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**Red Junglefowl (*Gallus gallus*) selected for low fear of humans are larger,
more dominant and produce larger offspring**

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Abstract

Many traits associated with domestication are suggested to have developed as correlated responses to reduced fear of humans. Tameness may have reduced the stress of living in human proximity, and improved welfare in captivity. We selected Red Junglefowl (ancestors of all domestic chickens) for four generations on high or low fear towards humans, mimicking an important aspect of the earliest period of domestication, and tested birds from the third and fourth generation in three different social tests. Growth and plumage condition, as well as size of eggs and offspring were also recorded, as indicators of some aspects of welfare. Birds selected for low fear had higher weight, laid larger eggs and generated larger offspring, and had a better plumage condition. In a social dominance test they also performed more aggressive behaviour and received less of the same, regardless of whether the restricted resource was feed or not. Hence, dominance appeared to increase as a consequence of reduced fear of humans. Furthermore, egg size and the weight of the offspring were larger in the less fearful birds, and plumage condition better, which could be interpreted as the less fearful animals being better adapted to the environment in which they were selected.

Keywords: Red Junglefowl, domestication, fearfulness, selection, social behaviour

Implications

Many traits associated with domesticated animals may have originated as correlated side-effects of reduced fearfulness. We recorded social behaviour, weight and reproductive traits in Red Junglefowl selected for high or low tameness. Birds with low fear were more dominant in social encounters, weighed more, laid larger eggs and produced larger offspring and had a better plumage condition. Birds selected for low fearfulness may therefore be better adapted to the environment in which they are selected, and low fearfulness may be an important aspect to consider when assessing animal welfare.

Introduction

During domestication, animals have undergone immense changes in physiology, morphology and behaviour, creating an unprecedented within-species variation in an evolutionary short time (Price, 1999). A set of seemingly correlated traits have developed in a similar way in most domesticated species, which is often referred to as the domesticated phenotype (Jackson and Diamond, 1996, Clutton-Brock, 1999, Price, 1999). Examples of such traits are changes in reproductive physiology, pigmentation, body size and proportions and, in mammals, increased frequency of floppy ears, and short and curly tails.

It remains an open question whether the domesticated phenotype is a result of human selection on each of the separate traits independently, or whether selection has been focused on one or a few traits with others developing because of genetic correlations caused by, for example, linkage or pleiotropy. One trait that could potentially have such a master role is the tameness of the animal, defined as the degree of fear response towards humans. It would appear that tameness could

have been a prerequisite for successive breeding and domestication, since it would allow human handling and relaxing the stress associated with human proximity.

Although a tame animal is of course not domesticated, tameness may represent an essential first step towards domestication.

It is also possible that some of the domestic phenotypes arise due to shared genetic mechanisms with tameness. A famous example of the importance of reduced fear of humans during the early phases of domestication, is the suite of correlated phenotypic responses related to tameness in silver foxes (*Vulpes vulpes*) (Belyaev *et al.*, 1985). Traits typical of domesticates emerged in few generations, such as piebaldness, modified body proportions, floppy ears, and modifications of the jaw, in spite of selection being targeted only on tameness (Trut *et al.*, 2004), suggesting genetic correlations between reduced fear of humans and important aspects of the domesticated phenotype. Hence, although the foxes should not be regarded as domesticated already after the first few generations, they showed correlated responses which might indicate shared genetic mechanisms. Other selective breeding projects focusing on fear in other species have shown similar results, for example, in rats (*Rattus norvegicus*) (Albert *et al.*, 2008), mink (*Neovison vison*) (Malmkvist and Hansen, 2002) and quail (*Coturnix japonica*) (Jones *et al.*, 2002).

Some important aspects of the domesticated phenotype consist of changes in behavioural frequencies and intensities. For example, feralized dogs show a less rigid social organization than wolves (Boitani and Ciucci, 1995) and domesticated chickens are generally less explorative and less active than their ancestors, and show more crowing and wing display in a social situation although the Red Junglefowl show a larger variety of social behaviour (Schütz *et al.*, 2001,

Väisänen *et al.*, 2005) . Recently, we reported significant genetic correlations between fear of humans and several other behavioural traits in chickens, among others, the propensity to search for hidden high energy feed vs visually presented commercial chicken feed (Agnvall *et al.*, 2012) that resembles the differences earlier reported between Red Junglefowl and White Leghorn (Lindqvist *et al.*, 2002). The significant genetic correlations between fear of humans and these traits ranged from 0.6 – 0.95 (Agnvall *et al.*, 2012). This suggests that many behaviours may have been modified secondarily to increased tameness.

The animals used in this current study are from an outbred population, which had subsequently been selected for three or four generations on high or low fear response towards humans in a standardized test. Previous findings based on the two first generations only, have shown a significant heritability (0.17 ± 0.09) of the trait under selection and a genetic correlation between the fear response and several other traits (Agnvall *et al.*, 2012).

