

# Causes and Consequences of Impulsivity in Red Junglefowl

Laura C Garnham



Red Junglefowl in a detour task used to measure impulsivity.

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## Abstract

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Throughout the animal kingdom, animals vary in cognition (i.e., how they acquire, process, store, and act on environmental information). Yet, the causes and consequences of this variation are currently unclear. Inhibitory control is one such aspect of cognition that typically varies between individuals within all species investigated. Variation in inhibitory control underlies variation in impulsivity (i.e., the tendency to act without planning or considering the consequences). The causes and consequences of variation in impulsivity are, themselves, rarely explored, despite that these may have important ecological and evolutionary implications. My thesis (spanning 5 papers), therefore, aimed to fill some of these gaps by taking a holistic approach and investigating causes and consequences of variation in impulsivity (specifically, impulsive action and persistence measured in a detour task) in red junglefowl (*Gallus gallus*) males and females, chicks and adults. The red junglefowl was an ideal species for this investigation. Firstly, they show individual variation in impulsivity throughout their lives. They are also typically food motivated, and easily habituated to handling and new situations, which means they commonly willingly participate in behavioural and cognitive tests. Furthermore, they are precocial, which means that they can be hatched and raised without mothers, thus reducing parental effects. Finally, the large, accumulated knowledge of red junglefowl behaviour and cognition aids interpretations regarding this. As differences in experience early in life have been found to affect impulsivity, **papers I and II** empirically explored whether variation in two previously uninvestigated experiences in early life (exposure to enrichment, and social group size, respectively) influenced impulsivity. The dopaminergic and serotonergic systems are important signalling systems in the brain, which have been found to link to impulsivity in other species. Therefore, in **paper I**, I also explored if variation in impulsive action and persistence was connected to variation in dopaminergic or serotonergic gene expression. As impulsivity links to inhibitory control, in looking at the effect of group size on impulsivity, **paper II** explored the hypotheses that social environment affects cognition (e.g., that social environments which are assumed to be more cognitively demanding will lead to better cognitive performance, a.k.a., the social intelligence hypothesis). To uncover potential mechanisms by which group size could affect impulsivity, besides from variation in cognitive demand, **paper II** also investigated if behaviours that could covary with group size linked to impulsivity. As emotional arousal has been linked to impulsivity, in another species, and impulsivity is implicated in welfare issues, **paper III** looked into how both positive and negative affective states (which can be used to measure welfare) related to

impulsivity. Prior to my thesis, whether variation in impulsivity could potentially affect animal welfare was scarcely explored. To better understand the potential consequences of impulsivity, and, thus, how selection could act on impulsivity, **papers IV and V** looked at potential implications of variation in impulsivity for social status (**paper IV and V**), foraging efficiency, and risk taking (**paper V**). My results showed that impulsivity could be consistent over time periods of weeks (in chicks, **paper II**) to months (in adults, **paper V**). Thus, impulsivity describes a characteristic of the individual. However, individuals could still learn to become less impulsive (**paper I**). Exposure to enrichment in early life could affect how impulsively individuals behaved. Environmental enrichment increased impulsivity, as did cognitive enrichment to a greater degree (**paper I**). Impulsive action, and persistence, correlated somewhat with brain gene expression of dopaminergic and serotonergic genes (DRD1, TPH; **paper I**). The social group size individuals experimentally experienced in early life did not affect their impulsivity (**paper II**). However, variation in impulsivity was connected to variation in activity, boldness, neophobia, and stress (**paper II**). Further, more impulsive individuals had less negative, more positive, affective states, but only when they were young chicks, and not as older chicks or adults (**paper VI**). No links were found between impulsivity and social status (**paper IV and V**), foraging efficiency, or risk taking (**paper V**). Taken together, **paper I** suggests that underlying explanations to observed individual variation in impulsivity could include variation in early life experiences and in dopaminergic and serotonergic gene expression, while **paper II** suggests that impulsivity may not be influenced by social aspects early in life. **Papers II and III** demonstrate that variation in impulsivity can associate with variation in behaviours and affective states (though these associations may vary over ontogeny), with the latter finding implying that variation in impulsivity could have welfare implications. **Papers IV and V** indicate that variation in impulsivity may have limited consequences for individuals in contexts that could affect reproduction or survival. Thus, it may not necessarily be costly to individuals if they are more impulsive than others. This, in turn, could help explain why variation in inhibitory control exists, because limited consequences of variation could result in low selection against variation. Overall, through the investigations conducted in its 5 papers, my thesis improves our understanding the potential causes and consequences of variation in impulsivity. As impulsivity is underlain by an aspect of cognition (inhibitory control), in exploring the causes and consequences of variation in impulsivity, my thesis also provides knowledge on causes and consequences of individual variation in cognition.

**Keywords:** Behaviour, Cognition, *Gallus gallus*, Impulsivity, Inhibitory control, Red junglefowl

## Popular science summary

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Even though it plays a fundamental role in the lives of all animals, we still don't understand why individuals vary in cognition (that is, how they acquire, process, store, and act on environmental information) or the consequences of this variation. Not just in humans, but across the animal kingdom, individuals vary in inhibitory control, an aspect of cognition, which influences how impulsive they are. This means that some individuals are more likely than others to act without planning or considering the consequences of their actions. But what causes this variation? And what are the consequences for individuals that act more impulsively? This is unclear for all species, including our own. Therefore, I aimed to experimentally investigate these questions in my thesis, using red junglefowl (*Gallus gallus*) as my study species. I took a holistic approach and investigated the causes and consequences of variation in impulsivity in red junglefowl males and females, chicks and adults. I chose to use red junglefowl (the ancestor of domestic chickens) because of the large, accumulated knowledge and understanding of their behaviour and cognition, which aids interpretations regarded this. In addition, junglefowl can often be habituated to handling and new situations, and are mostly willing to work for food rewards, which makes cognitive and behavioural studies easier. This was very useful as the data collection for all the papers in my thesis involved empirical testing of behaviour and cognition.

In **papers I and II**, I set out to explore multiple potential underlying causes of variation in impulsivity. Because experiences early in development have been shown to influence later cognition and behaviour in other species, I focused on how early life experience affected impulsivity. By rearing chicks in different treatment groups, I looked into whether exposure to enrichment (**paper I**), or social group size (**paper II**), in early life could causally affect how impulsive individuals were. As part of **paper I**, I also investigated how variation in impulsivity correlated with variation in expression in the brain of dopaminergic and serotonergic genes (genes of important signalling systems in the brain known to play various roles in behaviour and cognition in other species, including humans). In **paper II**, I also looked at whether variation in behaviours, which could covary with group size, linked to variation in impulsivity, thus exploring potential mechanisms by which group size could affect impulsivity.

In **paper III**, I explored whether variation in impulsivity was associated with variation in positive or negative affective states (i.e., mood or emotions). In doing so, I investigated whether impulsivity could have implications for individual welfare as less negative (e.g., less stressed or fearful), more positive (e.g., more

optimistic, yes, it is possible to measure optimism in animals!), affective states imply good welfare. Prior to my thesis, whether variation in impulsivity could potentially affect animal welfare was scarcely explored.

For the final part of the thesis, **papers IV and V**, I investigated multiple potential consequences that individual differences in impulsivity could have for individuals. I explored how impulsivity linked to individual outcomes in the contexts of social status (**paper IV and V**), foraging efficiency, and risk taking (**paper V**). If impulsivity affected outcomes in these contexts, this could have implications for individual survival and reproduction, and, therefore, for how impulsivity and inhibitory control evolve. This is because, for example, individuals that have higher social status often have improved access to food and resources, and individuals that take less risks may be more likely to miss out on opportunities (but also less likely to get injured or killed).

So, after all this investigation, what did I learn about the causes and consequences of variation in impulsivity, in red junglefowl? To begin with, how impulsive individuals were was moderately consistent over time periods of weeks (within chicks, **paper III**) to months (within adults, **paper V**). Thus, impulsivity describes a characteristic of an individual. Yet, individuals could still learn to become less impulsive (**paper I**). In terms of the underlying causes of impulsivity, exposure to cognitive and environmental enrichment in early life causally affected how impulsive individuals were (**paper I**), while social group size differences experienced early in life did not (**paper II**). That social life affects cognition is a long-standing idea in science (e.g., the social intelligence hypothesis), but is scarcely tested experimentally. Against theoretical predictions, my findings regarding the lack of effect of group size on impulsivity show that social life may sometimes not affect cognition.

