# Avian cognition in a changing world

Submitted by Victoria Ellen Lee to the University of Exeter

as a thesis for the degree of Doctor of Philosophy in Biological Sciences,

September 2019.

I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

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# Abstract

Humans are altering the natural environment at an unprecedented rate, with profound consequences for non-human animals. However, species differ in how they respond to these ecological changes. Understanding the responses of wildlife to environmental change is vital to conserve biodiversity and mitigate anthropogenic impacts. Behaviour can often act as a rapid adaptation to ecological change, and is influenced by an organism's ability to acquire and process information from their environment. Despite the importance of cognition in shaping behaviour, little is known about the role of cognition in allowing some species to thrive in human-dominated habitats. In this thesis, I examine how the cognitive abilities of wild jackdaws allow these birds to cope with the challenges of a rapidly changing world. Specifically, I focus on the need to navigate a dynamic social environment, and the need to learn about anthropogenic threats. Firstly, I investigate how jackdaws track their social environment by recognising conspecifics and their relationships. In Chapter 3, I demonstrate that jackdaws individually recognise the contact calls of their breeding partner, but I find no evidence of vocal discrimination beyond the pair bond. In Chapter 4, I use infidelity simulations to investigate whether jackdaws track changes to prevailing social relationships, although I find no evidence that jackdaws respond to relationship information in this experimental context. Secondly, I investigate how jackdaws' cognitive abilities shape their behaviour during encounters with people, allowing birds to avoid danger whilst exploiting anthropogenic resources. I test the commonly-held preconception that jackdaws identify people carrying shotguns as dangerous (Chapter 5), but find no evidence that jackdaws use objects being carried by people to inform their escape decisions in this case. I also demonstrate that jackdaws learn socially about dangerous people (Chapter 6). Throughout these experiments, jackdaws differed considerably in their behaviour, which may influence individual success in anthropogenic habitats. In Chapter 7, I find that individual jackdaws differ consistently in their responses to human disturbance, but that these differences do not appear to impact reproductive success. Together, my findings highlight the importance of fundamental behavioural and cognitive research in predicting animals’ responses to environmental change.

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# Acknowledgements

I have thoroughly enjoyed the four years that I have spent working on this thesis, and that is largely thanks to all the fantastic people who have helped me along the way.

Since I joined his research group in 2014, Alex Thornton has been endlessly supportive. As my primary supervisor, Alex encouraged me to pursue questions that I found interesting, helping me to see the big picture and to express my ideas coherently. As well as being a brilliant and inspirational scientist, Alex's positivity and genuine kindness is always uplifting; I am extremely grateful for his support and guidance throughout my PhD journey. I would also like to thank my secondary supervisors, Martin Stevens and Andy Radford, for their valuable advice and insights on experimental design and analysis, as well as during my write-up.

As well as having a brilliant supervisory team, I have been lucky enough to be part of a wonderful, collaborative research group. I would like to thank all the members of the Cornish Jackdaw Project, both past and present, without whose dedication and hard work this thesis would not exist. Special thanks go first and foremost to the inimitable Guill McIvor, for helping me go from being unable to climb a ladder, to becoming a fully-fledged jackdaw Jedi. Guill's hard work managing the team and ringing thousands of jackdaws is central to keeping such a unique and special project running so well. I owe more to Guill than will fit on this page, but suffice to say that his dedication, wealth of knowledge and unfailing good humour have made my PhD journey both infinitely smoother and hugely enjoyable. I would also like to thank Rich Woods, Mike Kings, Alison Greggor and Gabrielle Davidson for their valuable advice and support at various

stages throughout my PhD. Noémie Régli and Max Lauvergeon spent long hours in all weathers collecting data for this thesis as part of their Masters projects, for which I am immensely grateful. I am also grateful to Robin Joy, Lewis Flintham, Beki Hooper and Joe Wilde for their assistance with video coding, and the many students and volunteers who helped record vocalisations and collect life history data.

There are many wonderful people who allowed me to run some very strange experiments on their land. I am eternally grateful to Paul Gluyas and family, and all the staff at Pencoose, who very kindly allowed me to use their farm as a study site. It has been a joy and a privilege to work alongside such lovely people, who always brighten my day with a wave, a smile or a chat, no matter how busy they are. Similarly, I would like to thank Odette Eddy, Stithians Church and the people of Stithians for their patience, understanding and kindness.

Having been at the University of Exeter’s Centre for Ecology and Conservation for nine years, I have seen this supportive community go from strength to strength. Everyone that I have met in the department has been very approachable and always quick to offer advice and assistance. In particular, I would like to thank Tom Houslay for his help with study design and analysis for Chapter 7; Joah Madden at the Centre for Research in Animal Behaviour for his advice on shotgun licences for Chapter 5; and Nick Royle and Andy McGowan for encouraging me to do a PhD in the first place. I feel very fortunate to be part of a thriving community of PhD students and postdocs, and I am very grateful for their support and friendship. I would especially like to thank the ever-growing group of people affiliated with the Tremough House office, for countless lunches, beach barbeques and cheese-and-wine nights, as well as careers advice, stats chat and emotional support.

Most important of all, I would like to thank my family for supporting me every step of the way, and for always encouraging me to do what I love – I could not be more grateful. I am also incredibly lucky to have a wonderful ‘Falmouth family’ in the form of Alexandra Gardner, Emma Inzani, Cally Ham, Mike Collins, Lindsay Leyden, Kyle Wotton and Kelly Astley. They have been a huge source of support, along with Verity Jones, who was always happy to take off on a micro-adventure at short notice.

Finally, I would like the thank the jackdaws. Over the last few years, I have spent thousands of hours observing the daily lives of these fascinating birds, and I would happily sit in my birdwatching hide with a packet of chocolate biscuits and do it all again.

# Declaration

All work contained in this thesis was carried out under supervision of Dr Alex Thornton (University of Exeter), Professor Martin Stevens (University of Exeter) and Professor Andy Radford (University of Bristol). No part of this thesis has previously been submitted for any qualification. All work is my own, apart from what is specified below:

**Chapter 3:** Vocalisations used in playbacks were previously collected by students and volunteers on the Cornish Jackdaw Project, under supervision of Guill McIvor. Richard Woods and Guill McIvor provided advice on experimental design; Robin Joy acted as an independent video coder; and Guill McIvor provided feedback on a final draft of the submitted manuscript. Field sites and study populations were maintained by Guill McIvor.

**Chapter 4:** Vocalisations used in playbacks were previously collected by students and volunteers on the Cornish Jackdaw Project, under supervision of Guill McIvor. Richard Woods and Guill McIvor provided advice on experimental design and Lewis Flintham acted as an independent video coder. Field sites and study populations were maintained by Guill McIvor. Guill McIvor provided feedback on a final draft of the published manuscript, which also incorporates feedback from two anonymous reviewers.

**Chapter 5:** Gabrielle Davidson provided advice on experimental design for Experiment 1, and Joah Madden provided guidance on shotgun legislation. Some trials in Experiment 1 were carried out by Guill McIvor, and Joe Wilde acted as an independent video coder. Max Lauvergeon ran the experimental trials for Experiment 2 as part of his Masters project, using a protocol I developed and under supervision from Neeltje Boogert and Alex Thornton. Field sites and study populations were maintained by Guill McIvor.

**Chapter 6:** Noémie Régli assisted with data collection as part of her Masters project. Vocalisations used in playbacks were originally collected by Richard Woods, Jenny Coomes, Charlie Savill and several other students and volunteers. Beki Hooper acted as an independent video coder. Field sites and study populations were maintained by Guill McIvor, and Alison Greggor assisted with ringing the birds involved in the study. Guill McIvor provided feedback on a final draft of the submitted manuscript, which also incorporates feedback from two anonymous reviewers.

**Chapter 7:** Tom Houslay provided advice and guidance on study design and statistical analysis. Guill McIvor and Noémie Régli assisted with data collection in the original experiments, and life history data were collected by students, volunteers and staff at the Cornish Jackdaw Project. Field sites and study populations were maintained by Guill McIvor, and Alison Greggor assisted with ringing the birds involved in the original study.

Photographs are used with permission of Richard Woods, Jenny Coomes and the Cornish Jackdaw Project.

Note: Because each chapter is written as a stand-alone piece of work, there is some repetition in methods and descriptions of study sites.

# Publication List

**Chapters 1 & 8** contain material adapted from: *Lee, V. E., Greggor, A. L., Thornton A. Social learning in birds. In: The Cambridge Handbook of Animal Cognition (eds. Kaufman, A., Call, J., Kaufman, J.). In review.*

**Chapter 4** has been adapted from: *Lee, V. E., McIvor, G. E., Thornton, A. 2019 Testing relationship recognition in wild jackdaws (Corvus monedula). Scientific Reports 9 (6710).*

**Chapter 6** has been adapted from: *Lee, V. E., Régli, N., McIvor, G. E., Thornton, A. 2019 Social learning about dangerous people by wild jackdaws. Royal Society Open Science 6 (191031).*

**Chapter 7** contains data from Chapters 5 and 6. Data from Chapter 6 has been published as: *Lee, V. E., Régli, N., McIvor, G. E., Thornton, A. 2019 Social learning about dangerous people by wild jackdaws. Royal Society Open Science 6 (191031).*

# Chapter 1

# Introduction

*This chapter contains material adapted from: Lee, V. E., Greggor, A. L., Thornton A. Social learning in birds. In: The Cambridge Handbook of Animal Cognition (eds. Kaufman, A., Call, J., Kaufman, J.). In review.*

Although human activity has been altering the natural environment for thousands of years, the current rate and scale of anthropogenic change is unprecedented (Barnosky et al., 2012) and humans now have a pervasive influence in almost every ecosystem on the planet (Ellis, 2011; Waters et al., 2016). Human-induced rapid environmental change (HIREC; Sih, Ferrari, & Harris, 2011) continues to have profound effects on the natural environment through habitat conversion, overexploitation, climate change, pollution and the spread of invasive species (Ceballos et al., 2015). Understanding whether and how species will cope in an increasingly human-dominated world is vital if we are to mitigate the impacts of anthropogenic activity, conserve biodiversity and retain the delivery of ecosystem services underpinning human wellbeing (Millennium Ecosystem Assessment, 2005). However, species vary extensively in their responses to HIREC: while some show widespread and severe population declines, others appear to thrive in anthropogenic habitats (Sih, 2013; Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Sih et al., 2011). Explaining this variation in outcomes is therefore a major challenge: why do some species do well while others do badly (Sih, 2013)?

Although studying declining and endangered species is clearly of paramount importance (Buchholz & Hanlon, 2012), valuable lessons can also be learned from species that thrive under HIREC. Identifying the factors underlying this success allows us to predict species’ responses to human activity and minimise human-wildlife conflict (Barrett, Stanton, & Benson-Amram, 2018). Among these “urban exploiters”, research is biased towards introduced species and those inhabiting urban areas. Very few studies examine the factors influencing behavioural responses to HIREC in human-dominated habitats more generally; for example, given that agriculture provides an abundance of anthropogenic resources for wildlife, animals exploiting these resources often come into conflict with human interests. Understanding the factors that allow some species to thrive under these conditions may therefore provide vital insights for management and conservation of wildlife in rapidly changing environments.

## 1.1. Behavioural responses to a changing world

Humans can exert extremely strong selective pressures on wildlife (Darimont et al., 2009; Palumbi, 2001). Although human-induced environmental changes act in multiple dimensions, and vary over spatial and temporal scales, all result in novel ecological conditions which may differ from environments experienced in an organism's evolutionary past. This mismatch between the past and current environment has potential fitness consequences for individuals, with implications for population persistence, community composition and ecosystem function (Sih et al., 2011; Wong & Candolin, 2015). Behavioural responses can act as an initial, rapid adaptation to HIREC, with responses ranging from changes in foraging and habitat choice to altered reproductive and social behaviour (Sih et al., 2011; Wong & Candolin, 2015). These responses may confer benefits by allowing individuals to utilise novel habitat and food resources provided by human activity: for example, individuals may alter their dispersal behaviour and habitat use to take advantage of supplemental food sources (Baglione, Canestrari, Marcos, & Ekman, 2006). When exploitation of anthropogenic food resources generates human-wildlife conflict, individuals may alter their behaviour in order to mitigate this risk, by increasing social cohesion or modifying activity budgets (Beckmann & Berger, 2003; Duarte, Vecci, Hirsch, & Young, 2011; Hockings, Anderson, & Matsuzawa, 2012; Hockings et al., 2015; Wheat & Wilmers, 2016). As well as the risks posed by humans themselves, HIREC may alter the abundance, distribution and diversity of predators, pathogens and parasites. Behavioural alterations allow individuals to rapidly adjust to these threats: for instance, predator-naïve island songbirds alter nesting and parental care behaviour in response to increases in perceived predation risk (Peluc, Sillett, Rotenberry, & Ghalambor, 2008). Noise, light and chemical pollution resulting from human activity have also been demonstrated to have wide-ranging effects on wildlife (Halfwerk & Slabbekoorn, 2015), and in some cases behavioural responses may help in mitigating these impacts. For example, anthropogenic noise can reduce the efficacy of intraspecific communication, but urban songbirds alter the timing and structure of vocalisations to minimise masking by traffic noise (Slabbekoorn, 2013). Noise may also distract prey and reduce the ability of organisms to assess risk (Chan, Giraldo-Perez, Smith, & Blumstein, 2010): when foraging under high levels of traffic noise, individuals may increase their vigilance behaviour to compensate for this higher predation risk (Quinn, Whittingham, Butler, & Cresswell, 2006; Shannon, Angeloni, Wittemyer, Fristrup, & Crooks, 2014). Finally, behavioural adaptations can allow individuals to cope with altered spatiotemporal conditions, such as a changing climate. Studies have documented advances in egg-laying dates in line with rising temperatures in both birds and amphibians, although whether behavioural plasticity is sufficient to allow species to cope with projected future climate change remains to be seen (Charmantier et al., 2008; Phillimore, Hadfield, Jones, & Smithers, 2012).

Although there is no definitive list of attributes that confer benefits to organisms inhabiting human-dominated environments (Sih et al., 2011), a number of candidate traits have been identified. Among these traits, behaviour has been shown to play an important role alongside ecological and life history variables such as habitat and dietary generalism (Evans, Chamberlain, Hatchwell, Gregory, & Gaston, 2011; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005). In particular, a tendency to form social groups, greater within-population variation in behaviour, a high degree of behavioural plasticity and sophisticated cognitive abilities may be beneficial when adapting to novel conditions (Sih et al., 2011).

## 1.2. Cognition in changing environments

Altering behaviour in response to changing environmental conditions is likely to be facilitated by an enhanced ability to acquire, store and process information (Shettleworth, 2010). Cognitive processes, such as learning and memory, may be useful when environmental conditions change (Sol, 2009). However, developing and maintaining the neural architecture associated with these abilities is energetically costly (Kotrschal et al., 2013; Laughlin, de Ruyter van Steveninck, & Anderson, 1998; Navarrete, van Schaik, & Isler, 2011). As a result, cognitive abilities vary substantially between species, and considerable research effort has been dedicated to identifying the selective pressures driving this variation (e.g. Dunbar & Shultz, 2007; Emery, Seed, von Bayern, & Clayton, 2007; Rosati, 2017; Sol, 2009). There are several potential explanations as to why some species have much larger brains than expected for their body size, with the common theme that enhanced cognitive abilities confer benefits under ecological or social change.

### *1.2.1. Tracking the physical environment*

It has long been argued that enhanced cognitive abilities allow individuals to meet ecological demands, such as finding food. In this way, cognitive abilities such as learning and memory may ‘buffer’ individuals from the impacts of changing resource availability (Sol, 2009). Several lines of evidence lend support to ecological explanations for the evolution of enhanced cognition (reviewed in Ashton, Thornton, & Ridley, 2018; Rosati, 2017; Sol, 2009). For example, cognitive abilities may allow individuals to remember spatiotemporal locations of food. Among primates, increased relative brain size is associated with a frugivorous diet (DeCasien, Williams, & Higham, 2017); in birds, food caching is associated with enhanced spatial memory and hippocampal volume (e.g. Croston et al., 2016). Comparative studies have also shown that bird and mammal species with larger relative brain size have higher survival and establishment rates when introduced to novel environments (Sol, Bacher, Reader, & Lefebvre, 2008; Sol et al., 2005; but see Dale, Lifjeld, & Rowe, 2015). Empirical evidence of the relationship between environmental variability and cognition can be seen among mockingbird species (*Mimidae*): song complexity, as a putative proxy of cognitive ability, is higher in species living in habitats with increased climatic unpredictability (Botero, Boogert, Vehrencamp, & Lovette, 2009). Captive studies of cichlid fish (*Simochromis pleurospilus*) also show that individuals experiencing a 'switch' in early life conditions (food availability) later performed better in a learning task compared to individuals that experienced a stable environment. This effect was independent of the direction of the 'switch' (i.e. from high-low or low-high food availability) and persisted into adult life, suggesting that environmental variability acts as a signal to trigger increased cognitive development (Kotrschal & Taborsky, 2010). These results suggest that anthropogenic change may select for increased cognitive abilities (Kotrschal & Taborsky, 2010).  In theory, complex feedbacks may be created where ecological conditions selecting for improved learning and other cognitive traits increase the amount of 'realised' environmental variation that an individual is exposed to, by enhancing exploration and survival in a wider range of habitats. This ‘realised’ environmental variation then drives further selection for learning, cognition and behavioural plasticity, where feedbacks may only be limited by the relative costs of this plasticity (Snell-Rood, 2013).

### *1.2.2. Tracking the social environment*

For group-living species, individuals’ social environments may change rapidly, exerting selective pressures in addition to those of the physical environment (Shultz & Dunbar, 2007). The Social Intelligence Hypothesis posits that the demands of a complex social environment drive the evolution of cognition: for example, individuals may need to maintain social bonds, track third-party relationships and anticipate the actions of others, which may be cognitively demanding (Humphrey, 1976; Shultz & Dunbar, 2007). For many social species, social learning abilities may be essential in the acquisition and transmission of cultural behaviours (behaviours that are socially acquired and shared by members of a group; reviewed in Brakes et al., 2019). Given that similar cognitive mechanisms may underpin social learning and other learning mechanisms (Heyes, 2012; Mesoudi, Chang, Dall, & Thornton, 2016), selection for social learning may also enhance asocial learning and problem-solving skills (known as 'cultural intelligence'; Forss, Willems, Call, & van Schaik, 2016; van Schaik & Burkart, 2011). Comparative support for the Social Intelligence Hypothesis has linked measures of relative brain size and neuroanatomy with various measures of social structure (reviewed in Ashton et al., 2018). For example, relative brain size has been linked to group size in primates (Shultz & Dunbar, 2007) and cetaceans (Fox, Muthukrishna, & Shultz, 2017); whereas among birds, larger relative brain size has been linked to the formation of long-term monogamous pair bonds (Emery et al., 2007; Shultz & Dunbar, 2007). This has led to suggestions that socially monogamous bird species may require a kind of ‘relationship intelligence’, allowing individuals to retain a large amount of information about a relatively small number of high-quality relationships (Emery et al., 2007). Maintaining a strong bond with a breeding partner may confer benefits in terms of increased cooperation and behavioural coordination: according to the Relationship Intelligence Hypothesis, the need to maintain these valuable pair bonds may explain the evolution of large brains in some birds, such as corvids and parrots (Emery et al., 2007). However, the role of cognition in pair bond formation is poorly understood, and the idea of relationship intelligence remains speculative (Shettleworth, 2010). Moreover, many monogamous birds form social relationships beyond the pair bond, (whether affiliative or competitive; e.g. Boucherie et al., 2016, 2017; Braun & Bugnyar, 2012; Fraser & Bugnyar, 2012; Lewis et al., 2007) and these interactions are also likely to carry an informational load. Quantifying the specific cognitive demands associated with different types of social relationships may be key to explaining species differences in cognitive ability.

As well as comparisons between species, intraspecific studies have identified links between cognitive performance, or brain structure and function, with the size of an individual’s social group (Ashton, Ridley, Edwards, & Thornton, 2018; Fischer, Bessert-Nettelbeck, Kotrschal, & Taborsky, 2015; Kanai, Bahrami, Roylance, & Rees, 2012; Sallet et al., 2011). To date, one study has quantified the fitness benefits of these enhanced cognitive abilities in the wild. In Australian magpies (*Cracticus tibicen dorsalis*), performance in a range of cognitive tasks correlated positively with group size; performance in these tasks was also linked to female reproductive success, although the exact mechanism by which cognitive abilities yield these fitness benefits is yet to be established (Ashton, Ridley, et al., 2018).

Whilst ecological and social explanations for cognitive evolution are by no means mutually exclusive (Rosati, 2017), neither types of explanation have received unanimous support (Ashton, Thornton, et al., 2018; Healy & Rowe, 2007; Holekamp, 2007). For comparative studies in particular, the inconsistency in outcomes and high degree of methodological variation has generated much debate as to the general conclusions that can be drawn from these studies (Healy & Rowe, 2007; Holekamp, 2007; Wartel, Lindenfors, & Lind, 2019). Furthermore, that increases in relative brain size translate to changes in behaviour is often assumed and not explicitly tested (Healy & Rowe, 2007; Rosati, 2017); moreover, how these changes in behaviour confer fitness benefits in nature is not always clear (Ashton, Ridley, et al., 2018; Ashton, Thornton, et al., 2018). As a result, relatively little is known about exactly how cognitive abilities allow individuals to cope with the challenges of a changing world. In this thesis, I focus on two specific challenges faced by animals living under HIREC, and how cognitive abilities may allow animals to overcome these challenges. I begin by investigating how cognitive abilities allow individuals to navigate a changing social environment. Secondly, I investigate how cognitive abilities allow individuals to assess risk during encounters with humans.

### 1.3. Social cognition in a changing world

Sociality is often considered among the traits facilitating species persistence under changing environmental conditions (Sih et al., 2011). For instance, group living creates opportunities for social learning, allowing more rapid spread of novel behaviours than would be achieved through individual trial-and-error learning alone (Kendal, Coolen, van Bergen, & Laland, 2005; Laland, 2004). Social learning may therefore play a central role in influencing exploitation of novel resources (Aplin et al., 2015) and avoidance of novel threats (Curio, Ernst, & Vieth, 1978a, 1978b; Feeney & Langmore, 2013; Magrath, Haff, McLachlan, & Igic, 2015). For example, social learning has been implicated in the transmission of behaviours associated with exploiting anthropogenic food in birds and mammals (Aplin, Sheldon, & Morand-Ferron, 2013; Donaldson, Finn, Bejder, Lusseau, & Calver, 2012; Lefebvre, 1995; Schakner, Lunsford, Straley, Eguchi, & Mesnick, 2014) and facilitates the transmission of information about ‘dangerous’ humans among American crows (*Corvus brachyrhynchos;* Cornell, Marzluff, & Pecoraro, 2012). Socially acquired behaviours may spread through groups and persist over the long term, leading to the emergence of group traditions and culture (Whiten, 2017). Although research has yet to demonstrate that culturally-acquired behaviours enhance individual fitness (Aplin, 2018), culture has the potential to facilitate or hinder adaptation to environmental change by enhancing the spread of adaptive (or maladaptive) behaviours through populations (Greggor, Clayton, Phalan, & Thornton, 2014; Greggor, Thornton, & Clayton, 2017; Whiten, 2017).

At the same time, human activity may induce changes in an organism’s social environment, either through temporarily altering associations with conspecifics, or the addition or removal of individuals (Blumstein, 2012; Firth & Sheldon, 2015). For instance, this could involve the dispersal of new individuals to an area, alterations to social structure, or the loss of a mate. This may result in changes to prevailing social relationships, or alter opportunities for social learning (Aplin, Farine, Morand-Ferron, & Sheldon, 2012; Firth, Sheldon, & Farine, 2016). Individuals may modify their social behaviour in order to cope with these changes: for example, the clumped nature of anthropogenic food sources may alter competition dynamics, influencing foraging decisions and group sizes (Hockings et al., 2012). Fragmentation of resources may also influence competition, with potential population-level consequences (López-Sepulcre, Kokko, & Norris, 2010). Studies of wild songbirds show that social segregation caused by food availability in the environment may be carried over into other contexts, even without changes in population size or composition (Firth & Sheldon, 2015). On the other hand, animals may not be able to change their behaviour to cope with the social disruption caused by anthropogenic change. In these cases, human activities may have far-reaching, unexpected and potentially irreversible consequences (Brakes et al., 2019). For example, in long-lived social species such as African elephants (*Loxodonta africana*) and killer whales (*Orcinus orca*), keystone individuals – typically older, more experienced group members - possess vital social knowledge (Brent et al., 2015; McComb, Moss, Durant, Baker, & Sayialel, 2001). Consequently, the loss of these keystone individuals may compromise the survival and reproductive success of entire social groups (Shannon et al., 2013). Whilst these may represent extreme examples, they highlight the important role of socio-cognitive abilities in adapting to social change. Identifying how cognitive abilities such as learning and memory allow social animals to recognise individuals, track relationships and maintain social bonds not only provides crucial insights into social evolution (Wascher, Kulahci, Langley, & Shaw, 2018), but also sheds light on the cognitive challenges that animals may face when social environments change. A fundamental understanding of how different species cognitively represent their social world is therefore vital, both for conservation and the mitigation of human-wildlife conflict (Brakes et al., 2019; Greggor et al., 2014).

## 1.4. Navigating encounters with humans

Although human activity may expose wildlife to novel predators and/or alter the abundance of natural predators, humans themselves can also be a considerable threat (Frid & Dill, 2002). In addition to direct threats from harvesting and persecution, wildlife may experience frequent disturbance by humans. In these non-lethal scenarios, failing to respond appropriately during encounters with people may result in fitness losses and compromise population persistence (Frid & Dill, 2002). For instance, consistently fleeing in response to frequent (but benign) human disturbance may impact foraging activities and provision of parental care (Fernández & Azkona, 1993; Smith, Wang, & Wilmers, 2015; Thomas, Kvitek, & Bretz, 2002; Verhulst, Oosterbeek, & Ens, 2001). On the other hand, failing to flee from ‘dangerous’ people may also be detrimental (Bremner-Harrison, Prodohl, & Elwood, 2004). This may be particularly important for species targeted as pests as a result of their successful exploitation of anthropogenic habitats: in these cases, people may differ in their responses to wildlife, with some people providing resources (e.g. supplemental food) whilst others represent a genuine threat (e.g. hunters).

Fear and tolerance of humans can be learned, and therefore individuals that are able to discriminate between threatening and nonthreatening stimuli, remember relevant cues and apply previous experience in novel situations are more likely to respond appropriately (Sih et al., 2011). In environments where wildlife coexists alongside human activity, we may expect strong selection on cognitive abilities such as learning and memory. For example, many urban birds modify their response to individual humans based on prior learning, or subtle cues such as gaze direction (Bugnyar, Stowe, & Heinrich, 2004; Clucas, Marzluff, Mackovjak, & Palmquist, 2013; Davidson, Clayton, & Thornton, 2015; Goumas, Burns, Kelley, & Boogert, 2019; Lee, Lee, Choe, & Jablonski, 2011; Levey et al., 2009; Marzluff, Walls, Cornell, Withey, & Craig, 2010; von Bayern & Emery, 2009). Studies of American crows (*C. brachyrhynchos*) and Eurasian jackdaws (*Corvus monedula*) have demonstrated that these birds recognise individual people based on facial cues (Davidson et al., 2015; Marzluff et al., 2010), although the extent to which other human-associated cues inform risk assessment is poorly understood.

### *1.4.1. Social learning about dangerous people*

For group-living species, social learning may provide a mechanism by which information about threats can be rapidly transmitted through groups, reducing the need for costly individual encounters (Griffin, 2004). For example, birds will use conspecific cues to identify novel predators (Curio et al., 1978a, 1978b; Griffin, 2008; Griffin & Galef, 2005) and brood parasites (Davies & Wellbergen, 2009; Feeney & Langmore, 2013), and will even learn to associate the alarm calls of heterospecifics with the presence of a predator (Magrath et al., 2015; Potvin, Ratnayake, Radford, & Magrath, 2018). Although there is some evidence that organisms use social information to associate people with a dangerous place or event (Griffin & Boyce, 2009; Griffin & Haythorpe, 2011), only one study has demonstrated that information about dangerous people can be socially transmitted through groups. Wild American crows (*C. brachyrhynchos*) mob specific people that have previously captured them, or people that they have previously seen capturing other crows; this behaviour appears to spread to other birds not present at the initial capture event, and from parents to their offspring (Cornell et al., 2012). In this study, information about dangerous people was experimentally seeded during natural mobs: whilst these mobbing events are likely to have created significant opportunities for social learning, the exact mechanism by which social transmission occurs remain unclear. Moreover, for many animals such large-scale mobbing of dangerous people is likely to be infrequent because of the substantial costs (in terms of time, energy and risk; Dugatkin & Godin, 1992) associated with approaching a potential threat. More commonly, individuals will be exposed to a short-lived bout of conspecific alarm calling; it remains to be seen whether these events provide sufficient information for social learning to occur.

Using social learning over individual learning may not always be advantageous, if the information obtained from others is incorrect or out of date (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005). Consequently, individuals are expected to employ social learning strategies in deciding when, how and from whom to learn (Laland, 2004). For example, individuals are predicted to favour social over personal information when individual information is costly to obtain (e.g. Seppänen & Forsman, 2007; Templeton & Giraldeau, 1996). Conversely, social information may be less reliable if environmental conditions fluctuate rapidly, in which case individuals are expected to favour personal information when making decisions (Galef & Whiskin, 2004; Heinen & Stephens, 2016; Toelch et al., 2009; Wilkinson & Boughman, 1999). Alternatively, individuals may choose to learn from particular conspecifics when gathering social information (Coussi-Korbel & Fragaszy, 1995; Laland, 2004); when learning about danger, individuals may preferentially attend to information from familiar conspecifics if they possess more locally relevant knowledge about predation risk (e.g. Kavaliers, Colwell, & Choleris, 2005). Given that relatively little is known about how animals assess risk during encounters with people, further research investigating how information about dangerous people is obtained, applied and transmitted through populations is vital to predicting species variation in responses to human disturbance.

