ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

VETERINARIA 120

Cannibalism in Laying Hens

Characteristics of individual hens and effects of perches during rearing

Jenny Yngvesson

SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

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Akademisk avhandling som för vinnande av filosofie doktorsexamen kommer att offentligen försvaras i Hernquistaulan, J-huset, Sveriges Lantbruksuniversitet, Skara, fredagen den 8 mars 2002, kl. 13.00.
Av fakultetsnämnden utsedd opponent: Dr Beat Wechsler, Swiss Federal Veterinary Office, Schweiz.

Abstract

Cannibalism causes severe welfare and economical problems in modern egg production. This thesis aimed to identify differences between cannibalistic, pecked and neutral individuals and to investigate possible mechanisms for why perches reduce cannibalism. It combines theories and hypotheses from behavioural ecology and practical poultry production.

Individual characteristics were investigated in birds collected from commercial farms experiencing outbreaks of cannibalism. Birds were either classified as cannibals, victims or controls. The theory of developmental stability predicts that individuals with low stress tolerance show more fluctuating asymmetry. Cannibals were found to be larger than victims and both cannibals and victims were found to be more asymmetric than control birds, which may indicate that they are less stress tolerant.

Cannibalistic behaviour can be triggered by food shortage or nutritional deficiencies. Cannibals were therefore predicted to show signs of nutritional deficiency. However, no differences were found in body weight, production efficiency or resource allocation. Oviposition duration and egg weight was investigated as possible causes for why certain individuals become victims of cloacal cannibalism, but no differences were found between these individuals and control birds.

Earlier research has found that perches reduce mortality caused by cannibalism. In this thesis, rearing without perches was found to reduce spatial skill in layers and this effect was long lasting, even though birds were trained to use perches. Rearing with perches was also found to reduce latency and increase number of birds jumping up onto perches in a simulated cannibalistic attack. Merely providing perches, however, did not guarantee that birds would learn to use them and there was a large individual variation in whether or not birds learnt to perch.

In summary, cannibalism in laying hens has some similarities to cannibalism under natural conditions. It is also suggested that in commercial poultry rearing, a practical way to reduce cannibalism in loose housing systems is to ensure that birds learn to perch within the first few weeks of the rearing period.

Keywords: Laying hens, cannibalism, body size, fluctuating asymmetry, production, egg laying, perches, rearing, escape behaviour, welfare

Distribution:
Swedish University of Agricultural Sciences
Department of Animal Environment and Health
SE-532 23 SKARA, Sweden

Skara 2002
ISSN 1401-6257
ISBN 91-576-6360-2

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Doctoral thesis
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Acta Universitatis Agriculturae Sueciae
Veterinaria 120

ISSN 1401-6257
ISBN 91-576-6360-2

Tryck: SLU Service/Repro, Uppsala 2002

”- Titta! Vi har fått en tupp! Vad stilig han är, kacklade de.
Det var på tiden Pettson. Precis vad vi behövde.
Findus blängde tjurigt på hönorna. – Vadå behöver?
Det finns väl ingen som behöver en tupp. Jag har aldrig
i hela mitt liv behövt en tupp en enda sekund.
- Nä, *du* nä, sa Pettson. Men de här vimsiga tanterna
behöver nån som håller reda på dem.
- Ånä, du gubbe, sa Prillan. Är det någon som är vimsig
så är det du. Det är inte alls det det handlar om.”

Sven Nordqvist
Tuppens minut
Bokförlaget Opal
Stockholm, 1996

Abstract

Yngvesson, Jenny 2002. *Cannibalism in laying hens - Characteristics of individual hens and effects of perches during rearing.* Doctor's dissertation.
ISSN 1401-6257, ISBN 91-576-6360-2.

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Introduction

Cannibalism, in general, is the eating (usually after killing) of a conspecific. This is widespread across the zoological taxa from single cell organisms to chimpanzees (Elgar & Crespi, 1992). Furthermore, cannibalism is common in captive laying hens.

Cannibalism in laying hens has been a problem since the very start of intensive housing for efficient egg production. In 1937, Kennard wrote on "...cannibalism, including toe, tail, wing, and vent picking or pickouts among chicks, growing pullets, and mature birds" (Kennard, 1937). In 1947 Schaible et al. stated that injurious pecking was one of the serious problems with keeping poultry. In the 1950's there was already a research area dealing with cannibalism and associated problems in layers (Whittle, 1957a; Whittle, 1957b).

There has been a development of the definitions of cannibalism, reflecting both the state of knowledge and how hens and their welfare are viewed at different times. An early definition of cannibalism "a vicious habit of picking toes, comb, vent, feathers, and other parts of the bird's body" (Miller & Bearse, 1938) may give the impression of viciousness, evilness or cruelty of the birds performing it. The distinction between feather pecking and cannibalism was not clear: "...vices as feather picking, tail picking, toe picking, and vent picking" (Clark, 1953). Two more 'modern' definitions, both referring to laying hens as birds, are "The term cannibalism is used to denote damage inflicted upon a bird by its cage mates sufficiently severe to cause its death" (Allen & Perry, 1975) whereas Keeling (1994) defined cannibalism as the "pecking and tearing of the skin and underlying tissue of another bird". These two definitions reflect the shift in housing systems during the 1980's and onwards from solely cages to alternative systems, and also the increasing concern for farm animal welfare as opposed to cannibalism merely being a cause of mortality.

In modern egg production, cannibalism is a serious welfare problem and in Europe, mortality due to cannibalism has increased in recent decades (Preisinger, 1997). As it has not been observed in wild or feral hens, it is often regarded as an abnormal behaviour for laying hens. Cannibalism is also a significant economic problem as it causes mortality and decreased production in aviary type housing systems as well as in cages. Schaible et al. (1947) describe management risk factors for cannibalism and also mention that strain of birds is important for the development of cannibalism, and still in year 2002 this is where our knowledge is. Many proximate explanations for cannibalism in layers have been suggested. Research has focussed on nutrition, i.e. different components in the diet and their effect on cannibalism, on management, and on genetics behind the expression of cannibalistic behaviour. Hormonal aspects have also been investigated (Hughes, 1973; Zobundzija et al., 1972).

Cannibalism is a behaviour distinct from aggression in laying hens, as it is not preceded by any threat and aggressive pecks are usually directed from above at the head of the recipient (Savory, 1995). Cannibalistic birds studied for this thesis directed their attacks at victims from behind. Pecks were forceful and directed at the cloaca, belly or the tail base. One single peck was often enough to produce a haemorrhaging wound. Cannibalistic pecks may be directed at any part of the body of the victim, but are usually directed at the cloaca, belly or tail and most health problems are associated with pecks directed at these areas.

Cannibalism and its relation to feather pecking

Today most researchers agree on a distinction between feather pecking and cannibalism in laying hens. Feather pecking is "pecking directed at the feathers of other birds, with feathers sometimes being pulled out and eaten" (Bilcík & Keeling, 2000) and, unlike for cannibalism, there are well developed theories for the causal mechanisms of feather pecking (Huber-Eicher & Wechsler, 1997). A similarity between feather pecking and cannibalism is that early experience is important for the development of both these behaviours (Huber-Eicher & Wechsler, 1997; Johnsen et al., 1998). Feather pecking is more common than cannibalism and a welfare problem through the pain and stress it causes. Feather pecking is also an economical problem, since denuded birds need to eat more than feathered birds due to the heat loss (Tauson & Svensson, 1980). In severe cases feather pecking may lead to cannibalism when large feathers, e.g. from the wings or tail, are pulled out and birds start to bleed. The blood may attract pecking from group mates and in severe cases even lead to death of the pecked bird. Just manipulating the plumage, without causing any bleeding, has been shown to trigger cannibalism (McAdie & Keeling, 2000). However, feather pecking and cannibalism often occur independently and it has been shown that it is different individuals who perform the different type of pecking, when feather pecking and cloacal cannibalism occur in the same group simultaneously (Keeling, 1994).

Current methods of preventing and treating cannibalism

There are a number of actions taken in practice to control cannibalism. The most commonly used preventative method today is beak trimming. Beak trimming, and its effectiveness against cannibalism and other types of injurious pecking, has been extensively studied and there is a great body of literature on the subject (Gentle et al., 1982; Gentle, 1986; Craig & Lee, 1990; Kuo et al., 1991; Struwe et al., 1992; Hughes & Gentle, 1995; Muir & Craig, 1998). Beak trimming means removal of, usually not more than, half the beak in the young chicks using a hot blade. Trimming may be done on both mandibles or only the upper and it may be repeated on the older pullets as some re-growing occurs. Beak trimming is painful when the procedure is performed and probably also causes chronic pain (Gentle, 1986; Gentle et al., 1990; Hughes & Gentle, 1995). The potential for cannibalism varies between different strains of hens and therefore the benefit of beak

beak trimming, in reduced mortality, also vary between strains (Craig, 1992). For welfare reasons beak trimming has never been allowed in Sweden and hence other methods must be find to solve the problem with injurious pecking.

Various methods are used commercially to control and stop outbreaks of cannibalism once they have occurred. The light spectra may be altered from white to more red light, which has been shown to reduce cannibalism (Schumaier et al., 1968), however, light spectra was in this case confounded with light intensity. Decreasing the light intensity is probably the most commonly used method in Sweden today. Decreasing light intensity may have negative effects on production (North & Bell, 1990 p. 408) and is probably negative for bird welfare as hens are a species for which vision is relatively important. In addition, inspection and detection of injured or sick birds is difficult, and the working environment is poorer. Painting the injured birds with tar or commercial 'bad tasting' products to discourage the cannibals from pecking at the wounds is also used, but this is time consuming and needs to be repeated often. The painting is also ineffective against the cannibals finding new victims.

Historically, various devices have been put on the birds' beaks to prevent them from seeing other birds or rings have been put through the beak to prevent them from closing the beak completely (Kennard, 1937 ; Clark, 1953). During an outbreak in a housing system with a litter area, the hens can be distracted by feeding them whole grain in the litter. Also straw or root vegetables can be given to encourage pecking activity to the litter area. This is labour intensive and may have the effect that the hens do not eat enough commercial feed, exposing them to nutritional deficiencies and production decrease. Feed deficient in sodium has been correlated with outbreaks of cannibalism (Wahlström et al., 1998) and this may possibly be alleviated by giving the hens access to salt.

Photo 1. Beak trimmed bird, photographer unknown

Cannibalism and housing systems

As the animal welfare legislation in Sweden changed in 1988 and laying hens were not to be housed in cages after the start of 1999 (SFS 1988:539) the development of alternative housing systems increased also in Sweden, as it already had in other countries e.g. Great Britain, the Netherlands and Switzerland.