Similar to as seen in humans, variation in impulsivity was correlated with variation in dopaminergic and serotonergic gene expression in the brain (**paper I**), suggesting that variation in these important signalling systems could underlie individual variation in impulsivity. Variation in impulsivity linked to variation in behaviour (specifically, younger chicks that were less impulsive were more neophobic and tended to be less bold, while older chicks that were less impulsive appeared to be more stressed, less active and tended to be less bold, **paper II**) and affective state, though only in younger chicks, where more impulsive individuals had less negative, more positive, affective states (**paper III**). Thus, variation in impulsivity can link to variation in behaviour or affective state and these links may change with age. Selection on these behaviours could, thus,

potentially result in selection on impulsivity and vice versa. Furthermore, at least at certain ages, impulsivity could have implications for individual welfare.

In terms of potential consequences of impulsivity for individuals, I found no links between impulsivity and individual outcomes in the contexts of social status (**paper IV** and **paper V**), foraging efficiency, or risk taking (**paper V**). Therefore, impulsivity may not affect individuals' survival or reproduction by affecting outcomes in these contexts. This, in turn, could mean that it is not so bad for individuals to be impulsive after all, which might help explain why variation in inhibitory control is ubiquitous across the animal kingdom. On a broader level, a lack of effects on survival and reproduction could potentially help maintain individual variation in cognition.

Overall, with my thesis, I have added to our understanding of the nature of, and the causes and consequences of variation in, impulsivity. On top of this, as impulsivity is underlain by an aspect of cognition, inhibitory control, the findings of my thesis provide us with an improved understand of why individuals vary in cognition and the consequences of this.

## Populärvetenskaplig sammanfattning

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Även om det spelar en grundläggande roll i alla individers liv, vet vi fortfarande förvånansvärt lite om varför individer varierar i kognition (dvs. hur de förvärvar, bearbetar, lagrar och agerar utifrån information från sin omvärld), eller konsekvenserna av sådan variation. Inte bara hos människor utan över hela djurriket varierar individer i impuls kontroll, en aspekt av kognition, som påverkar hur impulsiva vi är. Detta innebär att vissa är mer benägna än andra att agera utan att planera eller överväga konsekvenserna av sina handlingar. Men vad orsakar denna variation? Och vilka är konsekvenserna för individer som agerar mer impulsivt? Detta är oklart för alla arter, inklusive vår egen. Min doktorsavhandling syftar därför till att experimentellt undersöka dessa frågor, med röda djungelhöns (*Gallus gallus*) som studieart. Jag använde ett helhetsgrepp och studerade orsaker och konsekvenser av variation i impulsivitet hos både hanar och honor, kycklingar och vuxna. Jag valde att använda röda djungelhöns (förfadern till tamhöns) eftersom vi har samlat på oss mycket kunskap och förståelse om deras beteende och kognition, vilket hjälper oss att göra tolkningar av dessa. Dessutom kan djungelhöns ofta vänjas vid hantering och nya situationer, och är oftast mycket villiga att jobba för matbelöningar, vilket förenklar kognitiva och beteendestudier. Detta har varit användbart eftersom datainsamlingen för alla artiklar i min avhandling involverade beteende tester. I **uppsats I** och **II** utforskade jag flera potentiella grundläggande orsaker till variation i impulsivitet. Eftersom

erfarenheter tidigt i livet, hos andra arter, har visat sig ha påverkan på kognition och beteende senare i livet, fokuserade jag specifikt på hur tidiga livserfarenheter påverkade impulsivitet. Detta gjorde jag genom att föda upp kycklingar i olika miljöer efter kläckning. Jag undersökte huruvida exponering för berikning (**uppsats I**) eller social gruppstorlek (**uppsats II**) tidigt i livet kunde kausalt påverka hur impulsiva individer var senare i livet. Som en del av **uppsats I** undersökte jag också hur variation i impulsivitet samvarierade med variation i gener från serotonin- och dopaminsystemen. Dessa är viktiga signalsystem i hjärnan, som är kända för att spela roll i beteende och kognition hos andra arter (inklusive människor). I **uppsats II** undersökte jag även ifall variation i beteenden som kunde uppvisa samvariation med gruppstorlek korrelerar med variation i impulsivitet, och således utforska de potentiella mekanismer genom vilka gruppstorlek kan påverka impulsivitet.

I **uppsats III** utforskade jag huruvida variation i impulsivitet förknippas med variation i positiva eller negativa känslotillstånd (dvs. humör eller känslor). Genom att göra detta undersökte jag ifall impulsivitet kunde ha konsekvenser för individens välfärd då mindre negativt (t.ex. mindre stressad eller rädd), mer positivt (t.ex. mer optimistiskt, ja det är möjligt att mäta optimism hos djur!) känslotillstånd innebär bättre välfärd. Innan min avhandling var det oklart ifall variation i impulsivitet potentiellt skulle kunna påverka djurens välbefinnande.

I den sista delen av avhandlingen, **uppsats IV** och **V**, undersökte jag flera potentiella konsekvenser individuella skillnader i impulsivitet kunde ha för individen. Jag undersökte hur impulsivitet kopplades till hur individer tar risker, hur effektivt de söker föda (**uppsats V**) och deras sociala status (**uppsats IV** och **V**). Om impulsivitet påverkade utfallen i dessa sammanhang kan detta få konsekvenser för individens överlevnad och reproduktion, och därför påverka hur impulsivitet och impuls kontroll evolverar. Detta beror på att individer som t.ex. har högre social status oftast har bättre tillgång till mat och resurser, och individer som tar mindre risker kan vara mer benägna att gå miste om möjligheter (men också mindre benägna att bli skadade eller dödade).

Så, efter alla dessa undersökningar, vad lärde jag mig om orsaker och konsekvenser av variation i impulsivitet, hos röda djungelhöns? Till att börja med var individers impulsivitet måttligt konsekventa över tidsperioder på veckor och månader (hos kycklingar, **uppsats III**, hos vuxna, **uppsats V**). Således beskriver impulsivitet aspekter i en individs beteende som utgör ett karaktärsdrag hos individen. Dock kunde fåglarna ändå lära sig att bli mindre impulsiva (**uppsats I**). När det gäller de underliggande orsakerna till impulsivitet, så påverkade kognitiv och miljömässig berikning tidigt i livet kausalt hur impulsiva individer var (**uppsats**

I), medan skillnader i social gruppstorlek upplevda tidigt i livet inte gjorde det (**uppsats II**). Att socialt liv påverkar kognition är en mångårig idé inom vetenskapen (t.ex. "the social intelligence hypothesis"), men som sparsamt har testats experimentellt. Dock visar mina resultat, avseende avsaknad av påverkan från gruppstorlek på impulsivitet, att socialt liv inte alltid påverkar kognition.

I likhet med hos människor, variation i impulsivitet samvarierade med variation i dopaminergiska och serotonergiska gener (**uppsats I**). Detta tyder på att variation i viktiga signalsystem i hjärnan kan ligga till grund för individuell variation i impulsivitet. Variation i impulsivitet korrelerade med variation i beteende (i synnerhet yngre kycklingar var mindre impulsiva, mer neofobiska och tenderade att vara mindre djärva, **uppsats II**) och känslotillstånd (dock enbart i yngre kycklingar, där mer impulsiva individer hade mindre negativa och mer positiva känslotillstånd, **uppsats III**). Variation i impulsivitet kan därför kopplas till variation i beteende eller känslotillstånd och dessa kopplingar kan förändras med tiden. Urval på dessa beteenden kan därför potentiellt resultera i urval på impulsivitet och vice versa. Dessutom kan, åtminstone under vissa utvecklingsstadier, impulsivitet ha konsekvenser för individens välfärd.

När det gäller potentiella konsekvenser av impulsivitet för den enskilda individen fann jag inga tydliga kopplingar mellan impulsivitet och individens sociala status (**uppsats IV** och **V**), risktagande eller födosökseffektivitet (**uppsats V**). Detta kan tyda på att impulsivitet inte påverkar individers överlevnad eller reproduktion genom att påverka utfall i dessa situationer. Detta kan i sin tur innebära att det inte är så illa för individer att vara impulsiva, vilket kan hjälpa att förklara varför variation i impulsivitet är allmänt förekommande i djurriket. Överlag kan en avsaknad av påverkan på överlevnad och fortplantning potentiellt förklara varför variation i kognition observeras mellan individer. Sammantaget har jag med denna avhandling utökat vår förståelse av impulsivitetens natur, och orsakerna och konsekvenserna av variation i impulsivitet. Utöver detta, eftersom impulsivitet underbyggs av den kognitiva egenskapen impulsivitet, ger resultaten av denna avhandling oss också en ökad förståelse för varför individer varierar i kognition och konsekvenserna av detta.

