



Behavioural consequences of divergent selection on general locomotor activity in chickens



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ABSTRACT

General locomotor activity is a highly variable phenotypic trait of animals. In domestic chickens it is different within and between breeds. The general locomotor activity is a substantially heritable trait and has been shown to be correlated with several other behavioural traits, such as for example feather pecking and anxiety in chickens. However, whether there is a relation between different levels of general locomotor activity and behavioural changes remained unclear. Therefore, a selection line model system has been established, where hens from the same founder population were selected over eight generations for either high or low general locomotor activity. The selection led to significant increases, respectively decreases in general locomotor activity and differences in growth. We here tested 128 hens of the 8th generation in three behavioural tests. We assumed fearfulness to be affected from selection on general locomotor activity, which we tested in a tonic immobility test. Socio-positive and socio-negative behaviours were tested in respective test paradigms. Fearfulness was higher in hens selected for high general locomotor activity. Social behavioural traits and feather pecking were not affected by selection for general locomotor activity. Evolutionary mechanisms that link fear and general locomotor activity are discussed and also why social behaviours and feather pecking seems not to be affected from selection on general locomotor activity. Our results provide interesting new insights on how selection on one trait, general locomotor activity, affects the behavioural phenotype in other dimensions too.

1. Introduction

General locomotor activity (GLA) is a phenotypic trait that is highly variable within and between different breeds of chickens (Bizeray et al., 2000; Kjaer, 2017). GLA describes the overall locomotor activity of an individual in its home range area while performing its undisturbed behaviour. GLA is not only variable among individuals but this variation can have direct influence on several other phenotypic traits in domestic chickens. Chickens with high locomotor activity have consequently also a higher energy expenditure and require a higher food intake (Gonyou and Morrison, 1983; van der Waaij, 2004; Phi-van et al., 2014, Kjaer and Phi-van, 2016). However, a higher locomotor activity seems to have a positive effect on the bone strength (Knowles and Broom, 1990) of chickens. The general locomotor activity (GLA) is also a substantially heritable trait with h^2 from 0.33-0.38 (Kjaer, 2017). Beside these direct effects of variation in GLA, also a potential correlation between high levels of feather pecking and high locomotor activity has been described (Kjaer, 2009), leading to the assumption that high GLA might also be a symptom of a kind of hyperactivity disorder

(Kjaer, 2009) related to feather pecking. Furthermore, the GLA level is affected by a genetic polymorphism in the serotonin transporter gene (5-HTT) (Phi-van et al., 2014). This polymorphism in the 5-HTT gene is not only associated with differences in GLA but also with different levels of fearfulness (Krause et al., 2019, Krause et al., 2017). However, whether these correlated effects of GLA are directly linked to other behavioural changes is not clear, so far. From other Galliform species, as for example for quail (*Coturnix japonica*) it has been reported that genetic selection on locomotor activity was accompanied by changes in fear-related behaviour so that quail that showed more locomotor activity were less fearful (Jones et al., 1982). In order to understand whether similar effects linked to GLA appear in domestic chicken, we here used adult hens that over eight generations (F8) were selected on either low (LGLA) or high general locomotor activity (HGLA) (Kjaer, 2017). We tested these selection lines for fear-related behaviour using a tonic immobility test (Gallup, 1977; Gallup et al., 1971; Jones, 1986; Krause et al., 2011; Albentosa et al., 2003). We assumed HGLA hens to be less fearful than LGLA hens. Although HGLA are more active than LGLA hens they were found to have a higher body mass (Kjaer, 2017),

Abbreviations: GLA, general locomotor activity; HGLA, high general locomotor activity line; LGLA, low general locomotor activity line; TI, Tonic Immobility test

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thus we expect the same pattern to be present. Furthermore, we tested how the selection on GLA affected social behaviour. We aimed to disentangle between two potential alternative scenarios how GLA may affect social behaviour. It might be either the HGLA is the result of a genetic based neuronal hyperactivity disorder (Kjaer, 2009) related to findings this disorder is potentially linked to the prevalence of abnormal behaviour such as feather pecking. Such increased behaviour may be the result of obsessive-like locomotor activity in order to e.g. feather peck. Thus, we expect in such a scenario HGLA hens in a socio-positive (Dudde et al., 2018) and a socio-negative aggression test (Dudde et al., 2018; Gallup et al., 1972) the HGLA to be less social and more aggressive. Alternatively, it might be that more active hens are also more engaged in social interactions (Schütz and Jensen, 2001) as they e.g. might be more likely to meet other hens. Here we would expect HGLA hens to be more social and less aggressive.