## 1.5. The importance of individual differences

Although there is considerable interest in investigating species differences in response to HIREC, intra-specific differences in behaviour may also play a vital role in influencing persistence in human-altered environments (Dingemanse, Both, Drent, & Tinbergen, 2004; Sih et al., 2012, 2011). Indeed, it has been suggested that species with higher inter-individual variation in behaviour may fare comparatively better under changing environmental conditions: the greater the range of behavioural phenotypes present at the population level, the greater the range of environmental conditions the population is able to cope with, thereby reducing the risk of local extinction (Sih et al., 2012). For example, if individuals differ in their behaviour or probability of success, larger populations may be more likely to contain individuals with the skills or previous experience required to solve novel problems (the ‘pool of competence’ hypothesis; Giraldeau, 1984; Morand-Ferron & Quinn, 2011).

Consistent inter-individual differences in behaviour (‘personality’) may also influence responses to human activity (Lapiedra, Chejanovski, & Kolbe, 2017; Sih et al., 2012). For example, individual differences in risk-taking behaviour may influence willingness to explore novel environments (Breck, Poessel, Mahoney, & Young, 2019; Kozlovsky, Weissgerber, & Pravosudov, 2017; Lapiedra et al., 2017; Sol, Griffin, Bartomeus, & Boyce, 2011; Thompson, Evans, Parsons, & Morand-Ferron, 2018), responses to threats (Evans, Boudreau, & Hyman, 2010; Schoener, Losos, Kolbe, Lapiedra, & Leal, 2018; Short & Petren, 2008) and aggression towards conspecifics (Duckworth &

Badyaev, 2007; Evans et al., 2010; Hardman & Dalesman, 2018); behaviours which may be correlated to form a behavioural syndrome (Adriaenssens & Johnsson, 2013; Dingemanse et al., 2004; Schoener et al., 2018; Sih, Bell, Johnson, & Ziemba, 2004). Although many studies have sought to link personality variation with survival or reproductive success (Dingemanse & Wolf, 2010; Réale, Dingemanse, Kazem, & Wright, 2010; Smith & Blumstein, 2008), few studies have investigated how personality variation influences fitness in human-altered habitats. Specifically, few studies have sought to identify how individual differences shape responses to human disturbance (Bonnot et al., 2015; Carrete & Tella, 2010, 2013; Martin & Réale, 2008; Runyan & Blumstein, 2004), and how these individual differences influence reproductive success (Ciuti et al., 2012; Greenberg & Holekamp, 2017).

### *1.5.1. Animal personality and cognition*

Individual differences in personality (including risk-taking behaviour) may influence the ways in which individuals acquire, store and process information from the environment. This in turn can influence learning and problem-solving performance, independent of an individual's actual cognitive ability (Sih & Del Giudice, 2012). For example, proactive individuals that are bolder and more exploratory may spend less time sampling the environment or be less cautious in their decision-making processes, in comparison with more reactive individuals (Sih & Del Giudice, 2012; but see Dougherty & Guillette, 2018). Although there is some support for the idea that an individual's personality may influence their 'cognitive style' (and vice versa), these relationships are not consistent across species (Dougherty & Guillette, 2018). Further, the interplay between personality and cognition may also vary between populations of the same species, and within the same population over time (e.g. Dalesman, 2018).

Investigating the causes and consequences of inter-individual differences in cognitive performance is receiving increasing attention, given the potential consequences for evolutionary processes (Boogert, Madden, Morand-Ferron, & Thornton, 2018). Moreover, if individuals differ in their responses to stimuli, these effects may have important implications for the design and interpretation of cognitive experiments (Thornton & Lukas, 2012). Until very recently, the field of animal cognition has tended to consider individual differences as ‘noise’ to be accounted for, and these differences have rarely been investigated explicitly (Boogert et al., 2018; Cauchoix et al., 2018; Griffin, Guillette, & Healy, 2015). In the limited number of studies quantifying individual cognitive differences to date, the majority have focused on performance in cognitive tasks or psychometric test batteries (Cauchoix et al., 2018). As a result, the effects of individual differences on performance in other types of cognitive experiments, including responses to novel threats, remains poorly understood.

## 1.6. Cognition and environmental change in jackdaws

In this thesis, I investigate how behavioural flexibility and cognitive abilities allow jackdaws, highly social members of the corvid family, to cope with the challenges of living in human-altered environments. Specifically, I ask:

- How does social cognition allow individuals to track changing social environments? (Chapters 3 and 4)
- How do cognitive abilities assist in informing behavioural responses to humans? (Chapters 5 and 6)
- How do individual differences in behaviour contribute to success in changing environments? (Chapter 7)

### *1.6.1. The Eurasian jackdaw (Corvus monedula)*

Jackdaws present an ideal model system in which to address how cognitive abilities facilitate success under human-induced rapid environmental change. Like many other members of the corvid family, jackdaws appear to thrive under HIREC by taking advantage of the abundant resources provided by human activity, including food and breeding sites. As a result, jackdaw populations have grown across most of their range: in the UK, for example, populations are estimated to have increased by 55% over a 20-year period (Gregory & Marchant, 1996; Harris et al., 2018). Although their high degree of habitat generalism (Holyoak, 1968; Lockie, 1956) is likely to have contributed in this regard, their cognitive abilities may also play an important role (Emery & Clayton, 2004; Sol et al., 2005). For instance, jackdaws readily discriminate between stimuli and learn cue associations; abilities that are likely to be useful in navigating both the physical and social aspects of their environment (Coomes, McIvor, & Thornton, 2019; Davidson et al., 2015; Greggor, McIvor, Clayton, & Thornton, 2018; Mikolasch, Kotrschal, & Schloegl, 2013; von Bayern & Emery, 2009; Woods, Kings, McIvor, & Thornton, 2018; Zandberg, Jolles, Boogert, & Thornton, 2014). Collectively, corvids have become a major focus of cognitive research in recent years; along with parrots, corvids have large brains in relation to their body size, containing large numbers of densely packed neurons, which may support their complex behavioural repertoire (Emery, 2006; Emery & Clayton, 2004; Olkowicz et al., 2016). Indeed, the performance of corvids has been shown to rival that of apes in several cognitive tasks including episodic memory, causal reasoning, and social cognition (Bugnyar, 2013; Emery & Clayton, 2004; Güntürkün & Bugnyar, 2016).

These cognitive abilities may allow jackdaws to navigate an ever-changing social environment. In jackdaw society, long-term monogamous pair bonds form the basic social unit: these bonds often persist throughout adult life (Henderson, Hart, & Burke, 2000) and are vital for reproductive success as both parents cooperate to raise young (Henderson & Hart, 1993; Röell, 1978). Breeding pairs form colonies that are often stable over time and characterised by a dominance hierarchy, with pair-bonded birds working together to defend a nest site (Röell, 1978; Verhulst & Salomons, 2004; Wechsler, 1988). Outside the breeding season, pairs join mixed-species flocks with rooks (*Corvus frugilegus*) that may contain thousands of other individuals (Jolles, King, Manica, & Thornton, 2013). Under these fission-fusion social dynamics, socio-cognitive abilities that allow individuals to navigate this complex social world are likely to be favoured by selection. For instance, it may pay individuals to remember a large amount of information about their breeding partner, in order to coordinate biparental care (Henderson & Hart, 1993) and recognise their partner in a large flock (Jolles, King, et al., 2013; Ling et al., 2019). As maintaining a strong pair bond is essential for fitness, jackdaws are ideal candidates for testing the pre-requisites of relationship intelligence (Emery et al., 2007). Moreover, jackdaws live in fission-fusion societies where the composition of breeding colonies is relatively stable over time. This may present individuals with socio-cognitive challenges beyond the pair bond: for example, it may be advantageous to recognise other colony members and track third-party relationships in order to minimise conflict with more dominant individuals (Verhulst & Salomons, 2004).

Secondly, jackdaws' cognitive abilities may help them to cope with the challenges of living alongside humans. Jackdaws are widespread in urban areas and on agricultural land: in the UK, this has contributed to their status as vermin, with lethal control authorised under licence (Wildlife and Countryside Act, 1981). Many corvid species, including jackdaws, are also frequently persecuted as a 'general nuisance': as a group, these birds are perceived poorly (Cox & Gaston, 2015), partly due to their often exaggerated reputation as voracious nest predators (Madden, Arroyo, & Amar, 2015; Newson, Rexstad, Baillie, Buckland, & Aebischer, 2010; White, Stoate, Szczur, & Norris, 2014) and as cultural 'harbingers of death' in myths and legends across Europe (Marzluff & Angell, 2005, p.6). As a result of this divided public opinion, jackdaws face the challenge of discriminating between 'dangerous' and non-threatening people. Cognitive abilities may therefore help jackdaws to avoid threats whilst taking advantage of anthropogenic resources. Like many corvids (Bugnyar et al., 2004; Clucas et al., 2013; Lee et al., 2011; Marzluff et al., 2010), jackdaws show remarkable discrimination and learning abilities when assessing risk from individual people (Davidson et al., 2015; von Bayern & Emery, 2009). Positron emission tomography has revealed how these anthropogenic threats are represented in the corvid brain where encounters with dangerous people, unlike encounters with natural predators, induce activity in brain regions devoted to learning and spatial memory (such as the amygdala and hippocampus; Cross et al., 2013). Moreover, distinct neural circuitry also underlies corvids' representation of individual humans, depending on whether people have been previously associated with danger or reward (Marzluff, Miyaoka, Minoshima, & Cross, 2012). Most corvids, including jackdaws, are also proficient social learners (Bugnyar, 2013; Emery, 2006; Emery & Clayton, 2004; Greggor, McIvor, Clayton, & Thornton, 2016) and there is some compelling evidence to suggest that cultural transmission of human-related threats occurs in wild populations of American crows (*C. brachyrhynchos;*

Cornell et al., 2012), although this possibility has yet to be tested in other corvid species.

### *1.6.2. Studying animal cognition in the wild*

Both behaviour and the underlying cognitive abilities are the products of an organism's evolutionary and developmental environment and although behaviour is often studied under natural conditions, cognitive studies are often conducted in laboratory settings (Pritchard, Hurly, Tello-Ramos, & Healy, 2016). Whilst the laboratory provides a highly controlled environment in which to conduct cognitive experiments and disentangle multiple competing factors influencing observed behaviour, it is also essential to corroborate these findings with data collected from wild animals. For studies of cognition in particular, there is an urgent need for further research in a field context, where trade-offs exist (between processes such as foraging, social interactions and predator avoidance) and observed behavioural responses are more likely to be representative of real-world cognitive abilities (Pritchard et al., 2016; Thornton, Clayton, & Grodzinski, 2012). Conducting robust cognitive experiments under natural conditions requires long-term data from known individuals, in order to minimise psuedoreplication and allow the consistency of behavioural responses to be quantified over time and/or across contexts (Blumstein, 2015; Buchholz & Hanlon, 2012). The experiments carried out as part of this thesis were conducted using entirely free-living jackdaw populations, where individuals are colour-ringed and closely monitored to obtain information on social relationships.  An extensive life history dataset also allows for links to be drawn between behaviour and multiple measures of fitness over individual lifetimes.

## 1.7. Thesis structure

I begin in Chapter 2 by introducing the study system, providing general information about study sites and data collection protocols. This chapter sets the scene for the five data chapters which follow, as outlined in Table 1.1 below.

| Theme | Chapter | Research Questions |
|---|---|---|
| How do cognitive abilities allow jackdaws to navigate a changing social environment? | 3 | • Do jackdaws recognise the contact calls of conspecifics? |
| | 4 | • Do jackdaws track changes in social relationships? |
| How do cognitive abilities allow jackdaws to cope with the challenges of living alongside people? | 5 | • Do jackdaws assess risk from humans based on objects being carried? |
| | 6 | • Do jackdaws learn socially about dangerous people?<br>• Do jackdaws preferentially learn from familiar conspecifics? |
| How do individual differences in behaviour influence responses to human disturbance? | 7 | • Do jackdaws show consistent individual differences in risk-taking behaviour during encounters with humans?<br>• Does risk-taking during encounters with humans predict reproductive success? |

Table 1.1: Structure and themes of data chapters

The data chapters begin by addressing how socio-cognitive abilities allow jackdaws to track changes in their social environment. For jackdaws, recognising social companions is likely to be beneficial in mediating social interactions and is a fundamental prerequisite for relationship intelligence (Emery et al., 2007). Whilst corvids are considered likely candidates for exhibiting relationship intelligence (Emery et al., 2007), it is unknown whether these birds recognise their breeding partner under natural conditions. In Chapter 3, I investigate whether female jackdaws individually recognise the contact calls of their breeding partner. As partner recognition is likely to be crucial in this species (e.g. for coordination of biparental care and locating partners in a flock), identifying the mechanisms by which recognition occurs provides insights into the cognitive demands of maintaining pair bonds (Emery et al., 2007). True individual recognition involves integrating cues with information from previous interactions with the signaller, and is considered to be a more cognitively demanding process than discriminating cues based on the category to which the signaller belongs (e.g. familiar versus unfamiliar, kin versus non-kin; Tibbetts & Dale, 2007). Given that jackdaws frequently encounter other familiar colony members, in addition to their breeding partner, category-level discrimination based on familiarity is unlikely to be sufficient for accurate mate recognition in this context. The fission-fusion social dynamics of this species may also favour vocal discrimination abilities that extend beyond the pair bond (Kondo & Watanabe, 2009), allowing individuals to navigate a changing social environment. Therefore, I also investigate whether female jackdaws discriminate between familiar and unfamiliar conspecifics on the basis of contact calls.

In addition to recognising conspecifics, it may also pay individuals to track changes in existing social relationships within the group (e.g. during dominance interactions; Verhulst & Salomons, 2004). Although this ability has been widely demonstrated in primates (see Chapter 4 for a review), evidence for third-party relationship recognition in other species remains limited, despite many animals living in structured societies where it is likely to be valuable (Holekamp, Sakai, & Lundrigan, 2007). Furthermore, few experimental studies test relationship recognition under natural conditions, where multiple stimuli compete for individual attention (Cheney & Seyfarth, 2008; Pritchard et al., 2016; Thornton & Lukas, 2012). In Chapter 4, I use a violation-of-expectation paradigm to test whether female jackdaws respond to simulated changes in their own social relationships, and the relationships of other familiar individuals in the breeding colony.

In the second part of the thesis, I address how jackdaws' cognitive abilities influence decision-making during encounters with people. Corvids are renowned for their remarkable discrimination and learning abilities when assessing anthropogenic threats: for example, it is widely reported that corvids flee more readily from a person holding a shotgun than a person holding a similar but harmless object, such as a walking stick (Creagh, 2011; Forgrave, 2015; Marzluff & Angell, 2005, 2012). Despite the apparent popularity of this anecdote, the idea that corvids identify 'dangerous' people based on the objects being carried has never been explicitly tested. In Chapter 5, I sought to test this preconception by presenting jackdaws with people carrying guns and wooden sticks in two different contexts. If jackdaws integrate information about such objects when assessing risk, this may provide a powerful mechanism by which jackdaws avoid danger whilst continuing to exploit anthropogenic resources.

Although jackdaws have been shown to recognise individual people based on prior learning (Davidson et al., 2015), learning from others may allow jackdaws to identify 'dangerous' people without the need for potentially costly personal encounters. In Chapter 6, I investigate this possibility by determining whether jackdaws alter their behaviour towards an unfamiliar person depending on social information provided by conspecifics. In the only other study to investigate whether wild animals learn socially about anthropogenic threats, social information about dangerous people was experimentally seeded during natural mobbing events (Cornell et al., 2012). By providing specific individuals with a consistent, highly controlled social learning opportunity, I investigate whether short-lived, commonly occurring alarm calling events are sufficient to alter the responses of individual animals during encounters with individual people (see Chapter 6 for detailed discussion). By varying the identity of conspecifics providing this social information, I also assess whether jackdaws attend more to social information provided by familiar individuals possessing more locally relevant knowledge about danger (Coussi-Korbel & Fragaszy, 1995; Laland, 2004).

For jackdaws living in human-altered habitats, individual differences in tolerance of human disturbance may influence the ability of birds to forage efficiently (Smith et al., 2015; Thomas et al., 2002) and provide adequate parental care (Fernández & Azkona, 1993; Verhulst et al., 2001). Whilst a handful of studies have quantified how individual animals vary in their responses to encounters with people (Bonnot et al., 2015; Carrete & Tella, 2010, 2013; Martin & Réale, 2008; Runyan & Blumstein, 2004), very few studies have investigated how this variation influences survival and reproductive success (Ciuti et al., 2012; Greenberg & Holekamp, 2017). In Chapter 7, I use data gleaned from the field experiments conducted in Chapters 5 and 6 to quantify the individual consistency of jackdaws' responses to human presence near the nest, using a fitness-relevant behavioural measure. I then investigate potential links between these individual behavioural differences and reproductive success, in order to determine whether individual differences in tolerance of people influences breeding success in habitats characterised by frequent human disturbance.

Finally, in Chapter 8, I synthesise my findings, highlight avenues for future research and draw conclusions about how jackdaws' cognitive abilities allow these birds to thrive in a rapidly changing world.

# Chapter 2

# General Methods

## 2.1. Study species

The Eurasian jackdaw (*Corvus monedula*) is a small-bodied (<280g), highly social member of the corvid family. Commonly found throughout Europe and Western Asia, population numbers are stable across Europe (BirdLife International, 2018) with increases seen in the UK in recent decades (Gregory & Marchant, 1996; Harris et al., 2018). Reflecting their classification as being of “Least Concern” by the IUCN Red List of Threatened Species (BirdLife International, 2018), sport hunting of jackdaws is permitted in some areas of their range and in the UK, culling of jackdaws is permitted in the interests of agriculture and public health (Wildlife and Countryside Act, 1981).

Jackdaws exploit a wide range of habitats including grassland, forest, coastal and urban areas (BirdLife International, 2018). This may be partly due to jackdaws’ high degree of dietary generalism, with seeds, grain and insects comprising a larger part of the diet in farmland areas (Holyoak, 1968). Current longevity records suggest that jackdaws may live up to 18 years in the wild, although birds tend to live around 5 years on average (Robinson, 2005). Jackdaws reach sexual maturity at two years of age and build nests in cavities found in trees, cliffs and buildings, and take easily to nest boxes. Clutch size varies from 3-8 eggs (BirdLife International, 2018), which are incubated for 20 days; offspring typically fledge 32-33 days after hatching (Robinson, 2005). Due to high rates of nestling mortality (c. 50%), raising young requires a high level of energetically demanding parental investment (Henderson & Hart, 1993).

Jackdaws breed in colonies that remain relatively stable across years (Henderson et al., 2000; Salomons, Dijkstra, & Verhulst, 2007). Bonds between breeding pairs form the primary units of jackdaw society: pair bonds are vital for reproductive success in this species, as mate loss during the nesting season often results in brood failure and/or loss of the nesting site (Röell, 1978). Both males and females invest heavily in pair bond maintenance through allofeeding and other sociopositive behaviours (Kubitza, Bugnyar, & Schwab, 2015). Pairs are thought to be sexually as well as socially monogamous (Henderson et al., 2000): although recent findings have cast doubt on whether extra-pair copulations are as rare in this species as previously thought (Gill, 2016), it has been suggested that the high energetic demands of offspring provisioning may constrain males to social monogamy (Henderson & Hart, 1993).

Beyond the pair bond, jackdaw societies are characterised by dominance hierarchies (Salomons et al., 2007; Verhulst & Salomons, 2004). Dominance status influences the ability of individuals to monopolise foraging opportunities and hold a nest site, with competition over suitable nest sites being particularly intense (Röell, 1978). However, these dominance relationships may be context-dependent: for example, individuals may be more successful in supplanting otherwise dominant competitors when defending their own nest, particularly when they are highly invested in the breeding attempt (Wechsler, 1988). It has also been suggested that the presence of a breeding partner may influence the outcome of dominance interactions (Röell, 1978; Wechsler, 1988). Outside the breeding season, jackdaws form large winter flocks with rooks (*Corvus frugilegus*), which may contain hundreds of birds (Jolles, King, et al., 2013; Ling et al., 2019).

## 2.2. Study system

The data contained in this thesis was collected over four consecutive jackdaw breeding seasons (April-June 2015-2018) from wild jackdaw populations maintained by the Cornish Jackdaw Project (University of Exeter, UK). Founded in 2012, the Cornish Jackdaw Project comprises three nest box populations of jackdaws across three study sites: Pencoose (35 nest boxes centred around an active farmyard; Figure 2.1), Stithians (33 nest boxes in a churchyard and surrounding fields; Figure 2.2) and the University of Exeter's Penryn Campus (11 nest boxes; Figure 2.3).

**Figure 2.1:** Map of Pencoose study site (50°11′56″N, 5°10′9″W) showing locations of nest boxes and feeding tables.

**Figure 2.2:** Map of Stithians study site (50°11′26″N, 5°10′51″W) showing locations of nest boxes and feeding tables.

**Figure 2.3:** Map of study site at University of Exeter Penryn Campus (50º17’32”N; 5º11’96”W) showing locations of nest boxes.

Over 2,000 jackdaws across the three study sites are individually identifiable by colour-rings, including the majority of nest box owners (c. 97% per year). Adult birds are colour-ringed following capture at nest boxes or in ladder traps. On capture, birds are fitted with a metal ring (issued by the British Trust for Ornithology), two colour rings and a third colour ring containing an RFID tag (radio-frequency identification; IB Technology, Leicester, UK). Biometric measures including wing length, tarsus length and body mass are also taken, as well as a sample from central tail feathers. The sex of birds is also determined via molecular sexing analyses using a small blood sample (1µl) taken during ringing. Chicks in nest boxes are colour-ringed and RFID-tagged using an identical protocol, 26 days following hatching of the first chick.

Throughout the nesting period, nest boxes are checked regularly using cameras (mounted inside the nest box or on long poles) to monitor nesting progress and obtain exact lay dates for eggs. Chicks are individually colour marked (using non-toxic marker pens) and weighed after hatching; broods are weighed daily until all chicks have hatched, and then every three days thereafter. After chicks are colour-ringed at 26 days post-hatching, nest boxes are checked daily to ascertain exact fledge dates for each chick in the brood. Survival estimates for juveniles post-fledging are not available, although many birds appear to disperse from the natal colony (colour-ringed individuals have been sighted or recovered up to 10km away from the study sites). On the other hand, many juveniles remain in the natal colony and are recruited to breeding population: from 2013-2019, 33.4% of 305 nest box owners were known to have hatched in a nest box themselves. However, due to the abundance of ‘natural’ nest sites available in the study colonies (in addition to nest boxes), this recruitment estimate is conservative. The fact that a moderate proportion of juveniles are recruited to the breeding population indicates that many colony members are related, although genetic estimates of relatedness are not currently available.

Behavioural experiments on individually marked pairs were carried out during the 2015-2017 breeding seasons. During this time, pairs breeding in nest boxes successfully fledged two chicks on average. In any given year, an average of 46.5% of nest boxes were occupied by the same individuals as the previous year; 34.2% of nest boxes were occupied by new recruits to the colony, and 17.5% of nest boxes were occupied by birds that had nested in a different nest box the previous year.

In each year, 4-6 supplemental feeders fitted with RFID-tag readers were installed at the Stithians and Pencoose sites, to record foraging associations between individual jackdaws and generate social networks (Kings, 2018). At the time of data collection, nest boxes did not include RFID-tag readers. Additional feeding tables are mounted in trees at each of the three study sites (two at Pencoose and Stithians, one at Campus). These feeding tables are baited with a mixture of oats and cheese at regular intervals during the breeding season, and hidden cameras (SJcam M10) used to record dominance interactions. The frequency of aggression and displacement between individuals is quantified, and individual dominance ratings calculated using the randomised Elo-method (Sánchez-Tójar, Schroeder, & Farine, 2018). Dominance interactions are likely to influence foraging opportunities and acquisition of a nest site (Röell, 1978), although studies of free-living populations are limited. Moreover, individuals' relative dominance may be influenced by motivation to defend a given resource (such as a nest site or brood), and the presence of a partner that may provide agonistic support (Röell, 1978; Wechsler, 1988).

## 2.3. Ethics statement

All work was carried out with landowners' permission, and in accordance with the Association for the Study of Animal Behaviour Guidelines for the Use of Animals in Research (Association for the Study of Animal Behaviour, 2012). Approval for all experimental procedures was obtained from the University of Exeter Research Ethics Committee (Chapter 3-4: 2015/974; Chapter 5-7: 2017/1680). Although no birds were directly handled during experiments, bird ringing was carried out under licence from the British Trust for Ornithology (C6449, C5752 and C6079) and the UK Home Office (project licence 30/3261).

# Chapter 3

# Jackdaws individually recognise the contact calls of their mate

## Abstract

In structured social environments, the ability to recognise other group members and integrate individual cues with previous experience is likely to be beneficial in mediating social interactions. Under these conditions, strong selection for individual discrimination and learning of conspecific vocalisations is expected. Recognition may be particularly important in structured societies in which individuals form enduring pair bonds and coordinate biparental care. The Relationship Intelligence Hypothesis posits that the cognitive demands associated with monogamous pair bonding drive the evolution of intelligence in birds: recognition of a breeding partner is therefore a fundamental prerequisite for relationship intelligence. Many corvids, famed for their remarkable cognitive abilities, form long-term pair bonds and are considered ideal subjects for investigating relationship intelligence; however, whether corvids individually recognise their partner under natural conditions remains to be determined. Here, I tested whether wild jackdaws, a colonial corvid, discriminate between the contact calls of individual conspecifics. Incubating females were presented with contact call playbacks from their long-term breeding partner, a male from a neighbouring nest, and an unfamiliar male. Females were quicker to respond to the calls of their partner, providing the first evidence of individual recognition in corvids in the wild.

## 3.1. Introduction

In many animal societies, the ability to recognise individuals is crucial for navigating a changing social world (Tibbetts & Dale, 2007). For example, recognising individual social companions allows group members to avoid conflict by integrating past experience into their current behavioural decision-making (Yorzinski, 2017). Recognition is also a prerequisite for tracking the relationships of others and maintaining valuable social bonds (Emery et al., 2007). The latter may be particularly important for species that cooperate with a long-term partner to raise offspring. Indeed, it has been suggested that the cognitive demands associated with pair bonding may have driven the evolution of large brains and sophisticated cognitive abilities in some bird and mammal species (‘relationship intelligence’; Dunbar and Shultz 2007; Emery et al. 2007). Although comparative studies of brain size provide some support for this idea (Dunbar & Shultz, 2007; Emery et al., 2007), empirical evidence is currently limited and the Relationship Intelligence Hypothesis remains the subject of debate (see Scheiber et al. 2008; Sayol et al. 2016). From insects to mammals, many animals appear to recognise their social companions; but the mechanisms by which this apparent recognition occurs may vary between species (Tibbetts & Dale, 2007). Responses to companions may involve ‘true’ individual recognition - a sophisticated cognitive process by which a receiver integrates unique cues from a signaller with information about identity (Tibbetts & Dale, 2007; Wiley, 2013) – or less specific discrimination based on category-level information about the signaller (Mendelson et al., 2016). Unlike category-level discrimination, where signallers are categorised at a group level (e.g. familiar versus unfamiliar, kin versus non-kin), true individual recognition involves memory of specific, known individuals, allowing recognition of, for instance, a single offspring or a single breeding partner (Tibbetts et al. 2008; Yorzinski 2017; but see Wiley 2013). Although category-level discrimination is widespread across taxa (Tibbetts & Dale, 2007), true individual recognition abilities have thus far only been explicitly demonstrated in a small number of mammals (Adachi, Kuwahata, & Fujita, 2007; Gilfillan, Vitale, McNutt, & McComb, 2016; Kulahci, Drea, Rubenstein, & Ghazanfar, 2014; Proops & McComb, 2012; Proops, McComb, & Reby, 2009; Sharpe, Hill, & Cherry, 2013; Sliwa, Duhamel, Pascalis, & Wirth, 2011; Townsend, Allen, & Manser, 2012) and birds (Berg, Delgado, Okawa, Beissinger, & Bradbury, 2011; Kondo, Izawa, & Watanabe, 2012; Wanker & Jennerjahn, 1998; Warrington, McDonald, & Griffith, 2015; see Yorzinski 2017 for a recent review). In either case, both true individual recognition and category-level discrimination are expected to facilitate social living by allowing individuals to predict the behaviour of others and adjust their own behaviour accordingly (Yorzinski, 2017).

For discrimination to occur, cues must contain a signature that is either unique to the individual (in the case of true individual recognition) or the category to which the individual belongs (for category-level discrimination; Yorzinski 2017). Indeed, studies of mammals (Gustison, le Roux, & Bergman, 2012; McComb & Semple, 2005; Pollard & Blumstein, 2011) and birds (Freeberg, 2006; Kroodsma, 1977) support the hypothesis that living in more complex societies (whether defined by group size, mating system or social structure) is associated with more complex communication systems, in terms of signal repertoire size and/or the amount of social information encoded in these signals (Sewall, 2015). With regards to acoustic cues, vocal individuality allows callers to signal their identity and allows receivers to attend to the calls of more reliable individuals. On the other hand, vocal individuality may also carry costs, by allowing receivers or eavesdroppers to target the caller for social punishment and territory disputes (Tibbetts & Dale, 2007). As a result, vocal signatures and acoustic recognition abilities are expected to evolve in environments where identity signalling is useful (Tibbetts & Dale, 2007; Wiley, 2013). Even in species exhibiting vocal individuality, the nature and extent of this individuality varies: in some cases, vocal individuality is seen in some call types but not others (Charrier, Jouventin, Mathevon, & Aubin, 2001; Rendall, Owren, & Rodman, 1998); in other cases, the distinguishing features of calls may differ between different call types. For example, the alarm and contact barks of chacma baboons (*Papio ursinus*) both show individual characteristics, but patterns of variation are not consistent between call types (Fischer, Hammerschmidt, Cheney, & Seyfarth, 2001).