## Papers written during, but not included in this thesis

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Garnham L & Løvlie H (2018). Sophisticated fowl: the complex behaviour and cognitive skills of chickens and red junglefowl. *Behavioral Sciences*, 8:13.

Sorato E, Zidar J, Garnham L, Wilson A & Løvlie H (2018). Heritabilities and co-variation among cognitive traits in red junglefowl. *Philosophical Transactions of the Royal Society*, 373:20170285.

Abbey-Lee RN, Uhrig E, Garnham L, Lundgren K, Child S & Løvlie H (2018). Experimental manipulation of monoamine levels alters personality in crickets. *Scientific Reports*, 8:16211.

Boddington R, Dunlop C, Garnham L, Ryding S, Abbey-Lee RN, Kreshchenko A & Løvlie H (2020). The relationship between monoaminergic gene expression, learning, and optimism in red junglefowl chicks. *Animal Cognition*, 23. DOI: 10.1007/s10071-020-01394-z

Lundgren KA, Abbey-Lee RN, Garnham LC, Kreshchenko A, Ryding S & Løvlie H (2021). Manipulating monoamines reduces exploration and boldness of Mediterranean field crickets. *Behavioural Processes*, 183:1-6.

## Papers included in this thesis

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**Paper I:** Ryding S\*, Garnham LC\*, Abbey-Lee RN, Petkova I, Kreshchenko A & Løvlie H (2021). Impulsivity is affected by cognitive enrichment and links to brain gene expression in red junglefowl chicks. *Animal Behaviour*, 178:195-207.  
\*Shared first authorship.

**Paper II:** Garnham LC, Garcia Dominguez S, Thornton A, Shaw R & Løvlie H. The effect of experimentally manipulating group size on cognitive performance in red junglefowl chicks. Manuscript.

**Paper III:** Garnham LC, Clarke C & Løvlie H (2022). How inhibitory control relates to positive and negative affective state in red junglefowl. *Frontiers in Veterinary Science*, in press. DOI: 10.1007/s10071-022-01598-5. To be part of a special issue on 'Captive Animal Behavior: Individual Differences in Learning and Cognition, and Implications on Animal Welfare'.

**Paper IV:** Garnham LC, Ahlgren-Porthén S, Child S, Forslind S & Løvlie H (2019). The role of personality, cognition, and affective state in same-sex contests in the red junglefowl. *Behavioral Ecology and Sociobiology*, 7:149.

**Paper V:** Garnham LC, Boddington R & Løvlie H (2022). Variation in inhibitory control does not influence social rank, foraging efficiency, or risk taking, in red junglefowl females. *Animal Cognition*. DOI:10.1007/s10071-022-01598-5

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## Introduction

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Throughout the animal kingdom, individuals within the same species vary in cognition (i.e., how they perceive, store and act on information from environmental stimuli, Shettleworth 2010) with the causes and consequences of this variation being largely unknown (Boogert et al. 2018; Shaw & Schmelz 2017; Thornton & Lucas 2012). One aspect of cognition, known to vary between individuals, is inhibitory control (e.g., Langley et al. 2020; Lucon-Xicatto et al. 2020a; MacLean et al. 2014; Szabo et al. 2020), which is the ability to inhibit impulsive responses in favour of more appropriate ones (Logan et al. 1997; Macario et al. 2021). Individuals with poorer inhibitory control are more impulsive than those with better inhibitory control (Dalley et al. 2011; Logan et al. 1997; Schippers et al. 2017), though individuals can learn to reduce how impulsive they are with repeated experience (Kabadayi et al. 2017; van Horik et al. 2018). More impulsive individuals are more likely to act prematurely without foresight (Dalley et al. 2011), or without completely processing available information (Moeller et al. 2001), than less impulsive individuals. Variation in impulsivity is relatively well studied, yet there remain clear gaps in our understanding of this. To begin with, previous studies have found impulsivity to be heritable (Gnanadesikan et al. 2020; Langley et al. 2020). This indicates that variation in impulsivity is temporally consistent and can be subject to selection (Smith & Blumstein 2008). When data for my thesis was collected and analysed, whether impulsivity was consistent over time had not yet been empirically investigated. Very recently, impulsivity has been found to be repeatable across time and contexts in great tits, *Parus major*, (Davidson et al. 2022). If variation in impulsivity can be subject to selection, the question arises as to why individuals vary in impulsivity, despite that higher impulsivity may lead to poorer outcomes for individuals (e.g., Amici et al. 2018; Boogert et al. 2011; Daruna & Barnes 1993). Finally, how variation in impulsivity affects individual outcomes in situations that can influence survival and reproduction, and, thus, how selection may act on impulsivity, is scarcely investigated. The aim of my thesis, therefore, was to help fill in some of these gaps in our understanding of the causes and consequences of impulsivity.

Impulsivity is a complex trait typically consisting of multiple distinct aspects (e.g., Brucks et al. 2017; Evenden 1999; Nautiyal et al. 2017). My thesis focuses mainly on one aspect, namely 'impulsive action' (i.e., the inability to inhibit a motor response, Broos et al. 2012; Diamond & Gilbert 1989; Winstanley 2006), and, to a lesser extent, on another aspect 'persistence' (i.e., continuing to use a previously adaptive response after it ceases to be adaptive, Evenden 1999). Additionally, as

measures of impulsive action taken in different tests may reflect different aspects of impulsivity (e.g., Vernouillet et al. 2018; Völter 2018), this thesis specifically focuses on impulsive action and persistence measured in a detour task (a.k.a., detour test, detour reaching task/test, cylinder task/test). This task has been used on a broad variety of species (exemplified below) and, as poor inhibitory control results in high impulsivity, can be used to assess both inhibitory control and impulsive action.

The following paragraphs of this introduction briefly discuss the current knowledge regarding potential causes and consequences of variation in impulsivity (i.e., mainly impulsive action, as studies on persistence are still lacking) measured in a detour test. Note that some of the studies discussed measured inhibitory control, but have been interpreted here in the context of impulsivity, which is possible due to the innate relationship between impulsivity and inhibitory control.

Regarding causes of variation in impulsivity, a handful of studies experimentally manipulated the experiences of some test individuals and compared their responses to unmanipulated control subjects (see examples discussed below). Such studies are ideal, as they can determine causality between impulsivity and other investigated factors. Some of these studies showed that changing an individual's environment could affect their impulsivity. For example, making the environment less predictable (by no longer rewarding previously rewarded cues) led to higher impulsivity in common pheasants, *Phasianus colchicus* (Griffin et al. 2020). Alternatively, if their environment was made less spatially predictable (i.e., if objects were regularly moved around), male common pheasants became less impulsive (van Horik et al. 2019). The effect of exposure to stressors on impulsivity has also been investigated. For example, common marmosets, *Callithrix jacchus*, that experienced regular separation from their mothers were more impulsive than those that did not (Pryce et al. 2005). Further, exposure to traffic noise, which could be stressful, increased impulsivity in zebra finches, *Taeniopygia guttata* (Osbrink et al. 2021). Some experimental studies have explored how neurochemistry affects impulsivity. For instance, depletion of serotonin or dopamine (important neurotransmitters that are active in the brain) led to higher impulsive action (e.g., southern pig-tailed macaques, *Macaca nemestrina*, Schneider & Roeltgen 1993; green monkeys, *Chlorocebus sabaeus*, Taylor et al. 1990; in common marmosets, Walker et al. 2006) and persistence (vervet monkeys, *Cercopithecus aethiops sabaeus*, Jentsch et al. 1999). Finally, in dogs (*Canis familiaris*) increasing emotional arousal decreased impulsivity when arousal was low, but increased it, when arousal was high (Bray et al. 2015).