2. Methods

2.1. Animals and general locomotor activity (GLA)

We used adult laying hens (*Gallus gallus* f. domestica) of about 10 months of age, from the 8th generation of lines selected on general locomotor behaviour (GLA) (Kjaer, 2017), a low general locomotor activity (LGLA) and a high general locomotor activity (HGLA) line which were selected for low, respectively high general locomotor activity in the home pens (Kjaer, 2017). These two lines originated from the same founder population which was the L68 line (Lieboldt et al., 2015; Lyimo et al., 2014; Krause and Schrader, 2018; Dudde et al., 2018) with a New Hampshire origin. The L68 line was not selected for general locomotor activity (GLA) or any other traits, but kept as a general random bred control line at the Institute.

The specific selection procedure for the GLA lines are described in detail elsewhere (Kjaer, 2017). Briefly, in each generation and line, ten sires and 20 dams produced around 200–300 offspring on which GLA records were taken in the home pens for five days at the age of about five weeks (Kjaer, 2017) using small RFID-transponders attached to the leg of each individual chicken. Individual GLA was recorded using antennas placed on the floor reading the transponders when birds passed over it (Ganter Pigeon Systems, Schruns, Austria). For each individual the average locomotor activity (reads/hour) was calculated (Kjaer, 2017).

We here used 51 adult laying hens of LGLA, 63 hens of the HGLA and 14 hens of the control line. The birds were housed together in a single stable (6.5 m x 4.5 m) with litter floor bedding and *ad libitum* access to standard layer food and water. All birds were hatched and reared together and were handled and tested under the same conditions. The observers were blinded to the three lines. All birds were weighed at day 30 of life when birds were fitted with RFID transponder and general locomotor activity (GLA) recording started. At 10 month of age, birds were weighed again immediately before the behavioural tests were conducted. The compartments were equipped with perches on an elevated dung area, which was otherwise covered with grid. Perches were provided after the GLA measurement have been taken at the age of five weeks of age. Group-nests were provided to the hens and eggs were collected on a daily basis. A temperature of about 20 °C and a light period of 14L:10D was provided, with lights on at 4am. Experiments started not before 8am to enable hens to lay their eggs before being tested.

At the age of 11 weeks, feather pecking observations were conducted (by JBK) in small sub-groups of 7 hens. After 24 h acclimatization, the groups were observed for 20 min and all incidents of gentle, severe or aggressive pecking were counted according to the criteria of (Kjaer and Vestergaard, 1999; Kjaer, 2009). In total 18 sub-groups were observed on three subsequent days, containing seven groups with only pullets of the LGLA, eight groups of HGLA and three control groups.

2.2. Behavioural tests

To measure selection-specific effects of low, respectively, high GLA on the behavioural phenotype we aimed to measure three behavioural dimensions. First, we aimed to test, whether the level of fear was altered by the selection for low and high GLA, using a tonic immobility test. Subsequently we aimed to test for effects of GLA selection on socio-positive behaviour and thirdly socio-negative behaviour (Dudde et al., 2018; Krause et al., 2019). After the end of each behavioural test, hens were returned to their home pen and remained there for further egg production.

i.) In the tonic immobility test (TI), which is a standard test to measure fearfulness in poultry (Albentosa et al., 2003; Gallup, 1977; Gallup et al., 1971; Krause et al., 2011; Jones, 1986, Krause et al., 2019), hens were individually tested in a room next to the home pen. Hens were laid on the back in a V-shaped cradle and once they remained 10 s immobile, the latency to rise was measured. One hen that needed more than three trials for inducing TI was excluded from the test. If a hen did not rise within 10 min the test was stopped and a value of 600 s of immobility was recorded. After the test, hens were immediately returned to their home pen.

ii.) In the social approach test, a runway (Hocking et al., 2001) was used to measure the socio-positive behaviour towards familiar conspecifics. The test was slightly modified after (Dudde et al., 2018; Krause et al., 2019). We used the identical setup with a runway of 1.5 m length (width: 45 cm; height: 50 cm) into which the hens were individually released from a start box. At the end of the walkway there was visual, acoustic and olfactory access to the pen mates as the walkway ended in the home compartment. The time from entering the runway to reaching the endzone was recorded, as this is a proxy for social motivation (Dudde et al., 2018; Hocking et al., 2001; Marin et al., 2001). If a hen did not reach the endzone the test was terminated after 30 s, this time was lower than in earlier studies (Dudde et al., 2018) as the present hens were more agile.