One type of vocalisation, the contact call, is widely used to advertise identity, coordinate behaviour and maintain group cohesion (Kondo & Watanabe, 2009). In many species, contact calls play a vital role in regulating social organisation: as a result, individual recognition of contact calls may be particularly valuable. Contact calls often encode information about individual identity, and many birds and mammals identify social companions (such as mates, Wanker and Jennerjahn 1998, Berg et al. 2011; kin, Wanker and Jennerjahn 1998, Charrier, Mathevon, et al. 2001; or individuals, Sharpe et al. 2013) based on contact calls. In many cases, category-level discrimination may be sufficient to identify social companions (e.g. discriminating siblings from other familiar individuals, Wanker and Jennerjahn 1998). However, in some cases, where there are numerous familiar conspecifics within a broad category, true individual recognition may be necessary to respond appropriately to specific individuals (e.g. a single mate or parent’s contact calls within a breeding colony: Wanker and Jennerjahn 1998; Charrier, Mathevon, et al. 2001; Berg et al. 2011). Contact call discrimination of bond partners and kin may be particularly valuable for colonial species (Charrier, Mathevon, et al., 2001; Clark, Boersma, & Olmsted, 2006) and those that engage in biparental care (Emery et al., 2007), while contact call discrimination beyond immediate pair or kin bonds allows individuals to navigate relationships that change over time (Kondo & Watanabe, 2009; Sewall, 2015).

In this study, I investigated contact call discrimination in wild jackdaws (*Corvus monedula*), a highly social corvid. Famed for their remarkable cognitive abilities (Emery & Clayton, 2004), corvids provide an ideal system in which to test the assumptions of the relationship intelligence hypothesis (Emery et al., 2007). Many corvids form long-term pair bonds, with pairs working together to acquire resources and raise young (Bugnyar, 2013; Clayton & Emery, 2007; Emery et al., 2007; Jolles, Ostojić, & Clayton, 2013; Röell, 1978): mate recognition is therefore likely to be a vital prerequisite for many of these activities. Several species, including jackdaws, exhibit fission-fusion social dynamics where advertising identity is predicted to be most valuable (Kondo & Watanabe, 2009), and where recognition within and beyond the pair bond is likely to be beneficial e.g. in large flocks (Jolles, King, et al., 2013; Ling et al., 2019) or dominance hierarchies (Kondo and Watanabe 2009; but see Wiley 2013). In support of this, acoustic analyses and playback experiments demonstrate that the calls of many corvid species encode information about individual identity, and that individuals discriminate between conspecific calls (American crow *Corvus brachyrhynchos*, Mates et al. 2015; pinyon jay *Gymnorhinus cyanocephalus,* McArthur 1982; rook *Corvus frugilegus,* Røskaft and Espmark 1984; large-billed crow *Corvus macrorhynchos,* Kondo et al. 2012; Mexican jay *Aphelocoma ultramarina*, Hopp et al. 2001). Previous studies have also shown that the food calls (Zandberg et al., 2014) and alarm calls (Woods et al., 2018) of jackdaws are individually distinct, and that birds respond preferentially to the antipredator recruitment calls of colony members over the calls of unfamiliar individuals (Woods et al., 2018). Alongside these more context-specific calls, contact calls are used widely by adult jackdaws. Contact calls are heard frequently in jackdaw breeding colonies and social foraging groups, and males will often make contact calls when returning to the nest to provision incubating females. Because these calls are used in a range of social contexts, contact calls are a likely cue for advertising identity and mediating social interactions. Given the importance of pair coordination for jackdaws (e.g. during offspring provisioning, Henderson et al. 2000; and collective movement, Ling et al. 2019), contact calls are likely to be used in mate recognition. Furthermore, this mate recognition may involve true individual recognition based on the memory of a specific partner: due to the abundance of other familiar birds in the breeding colony, category-level discrimination is unlikely to be sufficient for accurate mate recognition in this context. However, the function of jackdaw contact calls is still poorly understood: acoustic analyses have identified structural differences in the contact calls of individuals (Stowell, Morfi, & Gill, 2016), but it is unknown whether jackdaws perceive these differences, or how they respond to the contact calls of different conspecifics. Behavioural experiments of corvids to date have focused on discrimination of familiar individuals (Hopp et al., 2001; Kondo et al., 2012; Woods et al., 2018; Zandberg et al., 2014), offspring (McArthur, 1982) or siblings (Røskaft & Espmark, 1984); as such, no studies have tested recognition within the pair bond, or the cues used to do so. Furthermore, although captive large-billed crows (*Corvus macrorhynchos*) have been shown to individually recognise familiar conspecifics (Kondo et al., 2012), true individual recognition among corvids has yet to be tested under natural conditions. As captive populations are often small, with individuals housed in close proximity for extended periods of time, it is possible that subjects may have more opportunity to learn each other's vocalisations; field studies are therefore urgently needed to complement findings from laboratory systems. To address these research gaps, I used playback experiments to investigate the response of free-living female jackdaws to the contact calls of i) their male partner; ii) a familiar male from a neighbouring nest; iii) an unfamiliar male. I predicted that if females discriminate between individuals based on contact calls, subjects would vary in their behavioural response to playbacks depending on the identity of the caller. Given that lower response latencies reflect more efficient processing of familiar stimuli (see Miller et al. 2005; Landi and Freiwald 2017; Ramon and Gobbini 2018), I predicted that: i) females would respond more quickly to the familiar contact calls of their partner that signal the arrival of food, ii) females would show an intermediate response to the contact calls of their familiar neighbour, and iii) females would show longer response latencies for unfamiliar contact calls.. I also predicted that following the initial response, females may show a stronger overall response to the contact calls of unfamiliar individuals (e.g. by leaving the nest box to obtain more information about the potential intruder).

## 3.2. Methods

### 3.2.1. Study Population

This experiment was conducted during the breeding season (2015-2017) using free-living, individually colour-ringed jackdaws nesting in boxes provided by the

Cornish Jackdaw Project (University of Exeter, Cornwall, UK). The Cornish Jackdaw Project comprises three study sites: Stithians (a village churchyard; 50°11′26″N, 5°10′51″W; 33 nest boxes), Pencoose Farm (50°11′56″N, 5°10′9″W; 35 nest boxes) and the University of Exeter’s Penryn campus (50º17’32”N; 5º11’96”W; 11 nest boxes). Due to the close proximity of the Stithians & Pencoose sites (1.5km), some population crossover does occur with birds nesting at one site observed foraging at the other.  For the purposes of this study it was assumed, based on extensive observations, that birds from the Campus site (5km) had no contact with birds from Pencoose and Stithians (*pers. obs.*).

### 3.2.2. Playback Experiments

*Audio Recordings*

Early in the nest-building phase (late March - early April), nest boxes occupied by breeding jackdaws were fitted with CCTV cameras and lapel microphones (AKG-C417PP) concealed behind a panel. For playback experiments, focal nest boxes were selected with at least one colour-ringed individual (to ensure accurate identification of vocalising birds), and close neighbours (in order to ensure that the neighbouring male’s contact call would be an ecologically relevant stimulus for the focal female). Audio recordings were made early in the morning (start time: 0700-0900) during late March and early April, when birds were engaged in nest building or early egg incubation. Video recordings (using JXD 990 digital video recorders) and audio recordings (using Olympus LS-100 & Tascam DR-100MKII PCM recorders) were taken daily as required. Each recording ran for around 3.5 hours, when researcher activity at study sites was at a minimum. Where available, contact call exemplars were also extracted from recordings obtained using an identical protocol during previous seasons (2013-2015).

### *Call extraction*

Clear exemplars of male contact calls with minimal background noise were extracted from nest box audio recordings and normalised for amplitude using Audacity (audacity.sourceforge.net). Extracted calls were arranged into playback files comprising two bouts of three contact calls: within-bout, calls occurred at 2s intervals to simulate natural calling, with a 10s pause between the two call bouts (Supplementary Figure S1). Where possible, playback files contained six different contact calls from each male, with preference given to calls recorded on different days. Where fewer than six male contact calls were available, the number of repeated calls was kept as low as possible and call sequences were modified to ensure that focal females would not hear repeated calls presented in the same order. Each stimulus was 20s in duration (see Supplementary Material), and stimuli were played back once per experimental trial.

Each focal female was assigned three playback files: one containing the contact calls of her partner (‘Partner’ treatment), a second containing contact calls of a male from a neighbouring nest box (‘Neighbour’ treatment) and a third containing contact calls from an unfamiliar male at a different colony (‘Stranger’ treatment). Because of their close geographical proximity and the observed movement of birds between Stithians and Pencoose, only contact calls obtained from Campus were used in the ‘Stranger’ treatments at these sites. Within sites, the distance between focal and neighbouring nest boxes was 30m on average (range: 11-76m), with the same individuals occupying nest boxes for up to three years prior to the experiment. As the jackdaws in the study colonies begin to assert nest box ownership from late February (*unpublished data*), it was deemed likely that focal females would have had sufficient opportunities to learn their neighbours' contact calls before playback trials took place, even in cases where birds had not occupied neighbouring nest boxes in previous years.

### *Experimental Trials*

Playback trials were carried out in late April-early May, when females spend long periods of time inside the nest box incubating eggs (for logistical reasons, only females were tested). Several weeks prior to the experiment, a 'decoy' loudspeaker (plastic bottle wrapped in vegetation) was mounted on a hook adjacent to each focal nest box, to encourage habituation and minimise any neophobic behaviour in response to the loudspeaker itself. On the day of the experiment, decoys were replaced with a remote-controlled loudspeaker (FoxPro Fury 2) wrapped in similar vegetation, using a decorators' pole to minimise disturbance at the nest box.  Video recording equipment was also set up (DVR JXD 990) to record female behaviour inside the nest box. Following setup, the experimenter returned to a concealed location at least 50m away to control the loudspeaker and make additional behavioural observations. To allow birds to return to normal behaviour, a baseline period of at least 20 minutes elapsed between the female's first return to the nest box and presentation of the first playback stimulus. Playbacks only occurred when the focal female was inside the nest box for at least 5 minutes with no disturbance (including male visits). The order in which focal females received each playback treatment was counterbalanced across the experiment, and playback volume simulated natural calling at a distance of 6m (measured using a sound meter from inside a nest box). Playback trials were carried out between 10:00 and 19:00, when males were returning to the nest at regular intervals to provision the incubating female.

### 3.2.3. Video Coding

Video coding was carried out in BORIS (Friard & Gamba, 2016). I recorded the frequency and duration of all behaviours exhibited by the focal female in the two-minute period following each playback presentation. These included looking at the nest box entrance, arranging nest material, peeking out of the nest box entrance and leaving the nest box. All playbacks occurred at least 5 minutes after the last visit by the male; if the male returned to the box in the post-playback period, all female behaviours occurring during and after the male's visit were discounted. In total, I carried out 57 trials at 19 focal nest boxes; two trials were subsequently discounted (one due to camera failure, and one trial where the focal female appeared to be asleep during the playback presentation).

Twenty percent of videos were analysed by a second coder who was blind to treatment. Inter-rater reliability was analysed using the *irr* package in R (Gamer, Lemon, Fellows, & Singh, 2012), and coders showed a high degree of agreement for all behaviours analysed (latency to look at the nest box entrance following playback: ICC=0.95, p<0.001; time spent looking at and peeking out of the nest box entrance in the two minutes following playback: ICC=0.92; p<0.001. In 11/12 cases, coders agreed on the extent of female response to the playback; see 'Behavioural response to playback').

### 3.2.4. Statistical Analyses

All analyses were carried out in R (R Core Team, 2017), with models built using the *lme4* (Bates, Maechler, Bolker, & Walker, 2015) and *ordinal* (Christensen,

2018) packages. Models were simplified using log-likelihood ratio tests, following examination of model plots to ensure assumptions (homogeneity and normality of residuals) were met. Unless otherwise stated, sample sizes for models are comprised of 55 observations from 19 females (see *Video coding*).

### *Latency to look at nest box entrance*

In studies of recognition, the latency of test subjects to respond to stimuli is considered to reflect information processing time, as familiar cues (e.g. faces) are processed more efficiently than unfamiliar stimuli (Landi & Freiwald, 2017; Miller et al., 2005; Ramon & Gobbini, 2018). Here, I expected females to respond rapidly to the contact calls of their own mate, especially as this signals the arrival of food; due to the increased processing time associated with unfamiliar contact calls, I also predicted that females would exhibit the longest response latencies in the ‘Stranger’ treatment. In most cases, females initially responded to playbacks by looking towards the nest box entrance (69%). The latency of females to look towards the nest box entrance was analysed using a linear mixed model (LMM) with a Gaussian error distribution, following box-cox transformation of the response variable. Treatment (Partner, Neighbour or Stranger) and trial number (1-3) were included as fixed effects, and female ID as a random term. Females that did not look towards the nest box entrance in response to the playback were given a maximum score of 60 seconds.

### *Behavioural response to playback*

Although most females initially responded to playbacks by looking at the nest box entrance (LOOK), some individuals subsequently went on to peek out of the nest box entrance (PEEK) or leave the nest box (EXIT). The extent of female response was analysed using a cumulative link mixed model (CLMM) with an ordinal response term (NONE/LOOK/PEEK/EXIT). Treatment (Partner, Neighbour, Stranger) and trial number (1-3) were included as fixed effects, and female ID as a random term. To investigate whether individual identity influenced female response, the mixed model was compared to a cumulative link model (CLM) without the random term (Christensen, 2015).

*Time spent looking and peeking following playback*

The time that females spent looking at or peeking out of the nest box entrance in the two minutes following the start of the playback presentation was analysed using an LMM with a Gaussian error distribution (following box-cox transformation of the response variable). Treatment (Partner, Neighbour, Stranger) and trial number (1-3) were included as fixed effects, and female ID as a random term. This model comprised 54 observations from 19 females (an additional trial was dropped from the analysis as the focal female immediately left the nest box upon hearing the playback).

## 3.3. Results

### 3.3.1. Latency to look at nest box entrance

The identity of the calling male influenced the latency of females to look towards the entrance of the nest box ($X^2$=12.7, df=2, p=0.002; Figure 3.1, Table 3.1). Females were quicker to look towards the entrance following playback of their partner's contact calls (mean±SE: 8.5±4.7s), responding on average twice as fast as to contact call playbacks of neighbouring males and unfamiliar males (mean±SE: neighbour treatment=26.0±6.1s; stranger treatment=20.7±5.7s).

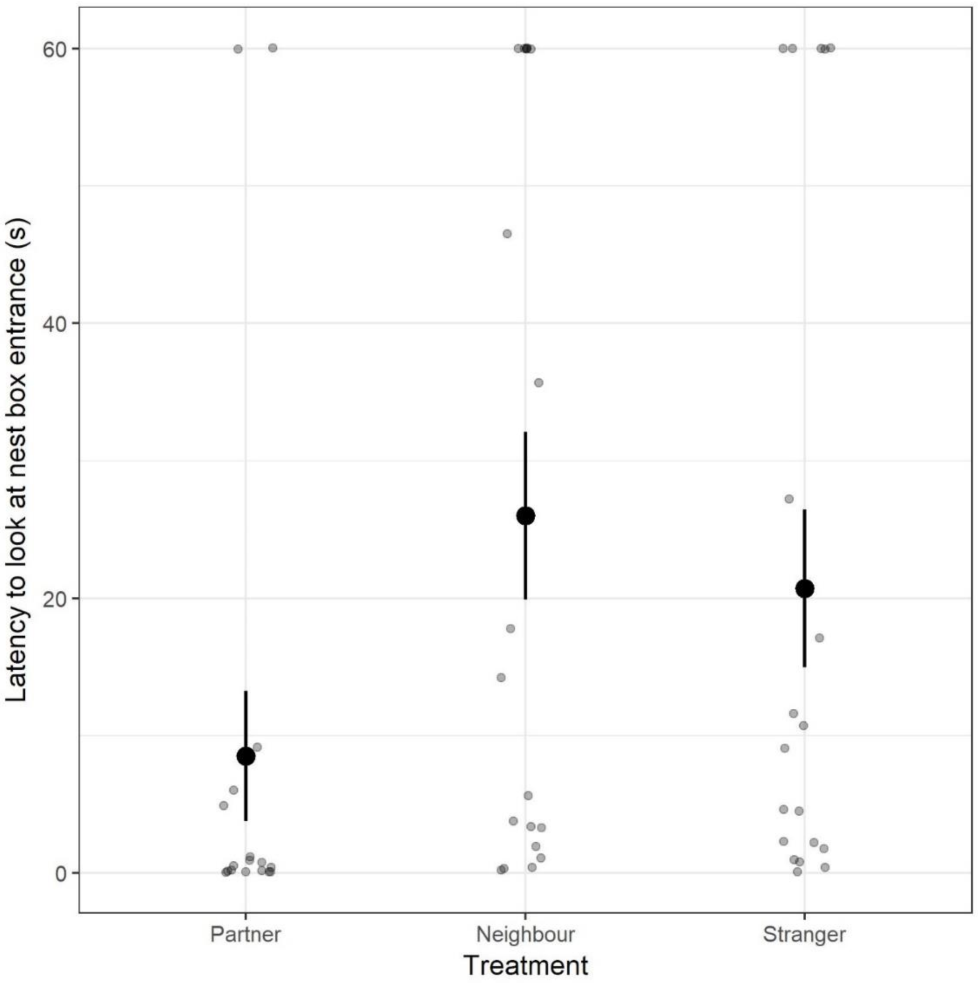


**Figure 3.1:** Latency of focal females to look towards the nest box entrance following playbacks, by treatment group. Grey circles denote individual data points, points and whiskers denote group means and standard error.

**Table 3.1:** Output of GLMM investigating the effect of treatment and trial number on the latency of females to look towards the nest box entrance after playback. Values are derived from full model with significant effects shown in italics (n=55 observations from 19 females).

| **Fixed effects** | | **β** | **SE** | **t-value** |
|---|---|---|---|---|
| Intercept | | 0.35 | 0.89 | 0.39 |
| *Treatment* | *Partner (reference)* | | | |
| | *Neighbour* | *2.35* | *0.67* | *3.50* |
| | *Stranger* | *2.11* | *0.66* | *3.20* |
| Trial number | | -0.18 | 0.33 | -0.53 |
| **Random effects** | | | **Variance** | **SD** |
| Female ID | | | 0.65 | 0.81 |
| Residual | | | 3.85 | 1.96 |

### 3.3.2. Behavioural response to playback

Females responded to playbacks by looking at the nest box entrance (LOOK), peeking out of the nest box entrance from a standing position (PEEK) or leaving the nest box (EXIT) (Figure 3.2a). The likelihood of females exhibiting each of these responses was not influenced by trial number ($X^2$=0.07; df=1; p=0.79; Figure 3.2c, Table 3.2) or the identity of the caller in the playback ($X^2$=2.04; df=2; p=0.36; Figure 3.2b, Table 3.2). The identity of the focal female did not significantly predict subjects' behavioural response to playbacks ($X^2$=1.44; df=1; p=0.23; Table 3.2).

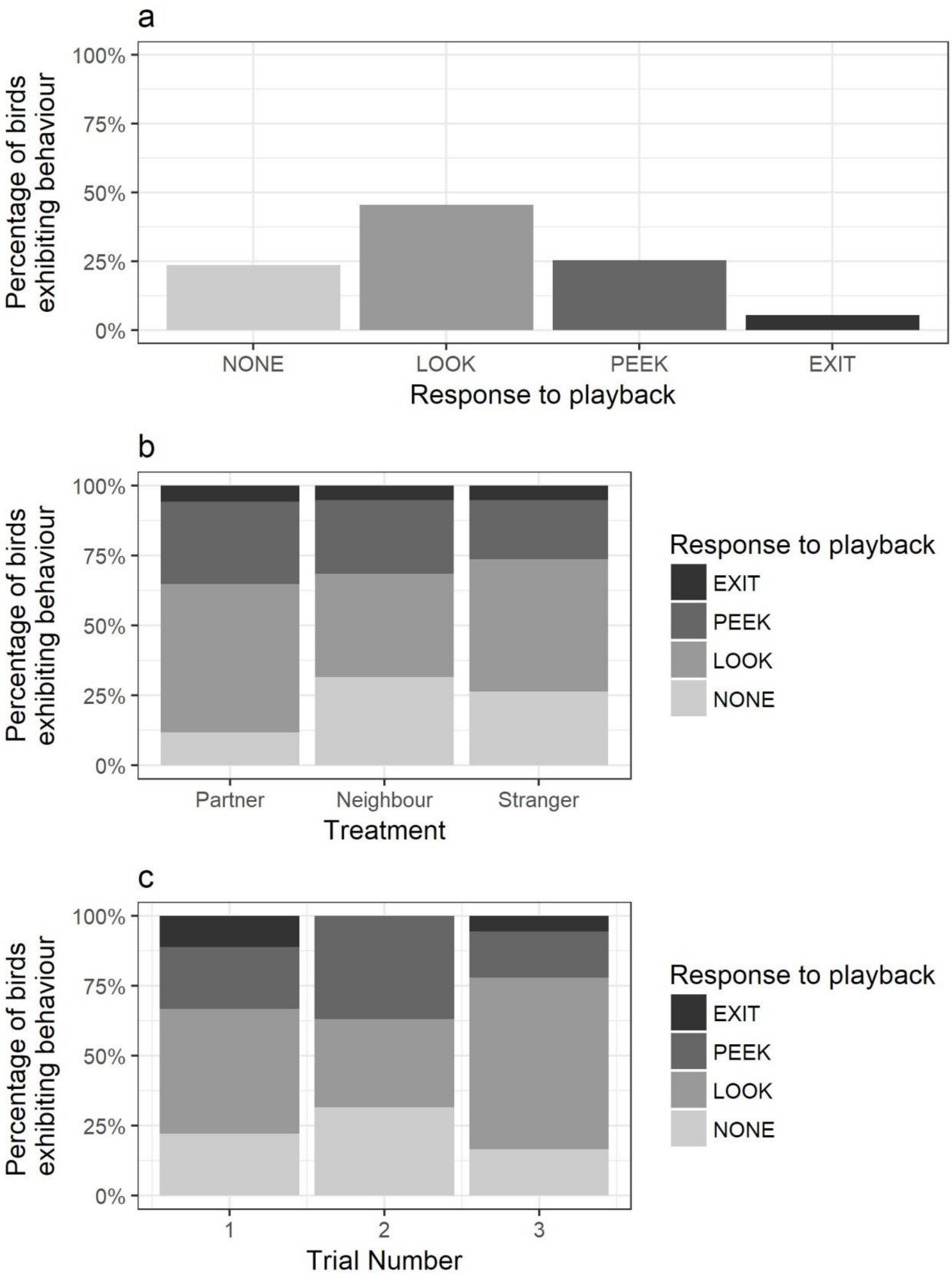


**Figure 3.2:** Percentage of females exhibiting each type of behavioural response to playbacks (LOOK: looking out of nest box entrance; PEEK: peeking out of nest box entrance; EXIT: leaving the nest box). Panels show proportion of females exhibiting each behavioural response a) across all trials; b) by treatment group (contact call playbacks from partner, neighbour or unfamiliar male); c) by trial number (1-3).

**Table 3.2:** Output of CLMM investigating the effect of treatment group and trial number on the behavioural responses of focal females to playbacks. Threshold estimates are calculated for each level of the ordinal response term at the reference level for each fixed effect (Treatment=Partner and Trial number=1). Values are derived from full model (n=55 observations from 19 females).

| **Model parameters** | **β** | **SE** | **z-value** | **p-value** |
|---|---|---|---|---|
| *Threshold (response)* | | | | |
| NONE\|LOOK | -2.33 | 0.99 | -2.35 | 0.02 |
| LOOK\|PEEK | 0.09 | 0.90 | 0.09 | 0.92 |
| PEEK\|EXIT | 2.49 | 1.07 | 2.33 | 0.02 |
| *Treatment* | | | | |
| Partner (reference) | -0.81 | 0.68 | -1.19 | 0.23 |
| Neighbour | -0.85 | 0.67 | -1.27 | 0.20 |
| Stranger | -0.15 | 0.33 | -0.44 | 0.66 |
| *Trial number* | -0.81 | 0.68 | -1.19 | 0.23 |
| **Random effects** | | | **Variance** | **SD** |
| Female ID | | | 1.03 | 1.01 |

### 3.3.3. Time spent looking/peeking following playback

In the two minutes following playbacks, the time females spent looking at or out of the nest box entrance was broadly similar across trials ($X^2$=0.12; df=1; p=0.73; Figure 3.3b, Table 3.3) and was not significantly influenced by the identity of the caller ($X^2$=1.40; df=2; p=0.50; Figure 3.3a, Table 3.3).

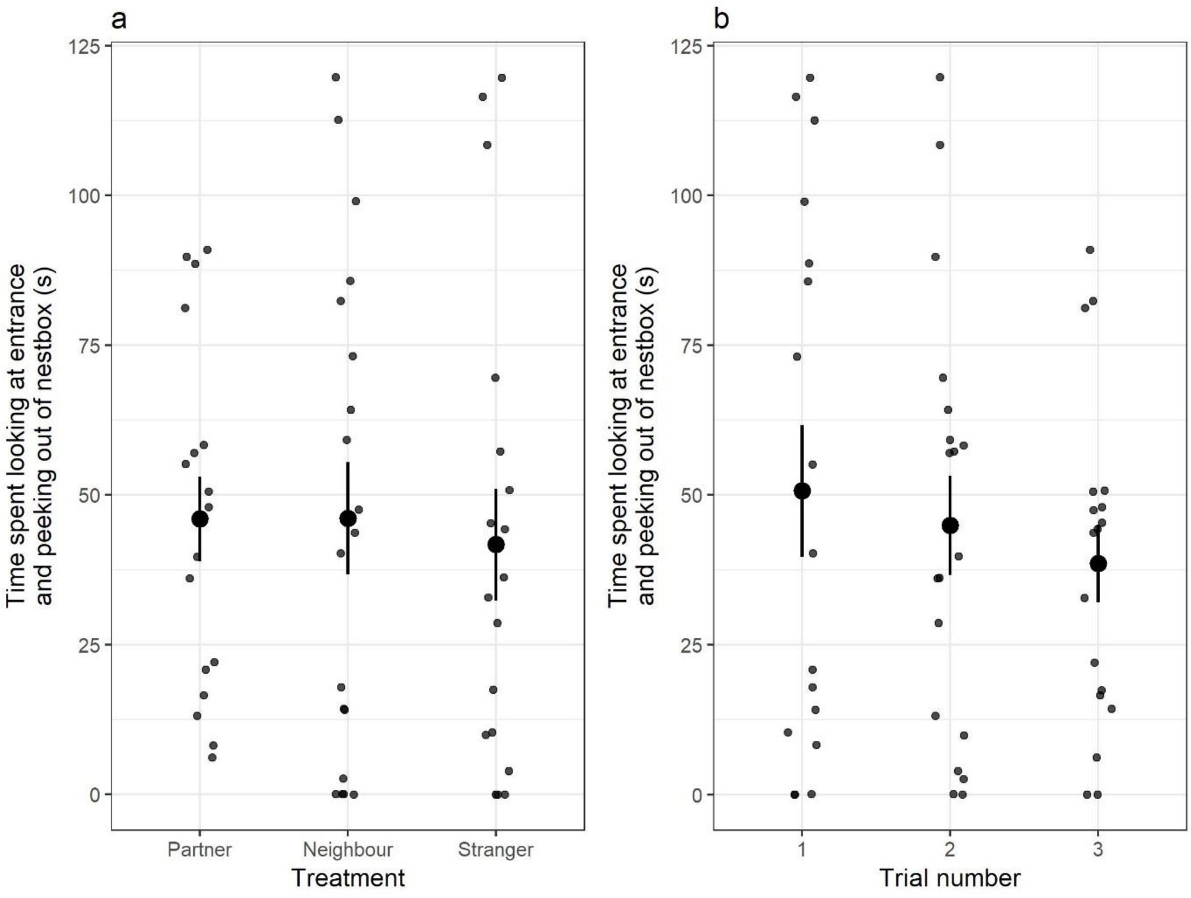


**Figure 3.3:** Time spent by females looking at or out of the nest box entrance in the two minutes following playbacks, by a) treatment and b) trial number. Grey circles show individual data points, black points and whiskers denote mean and standard error.

**Table 3.3:** Output of GLMM investigating the effect of treatment and trial number on the time spent by females looking at or out of the nest box entrance in the two minutes following playback presentations. Values derived from full model (n=54 observations from 19 females).

| **Fixed effects** | | **β** | **SE** | **t-value** |
|---|---|---|---|---|
| Intercept | | 9.90 | 2.14 | 4.63 |
| Treatment | Partner (reference) | | | |
| | Neighbour | -1.57 | 1.57 | -1.00 |
| | Stranger | -1.71 | 1.57 | -1.09 |
| Trial number | | -0.40 | 0.80 | -0.49 |
| **Random effects** | | | **Variance** | **SD** |
| Female ID | | | 4.72 | 2.17 |
| Residual | | | 21.15 | 4.60 |

## 3.4. Discussion

This experiment aimed to determine whether female jackdaws recognise the contact calls of their bonded partner, and discriminate between the contact calls of familiar and unfamiliar males. In line with predictions, female jackdaws differed in their response to playbacks depending on the identity of the caller. Incubating females were much quicker to look towards the entrance of their nest box upon hearing the contact calls of their partner compared to those of other males, likely anticipating the arrival of food. In contrast, female looking latencies did not differ in response to the contact calls of male neighbours and unfamiliar males. Upon hearing playbacks, although females initially responded by looking towards the nest box entrance, many females went on to peek out of the nest box or leave the nest box. However, the extent of female response was not influenced by the identity of the caller. The identity of the caller also had no significant effect on the length of time females spent looking at or out of the nest box entrance after hearing the playback. These findings demonstrate that female jackdaws individually recognise the contact call of their single, long-term breeding partner; providing the first evidence of true individual recognition among corvids in the wild (Tibbetts et al., 2008; Yorzinski, 2017).

