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Domestication effects on foraging behaviour  
- consequences for adaptability in chickens

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Front cover: Red jungle fowl and White Leghorn males  
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*To my mother*



## ABSTRACT

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The main aim of this thesis was to study domestication effects on foraging behaviour in chickens and to investigate whether and how domestication and selection for high production have influenced adaptability in chickens. Two domestic strains of chickens (egg layers and meat type chickens) and their wild ancestor, the red jungle fowl (RJF) were compared in different test situations with respect to foraging behaviour and adaptability. The domestic strains showed a modified foraging strategy, where they were less inclined to explore and feed from a hidden food source, *i.e.* they showed less contrafreeloading (CFL, the behaviour of working for food even though identical food can be easily obtained) than RJF. The difference in CFL between RJF and the layers were not altered by food deprivation, which suggests that the lower CFL in the layers represents a genetically based difference in feeding strategy. In addition, CFL decreased with age in RJF and layers and social isolation decreased CFL in RJF. Furthermore, when foraging, RJF acquired information about the quality of different food sources, which was utilised after a change in environmental conditions. Contrary to this, layers gained less information during foraging and showed an impaired spatial learning ability compared to RJF, and in this respect, layers showed a lower degree of adaptability. Chronic stress impaired the learning capacity of both breeds but RJF seemed to be overall faster to learn to locate food in a spatial learning task. Furthermore, stressed RJF started to eat faster in the spatial learning test than non-stressed RJF, and contrary to this, stressed layers showed a more passive response by prolonging the time to start feeding compared to non-stressed layers. This indicates a more active response to stress in RJF than in layers. Similarly, when RJF and layers were exposed to food deprivation, RJF showed an active response by increasing their time spent on foraging behaviour. The general results in this thesis most likely reflect different adaptive strategies, where RJF appear to be better adapted to a stochastic environment, and the domestic strains to grow and produce egg in a more predictable environment. The findings are in accordance with the resource allocation theory, which suggests that animals selected for high production are expected to reallocate a high proportion of resources into production traits and hence fewer resources might be left to other biological processes, *e.g.* exploratory behaviour. Selection for high production seems to influence the ability of chickens to cope with a changing environment, which may have implications for the welfare of chickens in a production environment.

## POPULÄRVETENSKAPLIG SAMMANFATTNING

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I denna avhandling används djungelhöns (ursprungsarten), värphöns och broiler (tamhöns) för att studera hur djuren har påverkats av domesticering och hur avel för produktionsegenskaper (äggproduktion, snabb tillväxt) har påverkat deras sätt att söka föda. Dessutom studeras vilken betydelse detta kan ha för deras förmåga att anpassa sig till olika miljöer och situationer. Generellt visar resultaten att höns avlade för att värpa många och stora ägg använder ett mer energisparande sätt att hitta föda än ursprungsarten och att de verkar ha svårare att anpassa sig till förändringar i sin livsmiljö. Både broilers och värphöns är mindre benägna att utforska nya matplatser. Värphönsen visar en försämrad inlärningsförmåga, är sämre på att skaffa information om kvaliteten på olika födokällor och verkar reagera mindre aktivt då de utsätts för brist på mat, jämfört med djungelhönsen. Skillnaderna i beteende beror antagligen på att hönsen utvecklade olika beteendestrategier. Djungelhönsen är anpassade att leva i en mer oförutsägbart miljö, där det antagligen är fördelaktigt att investera energiresurser i utforskande beteenden samt skaffa sig information om sin livsmiljö. Höns i produktionsmiljö är anpassade att växa snabbt och producera många ägg i en mer förutsägbart miljö (god tillgång på mat, vatten och skydd mot rovdjur), där mer resurser investeras i produktionsegenskaper. Om en orimligt stor del av djurets resurser investeras i produktionsegenskaper kan det ske på bekostnad av andra energikrävande livsprocesser, d.v.s. mindre resurser finns då kvar till energikrävande beteenden som t.ex. utforskande beteende. Utforskande beteende och en bra kognitiv förmåga har betydelse för djurets förmåga att anpassa sig till olika situationer. En försämring av dessa egenskaper kan eventuellt påverka djurets välfärd negativt, då det i produktionsmiljön kan möta olika utmaningar som att hållas i stora grupper, omgrupperas med nya individer, möta nya skötare och förflyttas till nya miljöer. Sammanfattningsvis visar avhandlingen att höns avlade för produktionsegenskaper använder ett mer energisparande sätt att söka föda jämfört med ursprungsarten, antagligen som en anpassning till att mer av djurets resurser investeras i produktionsegenskaper. Dessutom verkar värphönsens anpassningsförmåga ha försämrats vilket kan ha betydelse för deras välfärd i produktionsmiljö.

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## LIST OF PAPERS

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This thesis is based on the following papers, which will be referred to in the text by their Roman numerals:

- I. Lindqvist, C.E.S., Schütz, K.E. and Jensen, P. 2002. Red jungle fowl have more contrafreeloading than White Leghorn layers: Effect of food deprivation and consequences for information gain. *Behaviour* 139, 1195-1209.
- II. Lindqvist, C. and Jensen, P. Effects of age, sex and social isolation on contrafreeloading in red jungle fowl (*Gallus gallus*) and White Leghorn fowl. *Submitted manuscript*.
- III. Lindqvist, C., Zimmerman, P. and Jensen, P. 2006. A note on contrafreeloading in broilers compared to layer chicks. *Applied Animal Behaviour Science* 101, 161-166.
- IV. Lindqvist, C. and Jensen, P. Domestication and stress effects on contrafreeloading and spatial learning performance in red jungle fowl (*Gallus gallus*) and White Leghorn layers. *Manuscript*.
- V. Lindqvist, C., Lind, J. and Jensen, P. Domestication effects on food deprivation induced behaviour in red jungle fowl (*Gallus gallus*) and White Leghorn layers. *Manuscript*.