iii.) In the mirror test, aggression and pecking as proxies for socio-negative behaviour were measured (Dudde et al., 2018; Gallup et al., 1972; Krause et al., 2019). The same runway as described above was used, only without the startbox, and at the open end a mirror was placed. Hens were inserted into the runway at the end opposite to the mirror with the tail directed to the mirror. We measured the time hens required to reach the endzone at the mirror and counted the number of pecks on the mirror surface. The test lasted 300 s.

2.3. Ethical note

The study was conducted according to German laws and under permission of the local authorities LAVES (33.19-42502-04-16/2257). Daily visual controls for animal health status were conducted.

2.4. Statistical methods

The LGLA and HGLA paternities were known from the breeding scheme and were included in the analysis as random factors. The control hens' ancestry was unknown and thus they were only considered for additional post hoc testing, to get an impression of how selection on LGLA and HGLA affected the locomotor behaviour compared to the founder L68 line. GLA data were transformed [$\arcsin(\sqrt{\text{GLA}}/100)$] according to (Kjaer, 2017) to obtain normal distributions of the residuals. The transformed GLA of the two selected lines were compared in a Linear Mixed Effect model (LME) with Line ID (2-level factor: LGLA, HGLA) as fixed factor and sire and dam as nested random factors (dam within sire). The subsequent comparison with the control hens was calculated with a pair wise t-test. These comparisons were conducted to provide information on the relation of the behaviour of GLA-selected hens to non-selected control hens. Body mass at day 30 and at adulthood ($\log x + 1$ transferred) were analysed with identical LME's. In

all cases non-transformed data are presented in the figures.

The data from the feather pecking observations at the age of 11 weeks were group comparisons between LGLA and HGLA and the subsequent comparison with the control were calculated with non-parametric statistics, i.e. Mann-Whitney U-tests, as data was not normally distributed.

The latency to raise in the tonic immobility test, the time to approach the endzone in the social approach test and the time to approach the mirror were analysed using Generalized Linear Effect model (GLME) with the assumption of a Poisson distribution. Line was considered as fixed factor in these models and dam within sire as random factors. The peck rate at the mirror of those hens that reached the mirror was calculated as [peck rate per minute=(pecks at mirror/(maximal test time 300 s – time to reach the endzone))*60]. The peck rate was analysed in a LME as described above. All models were calculated in R 3.3.1 using the packages nlme (Pinheiro et al., 2017), lme4 (Bates et al., 2015) and car (Fox and Weisberg, 2011), non-parametric statistics were calculated using Dell Statistica 13.

3. Results

3.1. General locomotor activity (GLA) and body mass

The GLA of the two selected lines, i.e. the 8th-generation of LGLA (low) and HGLA (high), differed significantly from each other (LME, factor line $F_{1,17} = 294.32, p < 0.0001$, Fig. 1) and both differed in the subsequent post-hoc comparison from the unselected control birds (both $p < 0.0001$). HGLA hens had the highest GLA and the LGLA the lowest GLA (Fig. 1).

The body mass at 30 days of age was significantly different between the two GLA selected lines (LME, factor line $F_{1,17} = 15.55, p = 0.001$), LGLA birds (mean mass day 30 ± SE: 190.2 g ± 3.2 g) were significantly lighter than HGLA birds (214.4 g ± 2.9 g). A subsequent comparison with control birds revealed that LGLA birds were also lighter than the control birds (213.4 g ± 6.2 g) ($p = 0.001$), but HGLA did not differ in mass from control birds ($p = 0.87$).

These differences in body mass between the two selected lines disappeared by adulthood, i.e. when the behavioural tests were conducted (LME, factor line $F_{1,17} = 0.53, p = 0.48$; LGLA 1851.9 g ± 23.9 g (mean ± SE), HGLA 1809.7 g ± 21.5 g). Control hens weighed on average 1925.2 g ± 45.6 g and were significantly heavier than HGLA ($p = 0.02$), but not significantly heavier than LGLA ($p > 0.05$).