The motivation for the cage ban was to improve the welfare of laying hens. Aviary housing systems were, for example, encouraged by a higher egg price. Aviary type housing systems were tested as these systems provide the laying hens with several resources important for bird welfare, e.g. nests, litter, perches and ample space to move freely. Aviary housing systems are usually characterised by groups of several thousand birds housed in large pens without partitions. There is usually a littered area on the floor (wood shavings, sand, peat or a mixture), making up about one third of the total floor area. The room is usually long and narrow and the littered area goes from one end to the other. Along the litter area there is usually an elevated dunging area covered with a slatted floor. On the slatted floor the feeders and drinkers are placed. The dunging area can be constructed of tiers on top of each other with manure belts on each level or there can be a single level slatted floor with a perch structure placed on top of it. Nests are often placed to one or both walls of the room, usually raised from floor level.

It soon became obvious though, that the production results from the aviary systems used in large scale production were unpredictable and that the system itself could be difficult to manage. Farmers experienced, for example, how birds in one compartment of the poultry barn cannibalised each other, but not in another compartment with the same hybrid under the same management, or how they had cannibalism in their flocks some years, without any apparent cause. Mortality due to cannibalism could rise to over 40% of the flock in aviaries. One of the reasons for originally moving birds into cages in the 1940's was cannibalism (Appleby et al., 1992), which also shows that cannibalism was not a new phenomenon as such.

Apart from cannibalism, several health and management problems occurred in the aviaries (Abrahamsson et al., 1998; Gunnarsson et al., 1995; Gunnarsson et al., 1999), e.g. feather pecking, parasites, floor laying and dust, though they will not be discussed further in this thesis. Possible factors for the unpredictability of aviary systems could be that they were new to many farmers and therefore management difficulties may have arisen during the early years. Furthermore, birds in aviaries have other feed requirements than caged layers (North & Bell, 1990, p.661) and may possibly be more sensitive to accidental problems with the feed. Laying birds had been selected only for cage production and often in single cages. Single cage data collection of production traits is necessary, but the birds' social characteristics are also very important for successful production when birds are housed in large groups. Aviaries were in some cases not well designed to start off with, resulting in birds getting trapped or breaking their bones when moving.

The ability to move in the system is also important for nest site selection (Appleby et al., 1988) and floor laying can be a major problem in aviaries (Abrahamsson & Tauson, 1998). When aviaries first came into use all chicks were reared in cages and were therefore unprepared for the housing during the laying period. Cages are two dimensional, unlike aviaries, and the social environment is very different in a small cage group compared to in an aviary. Furthermore, in an aviary the care taker is in the same space as the birds, which may be perceived as more frightening than when the birds are caged. In summary, birds are provided with, to them, valuable resources in the aviary systems, but they are also subjected to great challenges.

Together with feather pecking, cannibalism is one of the major arguments against aviary type housing systems. It is important to point out that cannibalism always occurred in cages, but not to the same extent (Randall et al., 1977) and therefore cannibalism did not have the same welfare or economical implications. A cage has a limited number of potential victims and although cannibalism can be socially transmitted also in cages (Zeltner et al., 2000; Cloutier et al., 2001; Tablante et al., 2000), social transmission is potentially more pronounced in larger groups of hens.

Another alternative system of housing layers is the furnished cage. This is a cage equipped with a nest, a dust bath and perches. The furnished cages are new and not yet in major commercial use. This type of cages was evaluated in Oester & Wyss (2001). It has been reported that group size in the furnished cages may influence mortality due to cannibalism in that larger group sizes have greater problems with cannibalism (Fiks-van Niekerk, 2001; Tauson & Holm, 2001). There is also some evidence that furnished cages are more sensitive to light than other systems: Mortality due to cannibalism was reported to increase significantly with increasing light intensity (Fröhlich & Oester, 2001).

A brief comparison of mortality calculated as number of birds dead because of cannibalism by the original stock is given in Table 1.

Table 1. Mortality caused by cannibalism in different commercial or semi-commercial housing systems and countries. The abbreviation (b.t.) means beak-trimmed birds and it can be seen that even beak trimmed flocks may have mortality due to cannibalism.

Reference	Country	Aviaries	Conventional cages
Abrahamsson et al., 1998	Sweden	0.15-7.15% (5 flocks)	
Allen & Perry, 1975	UK		10.6% (1 flock)
Fiks-van Niekerk, Th. G. C. M. pers. comm.	Netherlands	1-2% (b. t).	
Gunnarsson et al. 1999	Sweden	2.65% (59 flocks)	
Moinard et al. 1998	France		3.0% (2 flocks)
Tablante et al. 2000	USA		0.84 %(1 flock, b.t).

There is a general opinion among farmers, the egg marketing industry and researchers that the situation in Swedish aviaries has improved during roughly the last perhaps ten years, though there are yet no figures showing that this is actually true. Cannibalism seems to be substantially more rare today and also many of the other problems with housing layers in aviaries are alleviated. There are several possible explanations for this:

1. The skill of the farmers is likely to have increased.
2. The breeding companies have selected new commercial hybrids to better suit production in aviaries.
3. Rearing is improving to expose the chicks to the resources they will encounter as adults.
4. Feeding formulas are improving.
5. Design of the aviaries is improving.

All these factors are applied in practice simultaneously and their relative importance is not known.

The importance of perches

A very important housing factor affecting cannibalism is access to, and use of perches during rearing of chicks aimed for egg production in aviary type housing systems. Gunnarsson et al. (1999) found, in an epidemiological study of Swedish layers in aviary type housing, that perches during rearing was the only factor significantly affecting the incidence of cloacal cannibalism. This was, however not unexpected. Already in 1988, Appleby et al. found that perches early in life were important for hens to find nests for egg laying and proposed that this affected the spatial ability of the hens. Fröhlich (1991) found that perches early in life decreased the mortality due to cannibalism in the adult hens. There seems to be a critical period less than 8 weeks after hatching for achieving normal spatial skills in hens (Paper III). Lack of the particular stimuli during the critical period

has long term effects on brain development and behaviour (Inglis, 1975 ; Rosenzweig & Bennett, 1996).

I can see several possible mechanisms for why rearing with perches has a reducing effect on cannibalism under aviary conditions. If perches, or more specifically the possibility to roost and rest on elevated locations, are essential for young chicks, perches may reduce the stress inflicted on young individuals. As stress seems to increase the risk of cannibalism, reduced stress should decrease this risk. Through this mechanism perches would lead to fewer birds developing into potential cannibals.

Perches could also act through an intuitively simpler mechanism. Namely that rearing with perches somehow make birds more suited to move in the three dimensional aviary production system and thereby escape cannibalistic attacks. This mechanism does not imply fewer potential cannibals in the hen population, but fewer suitable victims. The reason why cannibals are not expected to be easily able to follow the victim when it escapes is that hens are not predators. Active escape, onto a perch or not, might break off a chase effectively. Furthermore, under commercial aviary conditions it is very easy to lose track of a particular hen in the crowd. Rearing with perches would give the adult hens a better spatial ability and hens reared with perches would use these to a higher extent when escaping a cannibalistic attack.

Contradicting the positive influence of perches in aviary systems, it has been found that perches in cages increase mortality due to cannibalism (Moinard et al., 1998). However, these result probably reflect another mechanism as perches cannot be used for escape in a cage. The perches situated a few cm above the cage floor may facilitate the pecking at the rear part of the victims' bodies.

Genetical aspects of cannibalism in laying hens

It is well known that different strains and individual hens of the same strain differ in the expression of cannibalistic behaviour (Engström & Schaller, 1993; Craig & Muir, 1996; Keeling, 1994), i.e. the propensity to cannibalise varies between strains and between individuals. It is also clear that selection can be performed to reduce mortality due to cannibalism down to levels of beak trimmed birds (Kuo et al., 1991; Craig & Muir, 1996). Selection against injurious pecking is also carried out on a commercial level to produce birds suited for alternative egg production (Preisinger, 2001).

As the number of countries in the EU banning conventional cages increases and the demand for birds suitable for alternative housing increases, breeding companies seem to be focussing more attention to selection on behavioural traits of birds, combined with selection for egg production, e.g. (Preisinger, 2001).

Nutritional deficiency and cannibalism

Cannibalism in wild animals is often triggered by food shortage (Elgar & Crespi, 1992). When comparing hens within the same flock, but differing in their cannibalistic behaviour, cannibals might be expected not to have their nutritional needs covered. One would expect the cannibalistic propensity to co-vary with nutritional deficiency. This could for example be detected by a disproportionately high production relative to feed consumed, or by increased energy needs due to for example insufficient plumage cover, underweight, illness or injury.

Cannibalism in white leghorn cockerels has been reported to be triggered by a diet deficient in the amino acid arginine. When arginine was supplied in the feed again cannibalism stopped (Sirén, 1963). Cannibalism in laying hens has been triggered by protein (Ambrosen & Petersen, 1997) and sodium deficiency (Wahlström et al., 1998). In these cases, it was an imbalance in the feed rather than food shortage per se triggering cannibalism. Sodium has been shown to increase attraction to blood in pigs (*Sus scrofa*) (Fraser, 1987), though the individual variation was large. In particular, protein deficiencies may have the potential to alter the behaviour of animals as proteins are metabolised to, for example, hormones and brain neurotransmitters (see Fraser et al., 1991). Protein deficiency enhanced the attraction to blood and reduced weight gain in pigs (Fraser et al., 1991), so protein deficiency may be a triggering factor for tail biting (a form of cannibalism) in pigs.

Domestic animals have been selected for growth, production and reproduction traits. Their ability to ingest and digest nutrients has increased along with selection, but there is increasing evidence that energy input and output are no longer in balance (Rauw et al., 1998). For example, dairy cows and lactating sows today typically have a negative energy budget during the lactation peak (Freeman, 1986; Patience, 1996). Laying hens are also approaching a level of production efficiency where nutrient intake and output are not in balance (Flock, 1998).

Laying hens today are producing at extremely high levels compared to their ancestors the jungle fowl (Saeki & Inoue, 1979). Egg production is very protein demanding and high egg production would be expected to increase the need and appetite for protein. Protein is a major nutrient in meat and hence appetite for meat should be pronounced in high producing laying hens and the major source of meat in the poultry barn are conspecifics.

Cannibalism in other species of domestic poultry and in domestic pigs

Cannibalism seems to occur in most species of domestic poultry to lesser or greater extent. In this thesis I will consider examples from two species related to laying hens.