# INTRODUCTION

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## ***Domestication***

Wild animals that live in their natural environments are exposed to different challenges such as predation, unpredictable weather conditions and a variation in food supply. They adapt to their environment by genetic changes caused by natural selection. The adaptation can result in a higher success in avoiding predators, finding food, mates and shelter, which are factors that affect an animal's survival and reproductive success *i.e.* its fitness. Fitness is usually given in the number of offspring that survive to reproductive age, produced by an individual during its lifetime and the individual with the highest fitness is the one which is best adapted to its environment (Craig 1981, Price 1984, Alcock 2001). When it comes to domestic animals, they adapt to captivity and human proximity in the process of domestication (Price 1984, 1999).

Domestication is defined by Price (1984) as the “process by which a population of animals becomes adapted to man and to the captive environment by some combination of genetic changes occurring over generations and environmentally induced developmental events reoccurring during each generation”. Since domestication is a continuous and gradual process that involves genetic changes, it can be considered as an evolutionary process where animals exploit and adapt to a new ecological niche (Hale 1962, Price 1998, Trut 1999). The genetic phenomena that have the greatest influences on the domestication process are inbreeding, genetic drift and selection. Inbreeding and genetic drift produce random changes in gene frequencies, while the changes from selection are directional and can be divided into three processes (Price 1998, 1999). Firstly, there is a relaxation of natural selection factors, like food shortage, predation and unfavourable weather conditions, caused by human providing food and protection against predators and climate. Secondly, there is a natural selection in captivity, leading to adaptation to that particular environment. Thirdly, there is an artificial selection for traits preferred by humans, such as growth or tameness, which in turn can result in an unintentional selection of different traits correlated to the traits selected for. It is possible that these three selection processes can work simultaneously or at different times depending on environmental conditions (Trut 1999). Also, a wild animal's fitness is determined by adaptation to the wild environment, whereas an animal's fitness in captivity probably is, to a large extent, determined by whether the animal is allowed by humans to survive to maturity and reproduce (Craig 1981, Price 1984).

The process of domestication is accompanied by an array of morphological, physiological and behavioural changes that can be seen in many different species, and have been referred to as “the domesticated phenotype” (Hale 1962, Craig 1981, Clutton-Brock 1992, Price 1998, Jensen 2006). Typical morphological changes are reduced brain size, altered coat (*e.g.* changes in fur thickness and increased frequency of white and spotted colour), reduction of bone size and changes in the shape of the horns (Clutton-Brock 1992, Trut 1999). Examples of physiological and developmental changes are earlier sexual maturity, larger litter sizes, prolonged length of sensitive period of socialization and neotony *i.e.* retention of juvenile characters and behaviours into adult animals (Belyaev *et al.* 1985, Clutton-Brock 1992, Trut 1999, Schütz *et al.* 2002). Furthermore, examples of behavioural changes are reduced fear, reduced aggressiveness, increased sociability and reduced antipredator responses (Desforges and Wood-Gush 1975, Craig 1981, Price 1984, Schütz *et al.* 2001, 2004). However, domestication has not added or eliminated any behaviour to the animals’ behavioural repertoire, only changed the thresholds of the behaviours to be triggered (Hale 1962, Price 1998).

### ***Effects of artificial selection for increased production***

During the last century, artificial selection for production traits in farm animals has been strongly intensified and during the last 50 years, average production in farm animals has increased by more than 80% (Rauw *et al.* 1998). Development of highly efficient breeding programs, improved nutrients and farming systems have been the main reasons for this development (Bakken *et al.* 1998). Economically, feed is the most important cost, so the main goal in farm animal breeding has been to create a population with high production combined with relatively low food intake *i.e.* high economic production efficiency (Luiting 1990).

A number of undesirable side-effects with respect to metabolism, reproduction, health and behaviour have been reported in farm animals, and several of these side-effects are assumed to be genetically correlated to selection for high production (reviewed by Rauw *et al.* 1998, Schütz 2002). For example, disturbance in reproduction has been found in pigs, laying hens, quails, turkeys and broilers (Hunton 1984, Dourmad *et al.* 1994, Marks 1996, Sewalem and Wilhelmson 1999). Also, broilers which are chickens selected for high meat production, show high frequencies of leg abnormalities, lameness, and cardiovascular problems (Hughes and Curtis 1997, Julian 1998, Bessei 2006). When it comes to behavioural changes, it has for example been reported that broilers seem to spend more time resting and use a more efficient foraging behaviour than layers (Masic *et al.* 1974) and that laying hens selected for high

feed efficiency spend less time on social interactions, pecking for food and walking than layers selected for low feed efficiency (Braastad and Katle 1989).

### ***Resource allocation theory***

The resource allocation theory is a way to explain behavioural modifications towards less energy demanding behaviours in a biological evolutionary context. According to this, the fitness of an animal is a product of several different components, such as number of mating partners, average litter size and survival of progeny. An animal has a limited amount of resources available to be allocated to different biological processes such as reproduction, growth, general activity, immune defence and coping with its surroundings. The resources consumed by these processes give the total amount of resources consumed by the animal. In order to increase an animal's fitness, it is necessary to increase the resources consumed by one or more of the processes, *i.e.* fitness components, which thereby will increase the total need of resources of that animal. During evolution, animals have been adapted to their environment and the available resources have been optimally allocated to different biological processes in order to maximise the animals' fitness (Beilharz *et al.* 1993, Beilharz and Mitpaiboon 1994).