It is striking that the strongest correlated effects shown in previous studies of the population in this experiment relate to feeding and exploration. This suggests that tamer birds may have an increased ability to compete for limited food resources, and perhaps other resources as well. Early domesticated animals must also have been able to tolerate a higher density of conspecifics than in the wild in order to survive captivity. Therefore, we explore the possibility that changes in social behaviour may occur as correlated responses to reduced fear of humans, using Red Junglefowl (*Gallus gallus*) as study object, a species considered to be the wild ancestor of all domestic chickens (West and Zhou, 1988, Collias and Collias, 1996, Al-Nasser *et al.*, 2007). The aim of this study was to investigate the effects of fear-based selection on social behaviour and social dominance in both feed related and

non-feed related situations in divergently selected Red Junglefowl. In addition, we measured plumage condition, growth, egg weight and weight of offspring as other possible indicators of a better adaptation to the environment of selection (Campo *et al.*, 2001).

Materials and methods

Breeding

The animals in the study consisted of Red Junglefowl (*Gallus gallus*) from the third (S3) and fourth generation (S4), of a population divergently selected based on their level of fear of humans. In the selection program they were divided into three selected strains, one with high fear of human (H), one with low fear (L) and one unselected group (U). The parental generation of the selected animals consisted of a systematically outbred group of Red Junglefowl from two different populations, one of them from a free roaming zoo population in Copenhagen Zoo and one from a research facility in Sweden. The differences between the populations are described in (Håkansson and Jensen, 2005). Shortly, the animals from Copenhagen Zoo showed more fearful behaviours whereas the animals from Götala population performed more aggressive behaviours and weighed more than chickens from Copenhagen Zoo. Hence, the genetic variation in the parental generation was maximized with respect to these traits.

For details about the animals and breeding scheme, as well as for a description of the selection test, see (Agnvall *et al.*, 2012). Briefly, the birds were tested in a fear-of-human test when they were 12 weeks old. During the test, each bird was alone in an arena together with a human, who gradually approached the

bird until attempting to touch it. The fear reactions of the bird was scored during the test and merged into a composite fear score ranging on a continuous scale from 1.0 (indicating calm and unaffected behavior) to 5.0 (assigned to highly fearful birds). This index was used for subsequent selection of the most and least fearful birds in each generation. In each generation, we selected four to ten families in each selection line, and the offspring of all selection lines (113-135 birds per generation) were raised together in mixed groups in the same pens.

After pairing, fertile eggs were collected from hens while they were kept in individual cages, so family origin of each egg could be determined and noted directly on them. The eggs were placed in an incubator (Marsalles 25 DIGIT) with 37.5 C, 55% relative humidity, and egg rotation every hour. After 17 days of incubation the eggs were placed in hatching compartments separated by family. Immediately after hatching the chicks were weighed, vaccinated against Marek's disease and wing-tagged. During the first five weeks of life, the chickens were kept in the hatchery "Kruijt" situated at Linköping University. They were maintained in mixed groups of about 30 individuals on a 12:12h dark-light rhythm with a light level of approximately 11 Lux in littered floor pens measuring 0.75x0.75 m, which were gradually expanded to 2.25x2.25 m. The pens contained commercially available conventional chicken feed for chicks and water ad lib, a heat lamp, wood chips and perches. At five weeks of age, the animals were transported to the research facility "Wood-Gush" located about 10 km from the university. There, the birds were sex separated and kept in pens measuring 3x3x3 m, containing perches, nests, wood chips on the floor and water and conventional chicken feed for laying hens ad lib. Light schedule was kept at a 12:12 h dark-light rhythm with a light intensity of 5-8 Lux.

Experiment 1

Animals

Experiment 1 was carried out on the S3 generation, which comprised a total of 110 birds (60 males and 51 females). Nineteen females and 22 males were from selection line H, 17 males and 17 females from selection line L, and 21 males and 14 females from selection line U.

General routines and recordings

The weights of the animals were measured at hatching, and at 200 days of age. At day 200 the plumage condition was scored according to a standardized protocol (Gunnarsson et al 1995) with a 5 point scale, slightly modified to encompass three parts of the chicken (unlike Tauson *et al.* (1984) classification with 5 body parts on a 4 point scale); the head and tail was recorded separately, and wing and body together, and the average was then calculated from the three assessments (table 1) At 45 weeks of age the 5 highest, 5 lowest and 8 unselected females were mated each with a different male from the same selection line and with a similar fear score in order to generate the next generation. The collection of the eggs lasted for 3 weeks and the weights of the eggs collected were measured as well as the hatch weight of the 79 chicks in the fourth generation (S4).

At the age of 22 weeks, 99 animals (54 males, 45 females) were tested in a series of behaviour tests designed to measure different aspects of social behaviour.

Social behaviour test (SB)

The SB test was carried out to estimate the frequency of social behaviour performed. Three groups were tested in separate arenas at the same time. Each group consisted of three same-sex animals of the same selection strain. In this way one group from each of the three selection strains were tested every day in order to avoid any bias between the lines. The arenas measured 1*1*2 m and were built out of cardboard covered wooden frames with a littered floor. One side and the roof were made of wire mesh, to allow visual observations of the animals in the arena. In the arenas, the birds had free access to feed, water and perches, and the light was kept on 12:12 h light-dark rhythm.

