Social environment influences impulsivity in red junglefowl (*Gallus gallus*) chicks.

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Titel(/Title

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Sammanfattning/Abstract

Cognition (i.e. how individuals perceive, process and react to environmental cues) is fundamental to all animals' life. Despite this, what explains variation in cognitive abilities is still mainly unclear. Environment is assumed to influences cognitive variation, but the mechanisms for this are still unknown. According to the social intelligence hypothesis, living in a group with a rich social environment, generate challenges that can enhance cognitive abilities. Impulsivity (to not be able to inhibit impulses), one aspect of cognition, may be influenced by the social environment, however this has not yet been experimentally tested. Impulsivity can complicate life, both for humans and animals. In humans, high levels of impulsivity and lack of self-control are associated with addictions and psychiatric disorders, thus is considered to be maladaptive. In animals, impulsivity correlates with stereotypies. To improve our understanding of impulsivity, I experimentally investigated how early social environment affects individual variation in impulsivity. To test this, red junglefowl chicks were used because their group living nature, and our accumulated knowledge on their cognition and behaviour. To manipulate the social environment, chicks either grew up in larger groups (with 17 individuals) or smaller groups (with 7 individuals). During the chicks' first five weeks of life, three aspects of impulsivity were tested; impulsive action, persistence (in a detour reaching test) and routine formation (in a reversal learning test). Chicks that grew up in larger groups tended to perform less impulsive actions, while social environment did not explain variation in persistence. Chicks from larger groups had less strong routine formation compared to chicks raised in smaller groups. This partially supports the social intelligence hypothesis, and suggest that early social life can affect cognitive traits and explain individual variation in such.

Nyckelord/Keyword

Chicken, cognitive abilities, Gallus gallus, impulsive action, impulsivity, intelligence, persistence, routine formation.

Abstract

Cognition (i.e. how individuals perceive, process and react to environmental cues) is fundamental to all animals' life. Despite this, what explains variation in cognitive abilities is still mainly unclear. Environment is assumed to influences cognitive variation, but the mechanisms for this are still unknown. According to the social intelligence hypothesis, living in a group with a rich social environment, generate challenges that can enhance cognitive abilities. Impulsivity (to not be able to inhibit impulses), one aspect of cognition, may be influenced by the social environment, however this has not yet been experimentally tested. Impulsivity can complicate life, both for humans and animals. In humans, high levels of impulsivity and lack of self-control are associated with addictions and psychiatric disorders, thus is considered to be maladaptive. In animals, impulsivity correlates with stereotypies. To improve our understanding of impulsivity, I experimentally investigated how early social environment affects individual variation in impulsivity. To test this, red junglefowl chicks were used because their group living nature, and our accumulated knowledge on their cognition and behaviour. To manipulate the social environment, chicks either grew up in larger groups (with 17 individuals) or smaller groups (with 7 individuals). During the chicks' first five weeks of life, three aspects of impulsivity were tested; impulsive action, persistence (in a detour reaching test) and routine formation (in a reversal learning test). Chicks that grew up in larger groups tended to perform less impulsive actions, while social environment did not explain variation in persistence. Chicks from larger groups had less strong routine formation compared to chicks raised in smaller groups. This partially supports the social intelligence hypothesis, and suggest that early social life can affect cognitive traits and explain individual variation in such.

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Introduction

Cognition is defined as how individuals perceive, process, store and act on environmental information (Shettleworth, 2009). Cognitive abilities (e.g. learning, memory formation, impulse control), are crucial for individuals to be able to act appropriately in different situations (Boogert et al., 2018). Recent studies have revealed striking individual variation in cognition. Individual variation in cognition is thought to have important consequences, and individual differences are critical since they become the material in which natural selection acts on (Thornton & Lukas, 2012), but few experimental studies have been carried out regarding the source of such differences. Increased cognitive performance can be linked to increased reproductive success (Ashton et al., 2018a; Shaw et al 2019). Despite so, research on individual differences in cognition in non-human animals has tended to ignore variation until recently (Boogert et al., 2018).