Cannibalism occurs in turkeys (*Meleagris gallopavo*) as well as in laying hens. In turkeys, cloacal cannibalism is rare, and injurious pecking (feather pecking leading to haemorrhages) is mainly directed at particular sites on the wings and on the tail base (Hughes & Grigor, 1996). Turkeys, like other birds (Bennett & Cuthill, 1994), have the ability to detect ultra violet light and in UV light certain parts of their plumage show markings (Sherwin & Devereux, 1999). These markings vary with age (Sherwin & Devereux, 1999). Turkeys are usually housed in windowless houses without UV light. In UV-less housing, these markings on the turkeys' bodies and the age variations in the markings correspond to location and age at the occurrence of injurious pecking (Sherwin, 1998). It has also been shown that provision of UV light significantly reduces injurious pecking in turkeys (Moinard et al., 2001). I am aware of no research on how UV light relates to injurious pecking in laying hens. However, I would expect feather pecking and cannibalism originating from feather pecking to be more likely to be affected by UV light than cloacal cannibalism.

Cannibalism is perhaps even more serious in pheasants (*Phasianus colchicus*) than in any other species of domestic fowl. Cloacal cannibalism is one of the major causes of mortality in pheasants and may occur from seven days of age (Swarbrick, 1985). Beak trimming or beak devices preventing the birds from closing their beaks may be effective against cannibalism, but since these birds are reared to be released into the wild this is not a sustainable solution (Swarbrick, 1985). Furthermore there is no evidence that beak trimming would be less painful in pheasants than in laying hens. In a trial by Cain et al., (1976) it was found that when comparing two diets differing in the protein content, the low protein diet groups had significantly more cannibalism. Decreasing the feed content of the amino acid arginine has also been shown to trigger cannibalism in pheasants (Sirén, 1963).

Apart from cannibalism in domestic poultry, pigs show cannibalism that is in many ways similar to cannibalism in laying hens. The most common form of cannibalism in pigs is tail biting. Tail biting is a severe welfare and economical problem in modern pork production. The biting on the tail directed from one individual to another is painful and can lead to disease and mortality in the attacked animal. Victims of tail biting may seem surprisingly unconcerned with having the tail chewed on (Smith & Penny, 1981). However, the chances of escape is very limited in a commercial pig pen, so this may be an indication of the victim giving up rather than of tail biting being painless. Commercially, tail biting

is prevented by docking the tail of young piglets. The docking of the tail means amputation of the tail, leaving a short stump. This is however painful in a short and long term perspective (Simonsen et al., 1991) and is not allowed in Sweden. In the same way that beak trimming is not 100% effective against cannibalism in laying hens, neither is tail docking a guarantee against tail biting (Hunter et al., 1999). The causes of tail biting, as for cannibalism in laying hens, are thought to be crowded, intensive housing and dietary factors. (Dougherty, 1976; Smith & Penny, 1981). For example tail biting is more common when pigs are restrictively fed (Guise & Penny, 1998). It is also known that attraction to blood increases when the feed is deficient in protein or sodium (Fraser, 1987; Fraser et al., 1991). Tail biting can be reduced by providing the pigs with straw and, emphasising the importance of early experiences, the effectiveness of straw is increased if young piglets are given access to straw early (Arey, 1991). Tail biting has to my knowledge not been observed in wild or feral pigs, though cannibalism by wild boar sows on new born piglets does occur during food shortage (Andersson, M. 2002. pers. comm).

To conclude, cannibalism occurs in several domestic species and the factors triggering cannibalism or increasing its risk seem to be similar across species: Crowding, content and restriction of feed and the genetics of the breeds or lines used.

Ecological factors, individual variation and features of cannibals and victims

The evolutionary and ecological mechanisms of naturally occurring cannibalism in the wild may help to understand the underlying causes of cannibalism in laying hens. Cannibalism is widespread among zoological taxa. There are major advantages of cannibalism to the cannibals, and the ultimate explanation for cannibalism is that it increases fitness. Conspecifics constitute a perfectly balanced diet for carnivores and omnivores and therefore cannibalistic individuals have great nutritional advantages. Killing conspecifics may reduce the fitness for the victim in favour of the cannibal, as the dead individual will not reproduce. Cannibalism of own offspring, siblings or other close relatives may be a way of saving resources for later reproduction when environmental conditions are better. Letting yourself be cannibalised by your own offspring or by a female you just mated increases survival chances for your offspring and hence your fitness. Infanticide by males increases chances of mating with females who come into earlier oestrus, and consumption of the killed infant only increases the benefit due to its nutritional value. Cannibalism decreases population size and density and, hence, decreases the competition for resources from conspecifics. In cases of food shortage, cannibalism may be the only chance of survival (See Elgar & Crespi, 1992).

Increased group size and density are factors found to trigger cannibalism (Pfennig et al. 1998). Cannibalism is often triggered under particular conditions, for example when ponds are drying out or there is no other prey than conspecifics. In the dry season young caimans *(Caiman crocodilus)* become victims of cannibalism (Allstedt, 1994). Arctic charr (*Salvelinus alpinus*), in a lake in Svalbard, have 16-23 % of their diet made up of smaller fish of the same species (Svenning & Borgström, 1995). This lake contains no other species of fish and virtually all mortality of small charr is due to cannibalism.

In many species, where cannibalism is a normal behaviour pattern, a clear individual variation is seen in the expression of cannibalism. For example in the tiger salamander (*Ambystoma tigrinum nebulosum*) cannibalism in larvae is triggered by increased population density inducing certain individuals to develop into cannibalistic larval morphs. These cannibalistic morphs obtain physical features like enlarged jaws enabling them to eat conspecifics (Collins, 1983). Cannibalism of young is common among colonial see birds. Individual adults in the colonies specialise on cannibalism, whereas most adults do not express cannibalistic behaviour (reviewed by Stanback & Koenig, 1992). Cannibalism of pups has been observed in grey seals (*Halichoerus grypus*), where one single male was specialised on cannibalism (Kovacs et al., 1996). Individual potential for cannibalism is often consistent over time and genetically controlled although the expression of cannibalism may be triggered by environmental factors (Elgar & Crespi, 1992).

In all the above mentioned examples of cannibalism there are clear differences between the cannibals and victims. The cannibal is usually larger in size or in a later life stage but may also be healthier than the victim. These differences are explained as the cannibal decreasing the cost of cannibalism, by e.g. decreasing the risk of retaliation from the victim (Elgar & Crespi, 1992) since, for example, a small individual is less likely to attack a large individual. There are two anecdotal reports of adult birds cannibalising adult birds in the wild (Cawston, 1983; Paullin, 1987). Both these events have been observed during food shortage or wintertime and in both cases the attacked bird was or seemed weak because of sickness or injury. However, adult-adult cannibalism in wild birds is very rare. As there are always, when possible to verify, a difference between the cannibal and the victim in size, life stage, health or some other parameter affecting contest ability (see Elgar & Crespi, 1992 for a review) a difference between cannibalistic laying hens and their victims should be expected.

Ecology of hens in nature and in modern poultry housing

In the wild jungle fowl and feral hens are omnivores. They form small social groups of mixed sexes and ages. Group members vary over the season according to age and breeding status. These birds live in forest habitats where the different groups have hardly any visual contact, but mainly auditory contact. Chicks are

brooded by the mother hen, they forage with her and roost first on the ground and later on branches of increasing height. (Collias & Saichuae, 1967; Collias & Collias, 1996; McBride et al., 1969). Jungle fowl may spend over 90% of their active time foraging (eating, ground pecking and scratching) (Dawkins, 1989). A study comparing jungle fowl with modern laying hens showed no major breed differences in the total percent of observations the birds spent foraging (Schütz & Jensen, 2001), implying that laying hens, if possible, spend a large part of their active time pecking and scratching the ground and exploring their surroundings. All of these features of the ecology are dramatically changed for laying hens in commercial production.

Modern housing of layers is mainly designed to maximise egg production and to minimise feed, management and investment costs, though increasing attention is given to the welfare of the birds. All modern housing systems house birds at high densities. Laying hens and pullets are often fed ad libitum (i.e. free amount of food), although this is to some extent adjusted according to the weight increase of the birds. Furthermore, ad libitum, feed may not be perceived by the hens as continuous access to food. A common feeding system in Sweden and elsewhere is one long feed trough through the whole length of the house and where the food is distributed by a chain in the bottom of the trough. This feed chain runs at intervals and hens prefer to eat just after the chain has distributed fresh food. Also, there is a management trade-off between encouraging the birds to eat enough and minimising food wastage, which means that the feed trough is often empty before the chain runs. Therefore, birds may perceive a food shortage although no deliberate food restriction is imposed on them. In conclusion, hens are crowded and may experience temporary food shortages. As there are great similarities between the ecological factors when cannibalism was triggered in natural populations and the ecology of commercial laying hens, I find it likely that ecological factors constitute a large part of the underlying causes of cannibalism in laying hens.

Theory of developmental stability

Developmental stability is suggested to be the capacity of an individual with a given genotype to develop its phenotype under given environmental conditions. The developmental stability, or balance, is broken down by genetic factors like inbreeding and mutations and by environmental factors e.g. food shortage, sub-optimal temperature and chemical pollution etc (Møller & Swaddle, 1998). It has been suggested that developmental stability can be measured as increased fluctuating asymmetry (FA) in the phenotype (Swaddle & Cuthill, 1997; Palmer & Strobeck, 1986; Møller & Swaddle, 1998). FA is deviation, occurring during ontogeny, from perfect symmetry of bilateral body parts, where the optimum is perfect symmetry (van Valen, 1962). FA may be measured for example in length of flight feathers or thickness of legs. The theory behind the measuring and analysis of FA is debated (David et al., 1999; Swaddle et al., 1994; Palmer, 1999;

Thornhill et al., 1999; Van Dongen, 2000; Windig & Nylin, 2000), but may possibly be a measurement of how much an individual is affected by stress during its early life. FA, has been reported to be negatively correlated to secondary measurements of fitness, i.e. parasite resistance and individual reproductive success (Møller, 1994, 1997) and with stress tolerance in, for example, Japanese quail (*Coturnix japonica*) (Satterlee, 2000).

There is not a great deal of work on how FA and behavioural traits correlate and there is no general agreement among researchers that they do. However, FA was reported to be positively correlated with abnormal behaviour in humans (Thornhill & Møller, 1997), and in domestic poultry with tonic immobility, an expression of fear response (Møller, 1999). Broilers, which grow extremely fast, show more FA than jungle fowl (Møller et al., 1995) implying that high growth rate decreases developmental stability. Furthermore, Møller et al. (1995) found that FA in broilers was positively correlated with stocking density and with leg health problems, suggesting that FA may be a measure of stress experienced by broilers. It is possible that FA correlates with the expression of cannibalistic behaviour and with the likelihood of becoming a victim of cannibalistic attacks. Within a given flock of laying hens, individuals showing more FA could be less stress tolerant since all individuals have been hatched and reared together and presumably been exposed to a similar amount stress. Therefore, individual differences in FA should reflect differences in the genotype rather than differences in the exposure to stress. Cannibals may be expected to show higher FA than hens not showing cannibalistic behaviour, since they display an abnormal behaviour. Victims of cannibalism may also be expected to show higher FA than hens not being victims of cannibalism, since less stress tolerant chicks may grow up to be weaker or less healthy adults. I would hence predict that cannibalistic and victim hens would show higher levels of fluctuating asymmetry than hens neutral to cannibalism.