During domestication, several limiting factors are reduced, such as food shortage, predation and unfavourable weather conditions. The outcome is that more resources become available for the animal and during these conditions rapid genetic changes can occur in many traits such as growth, reproduction and production. The animal's fitness will increase until the resources become limited again. At this point any further increase in a given resource demanding production trait would result in a negative response in one or more of the other traits due to a reallocation of resources into the production traits. This will result in a new optimal resource allocation and new modified behaviours will be established (Beilharz *et al.* 1993, Beilharz and Nitter 1998, Schütz and Jensen 2001).

The selection pressure for high production has been intensified during the last century. Animals selected for high production may reallocate more resources into production traits, such as growth and reproduction and thereby, fewer resources may be left to other biological processes. Hence, these animals will be expected to use less energy demanding behaviours which may have consequences for the animals' capacity to cope with stressors and adapt to new or unpredictable environments.

## ***Studying domestication***

In general, there are three methods to study effects of domestication; comparative studies of wild and domestic stocks, longitudinal studies of wild animals kept in captivity, and molecular genetic studies. In comparative studies, wild and domestic animals of the same species are compared in captivity and/or in wild environments and this approach provides a description of differences between the populations at a single point in time. In longitudinal studies, a wild population is kept in captivity and phenotypic changes are studied over generations of breeding, which give information about the rate at which domestication occurs under different environmental conditions (Price 1998, Mignon-Grasteau *et al.* 2005). Molecular genetic studies involve comparisons between animals of different degree of domestication. For example there are studies of DNA and gene expression, which provide information about the history of domestication, to what extent gene frequencies have changed, and if there are any modifications in gene expression (Niu *et al.* 2002, Schütz *et al.* 2002, 2004, Saetre *et al.* 2004, Lindberg *et al.* 2005).

This thesis has a comparative approach and chickens are used as a model species. The ancestor, the red jungle fowl (*Gallus gallus*) (hereafter referred to as RJF) and two different strains of domesticated chickens (*G. gallus domesticus*), layers (selected for egg production) and broilers (selected for meat production) are compared.

## ***The history of chickens***

Archaeological and biochemical studies show that RJF is the main ancestor of all domestic chickens and that they became domesticated around 8000 years ago in Southeast Asia (Collias and Collias 1967, West and Zhou 1989, Fumihito *et al.* 1994, Niu *et al.* 2002). Wild populations of RJF still exist and the domesticated chicken can be regarded as a subspecies (Nishida *et al.* 1992, Fumihito *et al.* 1996). According to archaeological and historical records, the early reasons for domestication were mainly cultural, such as religion, art and entertainment and it was only later that chickens were exploited for egg and meat purposes (Wood-Gush 1959, Zeuner 1963, Crawford 1990).

The systematic selection for increased production was intensified during the 20<sup>th</sup> century and today there are two main kind of commercial hybrids; egg-laying hybrids and meat hybrids. The egg-laying hybrids originate primarily from White Leghorn or Rhode Island Reds, and have been selected for egg numbers, egg quality, early sexual maturity and food conversion efficiency. Broilers are primarily derived from crosses of Cornish and White Plymouth Rock and have

been selected for growth rate, meat yield, proportion of white meat and food conversion efficiency (Appleby *et al.* 2004, Al-Nasser *et al.* 2007).

### ***Red jungle fowl and natural behaviour of chickens***

RJF lives in Southeast Asia and inhabits forests and bushy areas (Collias and Collias 1967, Nishida *et al.* 1992). They normally form groups with a social rank order, where the dominant male lives together with one or several females. Juveniles and subdominant males take satellite positions in the periphery of the group. RJF is a seasonal breeder and the hens leave the groups in order to nest, incubate the eggs and raise their broods (Johnson 1963, Collias and Collias 1967). The birds' behaviours are synchronised in the group so they usually preen, rest and dust bath together in the same area, and since they are vulnerable to predation they have an extensive vigilant behaviour and spend their nights in trees (Collias and Collias 1967, Savory *et al.* 1978, Appleby *et al.* 2004, Wichman 2007).



Figure 1. Red jungle fowls in a natural environment. Photos: J. Håkansson (A, C, D) and H. Lövlie (B).

RJF is omnivorous with a mixed diet of fruit, seeds, herbage and invertebrates (Collias and Collias 1967, Collias and Saichuae 1967). When foraging, the birds first scratch the ground with their feet, thereby exposing possible food items, then take a step backwards, peck and eat edible items. Newly hatched chicks do not have an innate ability to recognize food (Hogan 1973) so they need to learn what is suitable food for them. The feeding behaviour is often synchronised and follows a diurnal rhythm with one peak of food intake in the morning and one at the end of the day (Savory 1979). Normally they do not feed in the dark so the peak in the morning is probably to refill the crop, which has been emptied overnight and the peak in the afternoon is in order to fill the crop to have enough food during the night (Collias *et al.* 1966, Savory 1979, Appleby *et al.* 2004). However, RJF spend a lot of time foraging between these peaks as well. Studies of free-ranging RJF in a zoo have estimated that they spend over 90% of their active time on foraging behaviours, such as eating, ground pecking and scratching (Dawkins 1989).