Individual variation in cognition is likely influenced by social environment (Langley et al., 2018), for example, during development (Tahamtani et al., 2015). Social factors, such as group size, have been linked with cognitive performance by using a comparative approach (Ashton et al., 2018a; reviewed in Langley et al., 2018). Living in a group creates certain challenges, such as the need to form and maintain social bonds, track third-party relationships and anticipate the actions of others (Ashton et al., 2018a; Wascher et al., 2018). According to the social intelligence hypothesis, these challenges faced by living in larger groups, enhance cognitive abilities (Ashton et al., 2018a; Ashton et al., 2018b; Wascher et al., 2018). However, it is not known if within-species variation in group size and cognitive performance are correlated (Langley et al., 2018) and if so, it is still ambiguous how sociality is correlated with increased cognitive performance, although larger groups are thought to be associated with higher cognitive performance. It is unknown if 'intelligent' animals are more likely to be drawn to larger groups, or if larger groups create possibilities for the individuals to improve their cognitive performance. Manipulations of group size would be required to disentangle this possibility and test the causal effect of social life on cognitive performance.

In this study I focus on impulsivity, one aspect of cognition. A higher cognitive performance is thought to correlate with lower impulsivity. Impulsivity is the mental processes occurring when the individual is not able to override/inhibit impulses, thus not enabling behaviour to vary adaptively from one situation to another (Inzlicht et al., 2014; Lindner et al., 2017; Winstanley et al., 2006). Self-control (i.e. being able to able to inhibit impulses), is often

important for success in life, both for humans and animals (Baumeister et al., 2007; Inzlicht et al., 2014; Winstanley et al., 2006). In humans, high levels of impulsivity and lack of self-control are associated with higher risk taking and problems such as addictions, (e.g. gambling- or drinking problems) and psychiatric disorders such as ADHD, mania and personality disorders (Winstanley et al., 2006). This, together with the lack experimental studies, makes impulsivity to an intriguing aspect to investigate further.

I investigated how social environment during early development affects cognitive performance, with focus on impulsivity, in red junglefowl (*Gallus gallus*) chicks. The prediction is that chicks that have grown up in larger groups will have elevated performance in cognitive tasks because of the challenges associated with a richer social environment. It was experimentally tested if and how group size affect performance in cognitive tasks in standardised conditions. To avoid other aspects other than differences in impulsivity (e.g. variation in motivation, body condition) to affect the result standardised conditions and repeated testing of known individuals are required. Therefore, the predictions were experimental tested with controlled surroundings

Methods

Red junglefowl, the ancestors of domestic chickens, are an ideal species to experimentally test this in because they are naturally social and group living animals, and has been used for animal behaviour research for a long time (Kim & Zuk, 2000;Garnham & Løvlie, 2018). Red junglefowl is a wild species and fearful of humans, and therefore difficult to observe in their native habitats (Collias & Collias, 1996). I therefore used a captive population of red junglefowls for this study.

Study population and housing
The study was conducted during April 2019 at Linköping University, on a population of red junglefowl monitored by Linköpings University and pedigree bred since 2011. Eggs (n = 151) were incubated on 2019-03-11 and candled on 2019-03-18 to check fertilization and development. To reduce maternal influences and to standardise incubation, chicks were artificially hatched and raised without mother hens. Chicks (n = 98) hatched on 2019-04-01 and were individually marked with an individual metal tag.

To manipulate social environment, at day one after hatching, chicks were randomly divided into seven different groups of two different group sizes; large (3 groups with 17 chicks) or

small groups (4 groups with 7 chicks). Of these 10 from each of the large groups were here tested and all chicks from the small groups (n = 58, n_{large} = 30, n_{small} = 28). Chicks were subjected to a series of cognitive tests, and all tests were performed between 8 am - 6 pm (light was on between 7 am - 7 pm). Chicks were individually tested.

During the study, chicks from both group sizes were housed in two sizes of pens, 60x42x49 or 72x71x53 cm (LxWxH), due to logistic constraints. Both large and small groups were housed in both cage sizes, to reduce the risk of housing area affecting the result. All cages had sawdust, a heater, perches and *ad libitum* access to food and water.

From day one, chicks were habituated to humans, being separated from their conspecifics and being alone in test arenas, and mealworms was used as a reward. At the end of the experiment, all birds were moved to Vreta, and kept in one big group until they were sexually mature. When sexually mature, birds were separated in two groups depending on sex.