Before the test started, the animals were left for 18 h in the test arenas to allow habituation. Following this, the behaviour of the birds was recorded during a three-hour period, commencing three hours after the onset of light in the morning. The social behaviours (see table 2 for ethogram) of the animals were recorded with continuous sampling for five-minute periods interspersed by 10 min pauses. The observer spent the first five minutes recording the behaviour of birds in the first arena, then moved to the second, and the third, before moving to the second and the thirds arena following the same procedure. This procedure was repeated in total 12 times, so the total recording time from each arena was 60 minutes, spread over the 180 min test period. All sampling was done at the same time of the day, starting at 12:00, which is when egg laying is usually completed. Hence, egg laying did not interfere with the sampling.

Social dominance test (SD)

Immediately after the Social behaviour test the same animals were tested in a Social dominance test. The birds were tested in groups of three of the same sex, one bird from each of the selection lines. This was accomplished by moving one bird from each of the three arenas used in the Social behaviour test (described above) into a new arena, similar to the one they were collected from with the difference that the feed bowls were replaced with small containers (21 x 9 x 7 cm) filled with mealworms and covered with a plastic lid with only one narrow hole measuring 2cm in diameter. In this way only one bird had access to the mealworms at a time. Before the experiment took place, all the birds had been trained in their home pen to eat mealworms from similar containers, both with and without the lid, for a week, so they were all well accustomed to them. In order to distinguish between the three different birds they were equipped with plastic leg rings with different colours. Behaviours reflecting position in the social hierarchy were recorded by continuous sampling for five minutes in each arena, where aggressive behaviours indicated dominance, and avoidance indicated submission. The first five minutes for each arena were recorded directly after regrouping of the animals, thereafter the observer rotated between the arenas, collecting data during in total 12 x 5 minutes for each group of birds.

During the test, we recorded the frequencies of the behaviours listed in table 2 for each of the three birds in the group, using continuous recordings.

Exploratory behaviour and sociality test (ES)

In order to investigate the propensity of the animals to explore a novel arena with unknown feed balanced with the propensity to maintain social contact, we tested the animals pair-wise in an L-shaped arena containing both familiar and unfamiliar feed, similar to the one described previously by (Håkansson and Jensen, 2005). All tests were carried out between 0900 and 1300. Two animals at the age of 27 weeks (familiar to each other), of the same sex and selection strain, were tested in an L-shaped arena made out of cardboard boxes and covered with wire mesh. The height of the arena was 40 cm and each of the arms was 1.5 m in length and 0,5 m in width. Hence, when a bird was situated about half way into one of the arms, the other arm and its content was not visible to it. In the distal end of each of the arms, one familiar (chicken feed) and one unfamiliar feed source (sun seed) was placed next to each other. The test arena thus allowed the birds a choice between foraging for novel or known feed either alone or together with another bird.

The animals were placed in the arena while in total darkness and the test started when the lights had been turned on for two minutes and continued for 60 minutes. The location and feeding activity of each of the animals were instantaneously sampled with an interval of 10 seconds. The position in the arena, and feeding (pecking at the feed source) from the familiar or unfamiliar feed was recorded. For statistical analysis, each tested pair of birds was treated as the independent replicate.

Experiment 2

Animals

Experiment 2 was carried out on birds from the S4 generation, which comprised a total of 79 animals (41 males and 38 females). Eight females and eight males were from selection line H, 20 males and eight females from selection line L, and 12 males and 22 females from the unselected line U.

Social dominance test (SD)

Since the dominance test in experiment 1 was related to competition over limited access to feed, we decided to investigate the dominance relations between birds from the different selection lines in the same test, but where competition was over a non-feed related resource. We studied 42 birds, seven females and seven males from each selection strain (H, U, L). Three dominance tests were carried out, and in each test we offered limited access to one of three resources: water, wood chips (for dust bathing), and mealworms (for comparison with experiment 1).

Before the dominance test started, the birds were isolated for 24 h in individual cages measuring 40x100x50 (WxLxH). Here, they had visual and acoustic contact with other animals, but no physical interaction was possible. During this period, they were deprived for 2 h from water, when that was the resource which they were going to be tested against, or for 24 h from access to wood chips to dust bathe in. This was done in order to increase the motivation to drink or to dust bathe. The 2 h of water deprivation was based on our previous experience of how chickens react to this, and previous research has shown that 24 h of deprivation from

substrate will significantly increase the motivation to dust bathe (Vestergaard, 1982). As in experiment 1, the birds were accustomed to eating mealworms from the same containers as used in the test, and their motivation to obtain this resource was always high. The dominance test was then carried out in the same way as in experiment 1, with the difference that the birds were collected directly from the isolation pens to the test pen.