Recognition of a partner's contact call is likely to be beneficial in the social life of jackdaws. In this species, contact calls are used in a wide range of contexts, and their primary function may be to advertise identity. For example, by emitting contact calls upon arrival at the nest, males and females may signal to their partner that they are not an intruder; for incubating females, male contact calls may also (but not always) be associated with the arrival of food. Pair bonds persist for many years, with individuals coordinating behaviour to raise young and defend a nest site. Biparental care is vital for reproductive success, with the loss of a partner during offspring provisioning often resulting in brood failure (Henderson et al., 2000; Röell, 1978). Recognition of a partner's unique cues may therefore allow pairs to coordinate their behaviour during the breeding season, and distinguish their partner from rivals and nest intruders. As a colonial species, jackdaws may also derive benefits from recognising their partner in a crowd (Aubin & Jouventin, 1998; Kondo & Watanabe, 2009). Adult breeding pairs often forage together (Valletta, Torney, Kings, Thornton, & Madden, 2017) and join large mixed-species winter flocks of hundreds, or even thousands of individuals. Analyses of flocking dynamics suggest that individuals travel close to their partner within these flocks (Jolles, King, et al., 2013; Ling et al., 2019). Given that contact calls are frequently given in flight, this provides a potential mechanism by which individuals might maintain pair cohesion even when flying at high speed among hundreds of other birds. In many species, conspecific recognition occurs via relatively simple mechanisms, such as category-level discrimination (see Wiley 2013). However, more complex forms of ‘true’ individual recognition are thought to be relatively cognitively demanding (Tibbetts & Dale, 2007; Yorzinski, 2017). Although true individual recognition has been demonstrated in several mammals and birds (reviewed in Yorzinski 2017), only one other study to date has investigated these abilities experimentally in corvids. Violation-of-expectation experiments by Kondo et al. (2012) demonstrate that captive large-billed crows (*Corvus macrorhynchos*) recognise group members individually, responding more strongly when a visual presentation of a social companion is combined with the ‘incorrect’ vocalisation. Here, my findings provide the first evidence that corvids individually recognise their breeding partner under natural conditions: a vital requirement for a colonially-breeding, socially monogamous species such as the jackdaw. Whether jackdaws discriminate between multiple individuals within the same category (such as offspring, kin or colony members) remains an interesting avenue for future study.

That test subjects did not differ in their response to the contact calls of neighbours and unfamiliar males is surprising. Whilst this could be interpreted as an inability to discriminate contact calls beyond those of an immediate partner, it may also be that there is no specific need for females to respond differently to the contact calls of neighbours and strangers. The fact that jackdaws have previously been shown to discriminate between familiar and unfamiliar alarm calls (Woods et al., 2018) suggests that the latter explanation is more likely. For example, if unfamiliar individuals are encountered frequently, or if neighbours and strangers are unlikely to pose a threat, their contact calls may not elicit a rapid response from the incubating female. Lack of motivation may also explain why playbacks of partner contact calls did not influence females’ responses beyond initially looking towards the nest box entrance:

these calls signal the arrival of the male with food, and do not require the female to gather additional information. Although females are likely to have been exposed to their partner's contact calls over a longer period of time, focal females would also have ample opportunities to become familiar with the contact calls of their neighbours. Of 19 focal females, seven had occupied the same nest box with the same neighbours in previous years. Of the 12 cases where birds were neighbours for the first time, females had sufficient opportunity to become familiar with the calls of their neighbours prior to the experiment being carried out. Jackdaws in the study colonies typically begin to take ownership of nest boxes from mid-February, spending a considerable portion of time each day at their nest (unpublished data). Given that this experiment was carried out several weeks later (beginning in late April), and contact calls are heard frequently around the colonies during the nesting season, it is likely that even first-time neighbours would be familiar with each other's contact calls. The failure of test subjects to respond as predicted in studies of vocal recognition may not necessarily reflect an inability to discriminate between the calls of different individuals, but rather that distinguishing between distinct vocalisations may not be relevant in a given context (Fischer, Metz, Cheney, & Seyfarth, 2001; Jansen, Cant, & Manser, 2013; Townsend, Hollén, & Manser, 2010). For example, meerkats (*Suricata suricatta*) do not appear to attend to individual signatures encoded in alarm calls, possibly as these calls are a highly reliable signal of an immediate threat (Schibler & Manser, 2007). Taken together, these findings highlight the need for behavioural experiments to complement analyses of individuality in call structure.

The idea that ‘relationship intelligence’ may have driven the evolution of sophisticated cognitive abilities has received widespread attention, but still lacks clear empirical support (see Scheiber et al. 2008). Although corvids are considered likely candidates for exhibiting relationship intelligence (Emery et al., 2007), the basic assumption that individuals recognise their bonded partner has yet to be formally tested in natural populations. Research suggests that corvid pair bonds are highly valuable relationships, with individuals investing significant time and energy in affiliative behaviours and agonistic support (Boucherie, Poulin, & Dufour, 2018; Emery et al., 2007; Fraser & Bugnyar, 2012; Kubitza et al., 2015; Röell, 1978). Moreover, many corvids (including jackdaws) compete with other pairs for access to resources (Clayton & Emery, 2007; Röell, 1978). Cooperating with a partner to navigate competitive interactions with other bonded pairs may therefore entail cognitive demands that extend beyond those associated with maintaining the pair bond itself (Massen, Szipl, Spreafico, & Bugnyar, 2014). However, our understanding of the fitness consequences of corvid social bonding is limited. If maintaining a pair bond is cognitively demanding but yields important fitness benefits, this may shed light on the evolution of corvids’ remarkable cognitive abilities (Emery et al., 2007). Currently, the theory of relationship intelligence remains speculative, as precisely whether and how maintaining pair bonds is cognitively demanding remains to be tested empirically. The cognitive demands of conspecific recognition provide a good starting point: for example, does relationship intelligence require explicit recognition abilities, or are simpler discrimination mechanisms sufficient (Mendelson et al., 2016)? Several methodological approaches can be used to investigate individual recognition abilities, including experiments involving presentation of multi-modal stimuli (Yorzinski, 2017). Due to the logistical challenges associated with implementing these experiments in the field, studies of captive individuals under controlled conditions are particularly valuable in this regard. On the other hand, captive populations may not always provide an accurate representation of a species' cognitive performance: small group sizes and physical proximity may allow individuals to become more familiar with each other's vocalisations. Consequently, captive studies must be complemented by field experiments where multiple cues compete for subjects' attention, and findings are more reflective of natural behaviour (McCune, Jablonski, Lee, & Ha, 2019; Pritchard et al., 2016; Thornton et al., 2012). Finally, although corvids and parrots provide ideal opportunities to test relationship intelligence (Emery et al., 2007), research should not be limited to these systems. By broadening our focus to other species with long-term pair bonds, we may be able to determine whether the nature of these pair bonds, and the cognitive demands associated with them, truly differ from those of supposedly more 'cognitively advanced' species (Scheiber et al., 2008; Thornton, 2014).

# Supplementary Material for Chapter 3: Jackdaws individually recognise the contact calls of their mate

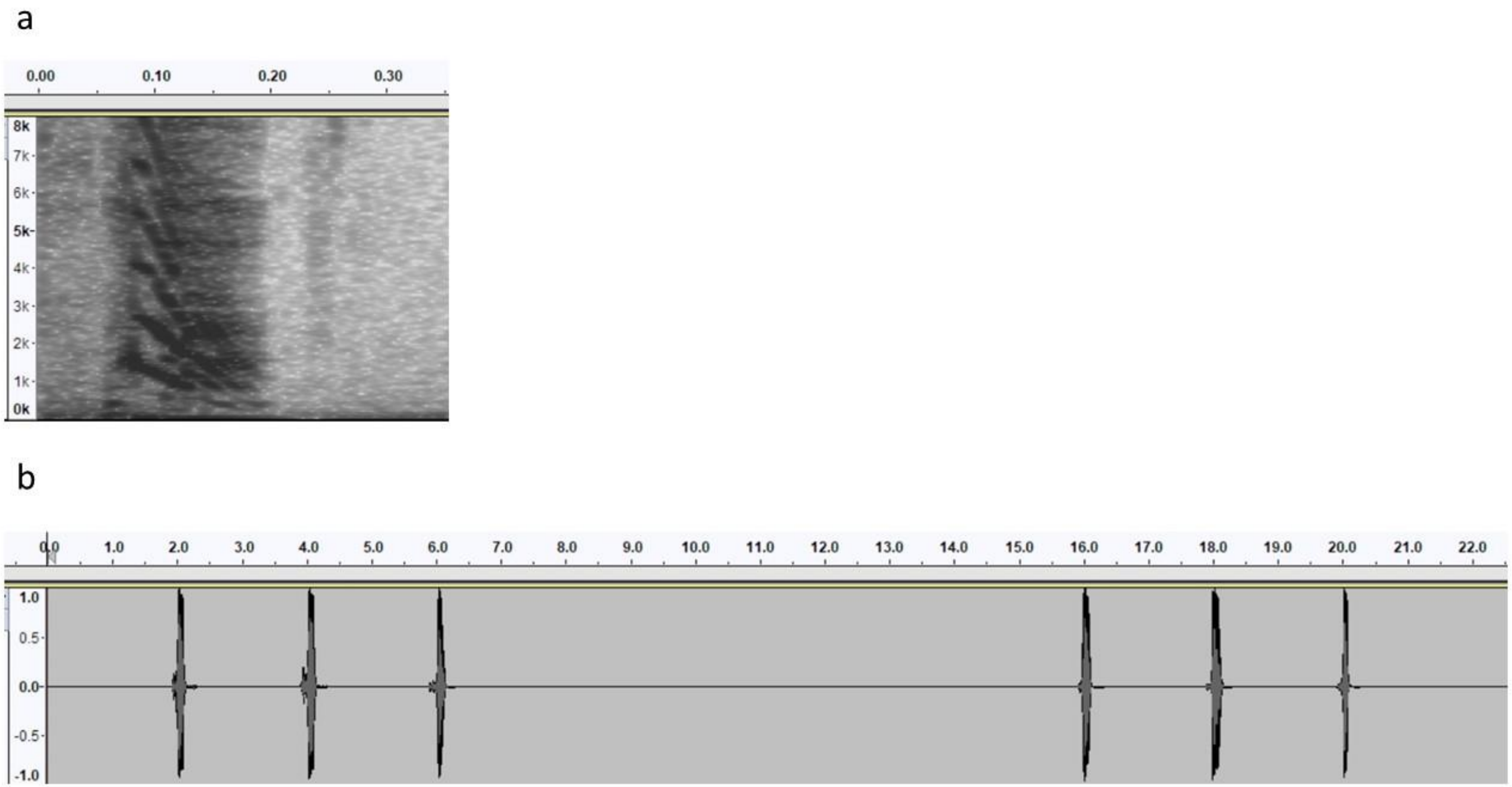


**Figure S1:** (a) Spectrogram of a contact call from a male jackdaw (b) waveform of a playback track, comprised of six contact calls from a male jackdaw.

# Chapter 4

# Testing relationship recognition in wild jackdaws

*This chapter has been adapted from:*

*Lee, V. E., McIvor, G. E., Thornton, A. 2019 Testing relationship recognition in wild jackdaws (Corvus monedula). Scientific Reports 9 (6710).*

## Abstract

According to the social intelligence hypothesis, understanding the challenges faced by social animals is key to understanding the evolution of cognition. In structured social groups, recognising the relationships of others is often important for predicting the outcomes of interactions. Third-party relationship recognition has been widely investigated in primates, but studies of other species are limited. Furthermore, few studies test for third-party relationship recognition in the wild, where cognitive abilities are deployed in response to natural socio-ecological pressures. Here, I used playback experiments to investigate whether wild jackdaws (*Corvus monedula)* track changes in their own relationships and the relationships of others. Females were presented with 'infidelity simulations': playbacks of their male partner copulating with a neighbouring female, and their male neighbour copulating with another female, against a congruent control. My results showed substantial inter-individual variation in responses, but females did not respond more strongly to infidelity playbacks, indicating that jackdaws may not attend and/or respond to relationship information in this experimental context. My results highlight the need for further study of relationship recognition and other cognitive traits that facilitate group-living in the wild, particularly in non-primates and in a wider range of social systems.

## 4.1. Introduction

The social intelligence hypothesis posits that the sophisticated cognitive abilities seen in some species may have arisen due to the selection pressures associated with group living (Dunbar, 1998; Humphrey, 1976). Several studies provide support for the social intelligence hypothesis, linking cognitive performance or brain size measures with various aspects of sociality (Amici, Aureli, & Call, 2008; Ashton, Ridley, et al., 2018; Bond, Kamil, & Balda, 2003, 2007; Dunbar, 1998; Emery et al., 2007). However, other studies have shown conflicting results (DeCasien, Williams, & Higham, 2017; Holekamp, 2007; Sayol et al., 2016; see Ashton, Thornton, & Ridley, 2018; Healy & Rowe, 2013 for a detailed discussion) and the social intelligence hypothesis remains controversial. To determine whether social life favours the evolution of associated cognitive abilities, it is necessary to understand how these cognitive abilities help individuals to navigate a dynamically changing social world.

Social species must solve ecological challenges within a social context (Ashton, Thornton, et al., 2018; Shultz & Dunbar, 2007). In these cases, the ability to recognise other group members and remember past interactions allows individuals to predict (and potentially manipulate) others' behaviour (Holekamp et al., 2007). Although obtaining, processing and applying this knowledge is likely to be cognitively demanding (Cheney & Seyfarth, 2008; Emery et al., 2007; Shultz & Dunbar, 2007), individuals who are more socially competent may derive fitness benefits as a result (Cameron, Setsaas, & Linklater, 2009; Campbell, Tkaczynski, Lehmann, Mouna, & Majolo, 2018; Silk, Alberts, & Altmann, 2003). In social groups where relationships persist over time, being able to track the relationships of other group members can be useful in predicting the outcomes of interactions (Holekamp et al., 2007). Knowledge of third-party relationships might allow individuals to adjust their own behaviour appropriately to avoid conflict (Bergman, Beehner, Cheney, & Seyfarth, 2003; Borgeaud, van de Waal, & Bshary, 2013; Massen, Pašukonis, Schmidt, & Bugnyar, 2014; Wittig, Crockford, Langergraber, & Zuberbühler, 2014), solicit and provide support during agonistic interactions (Emery et al., 2007; Engh, Siebert, Greenberg, & Holekamp, 2005; Schino, Tiddi, & Di Sorrentino, 2006; Silk, 1999; Slocombe & Zuberbühler, 2007; Szipl, Ringler, & Bugnyar, 2018), and take advantage of mating opportunities (Crockford, Wittig, Seyfarth, & Cheney, 2007). Third-party relationship recognition has been demonstrated in several primate species, originally leading some authors to suggest that this ability may be confined to the primate order (Tomasello, 1998; Tomasello & Call, 1997). Observations of agonistic interactions indicate that bonnet macaques (*Macaca radiata*) solicit support from individuals who are higher-ranking than their opponent (Silk, 1999) and chimpanzees (*Pan troglodytes*) will modify their recruitment screams depending on the dominance rank of bystanders (Slocombe & Zuberbühler, 2007). Playback experiments also provide evidence that primates track third-party relationships. For instance, vervet monkeys *Chlorocebus aethiops pygerythrus* (Borgeaud et al., 2013) and chacma baboons *Papio hamadryas ursinus* (Bergman et al., 2003) respond to simulated reversals in the existing dominance hierarchy, demonstrating an understanding of the dominance relationships between other group members. Chimpanzees (*P. troglodytes*) will avoid aggressive individuals who are socially bonded to their former opponent, for several hours following an agonistic encounter (Wittig et al., 2014); and male baboons (*P. hamadryas ursinus*) track consortships between other males and females in order to obtain sneaky matings (Crockford et al., 2007). In vervet monkeys (*C. aethiops*), playbacks of infant distress calls cause nearby females to look towards the infant's mother, demonstrating recognition of mother-offspring relationships within the social group (Cheney & Seyfarth, 1980).

Few studies have investigated third-party relationship recognition in non-primates, despite many other species living in complex societies where this ability is expected to be useful. For example, hyenas (*Crocuta crocuta*) live in complex social groups with multiple hierarchically structured matrilines, similar to many primate societies (Holekamp et al., 2007). Hyenas will join conflicts to support the higher-ranking individual even if the subordinate member of the fighting dyad is more aggressive, implying knowledge of the dominance relationships that exist in the group (Engh et al., 2005; but see Holekamp et al., 1999). Not only is it important to examine a diverse range of species, but also a diversity of social systems – for instance, little is known about the value of third-party relationship recognition in monogamous systems. Among birds, monogamy is the most common social system and has been argued to be central to the evolution of avian cognition (Emery et al., 2007), although little is known about the cognitive demands associated with maintaining long-term pair bonds. Furthermore, many monogamous bird species live in groups and form stable, individualised relationships with others in addition to their breeding partner (Emery et al., 2007). Corvids exhibit this type of social system, and their remarkable cognitive abilities make them ideal subjects for investigating the evolution of social cognition (Bugnyar, 2013; Emery & Clayton, 2004; Güntürkün & Bugnyar, 2016). Many corvids form long-term pair bonds and live in colonies characterised by dominance hierarchies between bonded pairs (Clayton & Emery, 2007). Empirical evidence supports the idea that recognising social relationships is beneficial in corvid colonies (Boucherie, Loretto, Massen, &

Bugnyar, 2019; Bugnyar, 2013). For example, playback experiments show that captive ravens (*Corvus corax*) respond to dominance rank reversals, both within their own social group and in a neighbouring group (Massen, Pašukonis, et al., 2014). Furthermore, observations of wild ravens indicate that victims will reduce the frequency of their distress calls during agonistic encounters, if the bonding partner of their aggressor is present in the vicinity; victims also call more frequently when their own kin are nearby (Szipl et al., 2018). Anecdotal reports suggest that rooks (*Corvus frugilegus*) engage in redirected aggression, where individuals are more likely to attack their aggressor's partner, or the aggressor of their partner, after a fight (Emery et al., 2007). Finally, ravens will intervene in the affiliative interactions of others that appear to be establishing a strong bond, which is likely to require knowledge of the relationships of group members (Massen, Szipl, et al., 2014).

In the only experimental test of third-party relationship recognition in corvids to date, Massen et al. (2014) found that ravens (*C. corax*) become stressed and engage in more self-directed behaviour after hearing simulated encounters that violate their expectation of the existing dominance hierarchy within their own colony. Male subjects also exhibited decreased calling and attention behaviour following simulated rank reversals in a neighbouring group, suggesting that ravens deduce third-party relationships by observation alone. However, this study was conducted under controlled conditions using captive individuals, where subjects could observe interactions between conspecifics very frequently. Consequently, it is not clear to what extent these results reflect the cognitive abilities animals employ in the wild, where a greater number of stimuli compete for individual attention (Cheney & Seyfarth, 2008; Pritchard et al., 2016; Thornton & Lukas, 2012). Furthermore, most of the research carried out under natural conditions has involved observations of naturally-occurring behaviour, and there is a lack of experimental evidence for third-party relationship recognition in the wild outside the primate order. To this end, a recent study by Pardo et al. (2018) describes the first experimental field test for third-party relationship recognition in a non-primate. This study found that acorn woodpeckers initiate defensive behaviour more quickly in response to simulated duets involving two birds from different social groups, compared to duets involving two birds from the same social group. As acorn woodpeckers only engage in duets with members of their own social group, these results suggest that subjects were aware of which individuals make up neighbouring social groups and responded more strongly to duets that violated their expectations. However, it is not clear to what extent this indicates knowledge of the dyadic relationship between the two callers, or whether it is possible that subjects were responding to the unfamiliar stimulus of two calls occurring in a chorus, when those calls had only been heard separately in the past. Consequently, much remains to be determined as to the extent of third-party relationship recognition in non-primates in the wild.

To address this research gap, I conducted an experiment to test whether wild jackdaws track changes in their own relationships and the relationships of other members of their social group. This ability is likely to be useful in jackdaw society: pairs form monogamous bonds and compete for nest sites in the dominance hierarchy of the breeding colony (Röell, 1978; Salomons et al., 2007). The composition of breeding colonies remains relatively stable over time due to high adult survivorship (c. 80%, although estimates vary) and low rates of ‘divorce’ (Röell, 1978), creating opportunities for frequent, repeated interactions between colony members. On the other hand, colony composition is not entirely fixed as new breeding pairs are formed, existing pairs move to new nest sites, and dominance relationships change over time (see Chapter 2 for estimates of the frequency of social change in my study colonies). For jackdaws, tracking relationships within the colony may allow individuals to avoid conflict with more dominant pairs, especially considering that competition over nest sites can be intense (Henderson & Hart, 1993; Röell, 1978). Relationship tracking may also allow individuals to notice if their partner is engaging in extra-pair copulations. Jackdaws are typically considered to be sexually as well as socially monogamous (Henderson et al., 2000; Liebers & Peter, 1998), with studies to date finding that extra-pair paternity is rare: it has been suggested that the high level of parental investment required to successfully raise offspring may prevent birds from seeking extra-pair copulations (Henderson et al., 2000). However, recent findings suggest that extra-pair copulations may not be as uncommon as previously thought (Gill, 2016); it may therefore pay females to track their partner's behaviour.

Following the 'violation of expectation' paradigm employed in similar studies (Borgeaud et al., 2013; Crockford et al., 2007; Massen, Pašukonis, et al., 2014), I used playback experiments to investigate whether female jackdaws respond to simulations of male infidelity. During mating, including extra-pair copulations, male jackdaws give loud copulation calls (Stowell, Benetos, & Gill, 2017), and the function of these vocalisations is currently unknown. In a recent study combining acoustic tracking and video surveillance, male jackdaws were recorded emitting copulation calls at the same time as the female was alone on the nest (Gill, 2016), suggesting that males do engage in extra-pair copulations and that this should be an ecologically relevant stimulus for the female. Furthermore, in my study population, intruder males are occasionally seen entering nest boxes and attempting to copulate with the incubating female (*pers. obs.*). Although it is not yet known whether male copulation calls encode information about caller identity, all other jackdaw vocalisations studied to date have been shown to be individually distinct (food calls: Zandberg, Jolles, Boogert, & Thornton, 2014; contact calls: Stowell, Morfi, & Gill, 2016; and alarm calls: Woods, Kings, McIvor, & Thornton, 2018). Using playbacks of male contact calls and copulation calls in conjunction with female contact calls, I simulated mating events occurring during the egg-laying period of the breeding season, when copulation calls are heard most frequently in the colony (*pers. obs.*). Contact calls were included to ensure that playback sequences simulated interactions between individuals: contact calls are individually distinctive (Stowell et al., 2016) and typically accompany jackdaw copulation events. I used three playback treatments to test whether females track changes in their own relationships and the relationships of other colony members. In the 'Partner Incongruent' treatment, the playback simulated the focal female's partner copulating with a female from a neighbouring nest, and this was expected to elicit a strong response from the focal female. A 'Neighbour Incongruent' treatment was designed to test third-party relationship recognition and simulated the male from a neighbouring nest copulating with another female who was not their usual partner. This was predicted to elicit an intermediate response from the focal female, as it violates expectations but does not involve the focal female's own partner. Using a within-subjects design (Figure 4.1), the responses of focal females to both 'Incongruent' playbacks were compared to a 'Congruent' control predicted to elicit a neutral response (playback of a neighbouring male copulating with their usual partner).

## 4.2. Methods

### 4.2.1. Study Population

This experiment was conducted during the 2015-2017 breeding seasons using free-living nest box populations of jackdaws, at three study sites in Cornwall, UK: a village churchyard (Stithians 50º11′26″N, 5º10′51″W; 33 nest boxes), an active farmyard (Pencoose Farm 50º11′56″N, 5º10′9″W; 35 nest boxes), and at the University of Exeter's Penryn campus (50º17'32"N; 5º11'96"W; 11 nest boxes).

### 4.2.2. Playback Stimuli

*Audio Recordings*

Nest boxes occupied by breeding jackdaws were fitted with hidden CCTV cameras early in the nest-building phase (late March-early April). A subset of nest boxes selected for this experiment were also fitted with lapel microphones (n=30). Focal nest boxes were selected with at least one marked individual, and with at least two nearby neighbouring pairs (within 50m). This was to ensure that neighbours' contact and copulation calls used in playbacks would be familiar and ecologically relevant stimuli for the focal female.

Audio recordings were made early in the morning (start time: 0700-0900) during late March and early April, when birds were engaged in nest building and copulation. Video recordings were made with digital video recorders (JXD 990) and audio recordings made with multitrack PCM recorders (Olympus LS-100 & Tascam DR-100MKII). Recordings were made daily as required to obtain the necessary vocalisations for use in playback experiments. Each recording ran for 3.5 hours. For some subjects, copulation and contact calls were extracted from recordings obtained during previous seasons (2013-2015) using an identical protocol.

*Call extraction*

Clear exemplars of contact calls and copulation calls with minimal background noise were extracted from nest box audio recordings and normalised for amplitude using Audacity (www.audacityteam.org). The context of vocalisations and the identity of the caller were ascertained using nest box videos collected alongside the audio recordings. In cases where females vocalised during copulation, female calls were removed from the audio track, leaving only the male copulation call. Extracted calls were arranged into playback files containing a male contact call, followed by a female contact call, followed by a male copulation call, to simulate a copulation event (see Supplementary Figure S1). Calls occurred at 2s intervals to simulate natural calling, and male copulation calls varied in length – this variation was retained to avoid excessively editing the acoustic stimulus and potentially altering important aspects of call structure, but playback duration was later controlled for statistically (see *Statistical Analysis)*. Playback duration varied from 7.8-25.5s (mean duration=16.1s), as recorded from trial footage taken inside the nest box. Each stimulus was played back once per experimental trial. Because of the limited number of suitable copulation call recordings, and the variation in copulation call duration within and between males, some copulation calls appeared in multiple playback trials. Focal females heard the same copulation call from the male neighbour in the Congruent and Neighbour Incongruent treatments, to ensure consistency across the experiment and minimise the potential confounding effects of call duration. Contact calls were not repeated across playback trials.

### 4.2.3. Experimental Design

This experiment followed a repeat measures design with each focal female (Female A) being assigned three playback files (one for each of the experimental treatments) as follows:

- Congruent treatment: Neighbour Male B ‘copulating’ with Neighbour Female B.
- Partner incongruent treatment: Partner Male A ‘copulating’ with Neighbour Female B.
- Neighbour incongruent treatment: Neighbour Male B ‘copulating’ with Neighbour Female C (Figure 4.1).

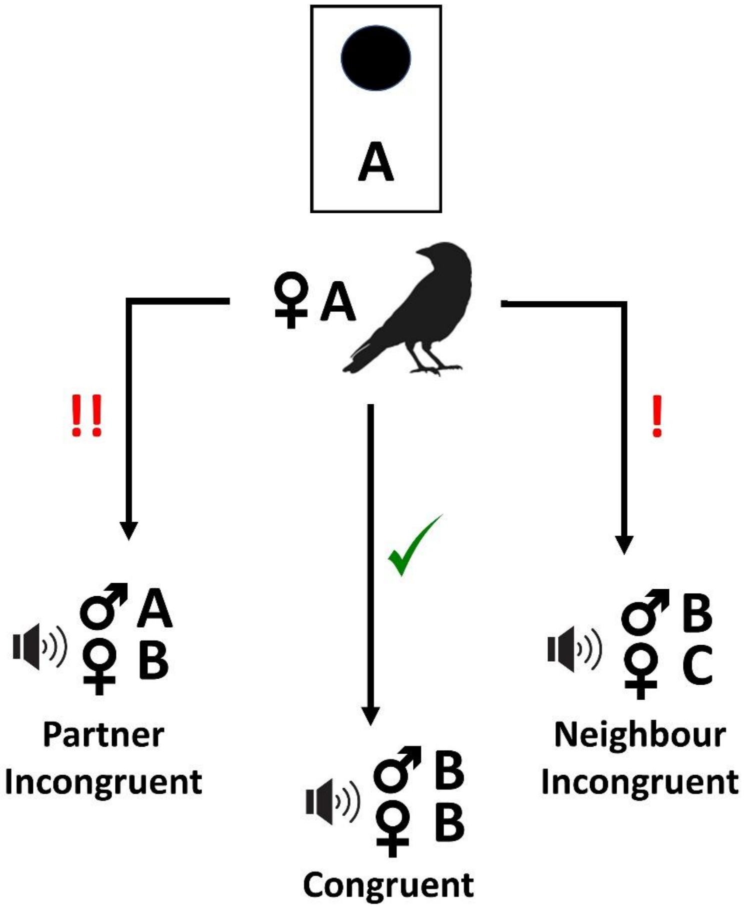


**Figure 4.1** Experimental setup for each nest box. The focal female from nest box A heard three playback presentations. In the ‘Congruent’ control treatment, focal female A heard a playback simulating a copulation event between the neighbouring male from nest box B and the female from nest box B (his usual partner). The focal female (A) was expected to show a weak response to this playback, denoted by a green tick mark. In the ‘Neighbour Incongruent’ treatment, focal female A heard a playback simulating a copulation event between the neighbouring male from nest box B and the female from nest box C (not his usual partner). The focal female (A) was expected to show a stronger response to this playback as it violated expectations, denoted by a red exclamation mark. In the ‘Partner Incongruent’ treatment, the focal female (A) heard a playback simulating a copulation event between her own partner (male

from nest box A) with the neighbouring female from nest box B. This playback was expected to elicit the strongest response from focal female A, denoted by two red exclamation marks.