Morphological measures
All chicks (n = 58, n_{large} = 30, n_{small} = 28) were weighted (to the nearest g), had their tars measured (to the nearest mm with digital callipers) and were individually body scored (0-3 point scale, by palpating its breast muscles, according to Gregory & Robin, 1998) on their 5, 19, and 33 day of life.

Cognitive tests
All chicks were individually tested for variation in impulsivity. During the chicks' third week of life, their level of impulsive action (i.e. difficulty in inhibiting a prepotent response) and persistence (i.e. tenacity to continue in way of action in spite of absent reward) in a detour reaching test (also called 'cylinder test', MacLean et al., 2014) were tested. During the chicks' fourth week of life, routine formation (i.e. difficulty changing a previously formed routine) was tested. Impulsive action and persistence were re-tested in the chicks' fifth week of life to investigate differences in these responses over time. In all tests, the observer did not know which group the test chick came from, with the aim to reduce the influence of previous knowledge or predictions of the observer.

Impulsive action and persistence

Prior to this test, each individual was trained to make a detour to obtain a reward (1/3 of a mealworm) from an opaque cylinder (Figure 1). A reward (ca. 1/3 of a mealworm) was placed in the middle of a cylinder (Figure 1), both during training and testing. Initially, during training, a second reward was placed on the opening of the opaque cylinder to encourage the chick to approach and look inside it. Once the chick approached and looked inside the cylinder, this extra reward was phased out. In addition to an extra reward, if needed, the chick could get more help during training to be able to learn where the middle reward was. Help could include guiding the chick towards, and/or by tapping at the cylinder. When a chick had eaten the reward, it was removed from the arena, and the reward and chick were replaced (Figure 1). When a chick was able to obtain the reward without any help five consecutive times, and did not peck at the cylinder, it progressed to testing.

During testing, chicks were never helped. Each chick was presented with a transparent cylinder (Figure 1), 30 consecutive times. The proportion of times where the chick failed to perform the detour response, in the first five trials, was recorded as a measure of impulsive action (Ashton et al., 2018a; MacLean et al., 2014). Chicks were always allowed to find and eat the reward to ensure that they remained motivated. Twenty-five additional trails were performed to investigate if number of pecks decreased, and self-control increased, with experience. Total number of pecks over 30 trials was recorded as a measure of persistence.
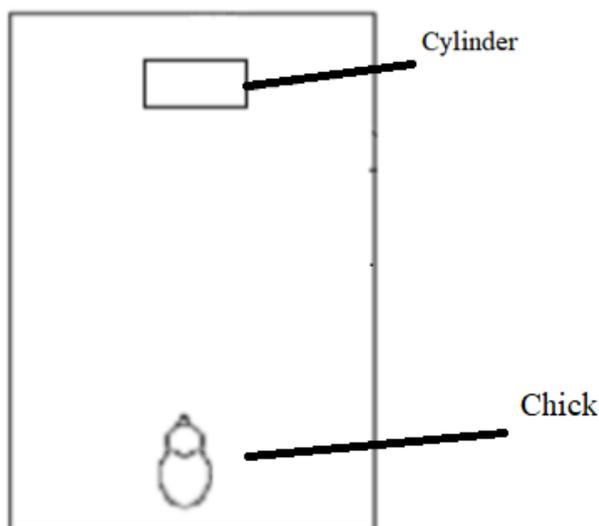

Figure 1: Setup for detour reaching test to measure impulsive action and persistence in red junglefowl chicks. Cylinder (5Ø x 8L cm), test arena (Arena = 48 x 39 x 15 cm).

Routine formation

Routine formation was measured in a reversal learning test. To measure learning speed (as part of another project), each chick was trained that a black bowl indicated a reward (ca. 1/3 of a mealworm) and that a white bowl did not (Figure 2). To ensure that chicks did not have an innate preference for right or the left, and therefore by chance chose the correct bowl, the rewarded bowl was placed on different sides by according to a predetermined, pseudorandomized schedule. When a chick selected the correct/rewarded cue (by putting its head in the bowl) six consecutive times, it was considered to have learned the association between colour cue and reward (Sorato et al 2018; Zidar et al 2018). When the chick had learnt this, a reversal learning task was performed, with the same setup and the same cues. However, in this test the white cue was rewarded instead of the previously rewarded black. Latency (measured in seconds) from when the chick checked the previously rewarded black bowl to when it found the white bowl that now was rewarded, was recorded as measure of routine formation. A longer latency indicates a higher routine formation.