Typically, studies on the potential causes of variation in impulsivity are correlative. The following two paragraphs discuss such studies that explored how variation in impulsivity or inhibitory control measured in a detour task correlated with other factors. In correlative studies, the causality in detected relationships is typically not known. For some of these relationships (e.g., between impulsivity and behaviour, social factors, or body condition) causality is challenging to predict, as it could go either way: impulsivity could affect behaviour, social factors or body condition, or these could affect impulsivity. In terms of behaviour, a more proactive personality (i.e., more active, bold, and explorative, Koolhaas et al. 1999; Sih et al. 2004) has been theoretically linked to higher impulsivity (Sih & Del Giudice 2012). There is some support for this, for example, in domestic chickens (*Gallus gallus domesticus*) birds that were more explorative were more impulsive (Ferreira et al. 2020). However, most empirical studies seem to link lower impulsivity with a more proactive personality type. Zebra fish (*Danio rerio*) and guppies (*Poecilia reticulata*) that spent more time in the centre of an open field arena (i.e., were bolder and more explorative) were less impulsive (Lucon-Xicatto et al. 2020b; Savaşçı et al. 2021). Common waxbills (*Estrilda astrild*) that were more active in front of, but less attentive to, a mirror (which associates with a more proactive personality in this species) had lower impulsivity (Gomes et al. 2020). Regarding social factors, some studies have investigated the effect of group size on inhibitory control (Ashton et al. 2018; Johnson-Ulrich & Holekamp 2020). Living in larger groups could be more cognitively demanding than living in smaller groups (e.g., Dunbar & Shultz 2007; Ferguson-Gow et al. 2014; Freeberg & Krams 2015), thus, these studies could potentially test the hypotheses that living in more cognitively demanding groups will lead to improved cognitive performance (a.k.a., the social intelligence hypothesis, Humphrey 1976; Jolly 1966). These studies found that living in larger groups was connected to less impulsive behaviour (in Australian magpies, *Cracticus tibicen*, Ashton et al. 2018; and spotted hyenas, *Crocuta crocuta*, Johnson-Ulrich & Holekamp 2020). In spotted hyenas, lower impulsivity was also associated with low social status, though this relationship was only found in larger groups (Johnson-Ulrich & Holekamp 2020). In terms of body condition, New Zealand robins (*Petroica longipes*) with better body condition were less impulsive (Shaw 2017).

In other cases, predicting the probable direction of correlative relationships between impulsivity and other factors may be easier. For example, sex, ontogeny and neurology have been shown in some studies to be associated with variation in impulsivity and could all, logically, be presumed to cause this variation. Regarding sex differences in impulsive behaviour, the nature of these differences can depend on the species investigated. For example, male guppies were more

persistent (Lucon-Xicatto & Bisazza 2017), while, in dogs, females showed lower levels of impulsive action (Junttila et al. 2021), and, in spotted hyenas, no sex differences were found (Johnson-Ulrich & Holekamp 2020). A range of behaviours (e.g., those describing animal personality, i.e., consistent individual differences in behaviour, Dall et al. 2004) are known to be affected by ontogeny (reviewed in Stamps & Groothuis 2010a). In terms of impulsivity, specifically, studies on the effect of ontogeny are scarcer. However, there appears to be a U-shaped effect, at least in guppies, where impulsivity is higher at young (10 days) and old (90 days) age and lower inbetween (20-40 days; Savaşçı et al. 2021). When it comes to neurology, individuals that have larger brains (in terms of absolute brain size, many species, MacLean et al. 2014), and process social information in the left hemisphere (guppies, Lucon-Xicatto et al. 2020c), have been found to be less impulsive.

Studies investigating the potential consequences of variation in impulsivity are less common than those investigating potential causes. Nevertheless, correlative studies suggest that variation in impulsivity may have implications for individuals' survival and reproduction. For example, impulsivity may affect foraging efficiency. First, increased impulsivity has been linked to increased foraging persistence in common pheasants (van Horik et al. 2018). Depending on whether other food is nearby, or whether the food the individual is attempting to access is obtainable, this could lead to lower or higher foraging efficiency. Second, great tits that are less impulsive were more able to switch to an alternative food source when this had higher value (Coomes et al. 2021). Reproductive success may also be influenced by variation in impulsivity. For instance, in threespine sticklebacks (*Gasterosteus aculeatus*) females preferred to mate with males that were less impulsive (Minter et al. 2017). Less impulsive stickleback males may be better at avoiding the impulsive behaviour of eating their fry (which can resemble prey) and so raise more offspring to independence (Minter et al. 2017). In song sparrows (*Melospiza melodia*), males with larger song repertoires (which are preferred by females), were less impulsive (Boogert et al. 2011). Furthermore, in female Australian magpies, better overall cognitive performance (a.k.a., 'general intelligence' or 'g'), of which inhibitory control is a part, linked to increased reproductive success (Ashton et al. 2018). Finally, while not demonstrating a direct effect on reproductive success, zebra finch pairs that were less impulsive were better at cooperating with each other, which could increase their chances of raising offspring to independence (Chia & Dubois 2017).

As can be seen, recent research has improved our understanding of the potential causes and consequences of variation in impulsivity. Yet, there are still gaps in this

understanding, some of which my thesis aims to help fill. To begin with, while numerous studies show that environment and experience can influence impulsivity (e.g., Griffin et al. 2020; Osbrink et al. 2021; Pryce et al. 2005; van Horik et al. 2019), and impulsivity is known to be underlain by an aspect of cognition (i.e., inhibitory control, Dalley et al. 2011; Logan et al. 1997; Schippers et al. 2017), if, and how, cognitive enrichment could affect impulsivity is not yet explored. Thus, **paper I** causally explored the effect of exposure to cognitive enrichment in early life on impulsivity. That depletion in serotonin and dopamine affects impulsive action (Schneider & Roeltgen 1993; Taylor et al. 1990; Walker et al. 2006) and persistence (Jentsch et al. 1999) measured in a detour task, implies that variation in dopaminergic and serotonergic genes could link to variation in performance on this task. Nevertheless, this lacks investigation, despite that genes of the dopaminergic and serotonergic systems are often implicated in variation in impulsivity (Dalley et al. 2011; Švob et al. 2016). Therefore, **paper I** explored whether variation in expression of dopaminergic and serotonergic genes in the brain of study individuals linked to variation in impulsive action or persistence measured in a detour task. To my knowledge, how variation in gene expression, in general, links to variation in performance on detour tasks had not yet been explored, despite that impulsivity appears to be at least moderately heritable and hence has a genetic component (Gnanadesikan et al. 2020; Langley et al. 2020). While individuals in larger groups have been found to be less impulsive, causality in this relationship is unclear (Wascher et al. 2018). Thus, **paper II** experimentally investigated if an individual's impulsivity was causally influenced by the size of the social group it was raised in. Moreover, **paper II** also investigated how variation in other behaviours (e.g., boldness, activity, neophobia) associated with variation in impulsivity with the aim to uncover mechanisms by which group size could affect cognition, besides the commonly predicted enhanced cognitive demands of living in larger groups. That changes in emotional arousal can influence impulsivity (e.g., Bray et al. 2015), suggests a link between affective state (i.e., mood and emotions) and impulsivity. Therefore, **paper III** explored how variation in both positive and negative affective states associated with variation in impulsivity. Here both younger chicks, older chicks and adults were used, thus making it possible to explore how relationships between impulsivity and affective state may change over ontogeny. The relationship between impulsivity and status is also currently unclear in the research field (i.e., whether status influences impulsivity or vice versa). Therefore, **paper IV** looked into whether an individual's level of impulsivity causally affected how likely they were to initiate and/or win a contest for status, while **paper V** looked at how an individual's level of impulsivity related to their current status. Finally, studies indicate that variation in impulsivity may have consequences for

survival and reproduction (e.g., Ashton et al. 2018; Boogert et al. 2011; Minter et al. 2017). However, no studies have yet explored the effect of impulsivity on multiple ecologically relevant consequences simultaneously. Thus, **paper V** did this by looking into how variation in impulsivity links, not only to social status, but also foraging efficiency, and risk taking.

## Methods

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### Study species and population

The study species used for my thesis was the red junglefowl (*Gallus gallus*). Red junglefowl, the ancestor of domestic chickens (Fumihito et al. 1994), are ideal for studies of behaviour and cognition (reviewed in Garnham & Løvlie 2018). Due to the accumulated research on the behaviour and cognition of red junglefowl, a lot is known about this, and how to measure it. Further, red junglefowl can be hatched and raised in large numbers, thus providing large sample sizes (small sample sizes are a common problem in animal cognition research). This, along with that they can also be relatively easily habituated both to human handling and being alone in testing arenas, made them ideal for the topic of my thesis. Red junglefowl are precocial, meaning that they can be raised without mothers, thus one can reduce maternal effects as a confounding factor (Langenhof & Komdeur 2018; Stamps & Groothuis 2010b). In addition, the red junglefowl is a good species in which to investigate social aspects, for example, how group size could affect impulsivity and how social status could relate to impulsivity. They naturally form social groups of typically 2-15 individuals (Collias & Collias 1996; McBride et al. 1969; Sullivan 1991) with social hierarchies in which individuals with high social status benefit from increased access to resources that can enhance reproductive success (Collias et al. 1994; Collias & Collias 1996). Junglefowl are also suitable for investigating consequences of impulsivity for foraging efficiency, and risk taking, as they forage on food which can be patchily distributed and, thus, vary in ease of access (e.g., seeds, fruits, and invertebrates, Collias & Collias 1967), and are a prey species in their natural habitat (Borah et al. 2009; Evans et al. 1993; Schaller 1984). Finally, there is a welfare incentive to investigate impulsivity in fowl, as feather pecking, which is a serious welfare issue in poultry, has been linked to impulsivity (de Haas & van der Eijk 2018; Kops et al. 2013).