### ***Layers and effects of selection for production***

A modern layer produces over 300 eggs in a year, and can be divided into light hybrids, derived from White Leghorn, that lay white eggs and have a body weight of around 1.5 kg and, medium hybrids, derived from Rhode Island Reds, that lay brown eggs and have a body weight of around 2 kg (Appleby *et al.* 2004). Several comparative studies between White Leghorn (hereafter referred to as WL), selected for commercial egg production and high feed conversion efficiency, and its wild ancestor RJF, have been performed (Schütz and Jensen 2001, Schütz *et al.* 2001, 2002). Differences between the breeds have been shown in several production traits. For example, WL grows faster and has a higher body weight. Also, the females have earlier onset of sexual maturity and lay heavier eggs and higher numbers of eggs (Schütz *et al.* 2002). Furthermore, the behaviour of WL has been modified towards less energy demanding behaviours in comparison to RJF. For example, WL show less active and social behaviours, react more passively in fearful situations and perform less costly foraging behaviours (Schütz and Jensen 2001, Schütz *et al.* 2001).

### ***Broilers and effects of selection for production***

During the last four decades, broilers have been subjected to increasingly intensive selection for growth and food conversion efficiency (Rauw *et al.* 1998, Appleby *et al.* 2004). A broiler female will reach 4.2 kg and a male 4.7 kg after 12 weeks of age which is more than four times the body mass of RJF (Havenstein *et al.* 1994, Jackson and Diamond 1996). The age at which

slaughter weight (approximately 2 kg) is reached, have been reduced from more than 10 weeks to less than 6 weeks and the amount of feed a broiler need to eat to reach a body weight of 2 kg has decreased by more than 30 % (EU 2000). In general, broilers use less energy demanding behaviours than layers. For example, broilers are extremely inactive and spend more than 75% of their time sitting/lying down (Bessei 1992, Weeks *et al.* 2000) which can be compared to laying strains which spend less than 30% of their time sitting/lying down (Savory and Mann 1997). Furthermore, broilers spend less time on actual feeding than layers do, but eat a higher amount of feed *i.e.* broilers have a higher feeding rate (Masic *et al.* 1974).

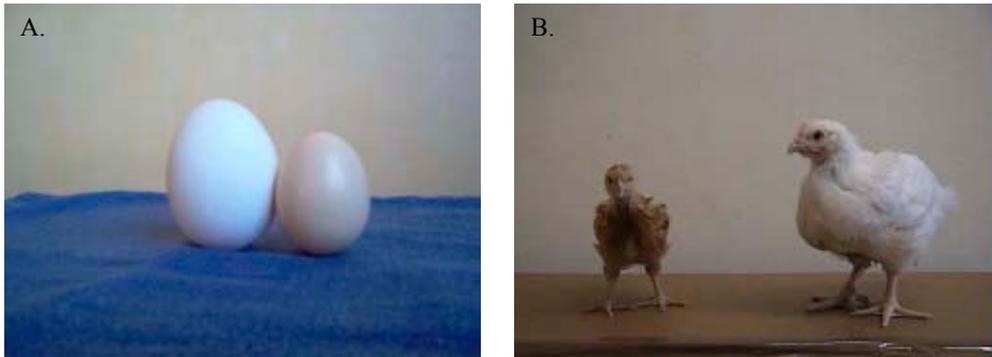


Figure 2. Differences in egg size and body size due to selection for increased production. A. Eggs from White Leghorn layers (left) and red jungle fowl (right). B. Chicks from a layer strain (left) and broiler strain (right) at three weeks of age. Photos: C. Lindqvist.

### ***Contrafreeloading***

One of the earlier mentioned behavioural difference between RJF and WL is that WL perform less costly foraging behaviours *i.e.* contrafreeloading (hereafter referred to as CFL) (Schütz and Jensen 2001). The term CFL is used for the feeding behaviour where an animal chooses to work for food even though identical food can be easily obtained. This phenomenon has been shown in several species, for example in Siamese fighting fish (*Betta splendens*), pigeons (*Columba livia*), chimpanzees (*Pan troglodytes*), mice (*Mus musculus*) and humans (*Homo sapiens*) (reviewed by Inglis *et al.* 1997). CFL is commonly studied by offering an animal a choice between two food sources, one with free food (*i.e.* less energy demanding) and one with identical food that requires more work (*i.e.* more energy demanding) in order to obtain the food. The work can consist of pressing a lever, moving long distances in a maze or searching for hidden food (Neuringer 1969, Larson and Tarte 1976, Forkman 1991, Schütz and Jensen 2001). In general, the degree of CFL is expressed as the percentage

of food obtained from the food source that requires more work. Different factors have been shown to decrease the level of CFL, such as increased food deprivation, increased environmental uncertainty and increased effort for the animal to obtain food (Inglis and Ferguson 1986, Rutter and Nevin 1990, Forkman 1991). Much is still unknown about how other factors affect CFL, *e.g.* age, sex and social isolation.

RJF show more CFL than WL and the reason to why there is a difference between the two breeds is still unclear. Schütz and Jensen (2001) suggested that the lower degree of CFL in WL may be a side-effect of selection for high production. It is likely that CFL is reduced in animals selected for high production since the resource allocation theory predicts that resource demanding behaviours should decrease in frequency in highly producing animals. However, it is also known that CFL decreases with increasing hunger (Inglis and Ferguson 1986) and another possible explanation to the lower degree of CFL in WL may be that a breed selected for high production and rapid growth might be more motivated to feed.