As in experiment 1, the animals were tested in groups of three, one from each selection strain and of the same sex. All the animals were tested with all the resources, one resource at the time. During three consecutive weeks they were tested once per week for one of the resources, so there was a resting period of one week in between tests. All tests were conducted between 10.00 am and 14.00 pm. After a 20 min habituation period in the empty test pen, the limited resource was presented to the animals. The water was presented in a water nipple which could only be operated by one bird at a time, the wood chips were introduced in a plastic box which would only allow one bird to dust bathe at a time (size of the box: 17 x 11,5 x 4 cm), and the mealworms were presented as in experiment 1, in a petri dish (13,5 cm in diameter) with a narrow hole of 1cm in diameter in the lid, only allowing one bird at a time to obtain worms. The resources were available to the animals throughout the 20 min test period. The behaviour of the birds was recorded on video during the test, in order to exclude any possible effects of the presence of a human in the test situation. During the entire test, we used continuous recording to score for each animal: access to the resource, and frequency of aggressive behaviour (table 2).

Statistics and data analysis

For each test and variable the mean and SEM within selection strain was calculated. Due to lack of normality the differences between selection strains in all the variables recorded in the Fear of human-test, SB, ES and SD tests were analysed with Kruskal-Wallis ANOVA with sex and selection strain as categorical predictors in separate models. For all statistical analyses, Statistica version 12 was used. Statistical significance was reported when $p < 0.05$.

Results

The selection regime caused a significant difference in fear-of-human score during the four included generations. In the parental, outbred and unselected population, the mean score was 3.31 (SEM: 0.07). In the fourth selected generation, the H line had a mean score of 3.43 (SEM: 0.1), the U line 2.92 (SEM: 0.11) and the L line 2.74 (SEM: 0.08). The effect of line was highly significant (Kruskal Wallis, $H(2) = 16.16$, $N = 79$, $P < 0.001$).

Experiment 1

The three strains in the S3 generation had a similar average weight at hatch (fig 1a). However, at day 200, birds from L were significantly larger than U and H (fig 1b). Furthermore, H females laid significantly smaller eggs than the other two strains and their offspring (i.e., the S4 generation) were on average significantly smaller at hatch than U and L (fig 2).

The overall average plumage condition score was significantly higher in birds from both H and U lines than L (fig 3), indicating a less damaged plumage in the L birds.

In the social behaviour test, there were no significant differences in any of the recorded behaviours. Hence, the frequency of social behaviour was unaffected by selection line.

In the social dominance test, birds from the H strain performed significantly less feeding and less overall aggressive behaviours than the other two strains. Consistent with this, they also performed more avoidance behaviour than the other two strains (fig 4). These results indicate that birds from the H strain were less dominant than those from the other selection lines. Considering differences between the sexes, males performed more aggressive behaviours (7.5 ± 1.19 vs 3.13 ± 0.65 SEM; $H(1) = 5.39$, $N = 99$, $P = 0.02$) and avoidance (0.27 ± 0.13 vs 1.35 ± 0.36 ; $H(1) = 8.73$, $N = 99$, $P = 0.003$) behaviour (nrs of recordings during 60 minutes)

In the exploratory and sociality test, the H strain performed significantly less total feeding as well as feeding from familiar feed. There were no significant differences between the selection strains with respect to the unfamiliar feed source (fig 5). Regardless of selection line, the time spent together in the same arm of the maze was significantly higher in the females than in the males (236 ± 14.96 vs 174 ± 17.02 nrs of recordings during 60 minutes; $H(1) = 6.19$, $N = 51$, $P = 0.013$), indicating a stronger social cohesiveness among females. However, this was not affected by selection.

Experiment 2

Birds belonging to the L-strain performed significantly more aggressive behaviours in all three test situations than both the U and H-strain, regardless of the resource (fig 6), indicating that L-strain birds were generally more dominant. There were no

significant differences in access to the resource between the three strains. There were no significant sex differences in any of the measured variables.

Discussion

In general, the results showed that chickens selected for a low fear response towards humans (L) secondarily had a higher weight, laid larger eggs and generated larger offspring than birds selected for a high fear response (H), and the unselected strain (U). They also had a less damaged plumage, indicating that they were less exposed to feather pecking. Furthermore, they were more socially dominant and received less aggressive behaviour in the Social dominance test. Finally, they also tended to be more feed motivated, both in the Social dominance test and in the Exploratory behaviour and sociality test. A possible interpretation of this is that birds selected for low fear were better able to cope with the experimental environment in which they had been selected.

Although we have only carried out selection for four generations in total, it was clear that this produced a significant difference in fear of humans. Since this was the target selection criterion, it is of course the expected result, and Agnvall *et al.* (2012) observed a significant genetic component to this trait after only two generations. In the present study, we found a number of correlated effects on traits related to ability to cope with captivity. which is a fast response to a simulated domestication event In foxes, Belyaev (Trut *et al.*, 2009) found that correlated responses to selection for tameness developed in a small proportion of the animals after eight to ten generations, which shows that domesticated phenotypes may start to occur within few generations of reduced fear of humans. The effects we found on social dominance were replicated in two consecutive generations, showing that this is

probably a stable behavioural difference between the selection lines in the present experiment. Hence our results indicate that the ability to obtain high social dominance (as assessed in this study) was affected by selection for high or low fear. Of course, there is a risk that our results are the result of genetic drift, since it comprises a relatively limited number of families. However, each selection line consists of four to ten families, which can be regarded as independent replicates, since selection is done on individual basis. Furthermore, the fact that the results were replicated in two subsequent generation strengthens the impression that they were due to the selection imposed, as does the fact that the unselected birds generally fall in between the selected lines in the variables measured.