The red junglefowl used in this thesis came from a population maintained by Linköping university and pedigree bred since 2011 (more details in Sorato et al. 2018). For this thesis, 3 successive cohorts of junglefowl were used (total N = 327),

one hatched in 2016, tested as both chicks (**paper II**) and adults (**paper IV**), one hatched in 2017, tested as chicks (**paper I, II**), and one hatched in 2019 tested as chicks (**paper I, III**) and adults (**paper V**).

## **Brief overviews of tests used in this thesis**

The behavioural tests described below are those that were directly involved in exploring causes and consequences of impulsivity. Other tests feature in the papers that make up this thesis, as these papers investigated also other themes, which are not discussed here. More detailed methods of all these tests can be found in the papers they are used in and in the corresponding '*sensu*' references. For all testing, to reduce effects of stress, individuals were carefully habituated to handling, and being alone in testing arenas, often from their first day of life. To reduce effects of variation in body condition and/or food motivation on our results, food was provided *ad libitum*. Finally, testing was non-voluntary, meaning that all personality types, and where possible, both sexes, participated in the studies. Note that, while I sometimes discuss the methods in first person singular, a team of people (see acknowledgements) were involved in the data collection for all studies.

### Detour task

In **papers I, IV and V**, I measured impulsivity, and in **papers II and III**, I measured inhibitory control in a detour task (a.k.a., detour test, detour reaching task/test, cylinder task/test). In **papers I and V**, this task was also used to measure persistence. In this task, an individual was first taught a detour to obtain a reward from the centre of an opaque tube. Once it had learnt this detour, I presented it 5 times with a reward in a transparent tube (the number of tube presentations in this test were kept low, to reduce effects of learning, e.g., Kabadayi et al. 2017; van Horik et al. 2018, but see **paper I**). As the individual could see the reward behind the barrier, it needed to inhibit the impulsive response (i.e., trying to reach the reward directly through the barrier) and instead use the previously learnt detour to obtain the reward. In **papers I, IV and V**, impulsive action was measured as the number of tube presentations, out of 5, an individual pecked at the tube in an attempt to get the reward (instead of using the previously learnt detour), and a higher measure implied higher levels of impulsive action. In **papers II and III**, inhibitory control was measured as the number of tube presentations, out of 5, an individual used the previously learnt detour to obtain the reward without impulsively pecking at the tube, where a higher measure implied higher levels of inhibitory control. Inhibitory control is, therefore, a reverse measure of

impulsivity. Persistence in the detour task was measured as the total number of pecks over these five presentations, where a higher measure indicated higher persistence. I accounted for that variation in previous experience of transparent objects can affect performance in detour tasks (van Horik et al. 2018), by ensuring that all individuals within a study had the same experience of transparent objects prior to the test. The only exception to this was in **paper V** where all females, bar 3, had experienced the detour test previously as chicks. To account for this, data in this study was analysed with and without these 3 females included, and any qualitative differences between these analyses were reported. To account for that how the detour is taught can affect performance in this test (van Horik et al. 2020), all individuals were taught the detour in the same way.

### Tonic immobility test

In **papers II** and **III**, a tonic immobility test was used (*sensu*, Favati et al. 2016). This test is commonly used to assess fearfulness in poultry (e.g., Forkman et al. 2007; Gallup 1979; Hicks & Patrick 2006), but can also be used to measure stress (Kozak et al. 2019; Zulkifi et al. 1998). Hence, tonic immobility tests were used to assess stress levels in **paper II**. As fearfulness and stress are both negative affective states, the tonic immobility test can also function as a test of negative affective state (Gallup 1979; Hansen et al. 1993) and, therefore, was used as such in **paper III**. I induced tonic immobility in an individual by laying it on its back in a V-shaped wooden cradle and gently holding it down, for 15 s, applying light pressure with one hand over its chest and, with another hand, covering its eyes. After this, I slowly removed my hands and measured (in s) how long it took for the individual to return to standing (a longer time indicated a higher stress level, Kozak et al. 2019; Zulkifi et al. 1998, and more negative affective state, Gallup 1979; Hansen et al. 1993). If an individual returned to standing within 3 seconds, tonic immobility was considered to have not been induced and the induction procedure was repeated up to five times. If tonic immobility could not be induced in an individual, it was given a measure of 0 s. If an individual remained immobile for 600 s, it was given a measure of 600 s and then gently brought it out of tonic immobility by hand. This test was also used in **paper IV**, which explored how variation in tonic immobility linked behaviour could influence social status.

### Novel arena test

In **paper II**, boldness, activity and exploration were measured in a novel arena test (*sensu*, Zidar et al. 2017a,b). As these behaviours have previously been shown to be temporally consistent among individuals in this population, that is, to describe variation in personality (Zidar et al. 2017a,b), they were only measured once in this study. Boldness was measured as an individual's latency to first movement after they were placed in the arena. Individuals were given a max time of 300 s to start moving and all did so within this time. After the individual had started moving, the test continued for a further 420 s. During this time, activity was measured as the number of times an individual transitioned between the sub areas in the arena and exploration as the total number of sub areas (out of six) an individual explored. A version of this test was also used in **paper IV** to study how variation in activity, boldness and exploration affected contest outcome. In this version the test took 10 minutes in total, and individuals were not given a time limit in which to start moving.

### Judgement bias test

In **paper III**, to measure positive affective state, I used a cognitive judgement bias test, which is a type of behavioural test commonly used to assess optimism (e.g., Lagisz et al. 2020; Neville et al. 2020). The version of the test I used was specifically developed to be used in the red junglefowl (*sensu*, Sorato et al. 2018). In this test, individuals were first taught to associate a white cue with a reward, and a black cue with the absence of a reward. Individuals were considered to have learnt this once they chose the rewarded cue in 6 consecutive cue presentations (in all cue presentations, rewarded and unrewarded cues were presented simultaneously, with the side of the rewarded cue varying according to a pseudorandom order). Once an individual had learnt the rewarded and unrewarded cues, it was presented with a novel, ambiguous cue that was intermediate between these (i.e., a mid-grey cue). A shorter latency to approach this novel ambiguous cue indicates higher optimism and, thus, a more positive affective state (Harding et al. 2004; Mendl et al. 2009; Zidar et al. 2018a). Average latency to approach the rewarded cue was used in analyses of this measure to account for that individuals may differ in approach speed to the ambiguous cue for reasons besides differences in affective state. This test was also used in **paper IV** when investigating the effect of optimism on establishment of social status.

### Staged contests

In **papers IV** and **V**, I staged intra-sexual dyadic contests (*sensu*, Favati et al. 2014a,b) to experimentally disentangle the relationship between impulsivity and status. These contests took place outside of the individuals' home pen in an arena that was familiar to them. Contest pairs were morphologically matched (i.e., had comb size, in mm, tarsus length, in mm, and weight, in g, within 10% of each other, *sensu*, Favati et al. 2014a,b) to reduce that morphology influenced the outcome of the contest. Contest pairs were also mismatched in terms of impulsivity (i.e., contest pairs consisted of one individual with a lower, and one individual with a higher, impulsivity measure). The winners and losers of contests were recorded by first-hand observation. An individual won a contest if its opponent avoided it 3 consecutive times. If a pair began to fight, I would quickly separate them. Most physical interactions did not escalate into fighting and no injuries were obtained (besides some minor bleeding resulting from pecks to the comb).

### Foraging test

In **paper V**, I developed a foraging test to assess if impulsivity linked to foraging efficiency. In this test, an individual was presented with nine glass petri dishes with lids, arranged in a grid. Each petri dish had three accessible mealworms on top of, and three inaccessible mealworms below, its lid. This created a foraging situation in which trying to obtain the inaccessible mealworms should lead to lower foraging efficiency. This could result in that individuals that are more persistent spend more time trying to obtain the inaccessible mealworms and, thus, have lower foraging efficiency. Foraging efficiency was measured as the number of patches and individual visited, divided by the time spent foraging, where a higher score implied higher foraging efficiency.

### Simulated predator attack test

In **paper V**, to assess how impulsivity connects to risk taking, specifically risk taking under perceived threat of predation, a simulated predator attack test was used (*sensu*, Favati et al. 2016). In this test, an individual, while foraging, experienced a black model outline of a hawk moving rapidly across a zip line, such that it appeared to be swooping to attack the individual. I measured both threat perception (intensity of response to the model hawk on a scale of 0-5, where a higher score indicated that the individual found the hawk more threatening) and time spent vigilant (latency of the individual to return to foraging after experiencing the model hawk). I combined these two measures to create a risk-

taking measure (time spent vigilant/threat perception), in which a lower value indicated higher risk-taking.