All experimental trials occurred soon after eggs were laid by the focal female, when females were motivated to remain in the nest box but copulation calls were still being heard frequently around the nesting colony. The order in which focal females received each playback treatment was counterbalanced as far as possible, to ensure a matched design across the experiment. At least 24 hours elapsed between trials for a given focal nest box. All trials were carried out between 09:00 and 18:30, to coincide with peak activity times of the birds (Henderson & Hart, 1993).

I carried out 28 trials across three sites in 2015-2017, at 10 focal nest boxes (two trials were discarded due to camera failure). This was the maximum sample size that could be achieved in this case, due to the limited number of nest boxes with at least two close neighbours and the difficulties in obtaining enough calls from these pairs. All females were colour-ringed, except one bird whose partner was colour-ringed enabling identification of individuals at the nest box. Trials were not carried out in the same area of the colony in the same year. In cases where trials were carried out in the same area in subsequent years, neighbouring birds from previous years were not included in the experiment as focal individuals.

### 4.2.4. Experimental trials

Prior to trials, a remote-controlled FoxPro Fury 2 loudspeaker (disguised with vegetation to avoid any neophobic responses) was attached to a tripod and placed approximately two-thirds of the distance between the focal nest and the neighbour nest (mean distance 13.6m between focal nest box and loudspeaker, range 8-21m). The loudspeaker was set up in the same location for all trials at a nest box. Video recording equipment was also set up (DVR JXD 990) to record female behaviour inside the focal nest box and neighbouring nest box.

Following setup, the experimenter returned to a concealed location a minimum of 50m away. Playbacks only occurred after the focal female had remained undisturbed in the nest box for at least 5 minutes (no disturbance outside the nest box, female had not left the box or appeared at nest box entrance), and at least 5 minutes following the most recent visit by the male. A baseline period of at least 20 minutes elapsed between the female’s first return to the nest box and presentation of the playback stimulus, to allow focal pairs to return to normal behaviour after setting up equipment.

### 4.2.5. Behavioural Analysis

Footage of focal females was analysed using BORIS (Friard & Gamba, 2016). The frequency and duration of behaviours exhibited by the focal female were recorded for the 2-minute period following the start of each playback presentation. These included: (i) categorical primary response to playback (looking at the nest box entrance, peeking out of the nest box, or leaving the nest box); (ii) time spent looking at the nest box entrance and peeking out of the nest box. All playbacks were conducted at least 5 minutes after the last visit by the male. There were 5 instances where males returned to the nest box in the two minutes following the playback, and in these cases all female behaviours occurring during and after the male's visit were discounted.

Twenty percent of videos were analysed by a second coder who was blind to treatment. Inter-rater reliability was analysed using a two-way intraclass correlation coefficient (ICC) and indicated a high level of agreement between coders for all behaviours analysed (time spent looking at entrance in the post-playback period: ICC=0.98, p<0.001; time spent peeking in the post-playback period: ICC=0.87, p=0.006. In all cases, both coders agreed on the categorical primary response to the playback).

### 4.2.6. Statistical Analysis

All analyses were carried out in R (R Core Team, 2017) with models built using *lme4* (Bates et al., 2015) and *ordinal* (Christensen, 2018). Model plots were examined to ensure that assumptions were met (homogeneity and normality of residuals), and minimum adequate models were obtained via log-likelihood ratio tests.

*Behavioural response to playback*

In all cases females looked towards the entrance in response to the playback, but some individuals subsequently went on to peek out of the nest box entrance or leave the nest box. The extent of female response was analysed using a cumulative link mixed model (CLMM) using female behaviour (LOOK/PEEK/EXIT) as an ordinal response term. In the model, leaving the nest box was considered the strongest response to the playback (EXIT=3), followed by peeking out of the nest box from a standing position (PEEK=2), with looking at the nest box entrance from a seated position taken to be the weakest response (LOOK=1). Treatment (congruent, partner incongruent or neighbour incongruent) and trial number (1-3) were included as fixed effects and female ID as a random term. The effect of female identity on response was analysed using log-likelihood comparison between the minimal model and a cumulative link model without the random factor (Christensen, 2015). Four trials were excluded from the analysis as the male returned to the nest box prior to the end of the playback, likely influencing female response.

### *Time spent looking and peeking following playback*

For the two-minute period following the start of the playback, the time that each female spent looking at the nest box entrance and/or peeking out of the nest box was analysed using a general linear mixed model (GLMM) with a Gaussian error distribution. Treatment (congruent, partner incongruent or neighbour incongruent), trial number (1-3) and length of playback were included as fixed effects with focal female ID as a random term. Of the 28 trials, 6 were discarded as the male returned to the nest within two minutes of the playback. One focal female responded to the playback by leaving the box immediately in all three trials, and these were likewise excluded from the analysis. An influential data point was also removed from the model following examination of Cook’s distances: in this case, the focal female spent the full two-minute period looking at the nest box entrance, but was also facing the nest box entrance when the playback started (and therefore may not have represented a reliable response to the playback).

## 4.3. Results

In all cases, females showed some form of response to the playback. These responses ranged from looking at the nest box entrance from a seated position during incubation (“LOOK”, 54% of cases), moving to look out of the nest box entrance (“PEEK”, 25% of cases) and leaving the nest box (“EXIT”, 21% of cases; see Figure 4.2). On no occasion did females vocalise in response to the playback. During the post-playback observation period, there were two occasions when an intruding male (not the focal female’s partner) entered the nest box and attempted to copulate with the focal female. These incidents both occurred during the first trial at the nest boxes in question and approximately half an hour after the playback presentation; once following a ‘Partner Incongruent’ playback (2015) and once following a ‘Congruent’ playback (2017). Intrusions by other males were not observed during any other trials, either before or after the playback presentation.

### 4.3.1. Behavioural response to playback

Females responded to playbacks by looking at the nest box entrance (LOOK), peeking out of the entrance from a standing position (PEEK) or leaving the nest box (EXIT). However, the likelihood of females exhibiting these behaviours was similar across treatment groups (CLMM: $X^2$=1.21, df=2, p=0.55) and was not influenced by trial order (CLMM: $X^2$=0.40, df=2, p=0.82) (Figure 4.2, Table 4.1). Instead, response to playbacks was strongly influenced by the identity of the female (CLM: $X^2$=12.3, df=1, p<0.001). For example, females that left the box in one trial were more likely to do so in subsequent trials (Figure 4.3, Table 4.1).

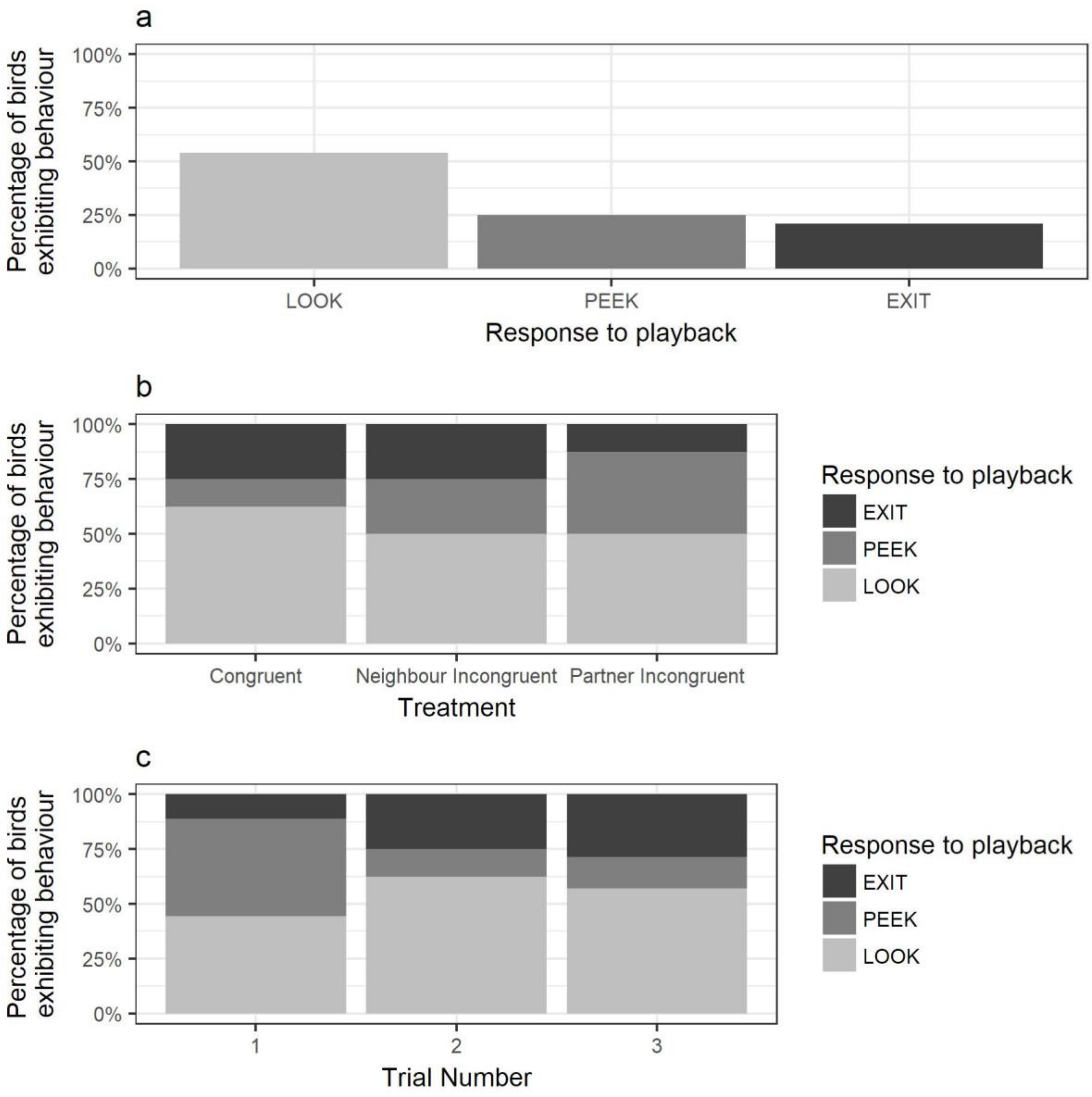


**Figure 4.2** Barplots showing behavioural responses of females to playback treatments: looking at the nest box entrance from an incubating position (LOOK, light grey bars); peeking out of the nest box entrance from a standing position (PEEK, mid-grey bars), and leaving the nest box (EXIT, dark grey bars). a) Percentage of females exhibiting each response across all trials; b) percentage of females exhibiting each behaviour by treatment (congruent, neighbour incongruent, partner incongruent); c) percentage of females exhibiting each behaviour by trial number (1-3, treatment presentations counterbalanced across trials).

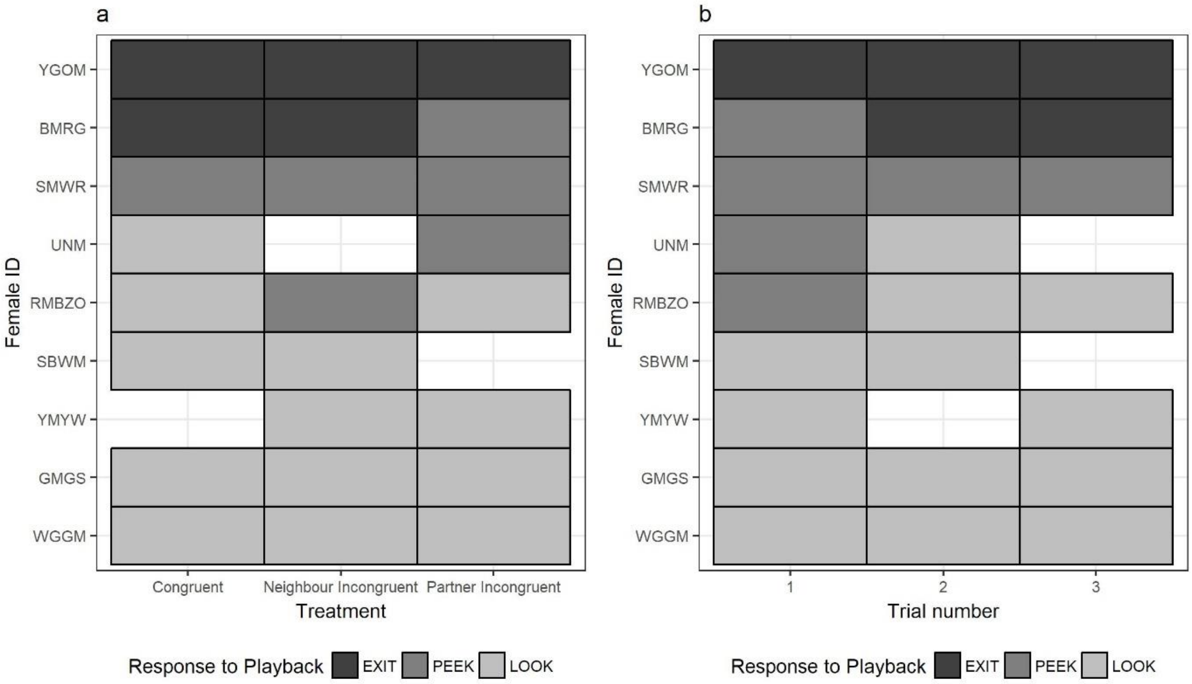


**Figure 4.3** Tile plots showing responses of focal females to the three playbacks, according to a) treatment (Congruent, Neighbour Incongruent, Partner Incongruent) and b) trial number (1-3). Female ID (y-axis) shows colour-ring combinations of focal females. Tile colour corresponds to the behavioural response of the female to the playback: looking at the nest box entrance from an incubating position (LOOK, light grey bars); peeking out of the nest box entrance from a standing position (PEEK, mid-grey bars), and leaving the nest box (EXIT, dark grey bars). Blank tiles represent trials where a reliable measure of females' initial response to the playback could not be obtained.

**Table 4.1** Output of CLMM investigating the effect of treatment (congruent, neighbour incongruent, partner incongruent) and trial number (1-3) on the ordinal response of females to the playback (LOOK=looking at nest box entrance, PEEK=peeking out of nest box entrance, EXIT=leaving the nest box). Congruent treatment and Trial 1 are the reference levels, n=24 observations of 9 females. Values shown from full model, statistically significant effects are given in italics.

| **Model parameters** | **β** | **SE** | **z-value** | **p-value** |
|---|---|---|---|---|
| Threshold (response) | | | | |
| LOOK\|PEEK | 1.47 | 2.74 | 0.54 | |
| PEEK\|EXIT | 6.31 | 2.74 | 2.30 | |
| Treatment | | | | |
| Congruent (reference) | | | | |
| Neighbour incongruent | 1.56 | 1.80 | 0.86 | 0.39 |
| Partner incongruent | -0.13 | 1.63 | -0.08 | 0.94 |
| Trial number | | | | |
| Trial 1 (reference) | | | | |
| Trial 2 | -0.53 | 1.62 | -0.33 | 0.74 |
| Trial 3 | -0.22 | 1.66 | -0.13 | 0.89 |
| **Random effects** | | | **Variance** | **SE** |
| *Female ID* | | | *31.89* | *5.65* |

### 4.3.2. Time spent looking/peeking following playback

In the two-minutes following the start of the playback, females spent an average of 54s (±7.3s) either looking at or peeking out of the nest box entrance. The length of time that females spent looking at or out of the nest box entrance did not differ between treatments (GLMM: $X^2$=0.58, df=2, p=0.75), and was not influenced by the duration of the playback (GLMM: $X^2$=1.12, df=1, p=0.29). However, females spent less time looking and peeking following playbacks as trials progressed (GLMM: $X^2$=10.13, df=2, p=0.006) (Figure 4.4, Table 4.2).

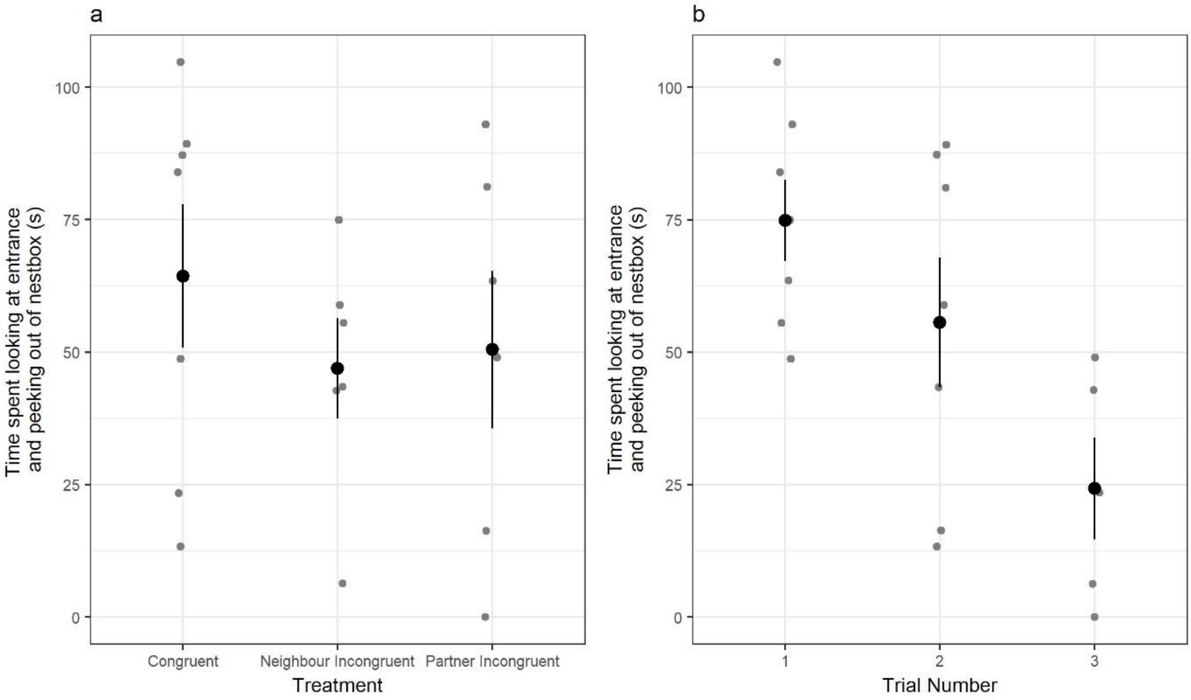


**Figure 4.4** Time spent by focal females looking at the nest box entrance or peeking out of the nest box entrance in the two minutes post-playback, by a) treatment (congruent, neighbour incongruent, partner incongruent) and b) trial number (1-3). Grey points represent individual data points (n=19 observations of 8 females), and black points with error bars denote mean and standard error.

**Table 4.2** Output of GLMM investigating time spent looking at nest box entrance and peeking out of nest box entrance in the two minutes following the start of playback. Full model includes treatment, trial order and playback duration as fixed effects (statistically significant effects given in italics). Congruent treatment and Trial 1 are the reference levels, n=19 observations of 8 females.

| | **Fixed effect** | | **β** | **SE** | **t-value** |
|---|---|---|---|---|---|
| **Full model** | | | | | |
| | Intercept | | 101.46 | 22.97 | 4.42 |
| | Treatment | Congruent (reference) | | | |
| | | Neighbour incongruent | -7.27 | 13.0 | -0.56 |
| | | Partner incongruent | -9.59 | 13.12 | -0.73 |
| | *Trial order* | *Trial 1 (reference)* | | | |
| | | *Trial 2* | *-16.72* | *12.31* | *-1.36* |
| | | *Trial 3* | *-47.20* | *13.55* | *-3.48* |
| | Playback duration | | -1.33 | 1.24 | -1.08 |

## 4.4. Discussion

I found no effect of treatment on jackdaws' responses to playbacks, with females behaving in a similar manner following simulations of their partner's infidelity, their neighbour's infidelity and a congruent control. There were no significant differences in females' initial response (looking at the nest box entrance, peeking out of the nest box entrance or leaving the nest box) or the duration of the response (time spent looking at, or out of, the nest box entrance). However, females appear to habituate to playbacks over time, as the length of time females spent investigating the stimulus (looking at or out of the nest box entrance) decreased over successive trials.

Each subject's initial response to the playback (looking at the nest box entrance, peeking out of the nest box entrance or leaving the nest box) was strongly influenced by the identity of the individual. Inter-individual variation between females was significant, with females' responses during their first trial strongly predicting their responses during subsequent trials, regardless of treatment. In terms of the duration of this response (time spent looking at/out of the nest box entrance), none of the test subjects behaved as predicted: I found no evidence of a stronger response to the 'Partner Incongruent' or 'Neighbour Incongruent' treatments compared to the 'Congruent' control. Two females looked/peeked for longer following the infidelity simulation of their partner compared to the control playback, but this may be because these subjects heard their partner's infidelity simulation first. Overall, these results suggest that individual variation likely plays an important role in influencing subjects' responses in these types of experiments, yet these individual differences are rarely examined or discussed explicitly in studies of cognition (Cauchoix et al., 2018; Griffin et al., 2015; Sih & Del Giudice, 2012).

Although these results do not provide any evidence that jackdaws track their own relationships and the relationships of others in their social group, this does not necessarily imply that jackdaws are incapable of third-party relationship recognition. Instead, it may be that birds simply failed to demonstrate this ability within the context of my experimental setup. The fact that females failed to respond to simulations of their own partner's infidelity, as well as the infidelity of a male neighbour, is consistent with this possibility. Whilst a larger sample size may yield an effect of playback treatment, the fact that none of the focal females responded to playbacks as predicted suggests that this is unlikely. There are several other potential explanations as to why female responses did not differ between experimental treatments. Firstly, the experiment was carried out during an ecologically relevant period when birds were copulating at a high rate compared to other stages in the breeding attempt. It may be that if copulation calls are heard frequently around the colonies at this time, individuals attend to (or ignore) all copulation calls equally. Moreover, it is possible that females do not discriminate between the copulation calls of individual males (although jackdaw contact calls are individually distinct, Stowell et al., 2016; and were included in playback sequences to simulate interactions between individuals). Furthermore, if extra-pair copulations are extremely rare (Henderson et al., 2000; Liebers & Peter, 1998), females may not perceive the playback stimulus as an 'infidelity'. However, recent evidence (Gill, 2016) and observations of intruder males in my study population suggest that extra-pair copulations in jackdaws may occur more commonly than previously thought. For this reason, it seems that it would be beneficial for females to notice when their partner is copulating with another female. If females do perceive the playback stimulus as an 'infidelity', perhaps there is no advantage to females in acting on this information (e.g. by leaving the nest to gather more information, or to retaliate against their unfaithful partner; Valera, Hoi, & Krištín, 2003). In a similar experiment, Crockford et al. (2007) found that subordinate male baboons respond to playbacks of female copulation calls that were indicative of a recent consortship having ended, as these cues provide highly relevant information which may allow them to gain ‘sneaky’ matings. In my study it is possible that, if there is no direct fitness benefit to females, the social information indicating male infidelity is not attended to or acted upon to the same extent. The fact that nest intrusions occurred following two of the playback presentations (where another male entered the focal nest box and attempted to copulate with the resident female) raises the possibility that male jackdaws may eavesdrop on copulation events in a similar way to baboons (Crockford et al., 2007). It is also possible that males may respond more strongly than females to simulations of their partner’s infidelity (for logistical and ethical reasons, only females were tested here). Finally, if male infidelity does not reduce subsequent paternal care, there may be little cost to their female partner. Given the high degree of social monogamy in this species (Henderson et al., 2000), it may be that male extra-pair copulation does not merit a response from females. It would be interesting to determine whether male extra-pair copulation behaviour, or playback simulations of male infidelity, influence female behaviour over the long term (e.g. in terms of mate choice, see Mennill, Ratcliffe, & Boag, 2002).

Females showed habituation to playbacks over time, suggesting that there may be aspects of my experimental setup that were incongruent with naturally-occurring copulation events. For example, the timings of calls in the playback sequence may not be a reliable indication of two birds being in close proximity at the same time. Each playback sequence consisted of a male contact call and female contact call, followed by a copulation call from the same male (Supplementary Figure S1). A pause of two seconds occurred between each call, which represents natural calling rates for individual birds (unpublished data). Playbacks were conducted when the area was quiet and no other birds were heard calling, but in busy areas of the colony where calling is generally frequent, it may be that the calls of multiple birds are frequently heard together without any direct interaction between callers. The fact that all playback calls were emitted from the same direction may have provided an additional cue that calls represent a social interaction; on the other hand, call direction may be difficult for a female jackdaw to discern from inside a nest box. Observations of female responses to naturally-occurring copulation events and male infidelity may shed light on why females failed to respond to my playbacks, and would be an important avenue for future study.

It could be that jackdaws are more likely to respond to relationship changes that influence agonistic encounters, such as changes in dominance rank. Jackdaw colonies are structured according to a dominance hierarchy, with pairs competing for foraging opportunities and nest sites (Henderson & Hart, 1993; Röell, 1978; Salomons et al., 2007). Recognising changes in dominance rank may be of fitness relevance to birds in allowing them to gain access to resources whilst avoiding conflicts that are potentially costly. Playback experiments have demonstrated that primates recognise changes in dominance rank (Bergman et al., 2003; Borgeaud et al., 2013), and hyenas also appear to apply knowledge of third-party relationships during agonistic interactions (Engh et al., 2005; but fail to demonstrate this ability in other contexts, e.g. Holekamp et al., 1999). Unfortunately, jackdaws do not give dominance calls, which would make an experimental test of knowledge of third-party ranks logistically challenging. Other corvids have been shown to respond to simulated changes in dominance rank, both within their own social group and a neighbouring group (Massen, Pašukonis, et al., 2014). However, this study was conducted in captivity with small groups of birds housed in close proximity. Birds therefore had extensive opportunities to learn about social relationships by observing frequent interactions between all group members; it is currently unknown whether these opportunities occur similarly under natural conditions. Therefore, the extent of third-party relationships knowledge in the wild, and the contexts in which corvids apply this knowledge, remains to be determined.

This study presents one of the first experimental tests of third-party relationship recognition in a non-primate under natural conditions. To date, only one other field experiment has been conducted on birds, and suggests that acorn woodpeckers are aware of which individuals make up neighbouring groups (Pardo et al., 2018). However, it is unclear whether the act of calling together in woodpeckers provides any information about the nature of the dyadic relationship between callers. Here, I used copulation calls, which are directed at specific individuals during a specific type of social interaction, to investigate dyadic and third-party relationship representation. I found no evidence that jackdaws track their own relationships and the relationships of other individuals in their social group. However, I cannot rule out that jackdaws possess this ability, as none of the test subjects responded in a manner consistent with the experimental predictions. Moreover, due to the difficulties in obtaining a sufficient number of calls from close neighbours in the experimental colonies, my sample size (n=10) is modest (see Methods). My sample size is in line with similar studies of corvids in captivity, both for tests of social cognition and cognitive abilities more generally (Dally, Emery, & Clayton, 2006; Kondo et al., 2012; Massen, Pašukonis, et al., 2014; Mikolasch et al., 2013; Paz-y-Miño-C, Bond, Kamil, & Balda, 2004; Seed, Tebbich, Emery, & Clayton, 2006). It could be that under natural conditions, where subjects' attention is divided and there are more confounding environmental variables, larger sample sizes are required to detect an effect. This emphasises the need to complement research in the laboratory with rigorous field studies addressing questions related to social cognition.

A growing body of research, both observational and experimental, shows that species that live in complex societies possess knowledge of third-party relationships and other socio-cognitive abilities considered to be relatively 'sophisticated'. To date, many of these studies have been carried out using captive populations, with field studies mostly confined to primates. More studies are needed in a wider range of species and social systems, especially in a field context where findings may be more likely to accurately reflect the cognitive processes animals use to solve real-world socio-ecological challenges (Pritchard et al., 2016; Thornton & Lukas, 2012). Studies of this kind would make a valuable contribution to our understanding of social cognition in different species, and how these abilities help individuals to navigate a changing social world.