In a similar type of test on foxes, Harri *et al.* (2003) found that animals selected for tameness monopolized a feed source in 9 out of 10 tests. This was interpreted as a generalization of the reduced fear also towards conspecifics and the test situation, and a reduced stress susceptibility, which could perhaps also explain the effects observed in the present study.

The birds selected for low fearfulness grew larger than the other strains, and this may have confounded the social dominance results to some extent. As earlier reported (Craig *et al.*, 1975, Cloutier and Newberry, 2000, Müller *et al.*, 2002) body weight seems to be a reliable predictor of a chicken's position in a hierarchy. It is therefore not possible to distinguish cause and effects between the observed correlated selection responses, since high body weight may either have been a consequence of the increased social competitiveness, or it may have been the factor causing it. Moore *et al* (2002) proposed that social dominance is affected by additive genetic variation, which can lead to rapid changes. Fear of human traits may

therefore have a shared genetic component with social dominance, but to disentangle the genetic mechanisms, further experiments are needed.

Body weight may also be an indicator of overall welfare and capacity to cope with the environment (Tachè and Selye, 1985, Broom, 1991), since a calm and confident animal may be better at obtaining feed and growing. However, to establish the overall welfare of the animal, variables such as behaviour disorders, physiological measurements and diseases need to be assessed (Broom, 1991), and our results therefore remain suggestive. In a similar study of rats, Albert *et al.* (2008) found no differences in body weight between rats selected for tameness and those selected for aggressiveness, which indicates that correlated effects on body weight may not be universally present, but may depend on species and environmental context.

The larger L birds also laid larger eggs, in accordance with the study by Müller *et al.* (2002), reporting a positive correlation between body size and egg mass. Increased body size in L birds may reflect a better ability to cope and grow in the captive environment used in this experiment. Further in accordance with this, the L birds in this study also had better plumage condition, both on the head and on average on the whole body. Both exposure to abnormal feather pecking and aggressive pecking can cause deterioration of plumage condition, (Jensen *et al.*, 2005) and a larger and more dominant bird may be more resistant to this. In general, the plumage condition is regarded as good reflection of the welfare of chickens (Campo *et al.*, 2001). It has previously been shown that offspring of barn swallow mothers with high corticosterone levels produce offspring with lower hatch weight and slower plumage development (Saino *et al.*, 2005), and similar effects have been observed in chickens (Eriksen *et al.*, 2003). The fact that the offspring of the H

chickens weighed significantly less could therefore indicate higher stress levels in H chickens. Even though this is well in line with the overall impression, that L-birds were better adapted to the environment, this remains an interesting hypothesis, since at present we have no data on levels of stress hormones in the different selection lines. Japanese quail selected solely on high plasma corticosterone response, experienced human contact more aversive than quails selected on low response (Jones *et al.*, 1994), emphasizing the link between tameness and general stress susceptibility.

During domestication, chickens have been selected on maximizing the ratio between feed intake and egg laying (Kerje *et al.*, 2003). Probably due to this, domesticated chickens show a higher general feeding motivation and less explorative foraging (Schütz *et al.*, 2001). In our experiment, the animals selected for low fear response fed more both in the SD and ES tests, although the feed consisted of familiar and unfamiliar chicken feed in the ES and mealworms in the SD. This may imply that increase in feeding motivation could subsequently explain the difference in social dominance. Since feeding motivation could be the confounding variable behind the effects observed in experiment one, we performed the second experiment, which showed that regardless of resource, chickens from the L line were more dominant. Hence, it seems likely that the increased dominance resulting from selection was not merely caused by a generally increased feeding motivation. Since there were no overall effects of selection on frequency of social behaviour the increased social dominance cannot be explained simply by a higher degree of social activity in the L line birds.

In conclusion, birds selected for low fear of humans grew to a higher body weight and laid larger eggs, with consequently larger offspring, and the

plumage condition of these birds was better than in those selected for high fear. In spite of the fact that there was no difference in frequency of social behaviours between the selected strains, birds selected for low fear were more dominant in test situations both with and without feed. Overall, this indicates that the L-birds from the two tested generations were better adapted to the experimental captivity environment.

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Table 1.

The criteria for the scores in the plumage condition assessment. The assessment was done on the head and tail separately and the body and wings together, and the final score of the individual was the average of the three separate scores.

Score	Criteria
0	Intact feathers
1	Few feathers separated but no broken or missing
2	Many feathers separated and/or a few broken or missing
3	Most feathers separated, many missing or broken, bald patch <5 cm
4	Most feathers missing or broken, bald patch >5 cm
5	Almost all feathers missing, completely denuded area.