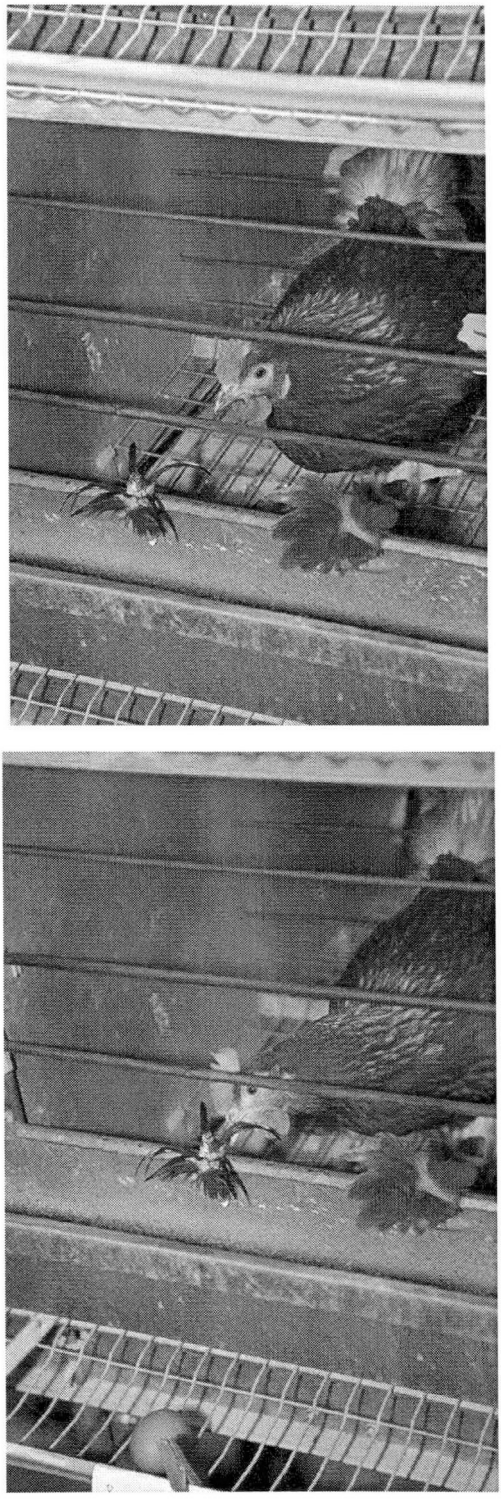
The resource allocation theory

The resource allocation theory (Beilharz et al., 1993) states that an animal has a limited amount of metabolic resources to invest in costly fitness related activities such as stress handling, anti-predator behaviour, growth, and reproduction. Resources allocated to one of these activities cannot be used for another activity. Selection for fitness will result in an optimisation of allocation of resources. Through domestication some resource constraints have been relaxed. When domestication started some activities, e.g. anti-predator behaviour and costly foraging behaviour, demanded less resources and so domesticated animals were able to reallocate more body resources to other activities such as growth and production. Simultaneously, the captive environment increased the amount of available resources (e.g. nutrients and time). Domestic animals have been selected for growth and (re)production to a level where they are approaching resource constraints and optimisation of resource allocation is necessary. In practice the

resource allocation theory may have the following implications for domestic animals; the selection pressure for growth, production and reproduction is so intense that resources for other activities may be reduced below the optimum level. Evidence for this is the increasing levels of health problems and abnormal behaviours correlated with levels of artificial selection (Rauw et al., 1998). I would hence predict that cannibalistic hens, i.e. those showing the abnormal behaviour, are the birds that have reacted to the artificial selection pressure to the highest degree.

Why are laying hens cannibalistic?

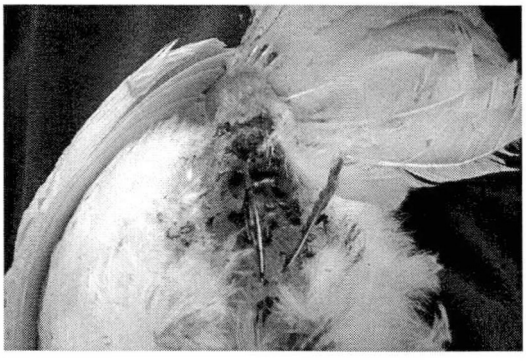
Cannibalism has, to my knowledge, never been observed in wild or feral hens, though there is a limited number of studies carried out. Furthermore, cannibalism may not always be reported as it is rare and may be perceived as 'accidental' or shown by an abnormal individual. However, hens find blood tasty under experimental conditions (Cloutier et al., 2001; Yngvesson & Keeling, 1998) and they do eat meat when given the opportunity. (McBride et al., 1969) observed a feral cockerel killing and eating a fledgling of another bird species and I have observed hens in the poultry barn killing and eating mice. Hens have sharp beaks which can inflict damage on a relatively immobile target animal. Considering the ecological factors triggering cannibalism, the crowding and feeding system in any poultry housing and considering cannibalism in other domestic species which have the physical possibility of eating meat, it may not be surprising that cannibalism occurs in laying hens.



Photos 2 and 3. Choice of chicken blood stained feathers over clean feathers. In this case the left feather bundle is soaked in blood. Photo Yngve Yngvesson.

Practical aspects of studying cannibalism in Swedish layers

The work for this thesis was carried out in Sweden during the years 1997 to 2002. Effectively I have worked with flocks with high mortality caused by cannibalism directed to the rear part of the victims' bodies, including cloacal cannibalism or vent pecking. There seems to be no major difference between cloacal cannibalism and rear body wounds, whereas cannibalism on other parts of the body, e.g. wings, presumably related to feather pecking. This is in consensus with e.g. Abrahamsson & Tauson, (1995).



Photos 4-7. Cannibalised hens used for Papers I-II. Photo J. Yngvesson

The work in this thesis concentrated on hens housed in aviary condition for several reasons: Commercial cages in Sweden are banned and going out of commercial use. Furthermore I wanted to study and compare cannibalistic hens, victimised but surviving hens and hens neutral to cannibalism. These three hens must come from the same group to be comparable. Commercial cages in Sweden house three hens, and if cannibalism occurs it is therefore very difficult to collect three individuals from the same group. The victim is usually dead and so it is impossible to collect one cannibal, one victim and one non-cannibalistic bird from the same social group. Furthermore, aviary housed flocks were, during 1997-1998, experiencing high mortality due to cannibalism and it was therefore relatively easy to find flocks from which to gather experimental birds.

Aims of this thesis

This thesis was initiated to identify causes to and offer some suggestions for how to prevent cannibalism in laying hens. Each of the four papers had specific aims.

The two first papers aimed to identify differences between individual hens who were defined as cannibals, victims or control hens, based on their behaviour during an outbreak of cannibalism.

Paper I. Does physical appearance differ between the different categories of hens? This question is asked with the background of cannibals in the wild being larger, healthier or of a later life stage than the victims. Cannibalistic behaviour may relate to stress tolerance, which might be measured as fluctuating asymmetry.

Paper II. Do production parameters vary between the different categories of hens? Cannibalistic behaviour is in many cases explained by food shortage and nutritional deficiencies. Abnormal behaviour may be related to low stress tolerance due to resources allocated from stress handling to production in cannibalistic birds. In addition, egg laying traits of victim birds may be of importance for cloacal cannibalism.

The overall aim of the two last papers was to test a possible explanation for why perches during rearing decrease mortality caused by cannibalism during the laying period.

Paper III. How is spatial skill affected by lack of perches during early rearing? The effect of rearing without perches on spatial skill was investigated and whether such an effect was long lasting or if adult birds reared without perches have the ability to learn to use perches as efficiently as birds reared with perches.

Paper IV. Does lack of perches during early rearing affect escape behaviour in the adult birds? It was investigated if perches affect escape behaviour in a simulated cannibalistic attack and whether or not chicks use perches when they are available.

Animals & Methods

Catching of experimental birds (Papers I and II)

For Papers I and II birds were collected from commercial farms during outbreaks of cannibalism and moved to the university research farm. The methodology for these two papers is made up of two parts; first the identification and the catching of the birds on the farms and second the experimental method for each individual experiment.

When a wounded bird was detected in a flock on a farm, it was caught, marked and released. This bird was then observed until another bird was seen pecking it in an injurious way. The pecking bird was then caught, marked and released and observed until it was seen pecking yet another bird in an injurious way. The pecker was then regarded as a cannibal and caught again and placed in a transport container. The marked victim and its surrounding birds were observed again and a focal bird, seemingly representative for the flock was chosen. This bird was followed for a minimum of ten minutes active time. It had to pass in close vicinity of a wounded bird's injury at least twice without pecking at it. If the focal bird was feather pecking it was excluded from the experiment, and another bird was chosen. If the criteria were fulfilled the focal bird was caught and regarded as a non-cannibalistic control bird. The last step was to re-catch the marked victim bird. On some occasions several sets of three birds could be caught from the same flock, or catching three birds could take a whole day or fail completely. In total the gathering of birds continued from August 1997 to April 1998.

After catching, the birds were taken to Götala research station and housed individually in standard commercial layer cages with one empty cage between each bird. The empty cage was necessary to avoid pecking injury. The daily light period was 12 hours and though this was a decreased light period for some of the birds, this decrease had no negative effect on production. The birds had ad libitum access to water and standard commercial layer feed.

A total number of 66 birds were caught. Due to poor bird health in some cases and improvement of the methodology in others, the number of birds used for each individual variable measured varied and is given in the papers. The age, breed, original flock, rearing system, feeding and lighting management varied between trios, but was always the same within trios. Hence the trio was the statistical unit for Papers I and II.

Measurements of body parts (Paper I)

Measurements were carried out using callipers with the bird placed on the lap of the observer. Each bird was measured twice, on two consecutive days four weeks after catching. We recorded the size of the following body parts: Wing length, leg length, thickness of the leg, thickness of the hock, length of the back toe and length of the mid toe (Figure 1).