Three chicks did not pass associative learning and therefore did not participate in the reversal learning test ($n = 55$, $n_{large} = 28$, $n_{small} = 27$).
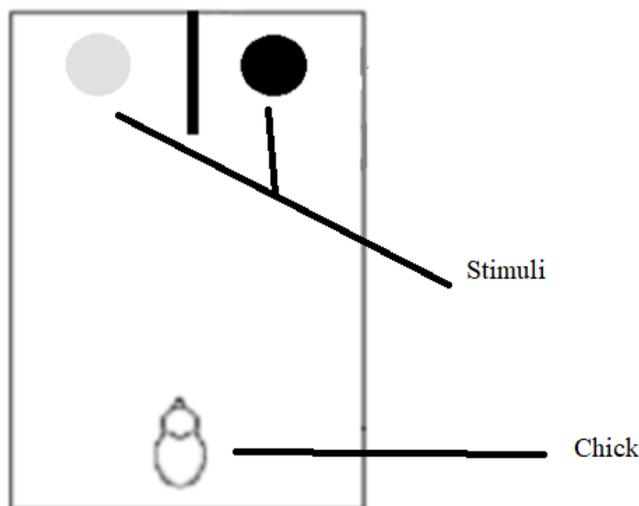

Figure 2: Setup for routine formation test for red junglefowl chicks. Each chick was trained to associate between colour and reward in a test area (Arena = 48 x 39 x 15 cm), before exposed to a reversal learning task. Latency (in seconds) to explore the new, previously unrewarded cue, was measured as strength of routine formation.

Food motivation

To investigate if lack of success in the cognitive test was due to variation in food motivation every chick was offered 1/3 of a mealworm, five consecutive times, after every test session. The mealworm was dropped ca five cm in front of the chick in the test arena and it was recorded how many times the chick ate the worm out of the five times. If the chick ate the worm it was regarded to be motivated.

Statistics

All analyses were carried out in R version 3.5.2.

Morphological measures

Weight (g), tars (mm), and condition (weight/tars), were compared between chicks of large and small groups using t-tests due to normally distributed data. For comparison of body fat score (0-3), a Mann-Whitney U-test was used due to non-normally distributed data.

Impulsivity

Impulsive action (proportion of times where the chick failed to perform the detour response, in the first five trials), persistence (total number of pecks on the tube over 30 trials) and routine formation (latency to explore a different colour cue), were compared with Generalized Linear Mixed Models (GLMM, 'lmer4' package), with either impulsive action, persistence, or routine formation as response variable, group size (small or large) as fixed effect, and cage ID (1-7) or test age (3 weeks or 5 weeks) as random effects. For these models, a Poisson distribution, with a log link function, was fitted.

Result

Morphological measures

During the chicks' first five weeks of life, there were no significant differences between individuals raised in large or small groups in weight, tars, weight/tars, or body fat score (Table 1).

Table 1. Morphological measures of red junglefowl chicks. Measures of weight, tars, weight/tars and body fat score did not differ between chicks raised in small or large groups during the first 5 weeks of life. Mean ± SE are presented.

Large groups	Week 1	Week 3	Week 5
Weight (g)	31.97 ± 0.58 g	92.96 ± 2.00 g	198.13 ± 5.10 g
Tars	26.00 ± 0.26 mm	36.61 ± 0.31 mm	47.83 ± 2.98 mm
Weight/tars	1.23 ± 0.02	2.53 ± 0.04	3.96 ± 0.09
Body fat score	1.77 ± 0.08	1.80 ± 0.07	1.86 ± 0.10
Small groups			
Weight	33.03 ± 0.52 g	90.10 ± 2.20 g	190.25 ± 5.30 g
Tars	25.89 ± 0.17 mm	36.61 ± 0.31 mm	47.76 ± 0.59 mm
Weight/tars	1.27 ± 0.02	2.43 ± 0.04	3.96 ± 0.07
Body fat score	1.64 ± 0.11	1.71 ± 0.53	1.86 ± 0.11
Test statistic			
Weight	$t = -1.35, p = 0.18$	$t = 0.96, p = 0.34$	$t = 1.10, p = 0.29$
Tars	$t = 0.45, p = 0.66$	$t = -0.70, p = 0.49$	$t = 0.09, p = 0.93$
Weight/tars	$t = -1.97, p = 0.06$	$t = 1.86, p = 0.07$	$t = 1.51, p = 0.14$
Body fat score	$W = 475.00, p = 0.29$	$W = 459.00, p = 0.44$	$W = 459.00, p = 0.46$