Table 2. Ethogram of the behaviour measured in the Social behaviour and in the Social dominance test. The behaviours were assessed through continuous recording of 5 minutes every 15 minutes, in total 12 x 5 minutes

Behaviour	Description
Feeding	Eating from feed container.
Avoidance	
Escape	Attempt to escape out from the test arena by jumping or making flight attempts towards the roof.
Avoidance	The bird sits in a corner and faces away from opponent
Aggressive	
Threat	The bird walks after the other with head held high, the other bird walking/running/jumping/flying away.
Severe feather peck	Pulling feathers.
Chase	Bird follows another bird, both running, jumping or flying.
Attack	Bird runs, jumps or flies when approaching another bird in order to give one or more aggressive peck. The head is kept above the receivers head
Fight	Bird being involved in an aggressive fight, more than just one single peck. Both birds are running, jumping or flying towards each other.
Aggressive peck	Bird gives a fast peck, directed to an anterior part of another bird's body.

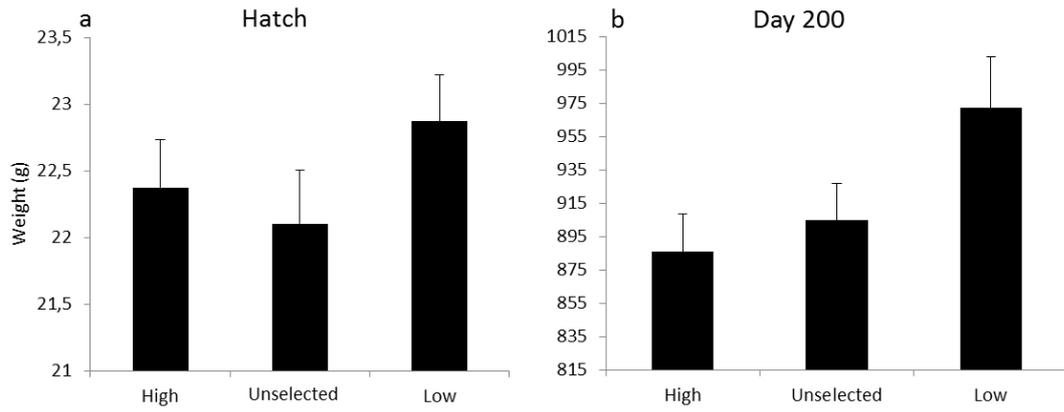


Figure 1. Weights of birds from the S3-generation. a. Hatch weight ($H(2)=2.27$, $N=142$, $P=0.32$). b. Weight at 200 days ($H(2)=6.16$, $N=101$, $P=0.04$).

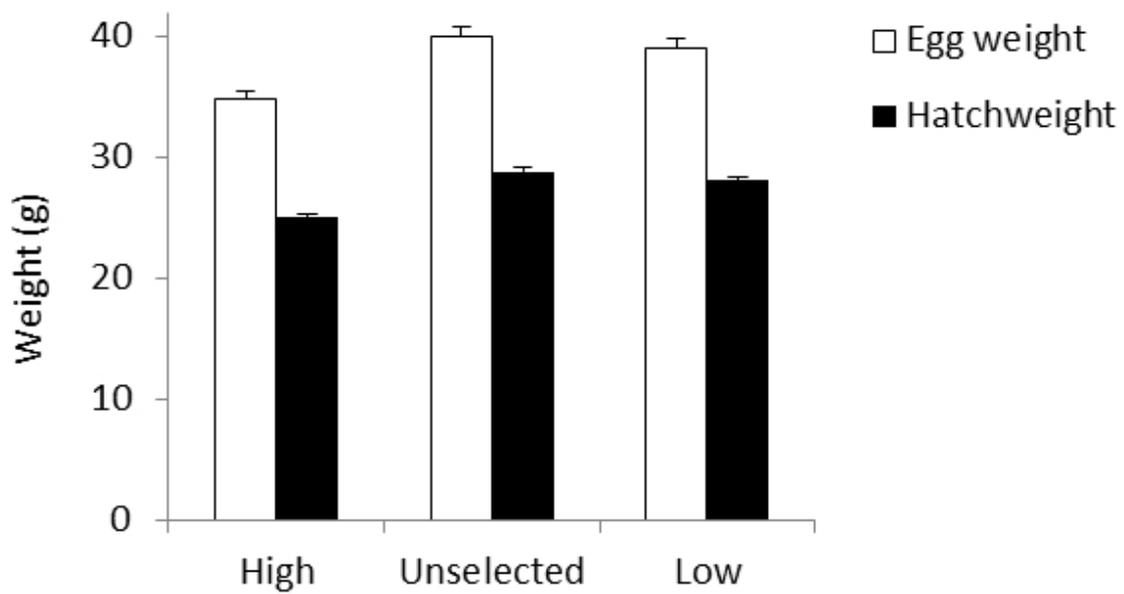


Figure 2. Weight of the eggs and the hatch weight of S4 generated from S3. (Egg weights: $H(2)=10.00$, $N=17$, $P=0.007$; chick weights: $H(2)=45.44$, $N=107$, $P<0.001$).