### ***A functional explanation to contrafreeloading***

An animal perform exploratory behaviour through active interaction with novel stimuli in order to gather information about its environment (Berlyne 1960 in Newberry 1999). In an evolutionary context, exploratory behaviour is important for an animal to weigh potential risks and benefits, such as predation, starvation and access to food and partners (Augustsson *et al.* 2005). It has been shown that wild starlings (*Sturnus vulgaris*) eat food that is freely available, but also work for food even though food is freely available *i.e.* they perform CFL. An explanation to CFL is offered in the “information hypothesis”, which suggests that the animals look for information as well as for food (Inglis and Ferguson 1986). It has also been shown that Mongolian gerbils (*Meriones unguiculatus*) prefer to work for their food if the food is hidden, but when the food is clearly visible they choose the most profitable food source. It was suggested by Forkman (1996) that an animal works for food if it gets information about the food source through its activity.

An animal that invests a certain amount of energy in exploratory behaviours, such as gathering information about alternative food sources, is probably better adapted to survive temporary fluctuations in food availability. The energy spent to obtain information from more unpredictable food sources is likely to be compensated by a long-term more efficient feed intake. If a lower degree of CFL is a side-effect of selection for high production, animals that are selected for high production may show lower levels of explorative behaviour, which in turn

may have consequences for the animals' capacity to learn about food sites, cope with stressors, and adapt to new or unpredictable environments.

### ***Natural environment versus captivity in chickens***

Risks occur in the natural environment of RJF, such as food shortage, injury or death by predators. In an unpredictable natural environment, a cautious animal with a high capacity to locate food sites, obtain information about quality of food sites and an ability to remember them, will probably be favoured by natural selection. In a captive environment, there is a relaxation of natural selection, since water and food normally are provided in sufficient quantities and there is an absence of predators (Price 1984, 1998). Besides, there is an intensified selection for high production in a production environment (Rauw *et al.* 1998). Hence, the fitness of the selected breed is probably more related to their ability to grow and reproduce efficiently than to their ability to be successful in foraging and avoiding predators.

A genetic difference in feeding behaviour between the two breeds makes it possible to use CFL as a model to study the change of an energy demanding behaviour, which is no longer directly linked to the fitness of an animal that has been selected for high production. It also provides an opportunity to study whether selection for high production in a predictable environment influences the animals' capacity to adapt to new or unpredictable environments.

## AIM OF THESIS

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The general aim of this thesis was to study domestication effects on foraging behaviour in chickens and to investigate whether, and if so, how domestication and selection for high production have influenced foraging behaviour and adaptability. This was done by comparing a layer strain (selected for high egg production), broiler chicks (selected for meat production) and the red jungle fowl (the ancestor of all domestic chickens) in different test situations designed to measure various aspects of feeding motivation under different environmental conditions.

**Paper I.** The aim was to study whether the lower level of contrafreeloading (CFL) observed in White Leghorn (WL) is a secondary effect of the fact that WL is more motivated to feed. Also, the aim was to study if the higher extent of CFL in the red jungle fowl (RJF) results in a higher gain of information about alternative food sources during foraging compared to WL.

**Paper II.** The aim was to study whether CFL varies with age, sex and social isolation within and between WL and RJF.

**Paper III.** The aim was to study to what extent broiler chicks perform CFL and to compare that with the CFL of a layer strain. Also, the aim was to do a comparison of general behaviours between broiler and layer chicks.

**Paper IV.** The aim was to study if there was a difference between WL and RJF in the ability to learn where food is located. Also, the aim was to study if the birds' behaviour, spatial learning ability and CFL were affected by being raised in an unpredictable (stressing) environment.

**Paper V.** The aim was to study whether the behaviour of RJF and WL was affected by an increased duration of food deprivation and how the both breeds in general cope with food shortage.

## CONCISE SUMMARY OF METHODS AND RESULTS

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### *Paper I*

RJF and WL were exposed to different levels of food deprivation, after which CFL was tested by offering the birds a choice to feed from freely available food or identical food mixed with wood shavings. Furthermore, both breeds were allowed to forage in a plus maze where symbols in each arm indicated the location of food sources of different quality. Thereafter the birds' capacity to find the food source of the highest quality was tested in a knowledge test.

In both breeds, CFL tended to decrease after food deprivation, but RJF had consistently a higher extent of CFL than WL. Furthermore, RJF significantly chose the food source of the highest quality in contrast to WL, which did not prefer any of the food sources.

### *Paper II*

The extent of CFL was studied by offering RJF and WL a choice to feed from freely available food or identical food mixed with wood shavings. The breeds were tested individually as young (8-10 weeks) and as sexually mature (27-29 weeks), and in pairs at an age of 30 weeks.

At the young age RJF showed more CFL than WL and both breeds showed more CFL at the young age compared to when they were sexually mature. There was no difference in CFL between the two breeds when they were sexually mature and tested individually, but when tested in pairs, RJF showed more CFL than WL. There was no difference in CFL between the sexes in either of the breeds.

### *Paper III*

The extent of CFL was studied by offering broiler and layer chicks a choice to feed from freely available food and identical food mixed with wood shavings. General behaviours such as foraging, activity and inactivity were also studied.

Broiler chicks performed less CFL, were more inactive and performed less active behaviours than the layer chicks.

#### ***Paper IV***

Birds of RJF and WL were raised in a stressful environment (unpredictable light:dark schedule) and in a control environment (12:12 h light:dark schedule). CFL was tested in birds from all groups by offering a choice to feed from freely available food or identical food mixed with wood shavings. Furthermore, the birds' behaviour and ability to learn the food location were studied in a T-maze, where food was located at the end of one arm.