Impulsivity

Chicks raised in smaller groups tended to perform more impulsive actions compared to chicks raised in larger groups (Figure 3a, 3c, Table 2). Persistence was affected by age, but did not differ between group sizes (Figure 3b, 3d, Table 3). Chicks from larger groups had less strong routine formation compared to chicks raised in smaller groups (Figure 4, Table 4).

Cage ID did not explain much of the variation (data not shown) and was therefore not considered further.
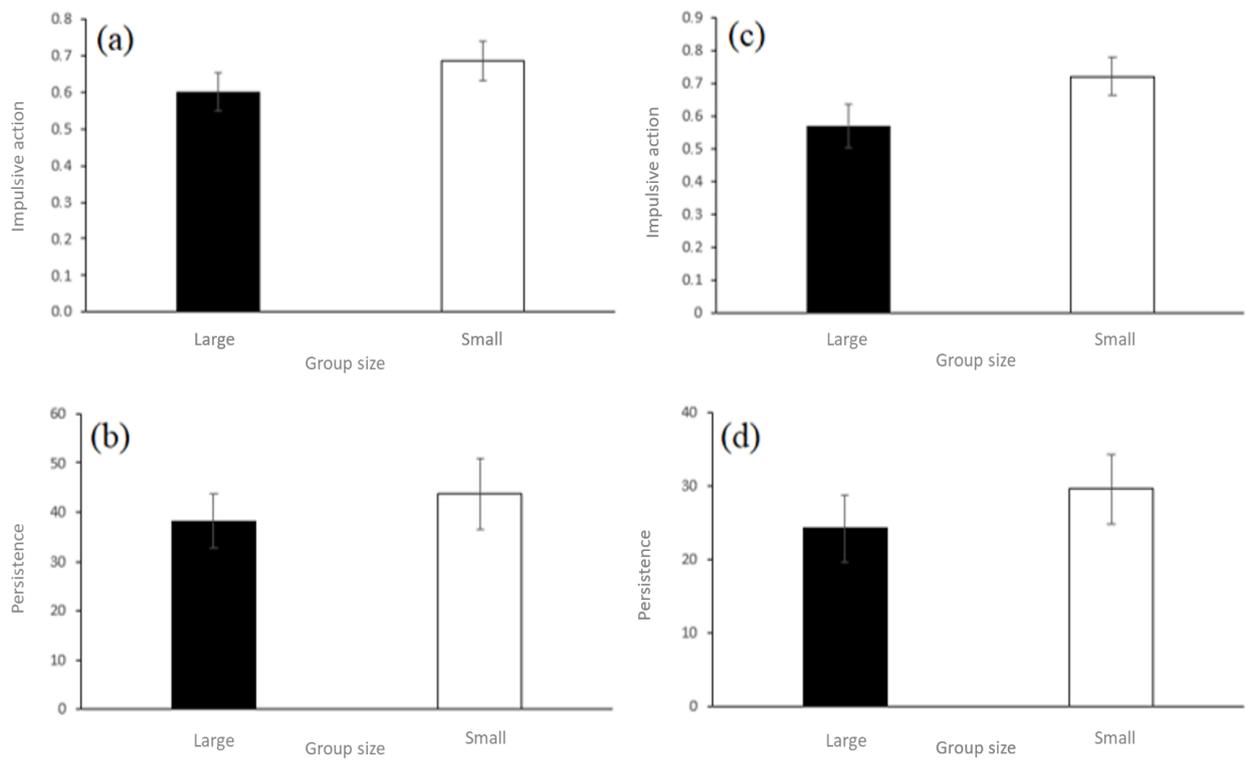
Figure 3. Behavioural responses to a detour reaching test in red junglefowl raised in large or small groups. (a) Impulsive action (i.e. proportion of times where the chick failed to perform the detour response, in the first five trials) week three. (b) persistence (total number of pecks on transparent tube over 30 trials) week three. (c) Impulsive action week five. (d) week five. Black = large groups, white = small groups. Mean ± SE are given.
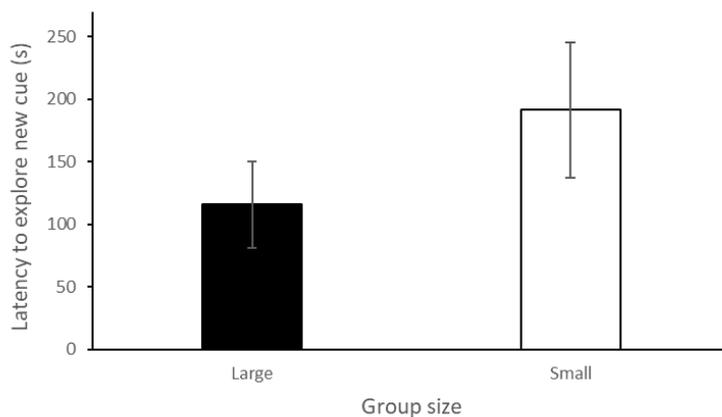