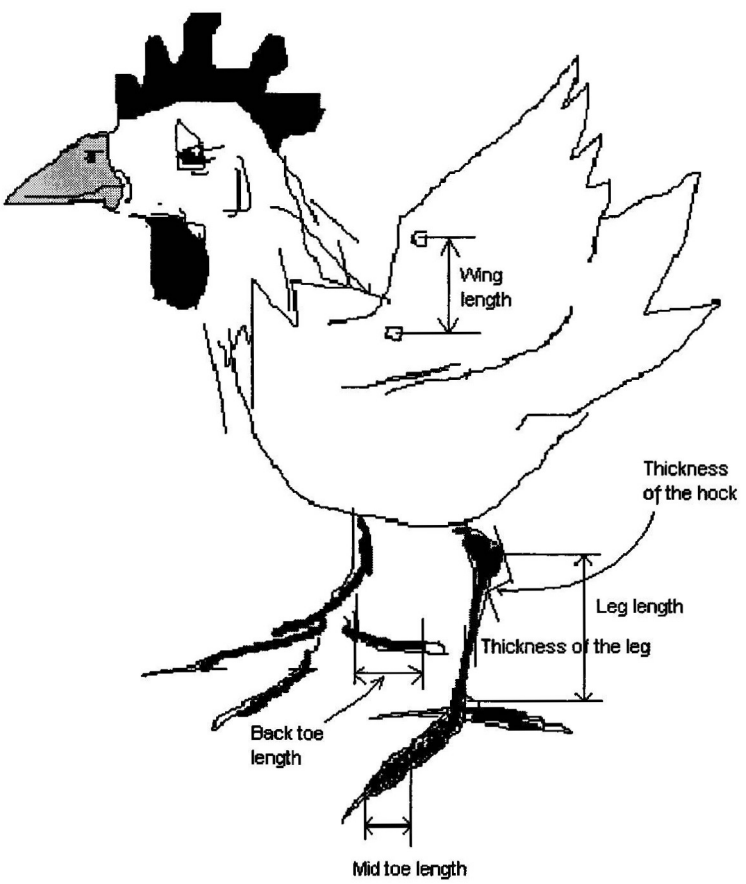


Figure 1. Measured body parts (Paper I).

Production parameters (Paper II)

Clinical examinations were carried out two days after catching. Production data recordings started four weeks after catching to allow injured birds to recover, and to standardise the environment for birds from different farms. Feed intake and egg mass produced was registered daily and weight weekly and from these, the food conversion ratio was calculated. A measure of the residual feed consumption, i.e. the feed consumption not explained by growth, production or heat loss, was also calculated. Plumage scores on the belly were correlated to the category of bird, to investigate if there was a connection between being denuded in this area and being pecked there. Egg laying times, egg weights and the bacterial flora of the victim birds' oviducts were analysed and compared to the control birds.

Birds and housing (Papers III and IV)

For Paper III, 30 Hisex brown chicks were bought as day old. The chicks were at first reared in two groups, one group without perches and one with perches. The density was 4 hens per m^2 and the birds were fed according to the breeders recommendations. The light period was constant at 12 h. At eight weeks of age the birds were mixed, i.e. all birds got access to perches and were trained to use them during daytime and at night. The food in the home pen was provided in feed troughs on an elevated shelf to ensure that all birds were capable of eating off the ground. As adults the birds were tested individually in a food searching task with increasing difficulty, in that food was placed on shelves of increasing height. Time until the birds reached the food was recorded.

For Paper IV, 100 Lohmann brown chicks were purchased as day old. The chicks were reared in ten groups with and ten groups without perches. These birds were housed at a density of 3.3 birds per m^2 until the age of seven weeks and thereafter at 1.7 birds per m^2 and fed according to the breeder's recommendations. The feeders were located on the floor. The light period was constant at 12 h. At seven weeks of age all birds got access to perches and at 13 weeks of age training started, by putting the birds on the perches just after dusk, to make the birds roost on the perches at night. Before any training was performed, at 12 weeks of age, recordings were made of whether the birds used the perches for roosting at night or not. In four of the ten pens reared with perches all birds were roosting on the perches at night. In six of the ten pens reared without perches no bird used the perches for roosting at night. These ten pens were classified as 'true perching' and 'true non-perching', respectively and analysed further. As adults the birds were tested in two social environments during a simulated cannibalistic attack (Photo 8). The cannibalistic attack was directed at the cloaca and consisted of spraying the birds with water at approximately two second intervals. Half of the birds from each treatment were tested first in a socially isolated test pen and then in the home pens with the pen mates present. For the remaining of the birds the first test was

in the home pen and the second in the test pen. Furthermore, registrations were carried out at 18 and 21 weeks of age of the birds' use of the perches when undisturbed in their home pens during day time.

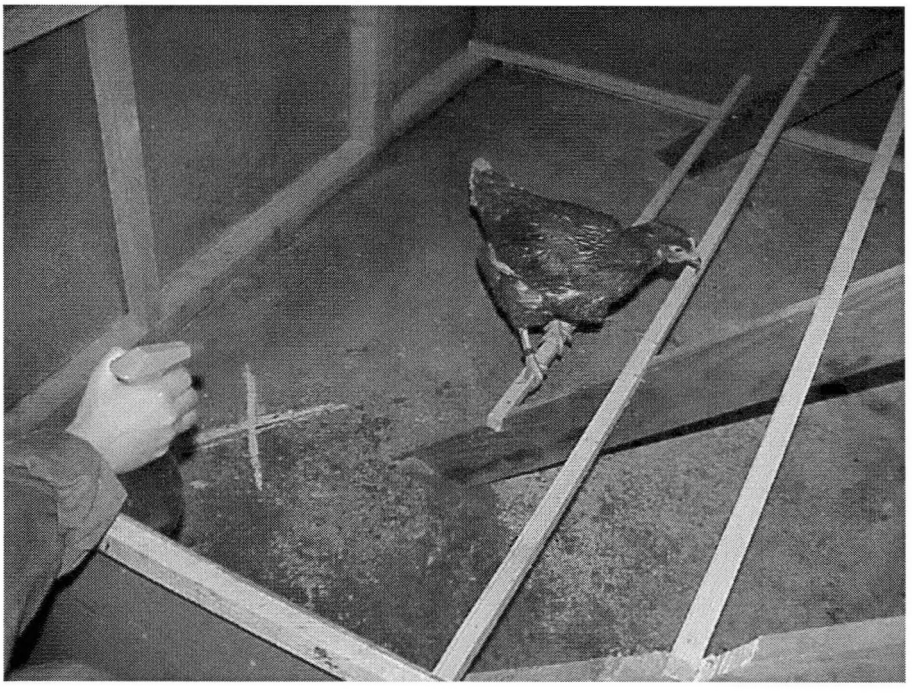


Photo 8. The escape behaviour in the test pen (Paper IV)

Statistical methods

For the data analysis in Paper I GLM ANOVA was used to investigate if trios from the same original farms could be treated as independent. A two-tailed paired *t* test was used to compare body weight at catching with body weight four weeks after catching. Repeatability of body measurements was analysed using GLM ANOVA to ensure that the two measurements of each side and body part could be carried out with sufficient repeatability. Normality of the asymmetry distribution was tested with the Kolmogorov-Smirnov test and a two-tailed one-sample *t* test was used to test if the signed asymmetry distribution deviated from zero, as fluctuating asymmetry is normally distributed and has no bias for left or right. Individual hens were ranked within their trio for character size and asymmetry. The number of rankings of each category of birds within their own trio, according to the hypothesis, was counted and compared with the expected result if size and asymmetry had been randomly distributed across category of bird. P values were obtained from the binomial distribution table. Analyses were performed in Minitab 12.

For Paper II a GLM ANOVA procedure was used to detect differences in production parameters between cannibals, victims and controls. In the cases where production parameters were non-normally distributed the non-parametric Friedman test was used. A Pearson correlation test was used to investigate the relationship between feathering on the belly and pecking damage to the cloaca and the belly skin. A Pearson correlation test was used to investigate the relationship between egg weight and oviposition time. Birds were ranked on the basis of bacterial count from oviduct samples and the data were analysed using GLM ANOVA. Mortality was analysed by means of a regression analysis. Analyses were performed in Minitab 12.

Body weight for birds in Paper III was compared between treatments, i.e. rearing with or without perches, using the Student's *t* test. Food searching test results, i.e. the time it took for the bird to reach the shelf where the food was located were analysed using the Wilcoxon generalised test for truncated data, as the test was interrupted after 600 sec. Jump quality was analysed for treatment effects using Wilxocon rank sum test. Analyses were performed in SAS systems for Windows 6.12.

For Paper IV a GLM ANOVA was used to investigate treatment effects, i.e. rearing with or without perches, on body weight. This test was also used to analyse for effects of rearing with or without perches on times to reach the different perch heights in all cases where test time data were normally distributed. In the cases were test time data were non-normally distributed the Friedman test was used. To analyse numbers of birds from each treatment group reaching specific perch heights the chi-square test was used. All analyses were performed in Minitab 12.

Summary of results

Experimental birds could be successfully collected from commercial farms during outbreaks of cannibalism, so avoiding the need to provoke cannibalism under experimental conditions. For ethical reasons it is desirable not to induce cannibalism experimentally and, furthermore, this shows that it is possible to detect and remove cannibals from flocks of layers during an outbreak of cannibalism. This removal of birds could be a method worthwhile trying by commercial egg producers, although very time consuming and difficult to carry out in nervous flocks where the light intensity is low.

The results from Paper I show that cannibalism in laying hens has parallels with cannibalism in wild populations of species where cannibalism is a part of the natural behaviour, i.e. cannibals were, as expected, larger than their victims and had longer wings and legs. Cannibals were heavier than other birds, both when caught and after four weeks. Victims increased significantly more in weight than cannibals and controls during four weeks of individual housing in cages, although all birds increased significantly in weight during this time. Controls were, as predicted, found to show a lower degree of fluctuating asymmetry (FA) in all body parts measured, though this difference was not always significant. More specifically they had significantly lower FA than cannibals and victims in wing length. Controls showed less FA than cannibals in the mid toe.

Results from Paper II show that variation in cannibalistic behaviour can not be explained by variation in production parameters between individual hens in a group. Cannibals did not eat less food to produce the same amount of eggs as birds from the other categories. Neither did body weight differ between birds of different categories. Plumage cover on the belly and peck wounds on the cloaca and belly did not correlate. Cannibals did not have a lower residual feed consumption than control hens. Hens which have become victims of cannibalism do not lay larger eggs or have longer oviposition durations after the cannibalistic attack had occurred. Nor do the victims have more bacteria in their oviduct than controls one month after the cannibalistic attack, or die sooner than other birds.