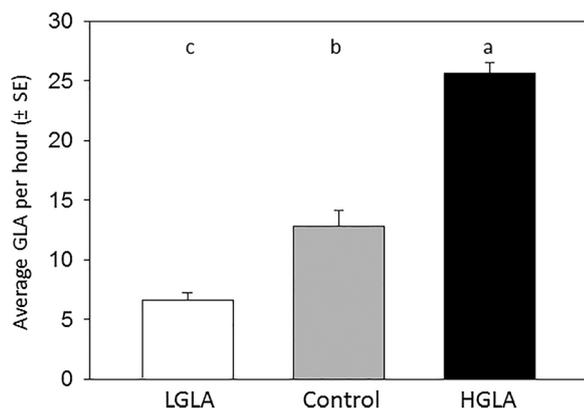


Fig. 1. The average general locomotor activity (GLA) of the hens selected on low general locomotor activity (LGLA) and high locomotor activity (HGLA) in comparison to unselected control hens. GLA was recorded individually in the home pens using a RFID an antenna system for one week starting in the fifth week of life. Different letters indicate significant differences.

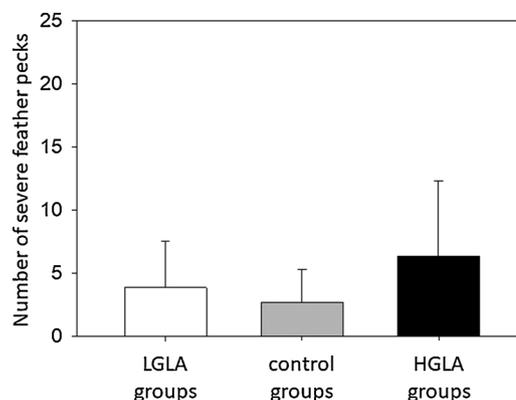


Fig. 2. Results from the feather pecking observations that were conducted in sub-groups at the age of 11 weeks with respect to LGLA (white bars), control (grey) and HGLA (black) chickens. No significant differences with in severe feather pecking were found.

3.2. Feather pecking and aggressive pecking observations

For the severe feather pecking no significant difference was found between LGLA and HGLA groups (Mann-Whitney, U-test, $N = 15, p = 1$; Fig. 2) and also subsequent comparison with the control revealed no differences (both $p = 1.0$; Fig. 2). Also the gentle feather pecking was not different between groups of LGLA and HGLA (Mann-Whitney U-test, $N = 15, p = 0.13$). Differences from groups of both selected lines to groups of the control were also not significant (both $p > 0.4$). Aggressive pecking was not different between groups of LGLA and HGLA (Mann-Whitney U-tests, $N = 15, p = 0.29$), from LGLA to control ($p = 0.33$) or from HGLA to control ($p = 0.061$).

3.3. Fear-reactions in the tonic immobility test

The time to rise in the tonic immobility test differed significantly between the two selected lines, HGLA remaining significantly longer immobile, indicating a higher fear response (GLME, factor line $\chi^2_1 = 41.26, p < 0.0001$; Fig. 3). A subsequent comparison with the control hens showed that only HGLA hens differed from them ($p < 0.0001$), while they did not differ in the latency to rise from LGLA ($p = 0.96$).

3.4. Socio-positive and socio-negative behaviour reactions

Social approach times, as proxy for socio-positive behaviour, did not differ between the two selected lines (GLME, factor line $\chi^2_1 = 0.20, p = 0.66$). LGLA hens required on average 7.5 s ± 1.2 s (mean ± SE)

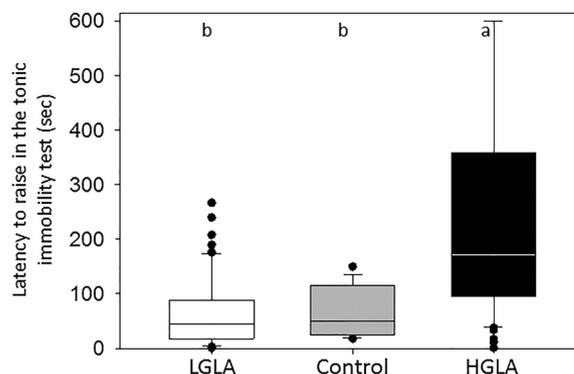


Fig. 3. The latency to raise in the tonic immobility test, a proxy for fearfulness. Hens selected for high general locomotor activity (HGLA) were most fearful compared to those selected for low general locomotor activity (LGLA). Different letters indicate significant differences.

to approach the conspecifics and HGLA hens $7.8 \text{ s} \pm 1.1 \text{ s}$. A subsequent comparison with the control hens ($6.3 \text{ s} \pm 2.4 \text{ s}$) revealed no significant difference to either of the two selected lines (both $p > 0.56$).