Figure 4. Red junglefowl raised in large groups had less strong routine formation (latency to explore a previously unrewarded colour cue, in seconds) than those raised in small groups. Black = large groups, white = small groups. Mean ± SE are given.

Table 2. General Linear Mixed Model output for analyses of impulsive action in red junglefowl. Chicks raised in small groups tended to perform more impulsive actions (proportion of times where the chick

failed to perform the detour response in the first five trials), than chicks raised in large groups. Age did not affect impulsive action.

	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	1.10	0.092	11.65	<0.01
Group size	0.18	0.11	1.73	0.08
Age	0.005	0.11	0.047	0.96

Table 3. General Linear Mixed Model output for analyses of persistence in red junglefowl. Chicks raised in small or large groups did not differ in persistence (total number of pecks on a transparent tube during 30 trials). Chicks got less persistent with increased age.

Total	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	3.60	0.17	20.59	< 0.01
Group size	0.16	0.23	0.70	0.48
Age	- 0.40	0.03	-11.98	< 0.01
Week three	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	3.60	0.18	19.40	< 0.01
Group size	0.08	0.24	0.34	0.70
Week five	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	3.10	0.19	16.50	< 0.01
Group size	0.24	0.25	0.97	0.33

Table 4. General Linear Mixed Model output for analyses of routine formation in red junglefowl. Chicks raised in large or small groups did differ in routine formation (latency to explore a different colour signal in a reversal learning task).

	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	4.50	0.26	17.50	< 0.01
Group size	0.40	0.024	18.50	< 0.01

Motivation

Chicks were highly motivated to participate in the cognitive tests (mean ± SE, 4.6 ± 0.11 pecks out of 5) and there were not any differences between group sizes (W = 223.00, p = 0.34).

Discussion

I have here investigated if group size has an influence on three different aspects of impulsivity in red junglefowl chicks, and I have shown that individuals raised in larger groups performed less impulsive action in a in a detour reaching test, and had less strong routine formation in a reversal learning test. Persistence was not affected by group size during development.

Red junglefowl chicks raised in large or small groups did not differ in weight, tars, weight/tars or body score over their first five weeks of life (i.e. during my study), and all chicks were highly motivated to participate in the cognitive test they were exposed to. Variation in these measures are thus not very likely to affect my result. I did neither observe any sex differences in impulsivity among the birds.

On the other hand, group size explained variation in impulsivity. Chicks raised in larger group tended to have less impulsive actions and had less strong routine formation compared to chicks raised in smaller groups. There were not any differences in persistence between chicks raised in larger or smaller groups, although with age all chicks became less persistence. This means that several aspects of impulsivity were influenced by the social environment during developmental in red junglefowl chicks. This aligns partly with my hypotheses that a 'richer' social group would lead to individuals with lower impulsivity (Adriani et al., 2010:Ashton et al., 2018a). Thus, my result partially support the social intelligence hypothesis which suggest that individuals raised in larger groups show enhanced cognitive abilities (such as performing less impulsive, enhanced performance in associative- and reversal- learning, and spatial memory tasks). This indicates that the challenges associated with living in larger groups can explain some of variation in cognitive performance of animals (Ashton et al., 2018a). Although, living in larger social groups can both have positive (Ashton et al., 2018a; Langley et al., 2018) and negative effects (Sandi, 2013) on cognition. Thus, differences between groups in competition and stress could also affect cognitive abilities, which may explain some of the variation I have found. For example, higher stress from too many/few conspecifics could lead to impaired cognitive abilities (Sandi, 2013). This could indicate that it is not the more complex social environment that enhances cognitive performance (as the social intelligence hypothesis suggests), but instead differences in competition or stress that influences cognition. The very few previous studies investigating the relationship between group size and cognitive performance (e.g. Asthon et al 2018), were not able to investigate the