Paper III found that rearing without perches impairs the spatial skill of adult laying hens. After placing the feeders on an elevated shelf, and training the birds to use perches by lifting them onto the perches, all birds learned to roost on elevated perches at night. There were no weight or other obvious physical differences between birds of the different treatments at any of the recording occasions. In the individual test situation, where food was placed on an elevated net shelf at increasing height, birds reared with perches were better at finding the food. The difference between the two rearing treatments increased with increasing food searching difficulty (i.e. the higher the food was placed the fewer of the bird reared without perches could solve the task).

The results from Paper IV found that rearing with perches increased the use of perches for escape during a simulated cannibalistic attack, even when all birds had been trained to use the perches. A higher number of birds reared with perches escaped onto the perches at the intermediate height in the test pen. Birds reared with perches tended to have a shorter latency to escape onto the middle and highest perch. On none of the registration occasions were there any rearing treatment differences in body weight or clinical condition. This study revealed a large variation in the use of perches among the chicks. Some chicks reared with perches did not learn to use them without human assistance and furthermore, some chicks reared without them did learn to use them effectively without human assistance. To investigate effects of this variation the analyses were repeated on pens where the birds had been reared with perches and learned to use them and on pens reared without perches where the birds did not learn to use them without training. This selection resulted in four pens of 'true perching birds' and six pens of 'true non- perching birds'. In the selected birds, treatment effects on escape behaviour were clearer than in the whole population. The 'true perching birds' used perches for escape significantly more and quicker than 'true non-perching birds'. Undisturbed use of elevated locations during daytime in the home pens, increased with age in the analysis of all hens. The use of elevated locations in pens of 'true perching birds' and 'true non-perching birds' was affected by treatment but not by age.

Discussion

Features in the appearance of the hens are correlated with the expression of cannibalistic behaviour. At least in the case of fluctuating asymmetry these features of appearance have their origin early in life. Access or, more importantly, the use of perches early in life affects the behaviour of the adult birds in situations relevant to cannibalism.

I will discuss what forces may act against cannibalism in laying hens, a possible link between fluctuating asymmetry and cannibalism, group size and density, nutrition and production, consistency of cannibalistic behaviour, importance of perches and the practical implications of the results presented in this thesis.

Forces acting against cannibalism in layers

If cannibalism is evolutionary new to *Gallus gallus spp.* then it should be expected to be not so well 'adjusted'. That is, cannibals may be expected not to have fully developed strategies to reduce the costs of cannibalism, though the benefits of cannibalism are there. It was surprising not to find greater size difference between the cannibals and the victims. From the literature size differences between cannibals and victims are commonly large, e.g. 50% or more (body length) (Svenning & Borgström, 1995), whereas in the laying hens I found weight differences of 1.3 % (Paper I, although the raw weight data is not shown in this paper) between the cannibals and the victims. Large variations in body size or weight increase the likelihood of cannibalism in the wild (Elgar & Crespi, 1992), but if this has any implications for cannibalism in laying hens is unclear. To my knowledge it has not yet been investigated whether or not variation in body size is larger in flocks developing cannibalism than in flocks which do not. Knowledge of the cost of cannibalism due to the size and condition of the victim hens is very limited and the small size difference could be due to that size of the victim is not of great importance for the cost of cannibalism in laying hens. Alternatively a size difference of a few percent is important. Cannibalism can be costly in other ways, e.g. the cannibal may eat a relative or be infected by a pathogen when eating a conspecific.

Pathogen transmission has been shown to be a major force against cannibalism, but disease is at the same time a factor increasing the risk for a certain individual to become a victim of cannibalism (Pfenning et al., 1998). In one report cannibalism and encephalomyelitis co-occurred in flocks of pheasants (Bryant et al., 1973). This case is not completely unambiguous as it is unclear whether the birds dying were cannibalised or just infected by the virus, i.e. did the cannibals become infected and die or did the cannibals attack sick birds? However, the rapid reduction in mortality when the flocks were beak trimmed, in order to stop the cannibalism, indicates that either the virus spread through cannibalism or the

disease created potential cannibalism victims. The disease itself could not have caused the high mortality or the number of deaths would have continued after beak trimming. As cannibalism probably does not appear to occur in nature among *Gallus gallus spp.* mechanisms for individuals to adjust their cannibalistic behaviour may not be well developed.

The behaviour of the victims, which to my knowledge has not been systematically studied, may also point at cannibalism being a relatively new behavioural pattern to *Gallus gallus spp.* In the commercial aviary situation, victims tend to be passive or immobile when attacked by a cannibal. Also, it seems to be common that victims are found dead in corners of the house facing the wall. Both these statements are based upon my own experience when visiting flocks during outbreaks of cannibalism. This would imply that victims do not have a well developed escape behaviour. For example, they might have been escaping along the wall but when reaching a corner the attacked bird could not make the decision to jump up to the dunging area or on a perch. Data from behavioural ecology shows that the in the vast majority of reports of cannibalism, the cannibal's choice of victim minimise the risk of retaliation or the cost spent on prey handling (Elgar & Crespi, 1992). Therefore, an active escape behaviour in victims may be a force acting against cannibalism in laying hens.

Fluctuating asymmetry and cannibalism in layers

In Paper I victims were found to show higher fluctuating asymmetry (FA), in wings and mid toes, than controls. FA levels, or traits correlated to the FA levels, may influence the risk of being attacked by a cannibal. As was outlined in the discussion of this thesis, FA is correlated with health parameters in broilers (Møller et al., 1995) and could likewise correlate with health parameters in laying hens. Furthermore, FA has been negatively correlated with mating in male barn swallows (*Hirundo rustica*) (Møller, 1994), and hence FA has implications for social interactions. In laying hens, FA may hypothetically be correlated negatively with active defence and hence the choice of a victim with high levels of FA may be a way for cannibalistic laying hens to reduce the cost of cannibalism. High FA may somehow detected by the potential cannibals searching for victims, though only small birds with high FA are attacked, possibly to minimise the risk of retaliation. Alternatively cannibals attack group mates randomly but only birds who are small and show high FA fail to retaliate or escape from the cannibal.

Cannibals also showed higher FA than control birds, however they were larger than the victims and may therefore either not be attacked or if attacked have the ability to retaliate or escape. The higher FA in both cannibals and victims may indicate that they are less stress tolerant than controls. However, the stress factors these two types of individual chicks have reacted to does not necessarily have to be the same. Hypothetically, one type of chick may be more sensitive to social

stress and one more sensitive to environmental stress. It has been reported that pecked hens and cannibalistic hens differ from hens neutral to cannibalism in the histological and histochemical characteristics of the adrenal glands (Zobundzija et al., 1972). Zobundzija et al., (1972) concluded that victims were stressed to the highest extent, cannibals intermediately and neutral hens the least. Hypothetically these differences in the adrenal glands could have occurred before the outbreak of cannibalism and be due to genetical variations in stress resistance.

Group or flock size, density and cannibalism in layers

Flock size on the farms, from where the birds were collected, varied considerably. There seemed to be fundamental differences in the expression of cannibalistic behaviour with regard to flock size, although these were not systematically studied. Nevertheless, it may be of value to speculate on them as ideas for future research. On the original farms large (>100 birds) flocks gave the impression that cannibals constituted a small minority of all birds. During the observations no victim bird was seen being attacked by a group of cannibals. In the small (15 birds) flocks, however, victims were observed being attacked by several cannibals simultaneously. It has been found that in small flocks affected by cannibalism, a victim bird taken out and put back after healing is immediately attacked again (McAdie & Keeling, 2000). However, if this bird was put back in an unfamiliar group it was not attacked. This could reflect partly different causal mechanisms for cannibalism in groups sufficiently small to allow for individual recognition and groups larger than the critical size for individual recognition. Individual recognition could increase the risk of retaliation from the victim, as the victim can also recognise the cannibal. The risk of retaliation, again, may be reduced if there is a group of cannibals attacking simultaneously. This, however, remains to be investigated.

When rearing animals for commercial egg production they are reared and kept at high densities which lead to higher variations in body weight between individuals (Møller et al., 1995). It is known that higher densities leads to a higher risk of problems with cannibalism (Carmichael et al., 1999). High stocking density may lead to a larger spread in body weights. In Paper I cannibals were larger than their victims. It remains unclear whether or not this can be interpreted as if a more even flock would have a lower risk of cannibalism. However, an even flock is a goal for egg producers and sometimes used as evidence of good management.

Nutrition and production traits

In Paper II cannibals, victims and controls were compared for their body condition, production efficiency, residual feed consumption and features of egg laying.

As cannibalism is often triggered by food shortage, cannibals were predicted to show some sign of a nutritional need that was not fulfilled. Cannibals may be birds getting insufficient access to the food, or they may have some nutritional deficiency because they are more active, more stressed or they are producing more efficiently. Body condition i.e. whether the birds were thin, normal or fat, did not differ significantly between the birds. In Paper I cannibals were found to be heavier and a higher body weight may indicate higher maintenance requirements, although feed consumption did not differ between the birds (Paper II). Furthermore, cannibals were not found to be higher producing or more feed efficient than other birds.

Furthermore, nutritional deficiency may act as a mechanism at the onset of the outbreak of cannibalism, whereas other factors may keep the outbreak going. Birds do alter their metabolism during the production period, e.g. production increases rapidly to a peak from where it slowly decreases. Birds' body weight increase slow down over time and in many flocks plumage deteriorates over time. However, in my study plumage cover did not vary significantly between the birds.

Residual feed consumption (see Luiting & Urff, 1991) did not vary significantly between the birds, providing no support for my prediction about cannibalism in laying hens based on the resource allocation theory and its possible practical implications (Beilharz et al., 1993, Rauw et al. 1998). The data recording for the analysis of residual feed consumption in Paper II was carried out four weeks after the birds had been removed from the flocks where cannibalism had occurred. It is possible that stress inflicted on the birds was different in the individual cages at the research farm compared to the aviary where flocks were housed during cannibalism, and hence resources needed for stress handling may have been different in those two situations.

Cloacal cannibalism has historically and in recent years been attributed to prolapse of the cloacal tissue (Savory, 1995). Paper II dealt with egg laying in victims of cloacal cannibalism. Victims were, contrary to prediction, not found to lay larger eggs, or show more of their cloacal tissue than control birds. However, at the onset of cloacal cannibalism, one single prolapsed cloaca may be enough to trigger one predisposed cannibalistic individual. An injured haemorrhaging bird may attract investigating pecks from other birds, some of which may be potential cannibals who will then continue to exploit this nutritional resources in new victims. (Pötzsch et al., 2001) found that early onset of egg production increased the risk of cloacal cannibalism, and possibly early onset of egg laying increases the risk of cloacal prolapse. However, early onset of lay could be induced by many factors, e.g. rapid increase of day length and body weight higher than recommended. Factors inducing early lay are simultaneously causing stress in the birds and thereby possibly increasing the risk of cannibalism, or other abnormal behaviours. At the onset of lay itself, the nutritional demands increase greatly. If, in the practical commercial case, the onset of lay comes earlier than intended the

diet may not have been adjusted from the grower diet to layer diet. For these reasons it does not necessarily have to be only the egg laying in itself that triggers cannibalism, but possibly a larger fraction of the birds become potential cannibals due to factors correlated with early onset of lay.