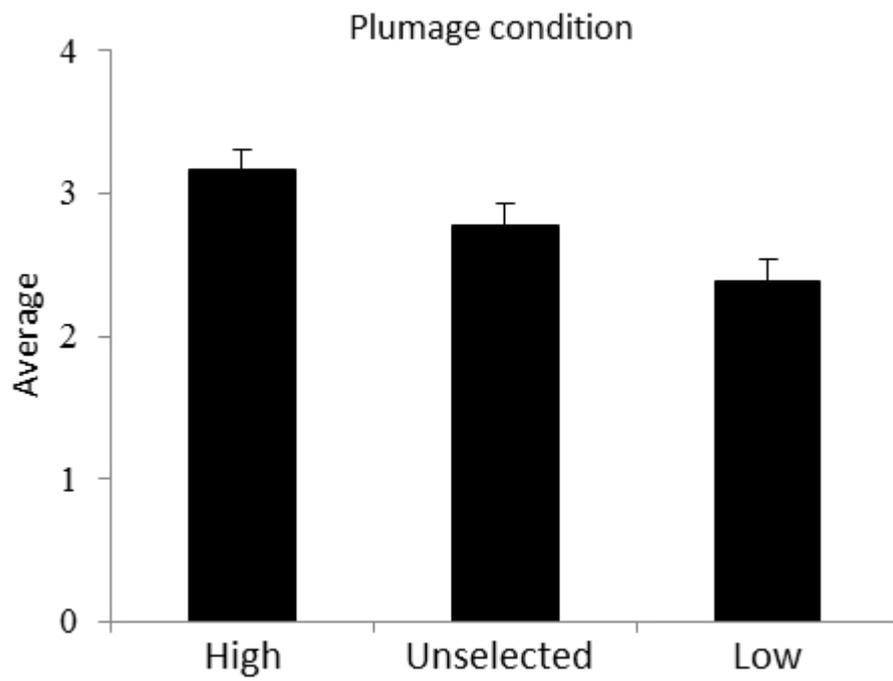


Figure 3. Average plumage condition scores of birds in the S3-generation at 200 days of age, on a scale 0-5, where 0 represents a completely unaffected plumage, and 5 severe damages on all body parts ($H(2)=11.55$, $N=101$, $P=0.003$).

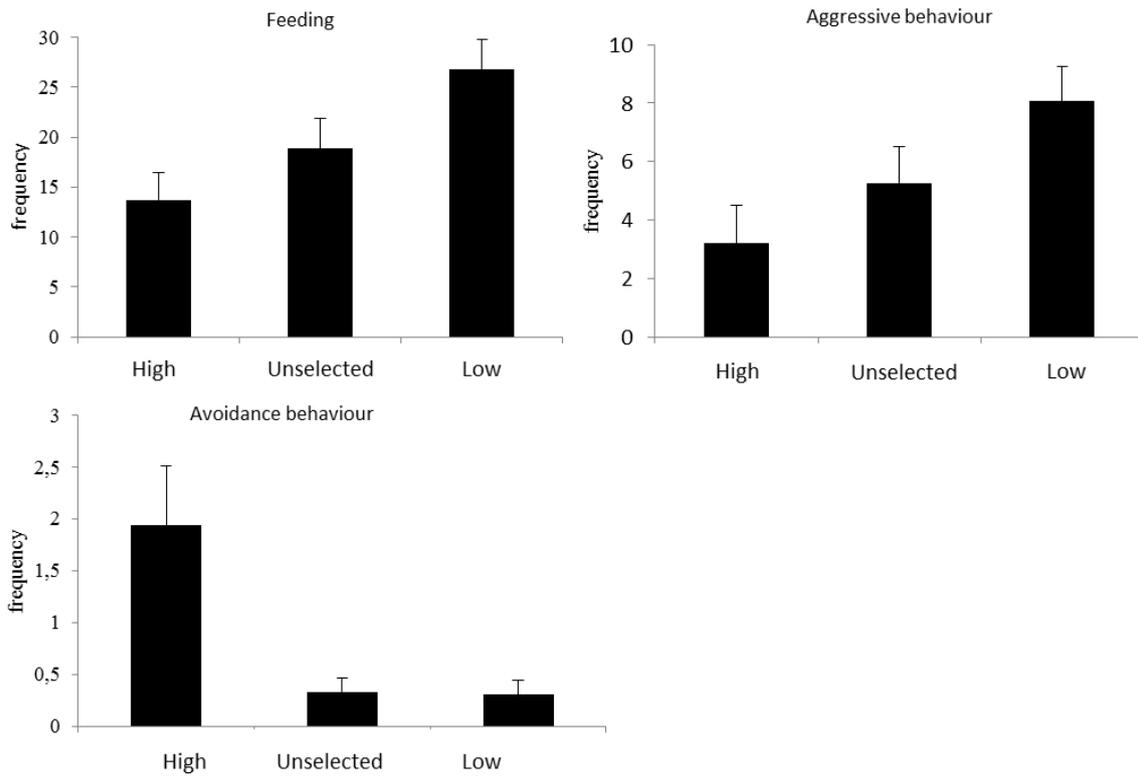


Figure 4. Average frequencies of feeding (Kruskal-Wallis: $H(2)=17.53$, $N=99$, $P<0.001$), aggression ($H(2)=11.20$, $N=99$, $P=0.004$) and avoidance ($H(2)=7.70$, $N=99$, $P=0.02$) in the Social dominance test in the S3-generation.