WL showed less CFL, was less cautious in the test arena and showed an impaired spatial learning ability compared to RJF. Stress treatment impaired learning capacity in both breeds, but stressed RJF showed an active response, by starting to eat faster in the first test session than the non-stressed RJF, while stressed WL prolonged their time to start eating compared to the non-stressed WL. There was no effect of stress on CFL in either of the breeds.

#### ***Paper V***

Both RJF and WL were exposed to different levels of food deprivation and thereafter general behaviours were studied in a series of tests; food intake, general activity, open-field test and novel object test.

In general, the results show that both breeds increased their feeding behaviour in relation to the duration of food deprivation. RJF showed an active response on food shortage, which was not as clear in WL. Furthermore, there were breed effects on the response in the open-field and the novel object tests, indicating that RJF was more cautious than WL.

## DISCUSSION

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### *Effects of selection on contrafreeloading*

WL which have been selected for high egg production, showed less active foraging behaviour *i.e.* showed less CFL, compared to their ancestor RJF (Paper I, II, IV). Schütz and Jensen (2001) and Schütz *et al.* (2001) showed that WL in general perform less active and social behaviours, react less actively in fearful situations, and perform less CFL compared with RJF. They suggested, according to the resource allocation theory, that WL allocate resources into production traits partly by reducing the frequency of energy demanding behaviours such as CFL, social interactions and more active responses in fearful situations. However, CFL decreases with increasing food deprivation (Inglis and Ferguson 1986, Inglis *et al.* 1997) and another possible explanation can be that a breed selected for high production and rapid growth might be more motivated to feed and therefore shows a lower degree of CFL.

Even though RJF and WL were exposed to food deprivation, RJF performed more CFL than WL (Paper I). This indicates that the breed differences between WL and RJF are not an effect of WL being more motivated to feed, but more likely an effect of correlated responses to selection for high production. Väisänen *et al.* (2005) showed that CFL correlates with production traits in a F3 progeny from an intercross between RJF and WL, where chickens with a more efficient feed utilisation, performed less CFL. This supports the suggestion that the breed difference most likely is due to a genetically caused strategy difference, probably as a result of selection for high production in WL. This is also supported in Paper III where broiler chicks, which are intensively selected for fast growth, showed less CFL compared to a layer strain, which grows considerably slower. Vilariño *et al.* (1998) showed that male broiler chicks show very little or no interest to explore a novel food source (*i.e.* hidden food) at an age of 16-18 days, which is in line with the results in Paper III where broiler chicks showed a very low level of CFL. Furthermore, broiler chicks were more inactive and performed less active behaviour than the layer strain (Paper III). It is well known that broilers are extremely inactive and become more inactive with increasing age, which can be due to factors such as high body weight, leg problems and pain (Julian 1998, Weeks *et al.* 2000, Bessei 2006). In general, the results in Paper III support the resource allocation theory and indicate that CFL seems to be a strategy that can change adaptively when resources are allocated into production traits as a result of selection.

## ***Effects of social isolation, age and stress on contrafreeloading***

CFL seems to be more common during stable conditions and if the conditions change to more unpredictable, like food shortage or increased environmental uncertainty, the animal will give priority to the less demanding food source (Inglis *et al.* 1997). In Paper II, when the birds were tested individually, both RJF and WL showed less CFL compared to previous findings, where they were tested in pairs or in groups of four (Schütz and Jensen 2001, Paper I). In a natural environment, chickens live and feed in groups, which gives benefits compared to feeding alone, since social feeding can facilitate food findings, reduce the time to be vigilant and lower the risk to be taken by predators (Collias and Collias 1967, Lazarus 1972, Krebs *et al.* 1972, Sullivan 1984). Feeding alone probably leads to a higher uncertainty in the environment and it is likely costly to sample different food sources. Hence, for an animal feeding alone it may be more adaptive to rely on the less demanding food sources. This is supported by the results where RJF showed more CFL when they were tested in pairs compared to when they were tested individually (Paper II).

The effect of age on CFL was studied in Paper II, where young birds of RJF and WL showed a higher degree of CFL than the sexually mature birds. It has been suggested that CFL consists of an exploratory element *i.e.* information gathering, and in an evolutionary context it can be considered as an adaptive behavioural strategy, since it increases the knowledge about possible food sources (Inglis and Ferguson 1986, Bean *et al.* 1999, Schütz and Jensen 2001, Paper I). Nature is full of possible food sources but there are also inedible and poisonous plants and animals. If an animal does not have a strong predisposition concerning what food looks and smells like it is necessary to learn it. A more explorative foraging strategy may be more adaptive for a young naive animal where it is especially important to learn about alternative food sources. When an animal reaches sexual maturity it needs to invest more energy into reproduction and with earlier experiences about different food sources, it may now be more adaptive to rely on less demanding food sources. A combination of a need to learn about possible food types and less need to invest energy in reproduction might explain the higher degree of CFL in young birds.

The effect of chronic stress on CFL was studied in Paper IV. Birds of RJF and WL were raised in a stressful environment (unpredictable light:dark cycle) and in a more predictable environment (12:12 h light:dark cycle). Previous studies have shown that CFL decreases when the conditions change to more unpredictable, like food shortage or increased environmental uncertainty (Inglis *et al.* 1997). In the stressful environment, the birds were not able to predict when and for how long the food would be accessible through the light regime, and hence it was expected that the birds would give priority to the less energy

demanding food source. Unexpectedly, there were no difference in CFL between the control and the stressed birds. As in previous studies, the birds in the present study had access to both food sources for a long time and the results from this and previous studies may reflect a more chronic difference on CFL, such as breed differences caused by domestication (Schütz and Jensen 2001, Paper II, III). Other studies that have investigated the effect of food deprivation or uncertainty in the environment on CFL have used shorter test periods (Forkman 1991, Paper I), since CFL probably tend to decrease when the birds are fully fed or adapted to the new environment. Hence, a different method of testing the effect of stress on CFL might have given another result. However, the present result indicates that there may not have been any chronic effect on CFL of being raised in an unpredictable environment.