Time to approach the mirror, as proxy for socio-negative behaviour, did not differ between the two selected lines (GLME, factor line $\chi^2_1 = 0.01$, $p = 0.93$). LGLA hens required on average $144.5 \text{ s} \pm 18.0 \text{ s}$ (mean \pm SE) to approach the mirror and HGLA hens $158.6 \text{ s} \pm 16.0 \text{ s}$. A subsequent comparison with the control hens ($157.0 \text{ s} \pm 33.8 \text{ s}$) revealed no significant difference to either of the two selected lines (both $p > 0.74$). Hens that reached the mirror did not differ significantly in their peck rate on the mirror (LME, factor line $F_{1,17} = 3.82$, $p = 0.07$). Subsequent comparison to the controls showed no difference between control birds and either of the two selected lines (both $p > 0.22$).

4. Discussion

We found that the selection over eight generations has led to a substantial difference in the general locomotor activity (GLA) of hens of the HGLA (high GLA) line and the LGLA (low GLA) line. Furthermore, early in life differences in body mass were apparent, with LGLA birds being lighter. These differences were compensated at adulthood. The selection on general locomotor activity affected also fearfulness, with HGLA hens being more fearful than LGLA hens. Social behaviour traits, feather pecking and aggression were not affected by selection on GLA.

The differences in GLA between the lines is the results of a diverging selection in eight generations and shows, in line with previous studies, that GLA is a heritable trait with heritabilities between 0.33 to 0.38, as shown previously (Kjaer, 2017). Beside the clear difference between HGLA hens and LGLA hens it is interesting to see that the unselected control hens seem to be intermediate in their GLA, which suggests that artificial selection on GLA, works indeed bi-directional, i.e. leads to an increase of locomotor activity in the HGLA and a decrease in the LGLA hens.

Probably differences in GLA might be linked to metabolism, which the differences in early growth might support. Body mass at the age of 5-weeks were different between LGLA and HGLA birds, with HGLA birds being heavier, in line with the data from the earlier selected generations (Kjaer, 2017). This is at first glance surprising, as one might have expected that a higher activity lead to a higher energy expenditure and thus a lower body mass. One potential explanation for this could be that HGLA pullets have a feeding strategy that enables them to buffer for the extra energy required from high activity. At adulthood, this difference in body mass has been compensated. Usually it is assumed that such compensatory growth can only appear on the price of trade-offs, i.e. in most cases only at costs on other traits (Monaghan, 2008; Krause and Naguib, 2011; 2015; Fisher et al., 2006), but not always (Krause and Caspers, 2016). In other bird species, such as the zebra finch (*Taeniopygia guttata*), it has been shown that compensatory growth was linked with behavioural changes in adulthood. Zebra finches that compensated for early low body mass were less explorative (Krause and Naguib, 2011; 2015). Whether cost of compensation appeared in the chickens needs to be examined further.

HGLA hens showed, in contrast to our initial assumption, an increase in fear, as measured in the tonic immobility test (Gallup et al., 1971; Jones, 1986). This is particularly interesting as studies on other Galliformes species, i.e. the quail selected over five generations for high respectively low locomotor activity, showed the opposite effect; i.e. that an increase of locomotor activity was negatively linked to fear (Jones et al., 1982) using the same test paradigm (TI-test). The authors concluded that fear seems to inhibit locomotor activity (Jones et al., 1982). In chickens, GLA does not seem to inhibit fear or vice versa, as HGLA hens were most fearful in the present study. Nevertheless, it is particularly interesting to see that in both studies the selection of GLA led only to a one-directional change in the fear response. In the quail experiment the physically less active birds were more fearful than the active birds (Jones et al., 1982), whereas in the present chicken