### Gene expression analyses

In **paper I**, to investigate whether gene expression of dopaminergic and serotonergic systems linked to variation in impulsivity, brain gene expression of dopaminergic and serotonergic genes were measured. Specifically, the caudal region of left hemisphere was focused on as this region is implicated in impulsivity (Vallortigara 1999; Walker et al. 2006). Chicks were culled at 9 weeks old and their brains rapidly frozen in liquid nitrogen (< 4 mins). RNA was extracted and its concentration (for all samples) and quality (for 12 samples, one per batch of extractions) was measured. Single stranded cDNA primers were created, including ones which targeted genes of the dopaminergic (DRD1 and DRD2) and serotonergic (5HT2A, 5HT1B, 5HT2B, 5HT2C and TPH) systems. The melting curve run on pooled cDNA from all individuals was inspected to check primer specificity. These primers were then used in a qPCR, to determine the expression of their target genes in the sample. While data from this analysis was used in my thesis, I did not carry out the molecular work.

## Paper Summaries

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The methods and results mentioned in these summaries are, specifically, the methods used, and results obtained, of relevance to the overall aims of my thesis. These papers had additional focuses besides from exploring causes and consequences of impulsivity, however, methods and results pertaining to these are mainly not covered here, as they were not the focus of my thesis. Note that, while **papers II** and **III** measured inhibitory control, I talk about methods and results for all papers in the context of impulsivity.

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**Paper I:** Ryding, Garnham et al. (2021). Impulsivity is affected by cognitive enrichment and links to brain gene expression in red junglefowl chicks. *Animal Behaviour*, 178:195-207.

### Methods

To investigate how exposure to cognitive enrichment experienced in early life influenced impulsivity, chicks of both sexes were raised in three different

treatments and their impulsive action and persistence later assayed in a detour task. Past the five tube presentations used to assay impulsive action and persistence, chicks experienced a further 25 tube presentations to explore how the treatments affected learning to overcome impulsive behaviours. The treatments were 'cognitively enriched', where chicks (N = 65) took part in cognitive tests, 'environmentally enriched', where chicks (N = 34) experienced the arenas and equipment used in cognitive testing, but were never cognitively tested, and 'nonenriched', where chicks (N = 34) did not experience cognitive testing equipment or arenas. We ensured that chicks from the same family were placed in different treatments, as genotype can affect cognitive performance (Aplin 2019; Lomanowska et al. 2017). By having three treatments, which aspects of cognitive enrichment may affect impulsivity could be determined (e.g., specifically participating in cognitive testing, or simply experiencing new situations). Brains were extracted from chicks that were culled after the experiment, to investigate brain gene expression of dopaminergic and serotonergic genes.

## Results

Chicks that were cognitively enriched early in life showed higher levels of impulsive action and persistence than nonenriched chicks. Cognitively enriched chicks also had higher levels of persistence, and tended to have higher impulsive action, than environmentally enriched chicks. Finally, environmentally enriched chicks appeared to be slower at learning to reduce impulsivity, compared to cognitively enriched or nonenriched chicks. Variation in impulsive action tended to correlate positively with brain gene expression of the serotonin synthesizer gene TPH. Variation in persistence was correlated negatively with gene expression of TPH and DRD1, and tended to correlate negatively with DRD2 (DRD1 and DRD2 are dopamine receptor genes). Finally, my behavioural measures of impulsive action and persistence were strongly correlated.

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**Paper II:** Garnham et al. The effect of experimentally manipulating group size on cognitive performance in red junglefowl chicks. Manuscript.

## Methods

To experimentally investigate whether the size of group individuals were raised in could causally affect how impulsive they were, chicks of both sexes (N= 76) were raised in small groups (N = 4, each consisting of 7 individuals) and large groups (N

= 3, each consisting of 16 individuals) from after hatching. As in **paper I**, we placed chicks from the same family in different treatments. The impulsivity of these chicks was assessed in detour tasks when 17-20 days old and when 34 days old. As well as exploring if group size causally affected impulsivity, to explore potential mechanisms behind this, how impulsivity was affected by various factors that could be predicted to covary with group size (such as activity, neophobia and stress) was investigated.

## Results

Although the group size chicks were raised in affected their performance in other cognitive measures (specifically, discrimination learning speed, and resampling in reversal learning, the latter in a sex specific manner), group size did not influence impulsivity, either when chicks were measured at 17-20 days or when they were measured at 34 days. When tested at 17-20 days old, chicks that were more neophobic (i.e., took longer to approach the testing equipment used in the detour task) and tended to be less bold (measured as latency to first movement in a novel arena) were less impulsive. Lower boldness also tended to be linked to lower impulsivity, when chicks were tested at 34 days, as was being more stressed and less active (the latter was a tendency). Finally, at 34 days, females were less impulsive than males.

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**Paper III:** Garnham et al. (2022). How inhibitory control relates to positive and negative affective state in red junglefowl. *Frontiers in Veterinary Science*, in press.

## Methods

To investigate how impulsivity may link to positive and negative affective states, these factors were measured in 3 cohorts of red junglefowl of both sexes. Impulsivity was measured in a detour task, negative affective state in a tonic immobility test, and positive affective state in a judgement bias test. Cohort 1 was tested as younger chicks (N = 70,  $\approx$  2.5 weeks old) and adults (N = 99,  $\approx$  28 weeks old), Cohort 2 was tested as younger chicks (N = 52), and Cohort 3 was tested as younger chicks (N = 58) and older chicks (N = 58,  $\approx$  5 weeks old). Total N = 206.

## Results

In younger chicks, individuals that were less impulsive had more negative affective state, less positive, affective states. In older chicks and adults, no connections between impulsivity and affective states were detected. Further, impulsivity was found to be moderately consistent over time between younger and older chicks (i.e., within the same developmental stage), but not between chicks and adults (i.e., across developmental stages).

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**Paper VI:** Garnham et al. (2019). The role of personality, cognition, and affective state in same-sex contests in the red junglefowl. *Behavioral Ecology and Sociobiology*, 73:149.

## Methods

To determine whether impulsivity plays a role in the establishment of social status, impulsivity was measured in adult female and male red junglefowl ( $N = 88$ ) and used to pair up individuals for staged same sex contests. Each individual was chosen an opponent that differed from it in terms of impulsivity and was similar to it in terms of morphology. The individual that initiated the contest was recorded. Typically, individuals that initiate contests win them, thus, if more impulsive individuals are more likely to initiate contests this could lead to more impulsive individuals having higher social status. I also recorded which individual won each contest.

## Results

Although other behavioural measures were linked to the initiation and/or outcome of contests (namely, activity, boldness and optimism), I found no evidence, for either females or males, that variation in impulsivity affected how likely individuals were to initiate, or win, contests.

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**Paper V:** Garnham et al. (2022). Variation in inhibitory control does not influence social rank, foraging efficiency, or risk taking, in red junglefowl females. *Animal Cognition*. DOI: 10.1007/s10071-022-01598-5

## Methods

In adult female red junglefowl (N = 30), how variation in impulsive action and persistence may influence individual outcomes in ecologically relevant contexts, was explored. These contexts were social status (specifically, current social status, measured in staged contests), foraging efficiency (measured in a foraging test) and risk taking under perceived threat of predation (measured in a predator startle test). The detour task was repeated  $\approx$  3 months after this study to investigate temporal consistency in impulsive action and persistence.

## Results

Neither impulsivity action nor persistence measured in a detour task linked to individual outcomes in terms of social status, foraging efficiency, or risk taking. Both impulsive action and persistence showed moderate consistency, over time, and were positively correlated.

## Discussion

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My thesis aimed to improve aspects of our overall understanding of individual variation in cognition, by filling in gaps our understanding of the causes and consequences of impulsivity, which is underlain by an aspect of cognition, inhibitory control. **Paper I** explored if enrichment experienced early in life could causally effect impulsivity, as well as how brain gene expression of dopaminergic and serotonergic systems linked to variation in impulsivity. **Paper II** investigated how early environment, in terms of social group size, could causally influence impulsivity and potential behavioural mechanisms by which this could occur. **Paper III** looked at whether differences in affective state could link to differences in impulsivity and if these links varied over ontogeny. **Papers IV and V** attempted to disentangle the relationship between impulsivity and social status, with **paper V** also exploring how variation in impulsivity could affect individual outcomes in foraging and risk taking. The results of these papers of relevance to the overall topic of my thesis are discussed below.