### ***Information gain and spatial learning***

In general, WL showed less exploratory behaviours and were less inclined to explore and feed from hidden food sources *i.e.* they showed less CFL than RJF (Paper I, II, IV). As mentioned earlier, a functional explanation to CFL is given in the “information hypothesis” which suggests that the animal is working for information as well as food (Inglis and Ferguson 1986, Inglis *et al.* 1997). The “information hypothesis” is supported by Paper I, where foraging RJF acquired information about the quality of different food sources, which thereafter appeared to be used to find the best food sources in a situation where food availability had changed. Similar results were found by Bean *et al.* (1999) where starlings acquired information by performing CFL, which they later used in food searching. However, WL did not perform better than expected from random choice. The differences in information gain between RJF and WL may be a result of RJF performing more CFL during the training sessions.

In the natural environment of RJF, there is a risk of food shortage and it is likely adaptive to invest a certain amount of resources in searching for food and information about future food sources. This will probably lead to a more long-term efficient food intake. In captivity, and particularly in production systems, water and food is normally provided in sufficient quantities and at the same location. In this environment it may no longer be adaptive to invest resources in searching for information about future food sources. Instead, fitness is probably related to production traits and the animals reallocate a higher proportion of resources into production traits to maximise their fitness. In a system where food has been provided *ad libitum* and the animals have been selected for high production, it is likely that CFL has been reduced, according to the resource allocation theory (Beilharz *et al.* 1993). The theory predicts that resource demanding behaviours which are not directly linked to fitness should decrease in

frequency in highly producing animals. This is supported by the results in Paper I, where WL showed less CFL than RJF. Also, WL showed a lower capacity to cope with environmental changes than RJF, by not being able to find the best food source in a situation where food availability had changed.

An alternative explanation for the difference in information gain between RJF and WL in Paper I may be that WL have a generally impaired learning capacity, which might affect their capacity to adapt in a wider set of situations than feeding. This is to some extent supported in Paper IV where WL showed an impaired spatial learning ability compared to RJF. However, chickens are able to locate a hidden object, and to find a hidden food reward in an octagonal maze using spatial memory and remember the location of a food reward based on colour and position of a visual cue (Regolin *et al.* 1995, Vallortigara 1996, Zimmerman *et al.* 2003). In Paper IV, WL did not fail to solve the task but needed a higher number of attempts to solve it compared to RJF. This suggest an impaired spatial learning ability in WL, but further research on the general learning ability of the breeds is necessary in order to investigate this explanation further. Exploratory behaviours as well as cognitive abilities, such as spatial memory, are important in order to locate, exploit and learn about resources. A degeneration of this ability could have implications for the animal's general capacity to adapt to changes in the production environment.

### ***Stressful environment***

Stress is often viewed upon as the biological response of an individual which perceives a threat (stressor) to its homeostasis (Moberg 2000). Factors that are important for the animal's capacity to cope with different stressors are predictability, controllability and feedback. If the animal can predict what will happen and also can control the situation by performing a relevant behaviour, then it will perceive the situation less stressful than if it was without these possibilities (Keeling and Jensen 2002). In Paper IV chicks of RJF and WL were raised in a stressful environment (unpredictable light:dark schedule) and in a control environment (12:12 h light:dark schedule). The challenge of the unpredictable light regime was that the birds were unable to predict important factors such as when to settle on perches for the night and when and for how long water and food would be available. These factors are important to chickens since they are vulnerable to predation in a natural environment and spend their nights in trees without eating and drinking (Savory 1979, Appleby *et al.* 2004, Wichman 2007).

It is known that stress can impair learning ability and cause memory disruption in animals (Mendl 1999, El Hage *et al.* 2006), which was also demonstrated in Paper IV. Stressed birds of both breeds showed an impaired spatial learning capacity compared to the control birds, but RJF seemed to learn faster where the food was located in the maze. Furthermore, stressed RJF started to feed faster than non-stressed RJF in the first test session. Opposite to this, stressed WL showed a more passive response by prolonging the time to start feeding compared to non-stressed WL. This indicates that stressed RJF respond more actively than stressed WL. Similarly, in Paper V, RJF showed a more active response on food shortage compared to WL, by reducing the time on perches and increasing the foraging exploration time on ground. This may be interpreted as a more risk-prone behaviour. In a natural environment, there is a trade-off between feeding and avoiding danger, and an animal will be more risk-prone with increasing hunger (Krebs and Davies 1996). In production environments, there is a relaxation of certain natural selection factors, such as starvation and predation but also an intensified selection for production traits (Price 1999, Rauw *et al.* 1998). The behaviour of RJF would appear more adaptive in an unpredictable natural environment where fitness probably is favoured by an active response to food shortage in order to prevent starvation and eventually death. The behaviour shown by WL may be more adaptive in a production environment, where fitness probably is more related to their ability to grow and reproduce efficiently. The results are in line with the resource allocation theory, which suggests that energy demanding behaviours may decrease in an animal selected for high production. RJF and WL showed different responses to stress and this may have implications for how selected birds are able to adapt to possible stressful production conditions.