experiment the active birds were more fearful than the less active birds (see Fig. 2). Thus, although the direction of effect of selection on general locomotor activity on fearfulness is opposite between quail and chickens, they have in common that fear seems to be affected from such selection processes only one-directionally. It seems that levels of fear can be increased but not decreased as a by-product for selection on GLA. That might be due to the evolutionary past, where an increase of fear might have been more flexible as fear has the potential to be adaptive in dangerous situations as for example predator encounters (Krause et al., 2017; Krause et al., 2019), while it may be maladaptive to reduce fear below a certain threshold. Whether the level of fear in the control birds as well as LGLA birds reflects the level of fear in the wild ancestors, i.e. the Red Jungle fowl, is unlikely as also the control birds are domesticated birds, and domestication has led to a reduction of fearfulness (Jensen, 2006; Schütz et al., 2002; Schütz et al., 2004; Campler et al., 2009). However, even artificial selection seems not to be capable to reduce fearfulness below a certain threshold. Fearfulness, as measured by the TI-test, seem to have certain heritable component (Mignon-Grasteau et al., 2017; Bertin et al., 2009) and furthermore it has been shown to be a highly repeatable trait, also in other birds (Wuerz and Kruger, 2015; Jones, 1989). Whether the increased fear of HGLA hens is now just back at the level of wild ancestors or even higher needs to be examined in future studies. However, it might be that selection for high GLA counteracts the taming effects of domestication. It would also be interesting to examine whether GLA of domesticated birds differs from that of the wild ancestors. There are a few hints indicating that locomotor behaviour in a specific context is lower in the wild ancestors (Campler et al., 2009), but this needs to be verified for the GLA.

Feather pecking was not different between HGLA and LGLA lines. Thus, it seems that the hypothesis of a hyperactivity syndrome (Kjaer, 2009) as being a cause of feather pecking could not be verified in the present genotypes. One possible reason for this discrepancy could have to do with the very low level of feather pecking in the lines of the present study in contrast to the high level in the White Leghorn lines used by (Kjaer, 2009). Earlier studies suggested one or a few major genes to be expressed in the White Leghorn lines and having a strong effect on feather pecking (Labouriau et al., 2009). These genes might be genetically correlated to activity and thus selection on feather pecking would co-select for activity in the White Leghorn lines. It is tempting to speculate that the low level of feather pecking in the LGLA/HGLA-lines might be due to the lack of these genes or their expression. This makes co-selection impossible, explaining the lack of correlated response in feather pecking behaviour when selecting on GLA. One need also to keep in mind that there is quite a genetic difference between brown and white layers (Lyimo et al., 2014).

The socio-positive as well as the socio-negative behaviour seemed not to be affected from the selection on GLA. Thus, GLA may only be linked to non-social behaviour traits. However, GLA could have affected social traits in an indirect way, as movement could have been important in an aggressive context and/or facilitate in general the likelihood of meeting conspecifics (Keeling and Duncan, 1991), but this was not subject of our experiments. None the less, we cannot fully exclude a link between GLA and social behaviour. Previous studies have found a positive correlation between activity and socio positive behaviour in commercial laying hens and bantam chickens (Schütz and Jensen, 2001).

Future studies may aim to validate the relation between GLA selection and social behaviours, probably also including male birds, as sex-specific effects might be possible. A higher GLA might be more beneficial for males under natural situations as one might speculate that this enables him to have better control over his group of females (Collias and Collias, 1996; Pizzari and McDonald, 2019), he will by chance meet competitors sooner and have more interactions with females.

Taken together, we found that selection on general locomotor

activity (GLA) works well in domestic chickens. The selection for high locomotor activity is accompanied by a higher level of fear, thus modification of a key personality trait.