causality of their observed relationship. I have here used an experimental approach, and thus can show that differences observed are indeed due to differences in group sizes. Future studies should explore further what aspect of different group sizes that actually cause differences in behaviour, where stress and differences in social interactions should be investigated further.

I chose to use group sizes that are biological relevant for red junglefowl (Collias & Collias. 1996). Social isolation can result in poorer overall cognitive performance (e.g. Cacioppo & Hawkley, 2009; Manni et al. 2009), which indicates that with more extreme group sizes there would be clear and more extreme differences in cognitive performance and impulsivity. Although, result from these kinds of studies may have other explanations than social complexity for the variation in cognitive performance, such as stress from being isolated impairing the performance observed. This shows that cognitive performance is likely complex and can likely be affected by more than how complex the social environment is. In other words, studies with more extreme group sizes may show more extreme difference in cognitive performance.

Further, both age and time spent in different social environment can potentially affect cognitive abilities (Ashton et al., 2018b). Therefore, it would be relevant to carry out similar cognitive testing later in life when the individuals have lived in the different social environments for a longer time. Longer time with social differences would expect to produce larger difference (Ashton et al., 2018 a; Langley et al., 2018). Whether an effect of social environment is current or persistent is unclear. For example, a barren social environment can cause long-term impairment of short-term memory in chickens (Tahamtani et al., 2015), thus investigation of whether the social environment during development causes long-term differences visible in adult life, or if it is only a short-time affect that disappear as soon as the treatment is removed. Knowledge of how early social environment may affect individual cognition is relevant in many aspects, both for animal welfare, but also for breeding, since individuals with elevated cognitive performance is thought to have elevated reproductive fitness (Ashton et al., 2018a; Ashton et al., 2018b). In general, improved understanding of how variation in social environment affects current and future cognitive performance is of interest to a range of species, including our own.

In conclusion, in the red junglefowl, manipulating group size early in life affected some aspects of impulsivity, namely impulsive actions and routine formation, but not persistence. This confirms that impulsivity is a heterogenic trait (reviewed in Dick et al., 2010), and partially supports the social intelligence hypothesis that the social environment can play an

important role in explaining variation in cognition. The results of this study can be useful for animal behaviour and animal welfare research since it emphasises the importance of social environment.

Societal and ethical aspects

This study shows that the social environment during development can play an important role in the development of cognitive abilities. By manipulating group sizes this study investigated how, and if, cognitive performance and impulsivity were affected by social environment. This can influence how we keep our animals, or how schools for our children are designed in the future. The understanding of the relationship between group size and cognition may have implications for improved animal welfare, maybe by management benefits, such as housing and conservation strategies. Furthermore, by using the ancestor of domestic chicken, the red junglefowl, this study may be particularly relevant to animal welfare of chickens. Chickens have become a very successful production animals, which has led them to become our most abundant bird. However, they face severe welfare issues (rewieved in Garnham & Løvlie, 2018), and it is therefore relevant to try to improve their welfare.

During this study, red junglefowl chicks were exposed to some mild stress by being separated from conspecifics, vaccination injections and identity marking by a metal tag. The stress of being separated from conspecifics was reduced by habituation. The experiment and all its procedures were approved by the Swedish Regional Ethical Committee.

Acknowledgment

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Appendix

Table 5. General Linear Mixed Model, show the influence of the random effect. Cage ID did affect persistence and routine formation, but not impulsive action.

Random effect	Variance	Std.
Impuslive action, Cage ID	0	0
Persistence, Cage ID	0.09	0.30
Routine formation, Cage ID	0.46	0.68