### *A note on fear behaviour*

RJF were in general less active in the open-field test than WL and similar results were found in the novel object and spatial learning tests where RJF took longer time to start feeding and fewer RJF started to feed at each food deprivation level compared to WL (Paper IV, V). The lower level of activity in the different test situations may reflect that RJF are more cautious, since fear related behaviours have been reduced or modified during domestication (Schütz *et al.* 2004). There was no difference in CFL between RJF and WL when they were sexually mature and tested individually (Paper II). This may also be an effect of RJF being more cautious and sensitive for social isolation than WL. In general, RJF have shown more variation in CFL depending on group size during testing (Schütz and Jensen 2001, Paper I, II), which further supports the suggestion that RJF are more sensitive to social isolation. Several studies have shown that fear and antipredation behaviours have been reduced or modified during domestication

(Desforges and Wood-Gush 1975, Andersson 2000, Schütz 2002, Håkansson 2007) probably since co-existence with humans has caused a relaxation of the natural selection pressure of predation. Schütz *et al.* (2004) showed that RJF males are less active in an open-field test and take longer time to approach a novel object than WL males. It was concluded that selection for high production in WL probably has led to less active responses in fearful situations in WL compared to RJF. A similar suggestion can be suitable for the findings in Paper II, IV and V.

### ***Implications for welfare***

“The welfare of an individual is its state as regards its attempts to cope with its environment” (Broom 1986) and the welfare will be poor in individuals which have difficulties in adapting (Broom 2006). The general results of this thesis probably reflect different adaptive strategies, where RJF appear better adapted to a stochastic environment, and WL to grow and produce eggs in a more predictable environment. In captivity there is a relaxation of certain natural selection factors such as predation, starvation and climate changes (Price 1998, 1999). The captive environment may be more predictable than the natural environment of RJF but there are still many challenges for the animals, especially in the production systems.

In current housing systems, the animals are often kept in large flocks, especially in poultry production where flocks of layers are kept on floor-housing or multi level systems, generally comprised of several hundred chickens while broilers are kept in flocks of several thousands (Mench and Keeling 2001, Appleby 1999, Appleby *et al.* 2004). In these housing systems, there is a development of technology such as electronic feeding and water stations, and different resources such as food, water, resting places and nest boxes are often provided in different areas. Animals going through the production systems meet several challenges by being exposed to environmental changes, such as introduction to new housing systems, mixing with unfamiliar individuals, exposure to new types of food and unknown animal keepers. The animals’ ability to adapt and cope with the production environment and changes in housing conditions is probably much influenced by learning processes (Appleby 1999, Wechsler and Lea 2007). In Paper I, II and IV, WL were less inclined to explore unknown food sources and were not able to find the best food source in a changing environment. Furthermore, both control and stressed WL showed an impaired spatial learning ability compared to RJF. Exploratory behaviours as well as cognitive abilities, such as spatial memory, are important in order to locate, exploit and learn about resources. Impairment in these abilities may weaken the animals’ capacity to cope and adapt to changes in housing conditions which may influence the

animals' welfare negatively. Several studies have shown that chickens selected for high production perform less energy demanding behaviours, with respect to exploratory, social and activity behaviours (Schütz and Jensen 2001, Schütz *et al.* 2001, Paper I-V). According to the resource allocation theory, animals selected for high production may reallocate more resources into production traits and hence fewer resources may be left to other biological processes, which seem to have consequences for the birds' ability to cope with a changing environment, and this may be the case in other species as well.

## CONCLUSIONS

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**Paper I.** The lower CFL in WL, compared to RJF, does not seem to be a secondary effect of different feeding motivation, but is most likely a genetically induced difference in feeding strategy. Compared to RJF, WL gained less information about the food sources during foraging, thereby suggesting that WL are less adaptable to variable environments. This may be a result of resource allocation favouring increased production on the expense of an energy demanding foraging strategy as CFL.

**Paper II.** In general, CFL was lower in WL than in RJF. CFL in both WL and RJF was influenced by age, and CFL in RJF was also influenced by social isolation suggesting that RJF are more sensitive to social isolation. There was no difference between males and females in CFL.

**Paper III.** Broiler chicks performed less CFL than layer chicks. This is in line with Paper I, suggesting that less CFL in domestic strains may indicate reallocation of energy resources into production traits as a response to selection for high production.

**Paper IV.** Compared to RJF, WL showed less CFL and poorer spatial learning ability. Chronic stress did not influence CFL in neither RJF nor WL, but impaired their learning capacity. RJF and WL showed opposite responses to chronic stress, where RJF were more active and WL less active compared to non-stressed birds. The behaviour of RJF would appear more adaptive in a natural and changing environment, while the behaviour of WL might allow a greater investment in production traits in a more predictable environment.

**Paper V.** In general, both breeds increased their foraging behaviour with increasing food deprivation. Compared to WL, RJF seemed to show a more active response to food shortage and a higher sensitivity to social isolation, which probably would be adaptive in a natural environment. On the other hand the behaviour of WL may be more adaptive in a more predictable production environment where fitness is more related to the capacity to invest in production traits rather than an active foraging behaviour.

**Overall conclusions.** Taken together, the differences between the ancestor, RJF and the domestic strains probably reflect different adaptive strategies, where RJF appear better adapted to an unpredictable environment and the domestic strains to grow and lay eggs in a more predictable environment. The findings are in accordance with the resource allocation theory, which suggests that animals selected for high production are expected to reallocate a higher proportion of resources into production traits and hence fewer resources might be left to other biological processes. Selection for high production seems to influence the ability of chickens to cope in a changing environment, which might have implications for their welfare in a production environment where there still are many challenges.

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