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References

- Albentosa, M.J., Kjaer, J.B., Nicol, C.J., 2003. Strain and age differences in behaviour, fear response and pecking tendency in laying hens. *Br. Poult. Sci.* 44, 333–344.
- Bates, D., Machler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48.
- Bertin, A., Richard-Yris, M.A., Houdelier, C., Richard, S., Lumineau, S., Kotrschal, K., Mostl, E., 2009. Divergent selection for inherent fearfulness leads to divergent yolk steroid levels in quail. *Behaviour* 146, 757–770.
- Bizeray, D., Leterrier, C., Constantin, P., Picard, M., Faure, J.M., 2000. Early locomotor behaviour in genetic stocks of chickens with different growth rates. *Appl. Anim. Behav. Sci.* 68, 231–242.
- Campler, M., Jongren, M., Jensen, P., 2009. Fearfulness in red junglefowl and domesticated White Leghorn chickens. *Behav. Processes* 81, 39–43.
- Collias, N.E., Collias, E.C., 1996. Social organization of a red junglefowl, *Gallus gallus*, population related to evolution theory. *Anim. Behav.* 51, 1337–1354.
- Dudde, A., Schrader, L., Weigend, S., Matthews, L.R., Krause, E.T., 2018. More eggs but less social and more fearful? Differences in behavioral traits in relation to the phylogenetic background and productivity level in laying hens. *Appl. Anim. Behav. Sci.* 209, 65–70.
- Fisher, M.O., Nager, R.G., Monaghan, P., 2006. Compensatory growth impairs adult cognitive performance. *PLoS Biol.* 4, 1462–1466.
- Fox, J., Weisberg, S., 2011. An {R} Companion to Applied Regression. Thousand Oaks, CA, USA.
- Gallup, G.G., 1977. Tonic immobility - role of fear and predation. *Psychol. Rec.* 27, 41–61.
- Gallup, G.G., Nash, R.F., Wagner, A.M., 1971. Tonic immobility reaction in chickens - response characteristics and methodology. *Behav. Res. Methods Instrum.* 3, 237–239.
- Gallup, G.G., Montevicchi, W.A., Swanson, E.T., 1972. Motivational properties of mirror-image stimulation in the domestic chicken. *Psychol. Rec.* 22, 193–199.
- Gonyou, H.W., Morrison, W.D., 1983. Effects of Defeathering and insulative jackets on production by laying hens at low-temperatures. *Br. Poult. Sci.* 24, 311–317.
- Hocking, P.M., Channing, C.E., Waddington, D., Jones, R.B., 2001. Age-related changes in fear, sociality and pecking behaviours in two strains of laying hen. *Br. Poult. Sci.* 42, 414–423.
- Jensen, P., 2006. Domestication - from behaviour to genes and back again. *Appl. Anim. Behav. Sci.* 97, 3–15.
- Jones, R.B., 1986. The tonic immobility reaction of the domestic-fowl - a review. *Worlds Poult. Sci. J.* 42, 82–96.
- Jones, R.B., 1989. Chronic stressors, tonic immobility and leucocytic responses in the domestic fowl. *Physiol. Behav.* 46, 439–442.
- Jones, R.B., Bessei, W., Faure, J.M., 1982. Aspects of fear in Japanese quail chicks (*Coturnix-Coturnix-Japonica*) genetically selected for different levels of locomotor-activity. *Behav. Processes* 7, 201–210.
- Keeling, L.J., Duncan, I.J.H., 1991. Social spacing in Domestic-Fowl under seminatural conditions - the effect of behavioral activity and activity transitions. *Appl. Anim. Behav. Sci.* 32, 205–217.
- Kjaer, J.B., 2009. Feather pecking in domestic fowl is genetically related to locomotor activity levels: implications for a hyperactivity disorder model of feather pecking. *Behav. Genet.* 39, 564–570.
- Kjaer, J.B., 2017. Divergent selection on home pen locomotor activity in a chicken model: selection program, genetic parameters and direct response on activity and body weight. *PLoS One* 12, e0182103.
- Kjaer, J.B., Phi-van, L., 2016. Evidence for the Association of a Deleted Variant in the 5'-Flanking Region of the Chicken serotonin transporter (5-HTT) Gene with a Temporary Increase in Feed Intake and Growth Rate. *Animals* 6, 63.
- Kjaer, J., Vestergaard, K., 1999. Development of feather pecking in relation to light intensity. *Appl. Anim. Behav. Sci.* 62, 243–254.
- Knowles, T.G., Broom, D.M., 1990. Limb bone strength and movement in laying hens from different housing systems. *Vet. Rec.* 126, 354–356.
- Krause, E.T., Caspers, B.A., 2016. Long-term consequences of early nutritional conditions on the behaviour and growth of fire salamanders. *Amphibia-Reptilia* 37, 69–77.