Consistency of cannibalistic behaviour

For Papers I and II the experimental birds were collected from flocks during cannibalism. Data were then recorded from these birds at fixed intervals after catching. When cannibalism occurs under commercial conditions, cannibals are removed from the group if identified, but to my knowledge consistency of cannibalism in domestic animals has rarely been investigated. In the wild cannibals often stay cannibals over several seasons (Elgar & Crespi, 1992a). It is known that infanticidal red fox vixens kill their cubs repeatedly if they are allowed to breed again (Braastad & Bakken, 1993). That cannibals remain cannibals, victims remain victims and controls remain controls, even eight weeks after being taken away from the environment where they were cannibalistic, is an assumption of this thesis. It is however, known that victims of cannibalism are immediately attacked by the cannibals if returned to the group, even many weeks after the cannibalistic attack (McAdie & Keeling, 2000), so in this case both cannibals and victims remained cannibals and victims over a long period of time even though they were kept separately.

The category of birds neutral to cannibalism, my control birds, is the only category for which there could have been some doubt of whether the choice of bird was correct. However, my impression is that the proportion of cannibals in a commercial flock during an outbreak of cannibalism is small, only a few percent of all individuals. This in itself makes the chances of accidentally catching a cannibal instead of a control very small. Furthermore, the definition used for controls was watching the bird for a minimum of ten minutes of active time meant, in practice watching it for a substantially longer time since resting time had to be discounted from the total time and, during this time, and it had to pass by a victim with a bleeding wound twice. This definition was developed after study visits to flocks with cannibalism and also from experience with research flocks where cannibalism had occurred. From this previous experience I knew that cannibals reliably peck at injuries on other birds.

On the other hand, control birds may also have been victims that had healed so well that any scars were invisible. This is also unlikely, as when victims included in the experiment healed most of them had pale but visible scars from their wounds. Also, experience has shown that on commercial farms, birds left in the flock when pecked in the cloaca or on the belly usually die. I therefore conclude that either controls were not previously pecked or these pecking injuries had been minor and healed without any scar formation.

The importance of perches

As described in the introduction of this thesis, perches are known to decrease the mortality due to cannibalism (Fröhlich, 1991; Gunnarsson et al. 1999). This could be due to fewer potential cannibals in the flocks reared with perches, or to victims being more difficult to attack, or to a combination of both. I do not exclude the possibility that fewer birds become potential cannibals in flocks reared with perches. Hypothetically rearing with perches could reduce the stress level inflicted on the young chicks to such an extent that fewer adults show cannibalism. This may be supported by the positive effects perches have on feather pecking (Wechsler & Huber-Eicher, 1998, Huber-Eicher & Audigé, 1999). However, Paper III shows that spatial skill is significantly affected by access to perches during early rearing and to me it is intuitively logical to see a connection between spatial skill and the consequences of escaping cannibalism, regardless of the underlying causes of cannibalism.

In Paper III we aimed to exclude the possibility that treatment effects were caused by differences in physical ability rather than mental ability. For example, between the provision of perches and the actual testing, birds reared without perches had 8 weeks to adapt physically and mentally to using perches. Furthermore, no weight differences were detected at any time and all birds in Paper III used perches for roosting at night and ate at an elevated shelf in the home pen before any testing to find food on a raised platform was started. Hence, the difference between the two treatments is likely to reflect a difference in mental spatial ability.

The experimental design in Paper IV could have involved training of the young chicks in the treatment with perches to make sure they all used the perches. This might have given clearer results, however, there was a point in observing that only 52% of birds learned to use perches without human assistance. Birds who were reared with perches but did not use them were not different, in their escape behaviour or daily perch use, from birds reared without perches. In commercial practice it is important to make sure that all chicks do use the perches.

Practical implications of the results

Paper I shows that cannibalistic behaviour may be linked to stress during early life, both for the cannibalistic hens and the victims. So one practical implication of the results of this thesis is to attempt to reduce the stress inflicted on young chicks. Another clear implication is to make sure that young chicks reared for egg production in aviary type housing systems not only have access to elevated perches during early rearing, but also use them. This may in itself reduce frustration and stress, but more importantly, the birds will develop normal spatial skills thereby making it more likely that they will show appropriate escape behaviour if attacked.

Conclusions

Paper I. I conclude that there are consistent differences in physical traits between cannibals, victims and control birds. Cannibals are heavier than their victims at catching directly in connection to an outbreak of cannibalism. This is possibly due to victims not being able to feed when and where they want. The weight differences even out after some time of housing in individual cages. Cannibals also have longer wings and legs and so seem to be genuinely larger individuals. This is in accordance with behavioural ecology data on cannibalism in a wide range of species. Furthermore, a perhaps more subtle aspect of appearance is the differences in fluctuating asymmetry. Cannibals and victims were found to be more asymmetric than control birds, which may imply that they are less stress tolerant individuals than control hens. Possibly the risk of outbreaks of cannibalism would decrease if the stress inflicted on the very young chicks, or even on the parental animals, could be decreased sufficiently.

Paper II. I have found no evidence for high production per se to be connected to cannibalism on an individual basis. Cannibals did not have a higher or more efficient production, that could have caused them some nutritional deficiency triggering the cannibalistic behaviour. There was no evidence that cannibals allocate more resources to production than other birds. The victims of cloacal cannibalism studied for this thesis did not produce larger eggs than the control birds. No cloacal prolapses were observed in any of the birds during the data collection. Hence there was no evidence found for the idea that large eggs cause cloacal prolapses which in turn facilitates cannibalistic pecking to the cloaca.

Papers III & IV. Earlier research has found that perches during rearing have a decreasing effect on cannibalism. In this thesis it was found that lack of perches during rearing impairs the spatial ability of adult hens. Furthermore, it was shown that perches during rearing alters the escape behaviour in that hens reared with perches use these to a higher extent for escape during a simulated cannibalistic attack. Perches do have a major effect on the behaviour of adult hens, but it is important to ensure that chicks really use the perches during early rearing.

Svensk sammanfattning

Kannibalism hos värphöns - Egenskaper hos individuella hönor samt betydelsen av sittpinnar under uppfödningen

Kannibalism hos värphöns är ett allvarligt välfärdsproblem och ett ekonomiskt problem i modern äggproduktion. Kannibalism innebär att en höna hackar sönder hud och underliggande vävnad hos en annan höna. Detta är smärtsamt och kan snabbt leda till döden för den angripna hönan.

Syftet med denna avhandling är att identifiera skillnader mellan kannibaler, hackoffer och neutrala individer samt att undersöka möjliga mekanismer för hur sittpinnar minskar kannibalism.

Individuella egenskaper jämfördes hos hönor insamlade från kommersiella gårdar under pågående utbrott av kannibalism. Dessa fåglar var antingen kannibaler, offer eller kontrollhönor med normalt beteende.

Kannibaler fanns vara större än sina offer. Teorin om utvecklingsmässig stabilitet förutsäger att individer med låg tolerans mot stress visar mer fluktuerande asymmetri (FA) i bilaterala kroppsdelar där optimum är perfekt symmetri. Kannibaler och offer förutsades visa mer FA än kontroller, eftersom kannibaler uppvisar ett, för höns, onormalt beteende samt eftersom låg tolerans mot stress kan leda till mer sårbara offer. Kannibaler och offer fanns visa mer FA än sina respektive kontroller (artikel I).

Kannibalism hos vilda djur startar ofta då det är ont om föda och experimentellt har man visat att kannibalism kan induceras genom att utsätta värphöns för näringsbrist. De hackande hönsen skulle därför vara individer som av någon anledning får för lite mat. Alternativt kan kannibaler vara de mest fodereffektiva individerna och på grund av fodereffektiviteten ha någon form av näringsbrist. Resursallokeringsteorin förutsäger att domesticerade djur som är avlade på hög och effektiv produktion avsätter så mycket av sina tillgängliga (näringsmässiga) resurser åt produktion att resurserna tillgängliga för ex. stresshantering inte är tillräckliga. Detta kan leda till en ökning av onormala beteenden och därför förutsades att kannibaler är individer som avsätter mer resurser till produktion jämfört med andra hönor. Jag fann dock inga skillnader i kroppsvikt, produktionseffektivitet eller resursallokering. Äggläggning och äggvikt hos offer och kontroller jämfördes för att undersöka möjliga länkar till kloakkannibalism. Tid för äggläggning och äggvikter skilde sig inte signifikant åt mellan offer och kontroller.

Tidigare forskning har visat att upphöjda sittpinnar minskar dödlighet orsakad av kannibalism i lösdriftsystem. Hönor är starkt motiverade att använda sittpinnar

och oförmåga att göra det kan i sig orsaka stress och samtidigt göra det svårt för attackerade fåglar att fly från en kannibal. Kycklingar föddes upp med resp. utan sittpinnar. De testades sedan som vuxna i ett försök där de fick leta mat placerad på en upphöjd plattform. Hönsen uppfödda utan sittpinnar var signifikant sämre på att lösa uppgiften, trots att de som vuxna fått träna på att använda sittpinnar. Slutsatsen är att uppfödning utan sittpinnar fanns försämra värphönsens rumsliga förmåga under lång tid. I ett ytterligare experiment föddes kycklingar upp med resp. utan sittpinnar. Som något äldre tränades de alla att använda sittpinnar och som vuxna testades deras flyktbeteende i en simulerad kannibalistisk attack. Uppfödning med sittpinnar ökade antalet hönor som flydde upp på sittpinnar vid en simulerad kannibalistisk attack. Latensen för att fly upp på sittpinnarna var kortare hos höns uppfödda med sittpinnar.

Sammanfattningsvis är resultaten av denna avhandling att kannibaler är större än sina offer. Kannibaler och offer är mer asymmetriska än kontrollhöns, vilket kan tolkas som att kannibaler och offer är mindre stresståliga. Jag fann inga skillnader i produktionsegenskaper eller produktionseffektivitet som kunde förklara varför vissa individer blir kannibaler eller offer. En trolig mekanism till sittpinnars dämpande effekt på kannibalism är att fåglar uppfödda med sittpinnar har bättre rumslig förmåga och därigenom visar ett effektivare flyktbeteende om de blir attackerade.