# Supplementary Material for Chapter 4: Testing relationship recognition in wild jackdaws

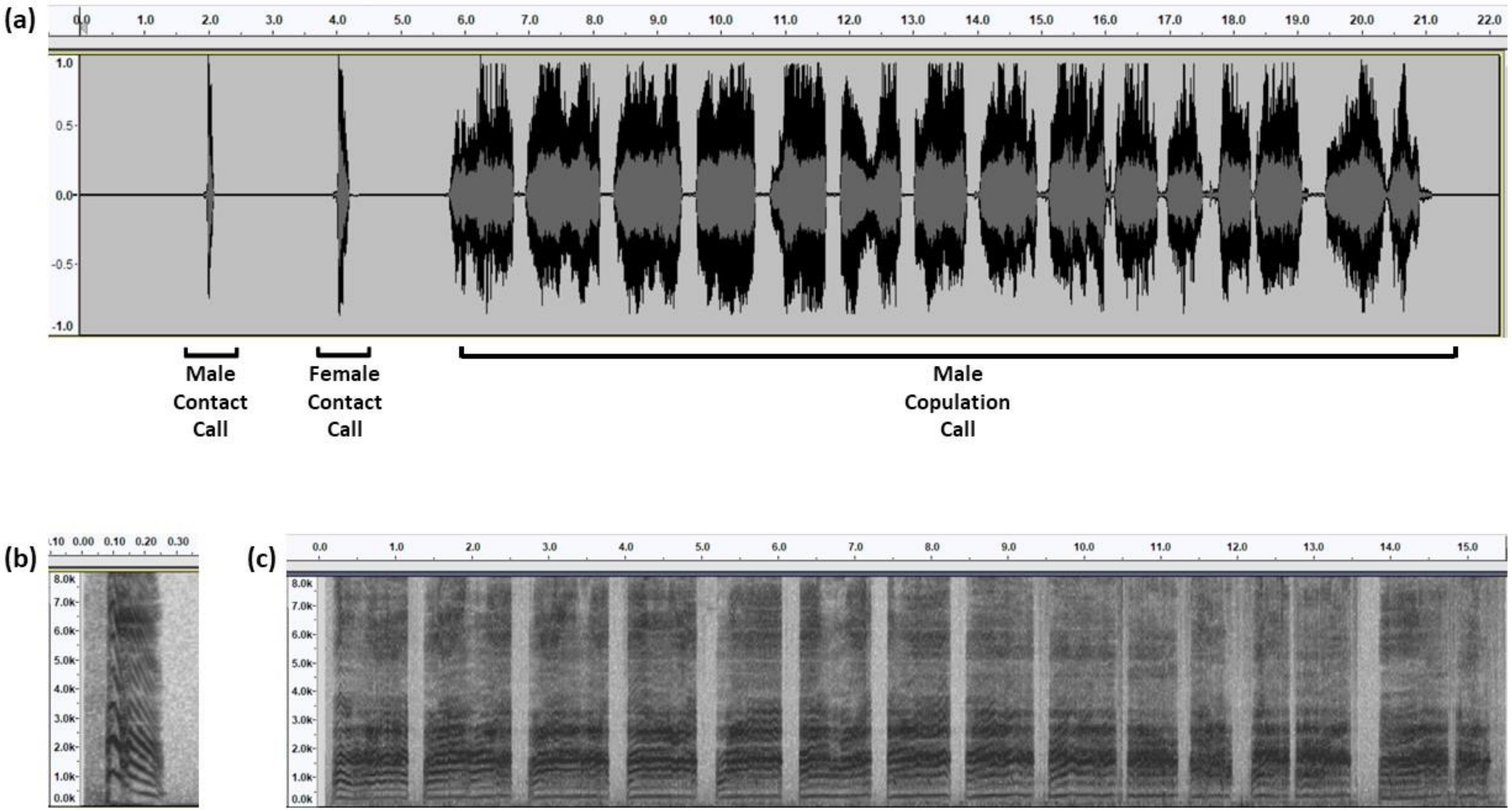


**Fig. S1: Diagram showing structure of playbacks.** a) Waveform of a playback track simulating infidelity at a neighbouring nest box. Each sequence was comprised of a male contact call, a female contact call and a copulation call from the same male. Male copulation calls varied in length; this variation was retained to avoid over-editing important call features and was later controlled for statistically; b) Spectrogram of a jackdaw contact call; c) Spectrogram of a jackdaw copulation call.

# Chapter 5

# Do jackdaws use anthropogenic objects to assess risk during encounters with people?

## Abstract

In habitats dominated by human activity, being able to discriminate between dangerous and non-threatening people may allow animals to avoid danger and exploit anthropogenic resources. When faced with a dangerous human, individuals that attend to relevant cues and integrate this information with previous experience are more likely to respond appropriately. However, little is known about the cognitive demands associated with gathering this information, and how these cognitive abilities facilitate survival in a changing world. It is often reported anecdotally that corvids in persecuted populations flee more readily from people carrying shotguns than people carrying similarly-shaped objects such as walking sticks, suggesting that corvids integrate information about anthropogenic objects in their assessment of risk. Here, I provide the first experimental test of this hypothesis by presenting wild jackdaws (*Corvus monedula*) with unfamiliar people carrying guns and wooden sticks. Birds did not show a heightened fear response to people carrying guns in two different experimental contexts, suggesting that existing anecdotal evidence may not be as widely representative of corvid behaviour as previously thought. Jackdaws also habituated to experimental presentations over time, highlighting a potential mechanism by which these birds learn about anthropogenic threats. Initial wariness followed by rapid habituation may allow jackdaws to exploit a wide range of habitats and thrive in a rapidly changing landscape.

## 5.1. Introduction

Although humans are often perceived by organisms as equivalent to natural predators in terms of threat (Conover, 1987; Frid & Dill, 2002; McLean, Smith, & Stewart, 1986; Murphy, 2006), fear of humans and habituation to human disturbance is often overlooked in discussions of traits adaptive in anthropogenic habitats (Carrete & Tella, 2013; Greggor et al., 2014; Hockings et al., 2015). Differences in behavioural responses to human disturbance may have an important influence on the success of individuals and species in coping with human-induced environmental change (Blumstein, Fernández-Juricic, Zollner, & Garity, 2005; Pelletier & Garant, 2012; Pirotta et al., 2018; Tuomainen & Candolin, 2011). For example, individuals or species that are intolerant of human presence are likely to show heightened antipredator responses (such as vigilance behaviour), limiting time and energy available for foraging (Thomas et al., 2002). Similarly, human presence at a breeding site may reduce offspring provisioning and result in inadequate parental care (Fernández & Azkona, 1993; Verhulst et al., 2001). Maladaptive responses and a lack of habituation to nonthreatening stimuli can therefore reduce individual survival and reproductive success, which (if widespread) may compromise population persistence (Pirotta et al., 2018). Conversely, individuals or species that habituate quickly to human disturbance, and/or are able to discriminate between threatening and nonthreatening people, may be more successful in human-altered landscapes (Carrete & Tella, 2013; Gravolin, Key, & Lill, 2014; Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2015; Tuomainen & Candolin, 2011).

In some cases, such as where populations suffer active persecution, fear of humans may be highly beneficial in allowing animals to avoid danger. However, exhibiting an inappropriate fear response to all humans would prevent wildlife from exploiting anthropogenic resources (e.g. in urban areas or farmland). Instead, it may benefit individuals to refine escape decisions by distinguishing between ‘dangerous’ and nonthreatening people. Indeed, experimental evidence indicates that some species (woolly monkeys *Lagothrix poeppigi,* Papworth, Milner-Gulland, & Slocombe, 2013; jackdaws *Corvus monedula,* Davidson, Clayton, & Thornton, 2015; elephants *Loxodonta africana,* Bates et al., 2007) assess risk during encounters with humans based on previous experience, although it is not always clear which cues are used to do so (Papworth et al., 2013). For example, attending to objects associated with dangerous people, such as guns being carried by hunters, may allow individuals to assess risk more effectively, but this has yet to be tested. Discriminating between threatening and nonthreatening stimuli, remembering relevant cues and applying previous experience in novel situations may be cognitively demanding (Sih et al., 2011). Therefore, we may expect stronger selection for these abilities in habitats where humans and wildlife coexist, and for species with these cognitive abilities to be more successful under human-induced rapid environmental change (Barrett et al., 2018; Greggor et al., 2014; Roth & Krochmal, 2015).

Corvids provide ideal model systems for investigating how cognitive abilities influence success in anthropogenic habitats. In the UK, corvid populations have increased consistently over recent decades, thriving in urban areas and on agricultural land by taking advantage of clumped, abundant resources made available by human activity (Gregory & Marchant, 1996; Harris et al., 2018). This has contributed to their resulting status as a crop pest, with persecution of corvids permitted under licence in the interests of agriculture and public health

(Wildlife and Countryside Act, 1981). However, not all people will be involved in this persecution: consequently, corvids show remarkable discrimination and learning abilities when encountering humans. For example, several studies show that corvids are able to discriminate between individual humans and associate these cues with previous experience (Davidson et al., 2015; Marzluff, Walls, Cornell, Withey, & Craig, 2010; see Chapter 6), and incorporate subtle human gaze cues in assessing predation risk (Bugnyar, Stowe, & Heinrich, 2004; Clucas, Marzluff, Mackovjak, & Palmquist, 2013; Lee et al., 2013; von Bayern & Emery, 2009). Positron emission tomography has identified how these different threats are represented in the corvid brain, suggesting that whilst corvids have an innate fear of natural predators, fear of dangerous humans is a learned response with associations being formed between identity of novel humans and the level of risk they pose (Cross et al., 2013; Marzluff et al., 2012). With regards to persecution, an early study of American crows found differences in nest defence behaviours in urban areas, where crows are protected, and in rural areas where they are persecuted (Knight, Grout, & Temple, 1987). Anecdotal reports also suggest that in areas where corvids are persecuted, birds flee more readily in response to a person holding a shotgun rather than a wooden stick, even before the gun is fired. This idea has received much attention in the media (Creagh, 2011; Forgrave, 2015) and popular science (Marzluff & Angell, 2005, 2012), and appears to be widely accepted despite a lack of empirical evidence.

This study aimed to address this research gap by investigating whether wild corvids infer threat based on the objects being carried by unfamiliar people. Specifically, I conducted two field experiments to test whether free-living jackdaws (*Corvus monedula*) exhibit a stronger response when encountering a human holding a gun rather than a wooden stick. Jackdaws are common in agricultural and urban habitats across Europe, and are frequently targeted as pests (BirdLife International, 2018; Wildlife and Countryside Act, 1981) due to their tendency to exploit anthropogenic resources, including food and breeding sites (Gregory & Marchant, 1996). Like other corvids (Bugnyar et al., 2004; Clucas et al., 2013; Lee, Lee, Choe, & Jablonski, 2011; Marzluff et al., 2010), jackdaws can learn to discriminate between individual people based on facial cues (Davidson et al., 2015; von Bayern & Emery, 2009). In the first experiment, I presented breeding pairs of jackdaws with an unfamiliar person sitting near their nest holding either a gun or a wooden stick of equivalent dimensions. I also investigated whether jackdaws use the orientation of objects as an indication of danger, predicting that birds would respond more strongly to an object being pointed in their direction rather than held horizontally across the experimenter's lap. By presenting jackdaws with guns and wooden sticks at their nest boxes (Experiment 1), I was able to target known individuals and control for any inter-individual differences in behaviour. However, as jackdaws are perhaps more likely to be targeted by hunters away from the nest box (e.g. whilst foraging), a second experiment was run to determine whether jackdaws respond similarly to anthropogenic objects presented in different contexts. To complement the data collected at nest boxes, a flight initiation distance (FID) experiment was carried out at feeding tables to investigate whether jackdaws flee more readily from an approaching human carrying a gun rather than a wooden stick.

## 5.2. Methods

### 5.2.1. Study Population

Experiments were conducted on free-living jackdaws at two study sites in Cornwall, UK (Stithians: 50°11′26″N, 5°10′51″W; Pencoose: 50°11′56″N, 5°10′9″W). Nest box presentations (Experiment 1) were carried out in 2016, and the flight initiation distance experiment (Experiment 2) was carried out in 2018, both during the jackdaw breeding season. Test subjects were members of nest box populations maintained by the ongoing Cornish Jackdaw Project (although not all birds present at the sites use nest boxes). At both field sites, resident jackdaws have experience of humans walking around the area – nest boxes at Pencoose are concentrated within an active farmyard and surrounding fields, while nest boxes at Stithians are located around a churchyard (used by the public) and nearby farmland (including public footpath). Jackdaws also frequently encounter fieldworkers during the nesting season, who check breeding progress daily using nest box cameras, remove chicks from nest boxes for weighing, ring adults and chicks and conduct various experiments at nest boxes and feeding tables. Whilst most other pedestrians are ignored, birds typically monitor researchers from a safe distance and give alarm calls, suggesting that some people are considered a threat (*pers. obs.*). Corvids, including rooks and jackdaws, have long been targeted in and around our study sites and shooting occurred in the area during the years prior to both experiments being carried out (*pers. obs.*). Several anecdotal reports suggest that jackdaws in the area will flee at the sight of a person carrying a gun (but not a person carrying a wooden stick), and most of the birds participating in the nest box presentations (Experiment 1) were at least 2 years old in 2016 (29/34). It was therefore considered that resident jackdaws at the study sites would have had some opportunity to learn about the dangers posed by humans carrying guns, and that this would be an ecologically relevant stimulus for test subjects.

### 5.2.2. Experiment 1: presentations at nest boxes

#### 5.2.2.1. Experimental Design

This experiment used a 2x2 factorial design to investigate whether jackdaws discriminate between a human holding a gun or a wooden stick, and whether the orientation of the object (held across the lap or pointed at the nest box) influenced birds' behavioural responses. Using a repeat measures design, focal birds were presented with four treatments at their nest box: a person holding a gun across the lap ('lap gun'); a person holding a stick across the lap ('lap stick'); a person pointing a gun at the nest box ('pointed gun') and a person pointing a stick at the nest box ('pointed stick'). To avoid pseudoreplication, three different gun stimuli and three wooden stick stimuli were used across the experiment (see Supplementary Figure S1). Gun stimuli were commercially available air guns with a shotgun-type design: due to changes to EU law in the weeks prior to the experiment (European Commission, 2015), I was unable to use deactivated 12-bore shotguns of the type commonly used to target corvids in the area; the airgun stimuli used were selected to resemble shotguns as closely as possible. The three air guns looked similar to each other, but were not identical. Likewise, wooden sticks were similar, but not identical: wooden sticks were cut to the same length as the guns and were of a similar diameter. Each focal pair encountered one of the sticks and one of the guns, allocated to ensure that individual sticks and guns were not consistently presented together and that no objects were overrepresented. Given that jackdaws and other corvids have been shown to recognise individual human faces (Cornell et al., 2012; Davidson et al., 2015), a mask and hat were worn during stimulus presentations to reduce any effect of familiarity with the experimenter. To avoid any potential confounding effects from a given mask, two masks were used for this experiment, with the same hat worn consistently with each mask (see Supplementary Figure S2). The identity of the mask was allocated at random for each box, and used for all trials at that box. Experimenters also wore a large raincoat to minimise body shape and gait cues, and clothing was kept consistent for all trials.

The study was carried out in early May, when adult birds were provisioning young nestlings and females were still spending some time incubating chicks. The first trial occurred 4-6 days after the first chick hatched in each nest. This was to ensure that the chicks would be young enough for the parents to be motivated to return to the box quickly, but that the health of chicks would not be compromised should the parents fail to return for the duration of the experimental trial. Subsequent trials were carried out on consecutive days, at a similar time (all trials at a given nest box were carried out in the same two-hour time period). Four trials (one per treatment) were carried out at 17 nest boxes in total (n=68 trials; 6 nest boxes at Stithians and 11 nest boxes at Pencoose). The order in which treatments were presented was randomised and balanced across the experiment as a whole, and effects of treatment order were later controlled for in statistical analyses.

#### 5.2.2.2. Experimental Trials

Before the start of the trial, the experimenter set up a chair approximately 30 m away and directly in line with the entrance of the focal nest box. Behind this, a camcorder (Panasonic HC-X920) and tripod were set up to record a close-up view of activity at the box, as well as a smaller camera (SJcam M10) to record a wide-angle view of the nest site that incorporated the experimenter in the chair. This was done to record the behaviour of birds on approach to the nest box, and control for any influence of experimenter behaviour (e.g. slight, inadvertent movements). Cameras were covered to protect from rain, but identical rain covers were used in all trials regardless of weather conditions.

Following setup, the experimenter left the area and returned to a concealed location to put on the mask and hat. The experimenter then approached the chair (whilst carrying the gun or stick horizontally), started the recording on both cameras and set a timer before sitting down. Once seated, the experimenter would arrange the object in the correct orientation (across the lap, or pointing at the box with the aid of a small stand) and remain motionless for 30 minutes with gaze directed towards the nest box entrance. Trials ended when the timer sounded, after which the experimenter turned off cameras, collected all equipment and left the area. Masks were not removed until the experimenter had returned to a concealed location. All trials at a given nest box were carried out by the same experimenter. I carried out trials at 14 nest boxes (n=56 trials), and trials at the remaining three nest boxes were carried out by a second experimenter using the same protocol (n=12 trials).

### 5.2.2.3. Behavioural Analysis

Videos of experimental trials were analysed using the open-source software BORIS (Friard & Gamba, 2016). From the close-up view captured by the HD camcorder, I recorded when focal birds landed on the nest box, entered the nest box and gave alarm calls. The identity of alarm calling birds was recorded where possible, using footage from both close-up and wide-angle footage and/or experimenter observation. The footage from the wide-angle camera was then aligned to the nest box footage using the built-in ‘offset’ function in BORIS. Using the wide-angle view, I recorded when birds returned to and departed from the area of the nest box (defined as landing within view of the wide-angle camera, usually in a tree or building). All focal nest boxes had at least one colour-ringed bird, enabling identification of individuals. Behaviours of both males and females were recorded, and analyses were carried out at the level of the individual (controlling for nest box ID). Trial start times were recorded, beginning when the experimenter sat in the chair (trial setup times were excluded). In cases where females were present in the nest box at the start of the trial, individual trial start times were recorded from when females first saw the experimenter.

A second coder who was blind to treatment coded around 20% of the videos. Inter-rater reliability was calculated for all behaviours recorded from the videos using the *irr* package in R (Gamer et al., 2012), and showed high agreement between coders in all cases (first return to vicinity of nest box: ICC=0.816, P<0.001; return to vicinity prior to first landing on the nest box: ICC=0.99, p<0.001; first landing on nest box: ICC: 1, P<0.001; first entry to nest box: ICC=1, P<0.001; time spent in vicinity over whole trial: ICC=0.98,p<0.001; time spent in box over whole trial: ICC=1, P<0.001).

### 5.2.2.4. Statistical Analysis

All analyses were carried out in R (R Core Team, 2017). Response variables were calculated from the behaviours recorded in the experimental footage, and general linear mixed models (GLMMs) were built using the *lme4* package (Bates, Maechler, Bolker, & Walker, 2015). Numeric response variables were

Box-Cox transformed prior to inclusion in models, and models were simplified using log-likelihood ratio tests.

### *Landing on the nest box*

Previous research on this species (Davidson et al., 2015; see also Chapter 6) suggests that jackdaws are quicker to approach their nest box when faced with a human threat, possibly to defend chicks and monitor the potential predator. I investigated the latency of birds to approach their nest box after first seeing the experimenter (see below), and also analysed whether the object held by the experimenter influenced the tendency of birds to return to the nest box at all. Whether birds landed on the nest box during a trial was analysed using a binomial GLMM with a binary response variable (1=Yes, 0=No). Trial number (1-4), object (gun/stick), orientation (pointing/lap) and the sex of the jackdaw (male/female) were included as fixed effects. An interaction between trial number and sex was included after inspection of exploratory plots (as preliminary analysis showed no interaction between object type and orientation, this interaction was omitted to avoid overfitting). Analysis was carried out at the level of the individual, with subject ID (nested within nest box) included as a random effect. This gave a sample size of n=136 (one male and one female from each of 17 nest boxes, presented with four trials at each nest box).

### *Entering the nest box*

Landing on the nest box may represent different responses to experimental stimuli, depending on whether birds remain on the nest box to monitor the threat or enter the box to feed chicks (Davidson et al., 2015; Greggor et al., 2018; Greggor, Spencer, Clayton, & Thornton, 2017). As above, whether birds entered the nest box during a trial (1=Yes, 0=No) was analysed using a binomial GLMM. Trial number (1-4), object (gun/stick), orientation (pointing/lap) and sex (male/female) were included as fixed effects, as well as the interaction between trial number and sex. Again, this analysis was carried out at the level of the individual (n=136), with subject ID (nested within nest box) included as a random effect.

*Time taken to approach nest box*

In similar experiments, jackdaws have been shown to return more quickly to their nest box when presented with a person previously identified as dangerous (through individual learning e.g. Davidson et al., 2015; or social learning, see Chapter 6). This may allow birds to defend their nest and monitor the threat; however, this may not be an appropriate strategy when the person is holding a gun. To determine whether birds were more hesitant to approach the nest box when faced with a person holding a gun, I calculated the time that individuals spent in the vicinity prior to first landing on the nest box. Approach time was included as the response variable in a Gaussian LMM, with trial number (1-4), object (gun/stick), orientation (pointing/lap) and sex (M/F) as fixed effects and an interaction between object and orientation (there was no discernible effect of an interaction between trial number and sex in this case, so this term was omitted to avoid overfitting). Subject ID (nested within nest box) was included as a random term. This model included 77 observations of 29 individuals (15 females and 14 males) at 16 nest boxes, after excluding cases where birds did not return to the nest box (n=50) or reliable measures could not be obtained due to poor lighting (n=9).

### *Latency to enter nest box after seeing object*

Again, returning quickly to the nest box may reflect differing responses to the human stimulus, depending on whether birds spend time on the nest box monitoring the threat or immediately enter the box to feed or incubate chicks, which involves losing sight of the person. To determine how long birds took to enter the nest box after first seeing the object, I calculated the length of time taken for birds to enter the nest box after first returning to the vicinity (appearing in the wide-angle footage). The behaviour of birds on their return to the vicinity of the nest suggested that they were attending closely to the experimenter (characterised by a gradual approach to the nest, orientation of the head towards the experimenter and frequent head saccades); therefore subjects are highly likely to have seen the object held by the experimenter. Latency to enter the nest box after first seeing the object was included as the response variable in a Gaussian LMM with trial number (1-4), object (gun/stick), orientation (pointing/lap) and sex (M/F) as fixed effects, an interaction between object and orientation, and subject ID nested within nest box as a random term. This model included 82 observations from 27 birds (14 females and 13 males) in 16 nest boxes, after excluding cases where birds did not enter the nest box during a trial (n=54).

### *Time spent vigilant*

To investigate whether birds spent more time vigilant when presented with a person holding a gun – as opposed to foraging or engaging in other activities – I quantified the length of time birds spent around the nest box over the whole trial (visible in the wide-angle footage) without entering the nest box to feed the chicks. Trial number (1-4), object (gun/stick), orientation (pointing/lap) and sex

(M/F) were included as fixed effects in a Gaussian LMM, with an interaction between object and orientation and subject ID (nested within nest box) as a random effect. 114 observations from 34 birds (17 females and 17 males) in 17 nest boxes were included in this model, after excluding cases where subjects did not return to the vicinity during the trial (15 cases).

*Time spent in nest box*

As cavity nesters, jackdaws typically respond to risk by leaving the nest to obtain more information about the potential threat (*pers. obs.,* see also Schneider & Griesser, 2013). Given that entering the nest box to feed or incubate chicks prevented birds from effectively monitoring the person sitting outside the nest box, spending longer periods of time inside the nest box (as birds are motivated to do when chicks are young) implies that subjects may be less afraid of the experimenter. To investigate this possibility, the length of time birds spent in the nest box over the whole trial was included as the response term in a Gaussian LMM. Fixed terms included trial number (1-4), object (gun/stick), orientation (pointing/not pointing) and the interaction between object and orientation. Subject ID was included as a random term. Separate models were constructed for males and females due to heterogeneity of variance between sexes in the response variable (see Supplementary Figure S3). Males typically spent a short length of time in the nest box during trials, whereas females showed more variability in response: this is to be expected given that females are primarily occupied with incubation at this stage in the reproductive attempt. Models included 44 observations from 14 females and 38 observations from 13 males, after excluding cases where individuals did not enter the nest box (24 cases for females; 30 cases for males).

### 5.2.3. Experiment 2: flight initiation distance (FID)

#### 5.2.3.1. Experimental design

*Feeding tables*

Early in the 2018 breeding season, two feeding tables were set up at each of the two study sites where nest box presentations were carried out in 2016 (Stithians and Pencoose). Feeding tables were wooden platforms 60 cm x 50 cm in size, attached to a post approximately 1.5 m high. Tables were located away from nest boxes, in open areas where birds are known to forage frequently. As distance to cover is known to influence the distance at which birds flee from approaching danger (Stankowich & Blumstein, 2005), all feeding tables were located a standardised distance from nearby trees (<5m), in which birds often perched before and after visiting the feeding table. To minimise any effects of starting distance on FID (Blumstein, 2003), a hide was set up at a similar distance from each feeding table (c. 80 m) from which the experimenter emerged. Hides and feeding tables remained in place throughout the experiment (March-May). Starting two weeks prior to the experiment, feeding tables were baited daily with a mixture of bread and grain and were regularly visited by jackdaws.

*Presentation stimuli*

To investigate whether jackdaws flee more readily from a person holding a gun, the experimenter approached birds at feeding tables whilst carrying one of three objects: a gun (dangerous object), a wooden stick (non-threatening object), or a bag of food (positive control). Three gun and stick replicates were used during the experiment, and were identical to those presented at nest boxes in 2016. The bag of food used during experimental approaches was the same bag used to bait tables prior to and throughout the experiment. The order in which objects were presented was counterbalanced at each feeding table and across sites. As in nest box presentations (Experiment 1), a mask, hat and large coat were worn during experimental approaches to avoid any effects of familiarity with the experimenter. Three different masks were worn at each site, with each mask allocated to a different treatment at each site. Masks were different to those worn during Experiment 1, and were unfamiliar to the birds at both sites (Supplementary Figure S4).

#### 5.2.3.2. Experimental trials

Trials were carried out between 06:00-12:00 from late March to early May 2018, covering the jackdaw breeding season from the nest-building stage to early chick rearing. On arrival at the site, the experimenter set up a small hidden camera on the feeding table (SJcam M10) and baited the table with a mixture of oats and cheese. The experimenter then retreated to the hide and set up a HD camcorder (Panasonic HC-X920) to record the experimental approach for data verification. Inside the hide, the experimenter also put on the coat, mask and hat. When birds had returned to normal behaviour and there was no other disturbance in the area, the experimenter emerged from the hide carrying the object (gun/stick/food bag) while at least one colour-ringed bird was feeding on the table (the ‘target bird’). After stepping away from the hide, the experimenter approached the feeding table at a rate of 1m/sec (measured with a metronome smartphone app). The experimenter dropped weights to mark the distance at which the target bird left the feeding table (FID1) and the distance at which all birds in the area left the trees surrounding the feeding table (FID2). The experimenter continued to approach to within 5 m of the feeding table before returning to the hide at the same pace. After the trial, the experimenter removed the mask, hat and coat and waited for birds to return to the feeding table. Once birds resumed normal behaviour, the experimenter emerged from the hide, collected recording equipment and took FID measures. Feeding tables were baited again before the experimenter left the area. At least 24 hours elapsed between approaches at a given table.

In total, 83 trials were carried out across the four feeding tables. On 21 occasions the experimenter was unable to approach the feeding table or obtain a measure of FID due to disturbance, poor weather or low visitation rates. This resulted in 62 successful approaches: 20 carrying a gun, 20 carrying a wooden stick and 22 control trials (carrying the bag of food).

#### 5.2.3.3. Statistical analysis

All analyses were carried out in R (R Core Team, 2017). Models were built using *lme4* (Bates et al., 2015) and simplified using log-likelihood ratio tests, after ensuring assumptions were met (normality and homogeneity of residuals).

*FID1: FID for target bird on feeding table*

The flight initiation distance of the target bird on the feeding table (FID1) was analysed using a linear mixed model (LMM) with a Gaussian error distribution. Treatment (gun/stick/control) were included as fixed effects, along with trial number. An interaction term (treatment x trial number) was included to investigate potential differences in habituation rates between treatments. Table ID was included as a random effect. This model contained 52 observations across four feeding tables: 8 trials were excluded where birds left the table too quickly to obtain a measure of FID1, and two erroneous outliers were removed (in one case, the target bird had been replaced by a second bird without the experimenter’s knowledge; in the second case foggy conditions meant that the target bird may not have had a clear view of the experimenter approaching the table).

*FID2: FID for last bird to leave area*

The distance at which the last bird left the trees surrounding the feeding table (FID2) was analysed in the same way as for FID1. The LMM contained treatment (gun/stick/control) and trial number as fixed effects, with an interaction term and Table ID as a random effect. This model comprised the full sample size (n=62), as the experimenter was able to obtain accurate measures of FID2 in all trials.

## **5.3 Results**

### **5.3.1. Experiment 1: presentations at nest boxes**

*Frequency of scolding*

When encountering a threat, jackdaws give repetitive, rattling alarm vocalisations (known as ‘scold’ calls) to recruit other birds to a mob (McIvor, Lee, & Thornton, 2018; Woods et al., 2018). Although jackdaws in our study population often scold researchers who handle chicks (see *Study Population*), scolding did not occur often enough during experimental trials to permit formal analysis. 15 focal birds from 12 nest boxes scolded the experimenter in 30/68 trials. Males scolded more often than females (scolds were recorded from 10 males and 5 females), but females that scolded gave a higher number of calls per trial (median 7.5 calls) than males (median 2.5 calls per trial). The number of birds scolding was approximately evenly distributed across treatment groups and showed no consistent trial order effect (see Supplementary Figures S5 and S6).

### *Landing on the nest box*

The object held by the experimenter (gun/stick) did not influence whether focal birds returned to the nest box during trials ($X^2$=2.47, df=1, p=0.12; Supplementary Figure S7). Likewise, whether the object was pointed at the nest box or held across the experimenter’s lap had no significant effect ($X^2$=0.72, df=1, p=0.40). However, birds were more likely to return to the nest box in later trials than in earlier trials. This effect was stronger for males, who showed a lower return rate than females in early trials (trial number x sex interaction: $X^2$=4.15, df=1, p=0.042; Figure 5.1a, Table 5.1).