Traits that are consistent over time can be subject to selection (Smith & Blumstein 2008). Therefore, I investigated consistency in impulsivity within chicks (in **papers I and II**), in adults (in **paper V**), and across the transition from chickhood to adulthood (in **paper II**). Impulsivity did not show temporal consistency over 1-2 days within younger chicks (**paper I**), whereas it did show temporal consistency over  $\approx 2.5$  weeks in somewhat older chicks (**paper II**). The reasons for this discrepancy could be that, in **paper I**, chicks experienced 30 tube presentations in the first detour task and participated in the repeat detour task within 1-2 days of the first, whereas, in **paper II**, chicks experienced only five tube presentations per detour task and at least two weeks before the repeat. Thus, there was greater potential for chicks to learn to overcome impulsivity, and to remember this for when they were tested again, in **paper I**, than there was in **paper II**. That chicks (in **paper I**), overall, performed better in the second detour task supports this idea, together with previous studies, which show that individuals can learn to respond less impulsively (Kabadayi et al. 2017; van Horik et al. 2018). In **paper V**, adult red junglefowl females (adult males were not tested because it is hard to keep them motivated with food reward) showed moderate consistency in impulsivity over a relatively long time ( $\approx$  three months). Finally, impulsivity was not consistent between chicks and adults (**paper II**). This result could be expected because, between chickhood and adulthood, red junglefowl experience two major developmental changes (becoming fully independent from their mother, at around 10-12 weeks of age, Collias et al. 1994; McBride et al. 1969, and sexual maturation at around 24-25 weeks of age, Delacour 1951; Wright et al. 2012). Both changes could result in changes to their behaviour and/or cognition (e.g., Favati et al. 2016; Zidar et al. 2018b). Overall, it appears that within developmental stages, and over a period of weeks to months, red junglefowl are moderately consistent in how impulsive they are. This finding supports another, very recent study, that found temporal consistency in impulsivity in great tits (Davidson et al. 2022). However, while impulsivity can be heritable (e.g., in dogs, Gnanadesikan et al. 2020; in pheasants, Langley et al. 2020), estimates of heritability are yet to be done in red junglefowl to confirm whether impulsivity is also heritable in this species. **Paper I** demonstrated that individuals can learn to adjust their impulsivity to respond more appropriately with repeated experience. This flexibility may reduce the degree to which variation in impulsivity could have negative consequences for individuals, which could help explain the apparent lack of consequences of variation in impulsivity seen in **papers IV and V**. On a broader level, if flexibility can reduce the negative consequences of impulsivity this could reduce selection on variation in impulsivity and, thus, help to explain why variation in impulsivity is commonly observed across species.

In **paper I**, early environment was found to affect impulsivity later in life. Cognitively enriched chicks (which experienced cognitive testing in early life), appeared more impulsive than environmentally enriched chicks (which explored cognitive testing equipment, but did not participate in cognitive testing, in early life). Both types of enrichment resulted in chicks that were more impulsive than nonenriched chicks (which were given no experience of cognitive testing equipment early in life). Therefore, experiencing enrichment early in life can increase impulsivity, with cognitive enrichment (i.e., participating in cognitive testing) having a greater effect than environmental enrichment (i.e., experiencing new or changed environments). That cognitive enrichment increased impulsivity may seem counterintuitive. As impulsivity is underlain by an aspect of cognition (inhibitory control, Dalley et al. 2011; Logan et al. 1997; Schippers et al. 2017), cognitive enrichment could be expected to improve inhibitory control and, thus, decrease impulsivity. Nevertheless, if cognitive enrichment functions similarly to environmental enrichment, our findings regarding both cognitive and environmental enrichment match with previous studies in which environmental enrichment increased impulsivity (Dalley et al. 2002; Kirkpatrick et al. 2013). Environmental enrichment may itself act as cognitive enrichment (e.g., if it stimulates social or spatial cognition, Dalley et al. 2002; Kirkpatrick et al. 2013). Overall, **paper I** adds to previous studies in showing that differences in early experience can causally result in variation in impulsivity (e.g., Griffin et al. 2020; Pryce et al. 2005; van Horik et al. 2019).

**Paper I** also found that both impulsive action and persistence correlated with brain gene expression of serotonin synthesizer gene (TPH), though for impulsive action the correlation was positive, while for persistence it was negative. Persistence also correlated negatively with expression of dopaminergic genes DRD1 and DRD2, however, the latter correlation was only a tendency. These results support previous studies which indicate that the dopaminergic and serotonergic systems may underlie variation in impulsive action and persistence (e.g., Jentsch et al. 1999; Schneider & Roeltgen 1993; Taylor et al. 1990; Walker et al. 2006). Further, results of **paper 1** tie in with earlier studies that find overall connections between dopaminergic and serotonergic genes and impulsivity (Dalley et al., 2011; Švob et al 2016). That impulsive action and persistence were linked to gene expression in different ways, and so appear to have different underlying genetic mechanisms, supports that they may be different aspects of impulsivity (Brucks et al. 2017; Harriman 1947). On the other hand, the strong correlation seen between my behavioural measures of impulsive action and persistence (**papers I** and **V**) could be due to that they are taken from the same test, and, thus, are not independent measures (similar to Garner & Mason 2002).

Therefore, impulsivity and persistence may need to be measured in separate tests to explore whether they are truly independent aspects of impulsivity.

In **paper II**, I experimentally assigned chicks to different sized social groups after hatching, to determine if social group size experienced early in life could causally affect impulsivity. Unlike previous studies (Ashton et al. 2018; Jonhson-Ulrich & Holekamp 2020; Langley et al., 2018), when controlling for that genetics and experiences can be more similar within, compared to between, groups, I found no connection between group size and impulsivity. This could potentially suggest that, where other studies have found group size to link to impulsivity, this could be due to individuals with particular levels of impulsivity preferring to congregate in particular group sizes. Alternatively, an effect of group size on impulsivity could appear in species in which inhibitory control correlates with other aspects of cognition that are affected by group size, even if group size would not directly influence inhibitory control. This is unlikely to happen in red junglefowl, as aspects of cognition appears to be domain specific in this species (i.e., they do show general intelligence, a.k.a., 'g', Sorato et al. 2018; Zidar et al. 2017a), but could happen in species where aspects of cognition interrelate (i.e., that have 'g'). For example, in both red junglefowl (**paper II**) and Australian magpies (Ashton et al. 2018), group size influenced another aspect of cognition, discrimination learning. If red junglefowl lack general cognition, but Australian magpies have it, a group size effect on discrimination learning will not affect inhibitory control in red junglefowl, but could affect it, indirectly, in Australian magpies. That group size did not affect impulsivity (i.e., did not affect inhibitory control) could go against the hypotheses that more cognitively demanding social environments (which larger groups have been considered to be, e.g., Dunbar & Shultz 2007; Ferguson-Gow et al. 2014; Freeberg & Krams 2015) lead to improved cognitive performance. However, whether larger groups are actually more cognitively demanding is unclear (Holekamp 2007; Kappeler 2019; Shultz & Dunbar 2007). We would first need to confirm or reject whether larger groups are more cognitively demanding for red junglefowl, before we can use the results of **paper II** to discuss if and how the social intelligence hypothesis applies to this species.

**Papers II** and **III** explored if, and how, various behaviours were associated with impulsivity. The connections found between impulsivity and other behaviours support predictions that more proactive individuals (i.e., those that are more active, bold, and explorative, Sih et al. 2004; Koolhaas et al. 1999) will be more impulsive (Sih & Del Giudice 2012). In **paper II**, higher impulsivity was found to connect with higher boldness, higher activity and lower neophobia (though the connections with boldness and activity were only tendencies). In **paper III**, more