Deutsche Zusammenfassung

Kannibalismus bei Legehennen – Individuelle Eigenschaften und Effekte von Sitzstangen während der Aufzucht

Kannibalismus verursacht bedeutende Tierschutz- und wirtschaftliche Probleme in der modernen Legehennenhaltung. Unter Kannibalismus ist das Picken durch die Haut in das darunterliegende Gewebe zu verstehen. Dies verursacht Schmerzen durch das Hacken und kann zum Tod der Tiere führen.

Diese Doktorarbeit untersucht individuelle Unterschiede zwischen einzelnen Hennen und deren Verhalten bezüglich Kannibalismus. Außerdem wird die Bedeutung von Sitzstangen während der Aufzucht für das spätere Auftreten von Kannibalismus untersucht.

In kommerziellen Beständen, in denen Kannibalismus auftrat, wurden einzelne Hennen gefangen und deren individuelle Eigenschaften untersucht. Diese Hennen waren entweder Kannibalen, Opfer oder neutrale Tiere als Kontrollgruppe. Die Theorie der Fluktuierenden (wechselseitigen) Asymmetrie (FA) besagt, dass Tiere mit geringerer Stresstoleranz eine größere FA aufzeigen. Die gefangenen Kannibalen waren schwerer als Opfer und Kontrolltiere. Sowohl Kannibalen als auch Opfer zeigten eine größere FA als die Kontrolltiere, was auf eine geringere Stresstoleranz hinweisen könnte.

Kannibalismus kann verstärkt bei Futterknappheit oder unausgewogener Fütterung auftreten. Da die Tiere auch bei freier Fütterung nur eine begrenzte Aufnahmefähigkeit von Ressourcen wie z.B. Energie haben, ist deren Verfügbarkeit begrenzt. Dies kann bedeuten, dass Hennen, die bei gleichem Futterverbrauch mehr Eier legen und dafür einen größeren Anteil ihrer Ressourcen verwenden, weniger Ressourcen für andere Bedürfnisse zur Verfügung haben. Dies wiederum kann eine geringere Stresstoleranz dieser Hennen zur Folge haben. Entgegen dieser Annahmen wurden in meiner Doktorarbeit keine Zusammenhänge zwischen Legeleistung, Produktionseffizient und Kannibalismus gefunden. Eigewicht und Dauer des Legevorgangs waren in anderen Studien mit Kannibalismus in Verbindung gebracht worden. Auch hier fand ich keine Zusammenhänge. Deshalb halte ich einen grundsätzlichen Zusammenhang zwischen Kannibalismus und Leistungsdaten für unwahrscheinlich. Damit erfolgt auch keine unabsichtliche Züchtung auf Kannibalismus durch Züchtung auf Legeleistung.

Frühere Studien zeigen eine Verringerung von Kannibalismus durch Sitzstangen in Volieren. Dies wurde mit verbesserten räumlichen Fähigkeiten durch frühen Kontakt mit Sitzstangen erklärt. In meiner Studie wuchsen Küken mit beziehungsweise ohne Sitzstangen auf. Später wurde bei den dann erwachsenen

Hennen untersucht, ob beide Gruppen in gleicher Weise Futter auf einer erhöhten Platte suchten. Hühner, die ohne Sitzstangen aufgewachsen waren, lösten diese Aufgabe signifikant schlechter, obwohl sie als Erwachsene trainiert wurden die Sitzstangen zu benutzen.

Für eine andere Studie wurden ebenfalls Küken mit beziehungsweise ohne Sitzstangen aufgezogen. Ab einem Alter von 8 Wochen wurden alle Junghennen trainiert, die Sitzstangen zu benutzen. Hennen, die ohne Sitzstangen aufwachsen waren, brauchten bei späterem Zugang länger, bis sie die Sitzstangen regelmäßig anwendeten. Als die Hennen erwachsen waren, wurde ihr Fluchtverhalten bei einem simulierten kannibalistischem Angriff untersucht. Hennen, die mit Sitzstangen aufwachsen waren, flohen schneller und öfter auf die Sitzstangen.

Die wichtigsten Schlussfolgerungen meiner Doktorarbeit sind folgende:
Kannibalen sind größer als Opfer. Da sowohl Kannibalen und Opfer asymmetrischer waren könnte dies möglicherweise auf eine geringere Stresstoleranz hinweisen. Ich fand keine Unterschiede bezüglich der Legeleistung die kannibalistisches Verhalten erklären könnten. Die Verminderung von Kannibalismus durch frühen Zugang zu Sitzstangen erkläre ich durch ein besseres räumliches Vermögen und dadurch effektiveres Fluchtverhalten.

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Acknowledgements

The Swedish Board of Agriculture provided the funding for this project.

Tack till SLU, som tillsammans med SJV sett till att jag kunnat genomföra min forskarutbildning med lön vilket gjort att jag omfattats av föräldraförsäkringen. Tack Svenska Staten för föräldraförsäkringen, utan vilken det inte hade blivit någon avhandling.

Tack alla ni äggproducenter som lät mig stöka omkring i deras redan stressade flockar då de hade utbrott av kannibalism. Tack för Ert tålamod och förstående.

Till ALLA doktorander vid institutionen för husdjurens miljö och hälsa vill jag säga tack för alla diskussioner, alla fikastunder och tips om hur man hanterar handledare, höns, hundar, statistiker och studenter!

Tack till ALL personal vid institutionen för husdjurens miljö och hälsa. Jag vet att många har sagt det redan, men det förtjänar att sägas igen; detta är en så otroligt trevlig plats att arbeta på!

Tack Maria Onila, som hjälpte mig att samla in blod på Kronfågelslakteriet i Skara.

Ingemar Ulinder på Svenska Lantägg i Skara hjälpte till med att lokalisera gårdar med utbrott av kannibalism. Tack även för att Svenska Lantägg hämtat våra ägg trots att vi inte alltid varit packeriets drömproducent...

Börje Hjalmarsson, lät mig öva fångst av höns under kommersiella förhållanden i en av hans flockar.

Biblioteksspersonalen vid Skara veterinärbibliotek; Beata Akersten, Britte Lindegren-Bohm och Per-Ola Rääf. Ni har letat upp referenser ur dammiga källare, från andra sidan jorden, vilket även i dessa IT dagar kan vara klurigt om referensen man vill ha är från 1940-talet... Stort tack för all er hjälp och vänlighet!

Jag vill uttrycka min uppriktiga tacksamhet till följande personer och personligheter:

Mina hönor från artiklarna I och II som jag samlade från gårdar runt om i södra Sverige; SD94, en riktig stygging, lilla Y1 med sina bleka, prickiga ägg, Y17, O11 som alltid hackade alla som vågade sticka handen i närheten av buren och alla de andra pullorna. Alla satt på min arm så stilla om de skulle flyttas till något nytt experiment, alla stod stilla på vågen utan att behöva någon 'papperskorg med

lock', som om de aldrig gjort annat i sitt liv. Jag hoppas att ni är i hönshimlen nu, med massor av sand att bada i, grönt gräs, pinnar och en skyddsängel (eller tupp) som ser till att ni inte hackar varandra! Tack till mina andra hönor också, som nu lever förhoppningsvis lyckliga liv i hobbyflockar runt om i Västergötland.

Linda Keeling, min handledare och medförfattare, som lärt mig så mycket om forskning och om att faktiskt få saker och ting gjorda. Tack för ditt enorma engagemang och stöd!

Ruth Newberry, my assistant supervisor and co-author, who managed to help me over a lot of thresholds despite the long distance between us.

Mina medförfattare, Björn Forkman, Stefan Gunnarsson och Linda Nedergård. Det har varit roligt och lärorikt att arbeta med er!

Per Jensen, som var handledare för mitt examensarbete under mitt första halvår i Skara. Sedan jag blev doktorand har Pelle varit ett stöd, bollplank och hållit entusiasmen för etologi och undervisning vid liv.

Jan Svedberg, som har delat med sig av sin stora kunskap om höns och varit så generös med idéer. Du har lärt mig allra mest om höns, men jag kommer aldrig att kunna avliva en höna på ditt sätt...

Alf Blomqvist och Anne Larsen, tack för er praktiska hjälp på Götala, er omtanke om hönorna och er entusiasm inför alla konstiga idéer och projekt!

Anders Linder, som hjälpt till när det gällde att hitta bakterier i kloaker (!), läst pek, delat med sig av idéer och som utfört obduktionerna på alla hönsen från de tre första artiklarna. Stort tack!

Ann-Sofie Wahlström, Klas Elwinger och Ragnar Tauson, vid institutionen för husdjurens utfodring och vård. Tack för hjälp vid olika tillfällen och för att ni alltid ställt upp och svarat på de mest kryptiska frågor!

Sverre Sjölander, som spädde på mitt nyvaknade intresse för etologi och tog oss (den första etologikursen vid Linköpings universitet) med till Skara där ett par av oss stannade längre än vi nånsin kunnat ana...

Tack Janne Nilsson och Gunilla Jacobsson, mina rumsgrannar, för all praktisk hjälp och tålamod med Zacco och hans mer eller mindre väluppfostrade polare!

Tack till Ulla-Britt Andersson, som är alltid varit så gullig mot Zacco trots att du fått ta hand om allt hundhår genom åren.

Jag är mycket tacksam mot Christine Brück, Tina McAdie, Tom Pizzari, Karin Schütz, Yngve Yngvesson och Thomas Östberg, för konstruktiva och ovärderliga kommentarer på ramberättelsen i elfte timmen.

Maria Andersson och Anna Lundberg, mina stora förebilder här i livet! Puss på er!

Tack till Agneta och Yngve Yngvesson, som fått ta ett allt större ansvar för sitt barnbarn ju närmare den 8 mars 2002 vi kommit!

Jens och Karl Jung, min livskamrat och mitt lilla barn. Tack för ert enorma engagemang i mina höns! Sticker jag en artikel under näsan på Jens så får jag tillbaka den med 'mega-major revisions' och Kalle kan inte gå förbi ett Gunnebostaket utan att fråga var tupparna är. Puss på er också!!! Stort tack till, framför allt, Jens för all praktisk hjälp med denna avhandling!

Acta Universitatis Agriculturae Sueciae
presents doctoral theses from the Faculty of Agriculture, Landscape Architecture and Horticulture, the Faculty of Forestry and the Faculty of Veterinary Medicine at the Swedish University of Agricultural Sciences. Each faculty has its own subseries, Agraria, Silvestria and Veterinaria, respectively, with separate numbering.

ISSN 1401-6257
ISBN 91-576-6360-2