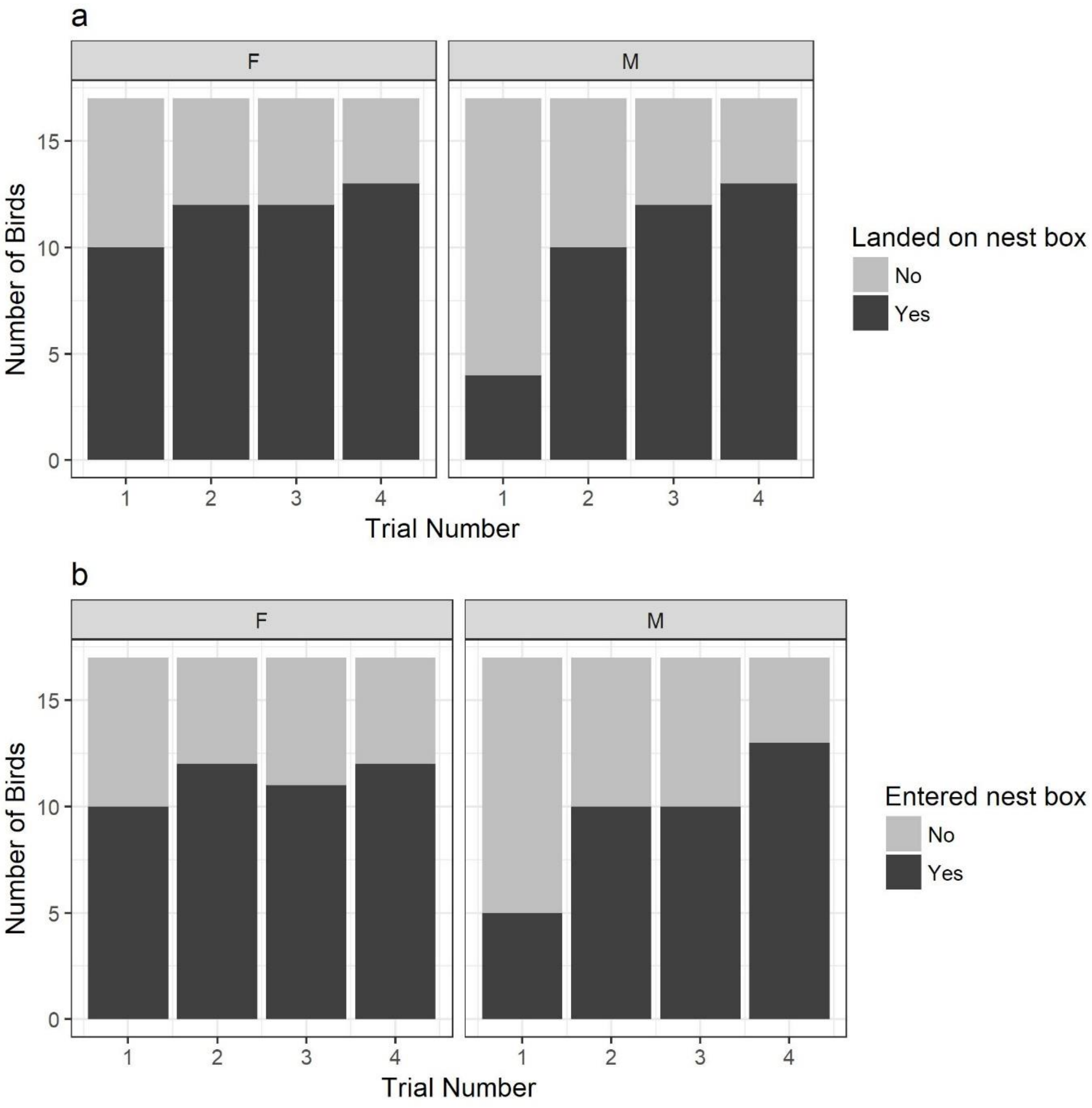


**Figure 5.1:** Number of birds that (a) landed on the nest box and (b) entered the nest box during trials, by trial number (1-4). Left panels show data for females, and right panels show data for males. N=136 observations from 68 trials at 17 nest boxes.

### *Entering the nest box*

Whether the experimenter was holding a gun or a stick had no significant effect on the tendency of birds to enter the nest box ($X^2$=1.31, df=1, p=0.253). However, the orientation of the object showed a non-significant trend, with birds being less likely to enter when faced with an object pointing at the nest box rather than held across the experimenter's lap ($X^2$=3.43, df=1, p=0.064; Supplementary Figure S8). Birds were more likely to enter the nest box and feed chicks in later trials than in earlier trials, with a stronger effect seen among males (trial number x sex interaction: $X^2$=4.44, df=1, p=0.035; Figure 5.1b, Table 5.1).

### *Time taken to approach nest box*

The length of time between birds returning to the area and landing on the nest box on their first visit did not differ significantly between treatment groups (object: $X^2$=0.05, df=1, p=0.820; orientation: $X^2$=0.24, df=1, p=0.621; object x orientation interaction: $X^2$=0.35, df=1, p=0.552). Approach times were also broadly similar across trials (trial number: $X^2$=1.29, df=1, p=0.256) and were not influenced by the sex of the focal bird (sex: $X^2$=1.38, df=1, p=0.241; Table 5.1).

### *Latency to enter the nest box after seeing object*

Subjects did not take longer to enter the nest box after seeing the experimenter holding a gun rather than a stick ($X^2$=0.11, df=1, p=0.743). Latency to enter the nest box was not affected by whether the object was pointing at the nest box ($X^2$=0.02, df=1, p=0.886), regardless of whether the object was a gun or a stick (object x orientation interaction: $X^2$=0.13, df=1, p=0.711). Trial number had a significant effect on the latency of birds to enter the nest box, with birds returning more quickly in later trials than in earlier trials ($X^2$=6.34, df=1, p=0.012;

Figure 5.2, Table 5.1). These patterns were similar for both males and females (sex: $X^2$=0.23, df=1, p=0.634).

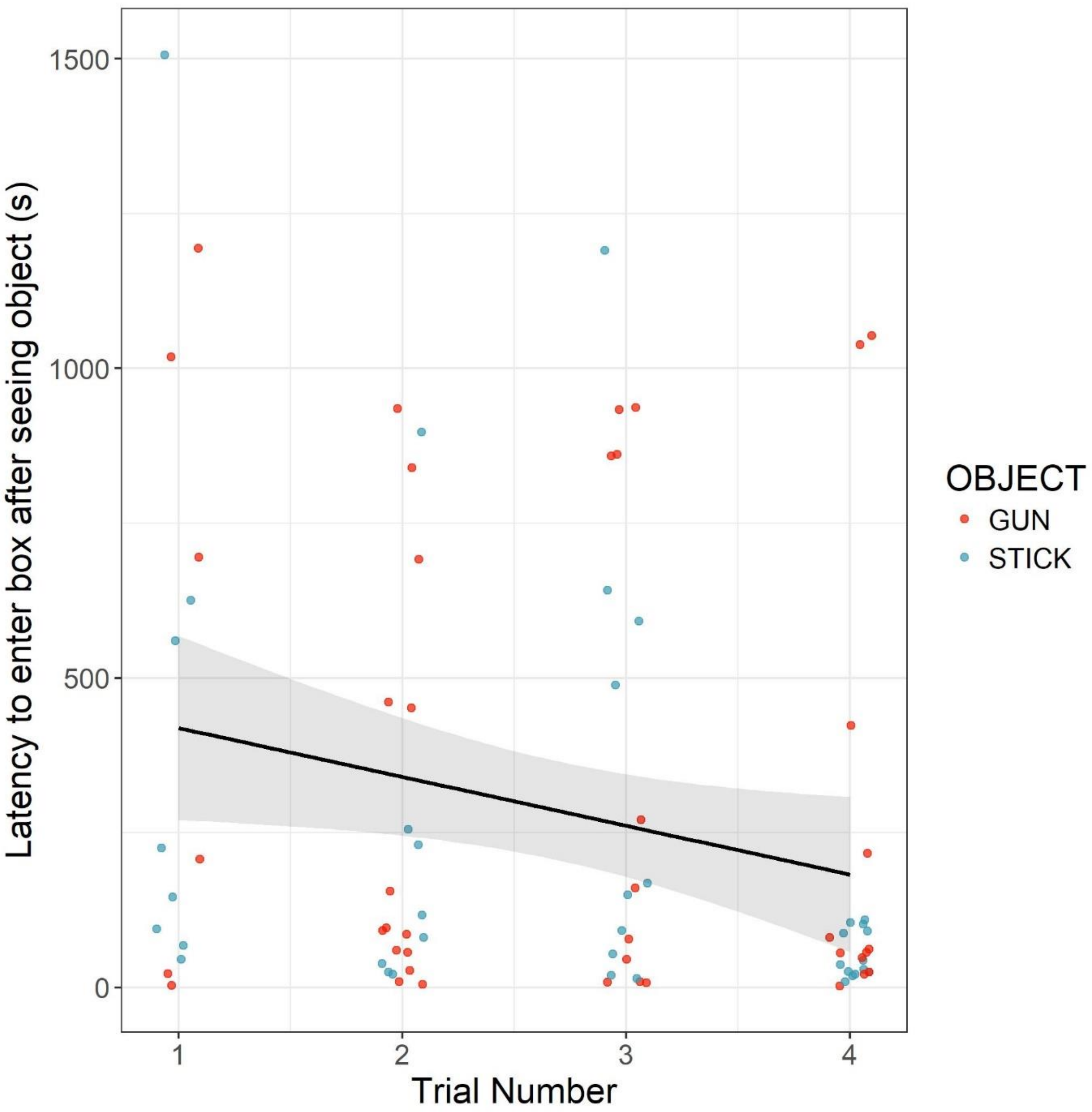


**Figure 5.2:** Time taken by subjects to enter the nest box after first returning to the vicinity and seeing the experimenter holding the object (gun/stick) by trial number (1-4). N=82 observations from 27 birds at 16 nest boxes.

### *Time spent vigilant*

The length of time that birds spent engaged in vigilance behaviour on the nest box and in the vicinity was similar between treatment groups (object: $X^2$=0.29, df=1, p=0.588; orientation: $X^2$=2.11, df=1, p=0.146; object x orientation interaction: $X^2$=1.06, df=1, p=0.303). Time spent vigilant did not differ between males and females (sex: $X^2$=0.41, df=1, p=0.521) but did decrease significantly over time, as more trials were conducted at the nest box (trial number: $X^2$=6.56, df=1, p=0.010; Figure 5.3, Table 5.1).

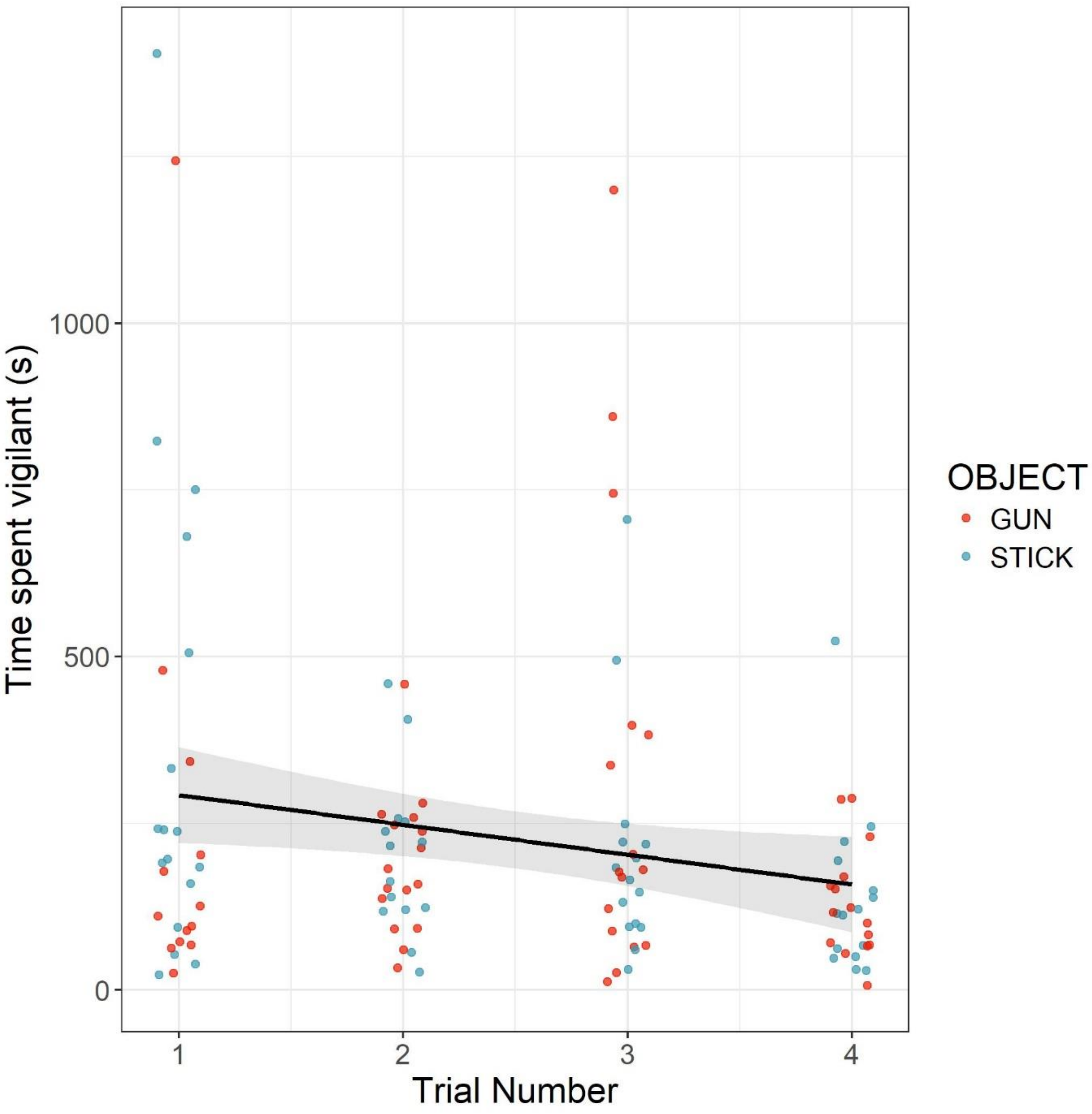


**Figure 5.3:** Time spent engaged in vigilance behaviour on the nest box and in the area over the whole trial, by trial number (1-4). N=144 observations from 34 birds in 17 nest boxes.

### *Time spent in nest box*

Females spent a similar length of time inside the nest box regardless of the object held by the experimenter, and whether the object was pointed at the nest box or held horizontally (object: $X^2$=0.69, df=1, p=0.405; orientation: $X^2$=0.51, df=1, p=0.474; object x orientation interaction: $X^2$=0.15, df=1, p=0.694; Table 5.1). The length of time that females spent inside the nest box did not differ significantly as trials progressed (trial number: $X^2$=1.15, df=1, p=0.283). Similarly, the length of time spent inside the nest box by males did not differ between treatment groups (object: $X^2$=0.17, df=1, p=0.677; orientation: $X^2$=0.12, df=1, p=0.728; object x orientation interaction: $X^2$=0.24, df=1, p=0.626). However, there was a non-significant trend for males to increase the length of time spent inside the nest box in later trials (trial number: $X^2$=3.06, df=1, p=0.080; Table 5.1; Supplementary Figure S9).

**Table 5.1:** Output of GLMMs for Experiment 1 investigating the effects of object (gun/stick) and orientation of object (pointing/lap) on (a) whether birds landed on the nest box during a trial; (b) whether birds entered the nest box during a trial; (c) time taken to approach box; (d) latency to enter nest box after first seeing object; (e) time spent vigilant in the area during the trial; (f) time spent in the nest box by females; (g) time spent in the nest box by males. Where relevant, sex and trial number were included as additional fixed effects. Values derive from full models with significant effects shown in italics.

| **Model** | **Fixed and random effects** | | **β ± SE** | **t- or z-value** | **Variance ± SD** |
|---|---|---|---|---|---|
| (a) Landed on nest box | Intercept | | 1.52 ± 1.47 | 1.03 | |
| | *Trial number* | | *0.57 ± 0.38* | *1.50* | |
| | Object | Gun | (reference) | | |
| | | Stick | -0.95 ± 0.62 | -1.54 | |
| | Orientation | Lap | (reference) | | |
| | | Pointing | -0.45 ± 0.62 | -0.73 | |
| | *Sex* | *Female* | *(reference)* | | |
| | | *Male* | *-4.41 ± 2.05* | *-2.15* | |
| | *Trial number x sex* | | *1.20 ± 0.63* | *1.89* | |
| | Subject | | | | 6.38 ± 2.53 |
| | Nest box | | | | 4.99 ± 2.24 |
| (b) Entered nest box | Intercept | | 2.22 ± 1.72 | 1.29 | |
| | *Trial number* | | *0.38 ± 0.39* | *0.96* | |
| | Object | Gun | (reference) | | |
| | | Stick | -0.68 ± 0.63 | -1.07 | |
| | Orientation | Lap | (reference) | | |
| | | Pointing | -1.18 ± 0.68 | -1.74 | |
| | *Sex* | *Female* | *(reference)* | | |
| | | *Male* | *-4.75 ± 2.36* | *-2.01* | |
| | *Trial number x sex* | | *1.24 ± 0.63* | *1.96* | |
| | Subject | | | | 12.59 ± 3.55 |
| | Nest box | | | | 1.82 ± 1.35 |

**Table 5.1 *(continued)*:**

| **Model** | **Fixed and random effects** | | **β ± SE** | **t- or z-value** | **Variance ± SD** |
|---|---|---|---|---|---|
| (c) Approach time | Intercept | | 3.82 ± 0.45 | 8.45 | |
| | Trial number | | -0.17 ± 0.13 | -1.39 | |
| | Object | Gun | (reference) | | |
| | | Stick | 0.09 ± 0.36 | 0.26 | |
| | Orientation | Lap | (reference) | | |
| | | Pointing | 0.33 ± 0.36 | 0.91 | |
| | Sex | Female | (reference) | | |
| | | Male | 0.32 ± 0.27 | 1.20 | |
| | Object x orientation | | -0.31 ± 0.52 | -0.60 | |
| | Subject | | | | <0.001 |
| | Nest box | | | | 0.58 ± 0.76 |
| (d) Latency to enter nest box | Intercept | | 6.37 ± 0.57 | 11.11 | |
| | *Trial number* | | *-0.39 ± 0.16* | *-2.46* | |
| | Object | Gun | (reference) | | |
| | | Stick | -0.22 ± 0.46 | -0.48 | |
| | Orientation | Lap | (reference) | | |
| | | Pointing | -0.18 ± 0.47 | -0.38 | |
| | Sex | Female | (reference) | | |
| | | Male | -0.24 ± 0.49 | -0.50 | |
| | Object x orientation | | 0.25 ± 0.67 | 0.37 | |
| | Subject | | | | 0.81 ± 0.90 |
| | Nest box | | | | 0.13 ± 0.36 |
| (e) Time spent vigilant | Intercept | | 6.44 ± 0.34 | 18.85 | |
| | *Trial number* | | *-0.21 ± 0.09* | *-2.41* | |
| | Object | Gun | (reference) | | |
| | | Stick | 0.31 ± 0.28 | 1.11 | |
| | Orientation | Lap | (reference) | | |
| | | Pointing | -0.09 ± 0.28 | -0.33 | |
| | Sex | Female | (reference) | | |
| | | Male | -0.14 ± 0.21 | -0.68 | |
| | Object x orientation | | -0.40 ± 0.39 | -1.04 | |
| | Subject | | | | 0.05 ± 0.22 |
| | Nest box | | | | 0.31 ± 0.56 |

**Table 5.1** ***(continued)*****:**

| Model | Fixed and random effects | | β ± SE | t- or z-value | Variance ± SD |
|---|---|---|---|---|---|
| (f) Time spent in nest box (females) | Intercept | | 6.54 ± 0.87 | 7.50 | |
| | Trial number | | -0.25 ± 0.24 | -1.05 | |
| | Object | Gun | (reference) | | |
| | | Stick | 0.22 ± 0.76 | 0.28 | |
| | Orientation | Lap | (reference) | | |
| | | Pointing | 0.25 ± 0.76 | 0.33 | |
| | Object x orientation | | 0.42 ± 1.07 | 0.40 | |
| | Subject | | | | 2.45 ± 1.57 |
| (g) Time spent in nest box (males) | Intercept | | 1.87 ± 0.12 | 16.27 | |
| | Trial number | | 0.05 ± 0.03 | 1.82 | |
| | Object | Gun | (reference) | | |
| | | Stick | 0.04 ± 0.08 | 0.47 | |
| | Orientation | Lap | (reference) | | |
| | | Pointing | -0.01 ± 0.08 | -0.12 | |
| | Object x orientation | | -0.06 ± 0.12 | -0.49 | |
| | Subject | | | | 0.07 ± 0.26 |

### 5.3.2. Experiment 2: flight initiation distance

*FID1: FID for target bird on feeding table*

Birds were quick to leave the feeding table when the experimenter left the hide (mean FID±SE=78.0±0.6m; range=65.7m-90.4m). FID1 varied between treatments ($X^2$=6.39, df=2, p=0.041), with birds taking slightly longer to flee in response to the experimenter carrying a wooden stick than when the experimenter was carrying a gun or a bag of food (mean FID±SE: gun=78.8±0.8m, stick=76.1±1.3m, control=78.6±0.8m; Figure 5.4a; Table 5.2). The distance at which birds left the table did not diminish over subsequent trials ($X^2$=2.36, df=1, p=0.124) for any of the experimental treatments (treatment x trial number interaction: $X^2$=0.38, df=2, p=0.826).

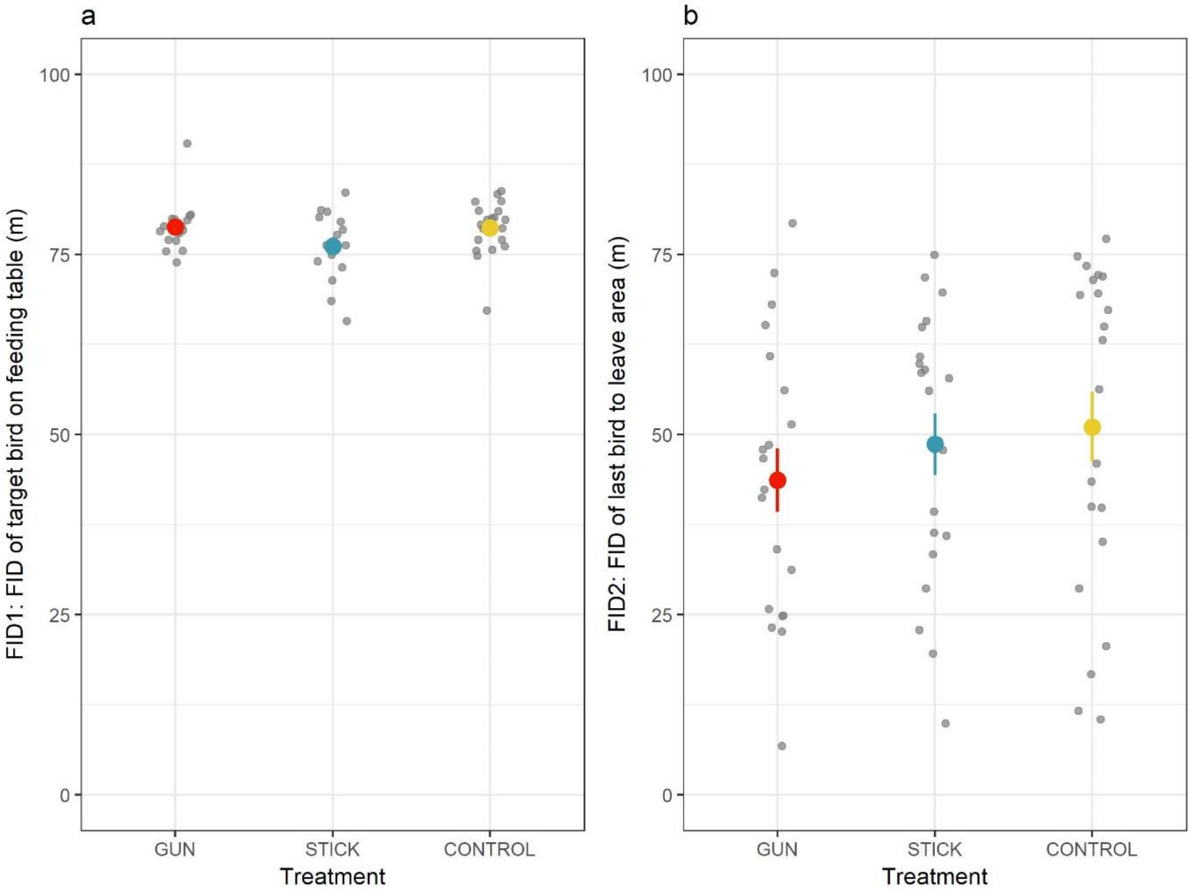


**Figure 5.4:** Effect of experimental treatment (gun/stick/control) on (a) FID of the target bird on feeding table (FID1) and (b) FID of the last bird to leave the trees surrounding the feeding table (FID2). Grey circles denote individual data points, points and whiskers denote mean and standard error. Point colour corresponds to object being carried by the experimenter (red=gun; blue=stick; yellow=food bag).

*FID2: FID for last bird to leave area*

In response to the experimenter leaving the hide, birds quickly left the feeding table and moved to trees in the immediate vicinity (<5m from feeding table). On approaching the table, the experimenter dropped a second weight when the last bird left the trees surrounding the feeding table (mean FID=47.9m, range=6.8m-79.3m). FID2 did not differ between treatments ($X^2$=2.10, df=2, p=0.350; Figure 5.4b) but birds habituated to approaches over time, taking longer to leave the surrounding trees in later trials (trial number: $X^2$=21.05, df=1, p<0.001; Figure 5.5; Table 5.2). Birds showed a similar rate of habituation in all experimental treatments (Treatment x trial number interaction: $X^2$=2.47, df=2, p=0.291).

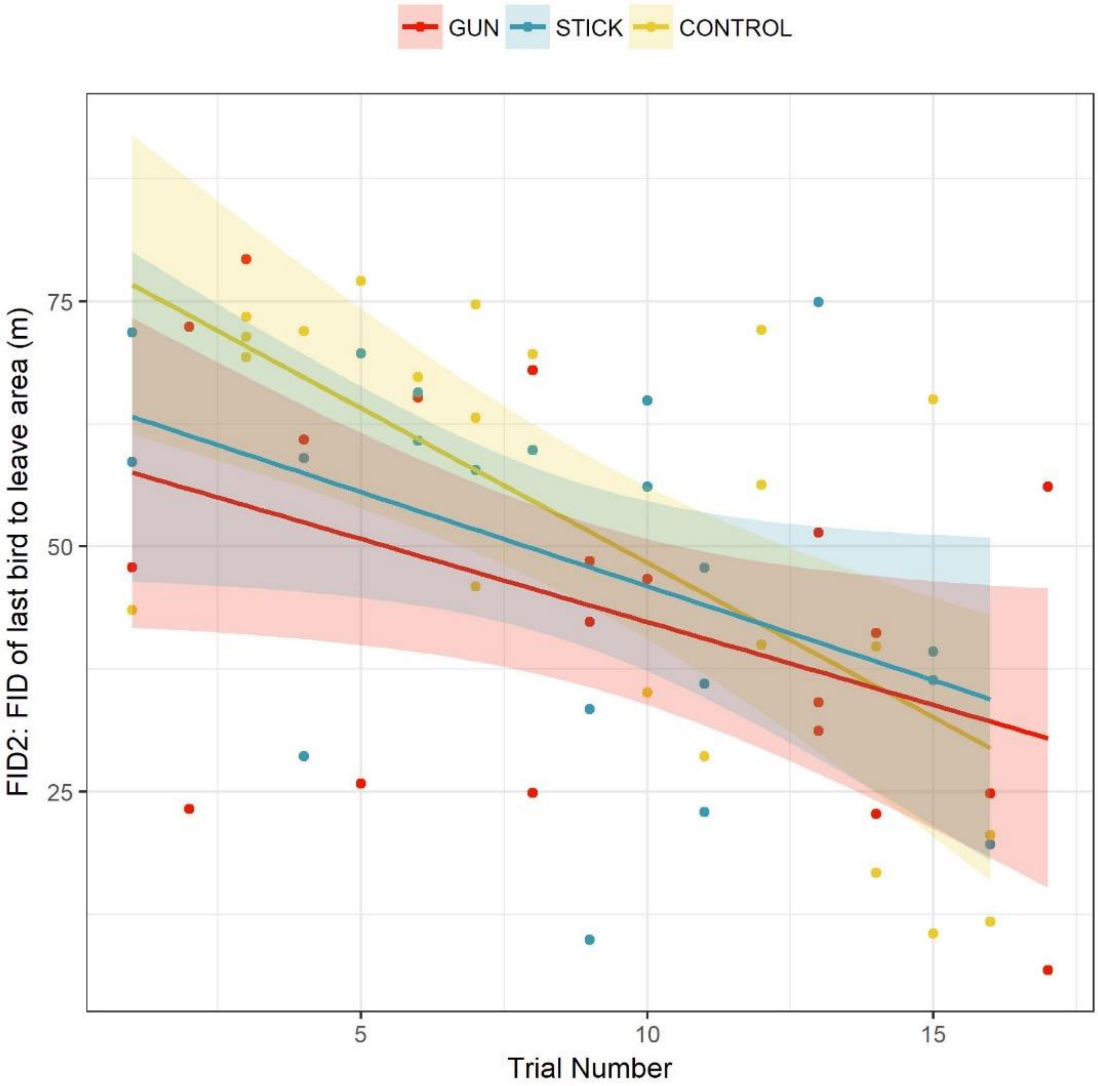


**Figure 5.5:** FID of last bird to leave the trees surrounding the feeding table (FID2) over subsequent approaches. Line colour corresponds to object being carried by the experimenter (red=gun; blue=stick; yellow=food bag).