- Krause, E.T., Naguib, M., 2011. Compensatory growth affects exploratory behaviour in zebra finches, *Taeniopygia guttata*. *Anim. Behav.* 81, 1295–1300.
- Krause, E.T., Naguib, M., 2015. Zebra finch males compensate in plumage ornaments at sexual maturation for a bad start in life. *Front. Zool.* 12, S11.
- Krause, E.T., Schrader, L., 2018. High, low, or familiar? Nest site preferences of experienced laying hens. *Br. Poult. Sci.* 59, 359–364.
- Krause, E.T., Petow, S., Kjaer, J.B., 2011. A note on the physiological and behavioural consequences of cannibalistic toe pecking in laying hens (*Gallus gallus domesticus*). *Archiv für Geflügelkunde* 75, 140–143.
- Krause, E.T., Kjaer, J.B., Luders, C., van, L.P., 2017. A polymorphism in the 5'-flanking region of the serotonin transporter (5-HTT) gene affects fear-related behaviors of adult domestic chickens. *Behav. Brain Res.* 330, 92–96.
- Krause, E.T., Kjaer, J.B., Dudde, A., Schrader, L., Loc, P.V., 2019. Fear but not social behaviour is affected by a polymorphism in the 5'-flanking region of the serotonin transporter (5-HTT) gene in adult hens. *Behav. Brain Res.* 361, 50–53.
- Labouriau, R., Kjaer, J.B., Abreu, G.C.G., Hedegaard, J., Buitenhuis, A.J., 2009. Analysis of severe feather pecking behavior in a high feather pecking selection line. *Poult. Sci.* 88, 2052–2062.
- Lieboldt, M.A., Halle, I., Frahm, J., Schrader, L., Baulain, U., Henning, M., Preisinger, R., Danicke, S., Weigend, S., 2015. Phylogenetic versus selection effects on growth development, egg laying and egg quality in purebred laying hens. *European Poultry Science* 79. <https://doi.org/10.1399/eps.2015.89>.
- Lyimo, C.M., Weigend, A., Msoffe, P.L., Eding, H., Simianer, H., Weigend, S., 2014. Global diversity and genetic contributions of chicken populations from African, Asian and European regions. *Anim. Genet.* 45, 836–848.
- Marin, R.H., Freytes, P., Guzman, D., Jones, R.B., 2001. Effects of an acute stressor on fear and on the social reinstatement responses of domestic chicks to cagemates and strangers. *Appl. Anim. Behav. Sci.* 71, 57–66.
- Mignon-Grasteau, S., Chantry-Darmon, C., Boscher, M.Y., Sellier, N., Le Bihan-Duval, E., Bertin, A., 2017. Genetic determinism of fearfulness, general activity and feeding behavior in chickens and its relationship with digestive efficiency. *Behav. Genet.* 47, 114–124.
- Monaghan, P., 2008. Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions Royal Society B-Biological Sci.* 363, 1635–1645.
- Phi-van, L., Holtz, M., Kjaer, J.B., van Phi, V.D., Zimmermann, K., 2014. A functional variant in the 5'-flanking region of the chicken serotonin transporter gene is associated with increased body weight and locomotor activity. *J. Neurochem.* 131, 12–20.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Team, R.C., 2017. Nlme: linear and non-linear mixed effects models. R package version 3, 1–131.
- Pizzari, T., McDonald, G.C., 2019. Sexual selection in socially structured, polyandrous populations: some insights from the fowl. *Adv. Study Behav.* 51, 77–141.
- Schütz, K.E., Jensen, P., 2001. Effects of resource allocation on behavioural strategies: a comparison of red junglefowl (*Gallus gallus*) and two domesticated breeds of poultry. *Ethology* 107, 753–765.
- Schütz, K., Kerje, S., Carlborg, O., Jacobsson, L., Andersson, L., Jensen, P., 2002. QTL analysis of a red junglefowl x white leghorn intercross reveals trade-off in resource allocation between behavior and production traits. *Behav. Genet.* 32, 423–433.
- Schütz, K.E., Kerje, S., Jacobsson, L., Forkman, B., Carlborg, O., Andersson, L., Jensen, P., 2004. Major growth QTLs in fowl are related to fearful behavior: possible genetic links between fear responses and production traits in a red junglefowl x White Leghorn intercross. *Behav. Genet.* 34, 121–130.
- van der Waaij, E.H., 2004. A resource allocation model describing consequences of artificial selection under metabolic stress. *J. Anim. Sci.* 82, 973–981.
- Wuerz, Y., Kruger, O., 2015. Personality over ontogeny in zebra finches: long-term repeatable traits but unstable behavioural syndromes. *Front. Zool.* 12, S9.