impulsive individuals were less fearful and more optimistic, which may indicate that they were more proactive (Asher et al. 2016; Sih & Del Giudice 2012; Sih et al. 2004; Uskul & Greenglass 2005). However, this contrasts earlier empirical studies, which suggest a link between a more proactive personality and lower levels of impulsivity (Gomes et al. 2020; Lucon-Xicatto et al. 2020b; Savaşçı et al. 2021). **Paper III** also implies that individuals may differ in impulsivity depending on how they trade off reward seeking vs. risk avoidance. More reward seeking individuals could be expected to be more impulsive, less fearful (lower negative affective state) and more optimistic (higher positive affective state), compared to more risk avoidant individuals, which is the pattern found in **paper III**. However, that, in **paper V**, risk taking was not linked to impulsivity suggests that this potential effect of reward seeking vs. risk avoidance on impulsivity, seen in younger chicks, fades with age. In older chicks, individuals that were more impulsive did not differ in their affective states, but tended to be bolder (**paper II**), compared to less impulsive chicks (in **paper III**). This suggests that a link between impulsivity with reward seeking vs. risk avoidance fades during chickhood, being less present in older chicks than it is in younger chicks. That, in **papers II and III**, chicks with lower impulsivity spent more time in tonic immobility (which can imply that they were more stressed, Kozak et al. 2019; Zulkifi et al. 1998) seems to contradict earlier studies that suggest that increased stress could lead to higher impulsivity (e.g., Osbrink et al. 2021; Pryce et al. 2005). Nevertheless, this could be because the stress our chicks experienced was mild, whereas the stress experienced by individuals in previous studies may have been more intense (mild stress can improve cognitive performance, while intense stress can worsen it, Kitaysky et al. 2003; McEwen & Sapolsky 1995; Sandi 2013). While **papers II and III** show links between impulsivity and other behaviours, it is important to point out the relationships detected were correlative, thus I cannot clearly infer causality in these relationships. Further, I must acknowledge that, as is the common approach when studying animal behaviour and cognition, I looked at relationships between single, rather than repeated measures of behaviour. Thus, the correlations I found were not partitioned into within and between individual variation and, thus, may not necessarily reflect among-individual patterns (Brommer 2013; Niemelä & Dingemanse 2018). Future studies should aim to explore relationships between impulsivity and other behaviours when able to partition variation into within and between individual variation. However, if behaviours do link to impulsivity, and if selection favours variation in these behaviours, it could indirectly select for variation also in impulsivity. This in turn could help explain why we continue to see individual variation in impulsivity within species.

In **paper III**, younger chicks that were more impulsive had less negative, more positive, affective states. This suggests that, as a more positive and less negative affective state could be presumed to indicate good welfare (Harding et al. 2004; Makowska & Wearing 2013), higher impulsivity may be associated with better welfare early in life. This could seem counterintuitive when higher impulsivity is linked to more inappropriate behaviour, in general (Daruna & Barnes 1993), and has been implicated in welfare issues for fowl (de Haas & van der Eijk 2018; Kops et al. 2013). I found that, in red junglefowl, links between impulsivity and behaviour (**paper II**), and impulsivity and affective state (**paper III**), changed over ontogeny. This is not surprising in fowl, as individuals undergo changes as they age in other aspects of behaviour and cognitive performance, and relationships between these (e.g., Favati et al. 2016; Zidar et al. 2018b). If, and how, changes in the factors that connect to impulsivity over ontogeny could help explain changes in impulsivity itself over ontogeny (e.g., as seen in Savaşçı et al. 2021) could be a focus for future research. Changes over ontogeny could also explain why sex differences were seen later and not earlier in life, in **paper II**. Red junglefowl become more sexually dimorphic up until reaching sexual maturation at around 20–25 weeks of age (Delacour 1951; Wright et al. 2012).

**Papers IV** and **V** attempted to disentangle the potential relationship between impulsivity and social status. **Paper IV** explored whether impulsivity could relate to social status through more impulsive individuals being more or less likely to initiate and/or win contests for social status. **Paper V** looked at how impulsivity associated with current social status, which could highlight if individuals with certain levels of impulsivity are better at holding on to higher status than others. Together, **papers IV** and **V** found no evidence that impulsive action influenced social status in red junglefowl. This contradicts an earlier study in which low levels of impulsive action were linked to low social status in spotted hyenas (Johnson-Ulrich & Holekamp 2020). This could, potentially, have been due to more impulsive hyenas being more likely to initiate contests (an effect which was not found in our junglefowl), as initiating contests often leads to winning them. However, the link between impulsivity and status was only found in larger groups of hyenas (Johnson-Ulrich & Holekamp 2020). It could, therefore, be suggested that I might have detected a link between impulsivity and social status, if I had used a larger study group. Nevertheless, as the social groups used for both **paper IV** and **paper V** consisted of 30 or more individuals (i.e., above the upper limits of red junglefowl group sizes observed in the wild, Collias & Collias 1996; McBride et al. 1969; Sullivan 1991), studying the effect of impulsivity and social status in larger groups would not have been ecologically relevant. Overall, the relationship between impulsivity and status remains unclear, especially as other studies, which

used different measures of impulsivity, have found high impulsivity to associate with lower social status (Higley et al. 1992; Krakowski 2003), contrasting what was found for hyenas with impulsivity measured in a detour task (Johnson-Ulrich & Holekamp 2020). Thus, more research is still needed to disentangle the relationship between impulsivity and social status.

In **paper V**, I looked into the implications of variation in impulsivity for individuals in multiple ecologically relevant contexts. As well as again finding no relationship between impulsivity and social status, I found no relationships between impulsivity and foraging efficiency, nor risk taking. While I aimed to set up the foraging test such that individuals that were more persistent would have lower foraging efficiency, this was not what I observed. Nevertheless, that great tits with lower impulsivity are more able to switch to an alternative food source when this had high value (Coomes et al. 2021) implies that impulsivity may influence at least some aspects of foraging efficiency. To my knowledge, **paper V** was the first study to explore whether impulsivity measured in a detour task could influence risk taking. Perhaps surprisingly, seeing as higher impulsivity, in general, appears to be more likely to result in more negative consequences (e.g., Amici et al. 2018; Boogert et al. 2011; Daruna & Barnes 1993), I found no relationship between impulsivity and risk taking here. As **papers II** and **III** suggest that a link between impulsivity and risk taking may exist in early life, but fade before adulthood, it would be interesting to see if, in chickhood, differences in impulsivity are linked to differences in risk taking (for example, risk taking under perceived threat of predation, as was tested in **paper V**). Overall, **papers IV** and **V** suggest that variation in impulsivity may not necessarily have clear consequences for individuals. As mentioned above, this, in turn, could reduce selection on impulsivity and help explain why individuals are often seen to vary in impulsivity within species. Nevertheless, it could be that, if individuals are relatively consistent, but somewhat flexible, in their risk taking, foraging efficiency and impulsivity, using single rather than repeated measures would have missed relationships between these that occur over time. Earlier studies in other species have found consequences of impulsivity for certain aspects of foraging and reproduction (Ashton et al. 2018; Boogert et al. 2011; Coomes et al. 2021; Minter et al. 2017; van Horik et al. 2018). Determining whether these consequences of impulsivity also occur in red junglefowl would aid our understanding of the consequences of impulsivity for, and, thus, how selection may act on variation in impulsivity, in this species.

In conclusion, my thesis demonstrates that, while variation in impulsivity is moderately consistent over time, it is not fixed. For example, how impulsive

individuals are can be influenced by their early life experiences. Further, individuals can learn to behave less impulsively in response to a situation with repeated experience of it. Future research could explore the stability, over time, of individual differences in impulsivity induced by differences in early life experiences, and also whether there are particular developmental windows in which experience can affect impulsivity. This could help improve our understanding of the stability and plasticity of impulsivity. Such research could also explore the long-term effects of differences in early life experience on impulsivity later in life. My thesis also showed that variation in impulsivity was linked to variation in expression in the brain of genes from dopaminergic and serotonergic systems, highlighting a possible genetic mechanism behind variation in impulsivity for this species. In species where gene knock-out studies can be done, the causality of this relationship could be investigated further. Moreover, despite being correlated, impulsive action and persistence linked to dopaminergic and serotonergic genes in different ways, indicating that these may be different aspects of impulsivity. My thesis specifically focused on impulsive action, and to a lesser extent, persistence, measured in a detour task. Therefore, further research could investigate whether the findings obtained in this thesis also apply to other aspects of impulsivity. In addition, my thesis found potential links between impulsivity, affective states and behaviours, suggesting that impulsivity may influence, or be influenced by, these behaviours and may have implications for welfare. Nevertheless, further research, able to partition variation of within and between individual patterns, is required before it can be certain that the patterns observed here, from analyses using single measures, reflect patterns found on the between individual level. Further, in some cases, my thesis did not find relationships between other factors investigated and impulsivity. For instance, group size differences did not affect impulsivity, and impulsivity appeared to play no role in social status, foraging efficiency, or risk taking (at least not later in life). Overall, while there is scope for further work based on my thesis, I have added to our understanding of the nature of impulsivity, and the causes and consequences of variation in this. On top of this, as impulsivity is underlain by an aspect of cognition, inhibitory control, the findings of my thesis help provide us with an improved understand of why individuals may vary in cognition and the consequences of this.

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Laura Garnham is an ethologist with a keen interest in animal behaviour and cognition. This is her PhD thesis.