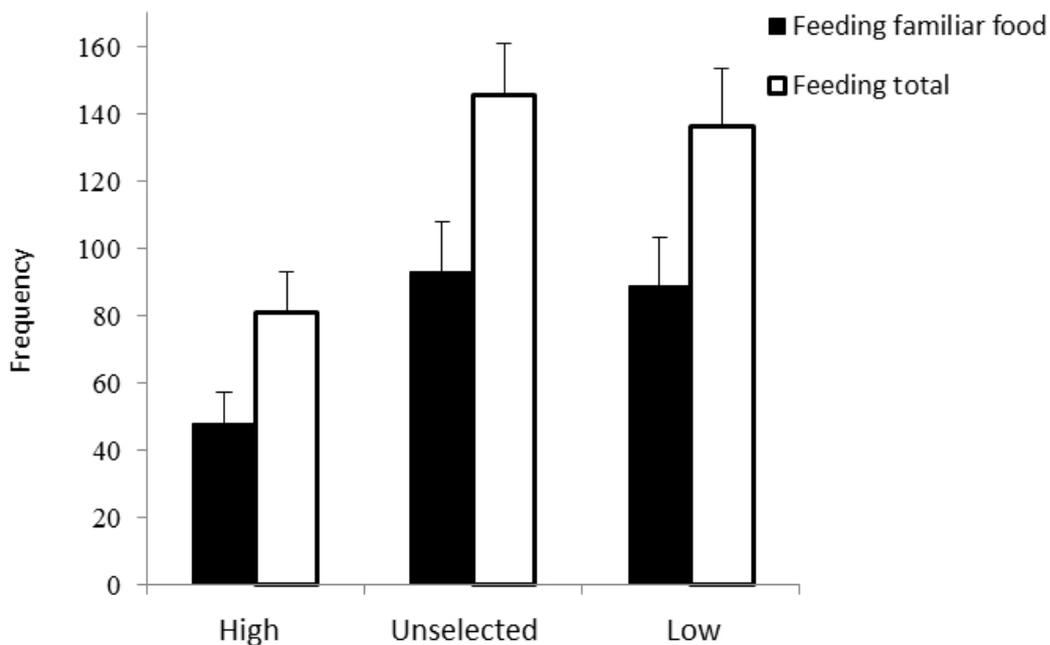


Figure 5. Frequency of total feeding ($H(2)=10.02$, $N=51$, $P<0.007$) and feeding familiar feed ($H(2)=7.70$, $N=51$, $P=0.02$) in the Exploratory behaviour and sociality test.

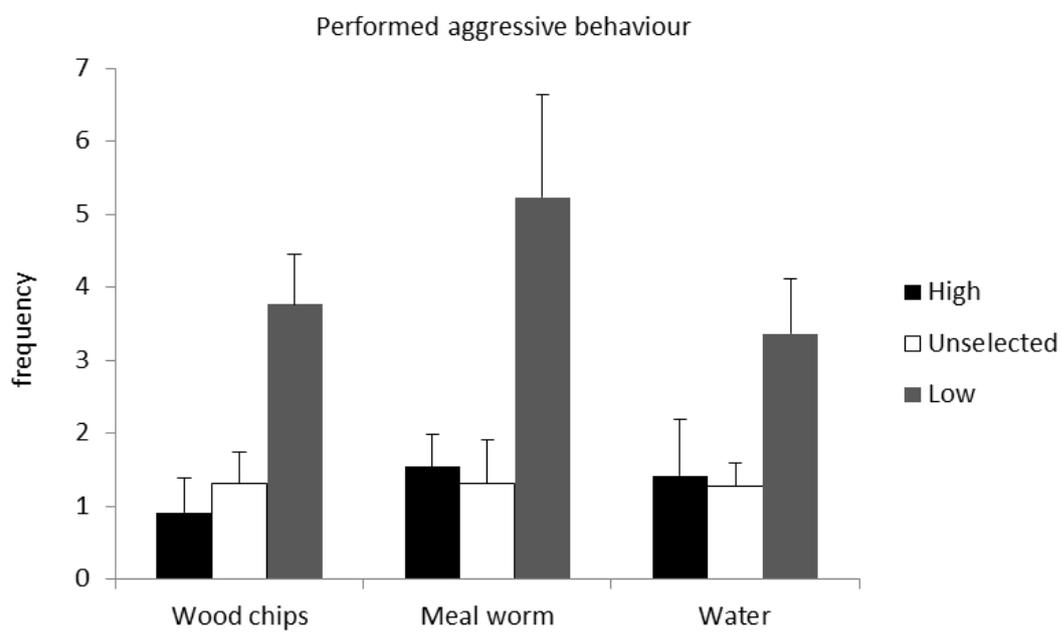


Figure 6. Frequency of aggressive behaviour performed during the three test situations with different limited resources in the S4 generation (Wood chips: $H(2)=11.90$, $N=39$, $P=0.002$; Mealworm: $H(2)=5.91$, $N=39$, $P=0.05$; Water: $H(2)=6.72$, $N=42$, $P=0.03$)