**Table 5.2:** Outputs for GLMMs for Experiment 2 investigating (a) FID of target bird on feeding table (FID1) and (b) FID of last bird to leave the trees surrounding the feeding table (FID2). Models investigated changes in FID across trials at each feeding table, according to objects being carried by the experimenter (gun/stick/control). Values are taken from full models, with significant effects shown in italics.

| **Model** | **N** | **Fixed effects** | | **β ± SE** | **t-value** |
|---|---|---|---|---|---|
| (a) FID1: target bird on feeding table | 52 | Intercept | | 78.87 ± 1.99 | 39.69 |
| | | *Object* | *Control* | *(reference)* | |
| | | | *Gun* | *1.06 ± 2.11* | *0.51* |
| | | | *Stick* | *-0.82 ± 2.25* | *-0.36* |
| | | Trial number | | -0.09 ± 0.14 | -0.63 |
| | | Trial number x object | Control | (reference) | |
| | | | Gun | -0.03 ± 0.20 | -0.13 |
| | | | Stick | -0.13 ± 0.22 | -0.60 |
| (b) FID2: last bird to leave area | 62 | Intercept | | 81.05 ± 7.81 | 10.37 |
| | | Object | Control | (reference) | |
| | | | Gun | -20.86 ± 10.52 | -1.98 |
| | | | Stick | -16.64 ± 11.07 | -1.50 |
| | | *Trial number* | | *-3.26 ± 0.73* | *-4.45* |
| | | Trial number x object | Control | (reference) | |
| | | | Gun | 1.46 ± 1.01 | 1.45 |
| | | | Stick | 1.43 ± 1.12 | 1.27 |

*Identity of birds visiting feeding tables*

As the identity of the target bird (FID1) was not recorded during the experimenter’s approach, it is not possible to identify whether individual birds were targeted for approach in multiple trials. However, the fact that the target bird fled almost immediately in all cases suggests that if any pseudoreplication occurred, it is unlikely to have biased the results. The identity of all birds visiting the feeding table over the course of a trial was recorded using the hidden cameras (SJcam M10). Whilst it was not possible to directly identify birds perched in the surrounding area during the experimenter's approach (FID2), visits to the feeding table give some indication of the number of birds that may have had the opportunity to observe experimental presentations. Across all 62 trials, 184 unique jackdaws could be reliably identified in 54 trials. In any given trial, 1-35 birds visited the feeding table (mean±SE=7.72±0.77 individuals). Of these 184 individuals, 83 birds (45.1%) were recorded visiting feeding tables in more than one trial (mean±SE=2.27±0.16 trials).

## 5.4. Discussion

In this study, I investigated whether jackdaws respond differently to individual humans based on the objects being carried. Numerous anecdotal reports assert that corvids identify people as 'dangerous' if they are carrying a shotgun (Creagh, 2011; Forgrave, 2015; Marzluff & Angell, 2005, 2012); an idea that is seemingly widely accepted despite a lack of empirical evidence. Contrary to predictions, I found no indication that jackdaws are more wary of a person holding a gun than a person holding a wooden stick. During nest box presentations (Experiment 1), jackdaws also showed no increase in fear behaviour when guns or sticks were pointed at them rather than held across the experimenter's lap. Previous studies have shown that breeding jackdaws respond to threatening anthropogenic stimuli (a 'dangerous' person near the nest, who had previously handled their nestlings) by returning more quickly to their nest box, perhaps to defend the chicks and monitor the potential threat (Davidson et al., 2015; see also Chapter 6). However, in this study, the time taken by birds to approach the nest box on the first visit did not differ between treatments. The object held by the experimenter also had no influence on whether birds returned to the nest box and fed their chicks, or their latency to do so. On the other hand, my results indicate that birds habituated to experimental stimuli over time. Test subjects were more likely to return and enter the nest box in later trials compared to earlier trials, with males (being more hesitant than females in earlier trials) showing a stronger habituation effect. The latency of birds to enter the nest box after first seeing the object decreased as trials progressed at a given nest box. Birds also spent less time vigilant in later trials: this is consistent with habituation but may also reflect the reduced urgency for parents to return to the nest and incubate older chicks that are better able to regulate their own body temperature. It may be that birds habituated quickly to the experimenter as their presence was not associated with a direct negative consequence (in contrast to previous studies; Davidson et al., 2015).

Consistent with the results of the nest box presentations (Experiment 1), there was no clear evidence that jackdaws attended to objects carried by an approaching human in a foraging context (Experiment 2). Birds foraging on feeding tables exhibited shorter flight initiation distances when the intruder carried a wooden stick (FID1), although the magnitude of this effect is very small. In all treatments birds fled within 5m of the experimenter beginning the 80m transect, with only a 2.5m difference on average between gun and wooden stick presentations, casting doubt on whether these effects are robust. Instead, all birds foraging around the feeding tables tended to move to the surrounding trees almost immediately after the experimenter emerged from the hide. Birds in the trees surrounding the feeding tables fled the area at a similar distance (FID2) regardless of whether the intruder carried a gun, a wooden stick or a bag of food, further suggesting that birds did not use the type of object being carried by the experimenter to inform their escape decisions. In the flight initiation distance experiment (Experiment 2), birds also appeared to habituate to experimental approaches over time in a similar way to birds tested at nest boxes (Experiment 1), regardless of the object being carried by the experimenter. The fact that a substantial proportion (45.1%) of colour-ringed birds were recorded at feeding tables on multiple occasions raises the possibility that some individuals may have had the opportunity to habituate to experimental presentations.

Despite presenting my test subjects with clear, highly salient experimental stimuli in two ecologically relevant contexts, birds did not appear to discriminate between people carrying guns or sticks. This may be because people carrying guns are not perceived as a threat: although jackdaws are targeted around the study site where the experiment took place, individual birds may not have sufficient prior knowledge of guns to discriminate these objects as dangerous. Given that birds are likely to require a certain amount of experience with guns before they recognise them as dangerous, the responses of corvids to objects being carried by people may differ depending on the frequency of hunting in a particular area. However, birds may not necessarily require direct experience of being shot at; it is possible that corvids learn to avoid people carrying guns based on the responses of conspecifics (e.g. Chapter 6). These results highlight the importance of establishing whether commonly held preconceptions are supported by empirical evidence, or whether other factors (e.g. observation bias) influence cultural perceptions of different species. For example, it is commonly accepted that magpies (*Pica pica*) steal shiny objects, such as keys and jewellery; but experimental tests found no evidence of a preference for shiny objects in either captive or wild birds (Shephard, Lea, & Hempel de Ibarra, 2015). The idea that corvids discriminate between guns and sticks is widely cited (Creagh, 2011; Forgrave, 2015; Marzluff & Angell, 2005, 2012) but my results suggest that not all corvid populations will respond in the same way, especially if birds do not experience many shooting events. Further studies are needed in populations experiencing varying levels of persecution, to determine whether jackdaws are more attentive to people carrying guns in areas where corvids are targeted frequently.

On the other hand, it is possible that jackdaws simply failed to respond to people carrying guns in the context of this study. Conducting experimental presentations at nest boxes allows the responses of individual birds to be quantified and controls for inter-individual variation in behaviour; however, the ecological relevance of the stimulus may be diminished if jackdaws are less likely to be targeted when returning to their nest site. The results of my second experiment, where foraging jackdaws were approached by a person carrying a gun, suggest that this is unlikely and that individuals in my study population respond similarly to these stimuli across contexts. Alternatively, it may be that any human presence near the nest box or whilst foraging is considered a threat and birds respond fearfully regardless of the object being held by the person. Birds at the sites where this experiment was carried out typically respond fearfully to researchers (see *Study Population*), although test subjects tended not to scold the experimenter as they would for researchers coming into direct contact with the nest box (*pers. obs.*). Moreover, although the airgun stimuli used were chosen to resemble real shotguns as far as possible, it may be that previous experience has led birds to acquire search images for larger shotguns. Therefore, birds may not have classified the gun stimuli as ‘dangerous’: although air guns are often used to target corvids, birds’ perception and recognition of guns may depend on the types of guns encountered in the past.

My findings also demonstrate that jackdaws habituate to the presence of a human sitting near their nest box, and to human approach whilst foraging, which may be beneficial for jackdaws and other species that breed in urban and agricultural habitats (Carrete & Tella, 2013; Gravolin et al., 2014; Samia et al., 2015). For these species, a balance must be struck between responding appropriately to potential threats whilst continuing to carry out vital activities. Consistently fleeing in response to frequent (but benign) anthropogenic disturbance may impact survival and reproductive success, through reducing time available for foraging and other activities (Bötsch, Tablado, & Jenni, 2017; Fernández & Azkona, 1993; Sih et al., 2011; Thomas et al., 2002; Verhulst et al., 2001). In this case, initial wariness followed by rapid habituation may be an adaptive strategy allowing jackdaws to flexibly modify their behaviour in response to threats, and may partly explain their success in exploiting human-dominated habitats (Greenberg, 2003; Greggor, 2016). How animals habituate to anthropogenic disturbance provides vital insights for conservation (Blumstein, Anthony, Harcourt, & Ross, 2003; Samia et al., 2015): whilst a small number of comparative studies have investigated species differences in habituation rates (reviewed in Blumstein, 2016), further study is urgently needed. Furthermore, individual differences in behaviour are likely to influence how organisms respond during encounters with people (Carrete & Tella, 2013; Sih et al., 2012, 2011); to this end, determining the causes and consequences of intraspecific variation in habituation rates is also vital to predict and mitigate the effects of human-induced rapid environmental change.

# Supplementary Material for Chapter 5: Do jackdaws use anthropogenic objects to assess risk during encounters with people?

**Figure S1:** Gun and wooden stick stimuli used in stimulus presentations (Experiment 1 and Experiment 2)

**Figure S2:** Mask stimuli used in nest box presentations (Experiment 1)

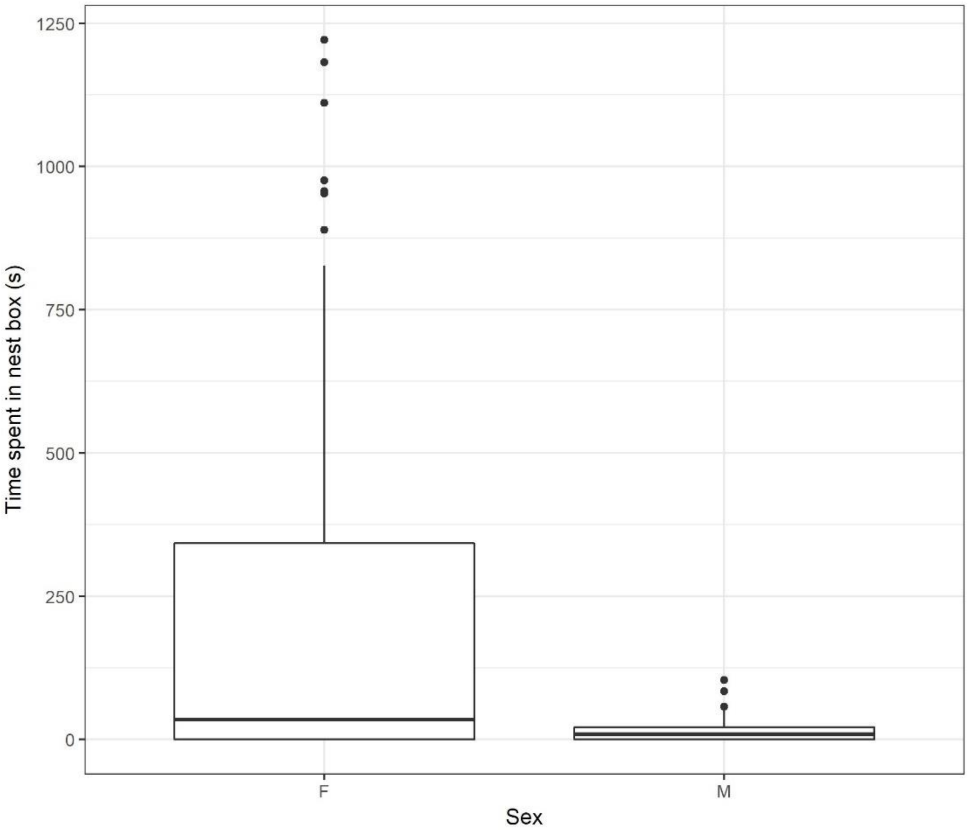


**Figure S3:** Heterogeneity of variance between males and females for time spent in the nest box during nest box presentations (Experiment 1). At this stage in the breeding attempt, females are primarily occupied with incubating young chicks.

**Figure S4:** Mask stimuli used in flight initiation distance experiment (Experiment 2)

| **Treatment group** | Gun | Stick |
|---|---|---|
| Pointing | 8/34 | 8/34 |
| Lap | 6/34 | 8/34 |

**Figure S5:** Frequency of scolding by focal birds during nest box presentations (Experiment 1), by treatment group.

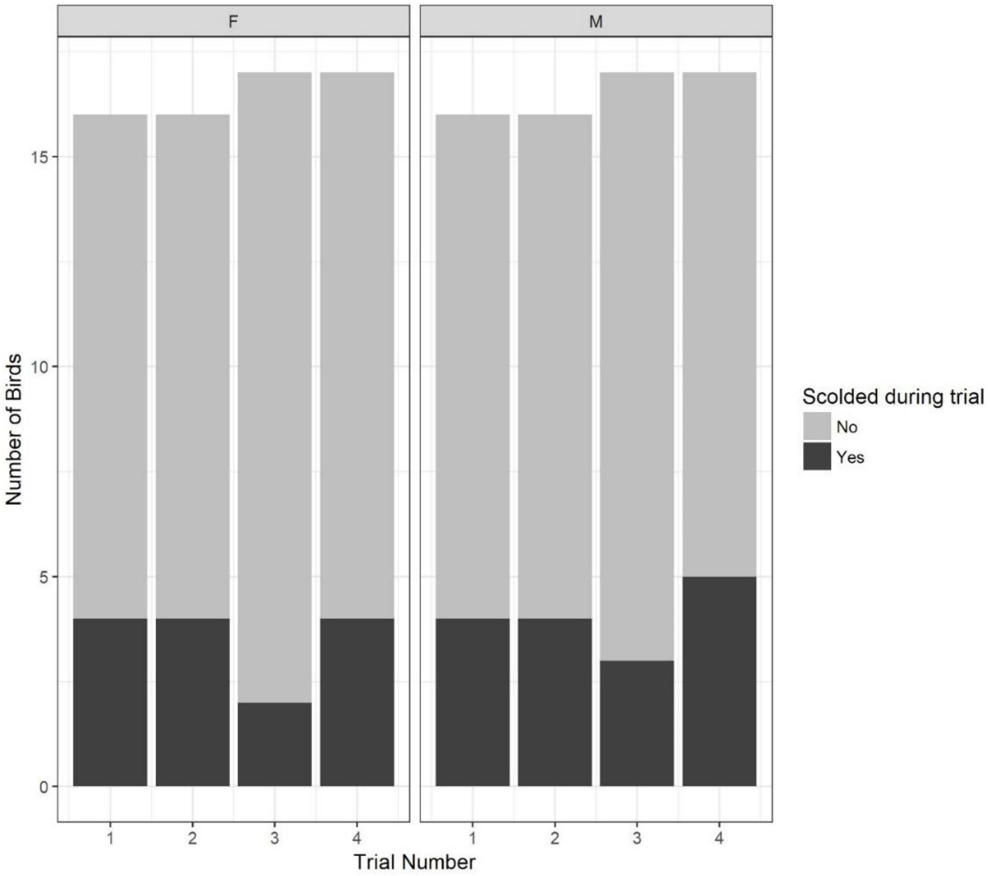


**Figure S6:** Frequency of scolding by focal birds during nest box presentations (Experiment 1), by trial number.

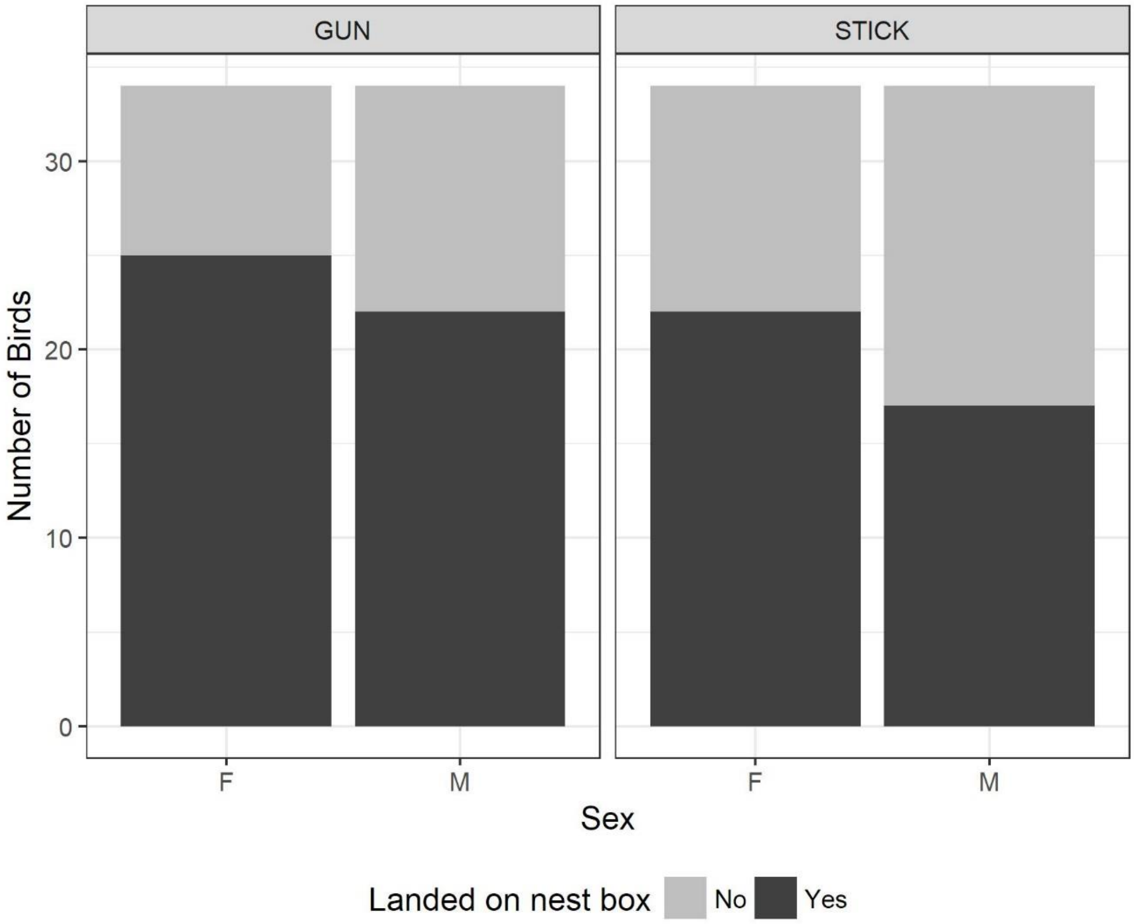


**Figure S7:** Tendency of birds to land on the nest box (0/1) based on object held by the experimenter (gun/stick) during trials in Experiment 1. Subjects were slightly more likely to land on the nest box during a trial if the experimenter was holding a wooden stick rather than a gun, but this relationship was not statistically significant.

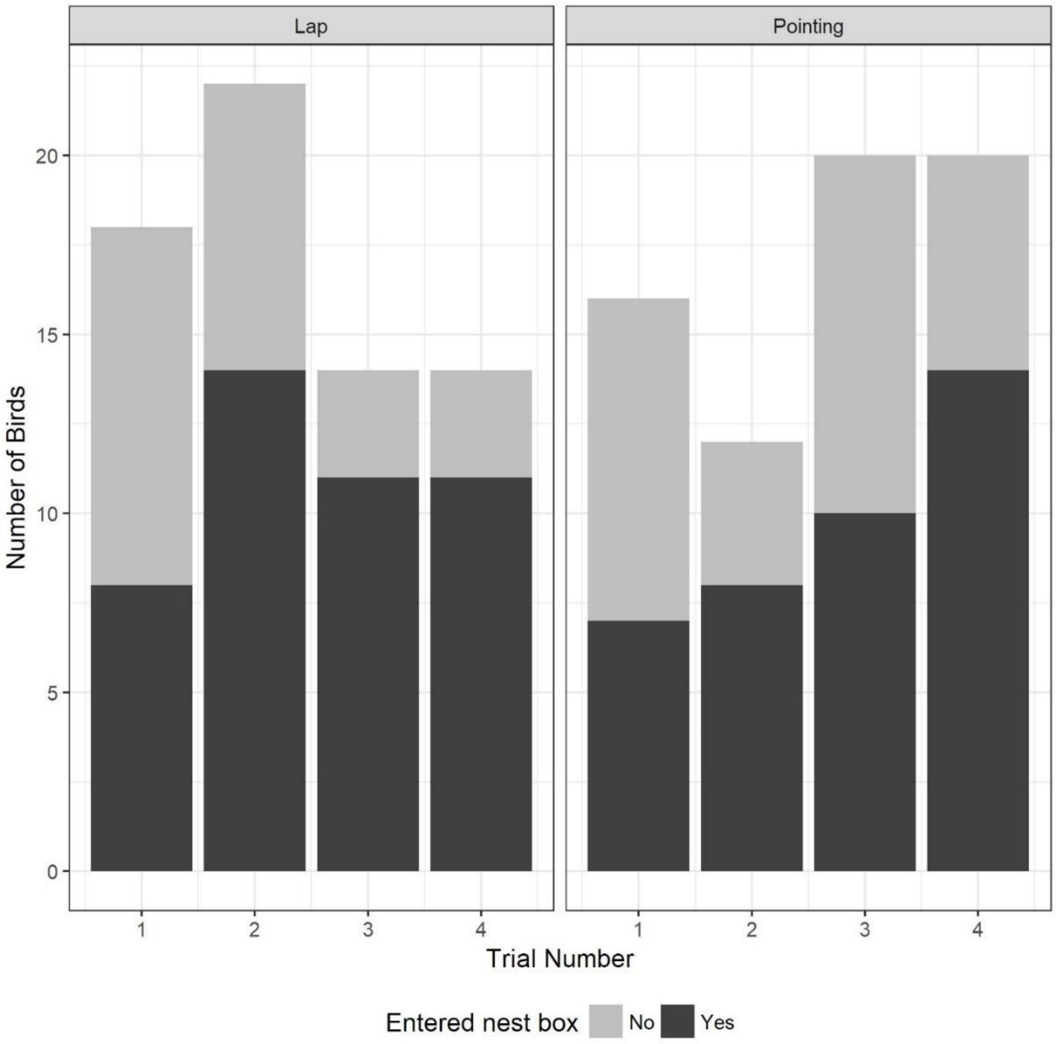


**Figure S8:** Tendency of birds to enter the nest box (0/1) based on orientation of the object (pointing/lap) during nest box presentations (Experiment 1). This relationship showed a nonsignificant trend (p=0.064) but may be an artefact of trial number, as focal birds were significantly more likely to enter the nest box in later trials.

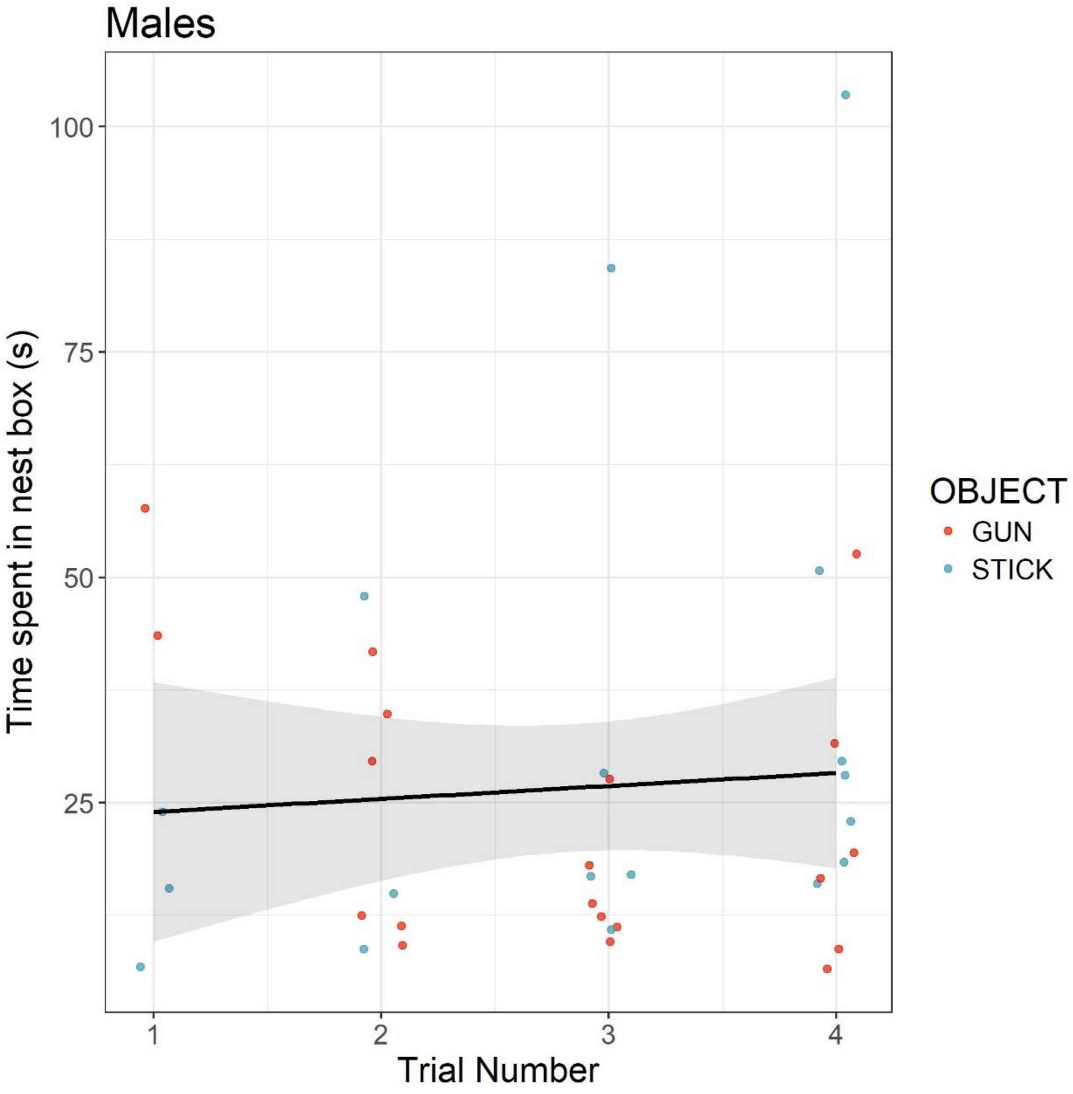


**Figure S9:** Time spent in the nest box by males during nest box presentations (Experiment 1) tended to increase over successive trials, but this relationship was not statistically significant (p=0.08).

# Chapter 6

# Jackdaws learn socially about dangerous people

*This chapter has been adapted from:*

*Lee, V. E., Régli, N., McIvor, G. E., Thornton, A. 2019 Social learning about dangerous people by wild jackdaws. Royal Society Open Science 6 (191031).*

## Abstract

For animals that live alongside humans, people can present both an opportunity and a threat. Previous studies have shown that several species can learn to discriminate between individual people and assess risk based on prior experience. To avoid potentially costly encounters, it may also pay individuals to learn about dangerous people based on information from others. Social learning about anthropogenic threats is likely to be beneficial in habitats dominated by human activity, but experimental evidence is limited. Here, I tested whether wild jackdaws (*Corvus monedula*) use social learning to recognise dangerous people. Using a within-subjects design, I presented breeding jackdaws with an unfamiliar person near their nest, combined with conspecific alarm calls. Subjects that heard alarm calls showed a heightened fear response in subsequent encounters with the person compared to a control group, reducing their latency to return to the nest. This study provides important evidence that animals use social learning to assess the level of risk posed by individual humans.

## 6.1. Introduction

In changing environments, social information allows organisms to learn about novel threats without the need for potentially costly encounters (Laland, 2004). Despite having received less attention than in foraging contexts (Griffin, 2004), the importance of social learning in avoiding predators has been demonstrated in a range of taxa (insects, Coolen, Dangles, & Casas, 2005; fish, Crane & Ferrari, 2015; Manassa & McCormick, 2012; birds, Curio, Ernst, & Vieth, 1978a; Griffin & Boyce, 2009; Griffin & Galef, 2005; mammals, Griffin & Evans, 2003; Mateo & Holmes, 1997; Mineka & Cook, 1993; see Griffin, 2004 for a review). However, with a few exceptions (Cornell et al., 2012; Griesser & Suzuki, 2016), most studies investigating aspects of socially acquired predator avoidance have been conducted in captivity. Field studies carried out under natural conditions are urgently needed in order to establish how social information influences antipredator behaviour in real-world settings (Griffin, 2004; Pritchard et al., 2016; Thornton et al., 2012). As socially-acquired predator avoidance is hypothesised to confer benefits when predation risk varies in space and time (Lima & Dill, 1990), when new predators are encountered (Berger, Swenson, & Persson, 2001) or when community composition is altered (Griffin, 2004), understanding how social environments shape antipredator responses is vital in predicting and mitigating the effects of environmental change (Sih, 2013). Furthermore, if potential predators vary in their level of threat, the ability to discriminate between individual predators of the same species is likely to be beneficial (Cornell et al., 2012). In this scenario, social learning may help prey to fine-tune their antipredator behaviour and avoid the costs of fleeing in response to benign encounters.

For many animals today, humans present a threat greater than or equivalent to natural predators (Conover, 1987; Lima & Dill, 1990; McLean et al., 1986; Murphy, 2006), but individual people can vary substantially in their behaviour towards wildlife (Cornell et al., 2012; Levey et al., 2009). In urban or agricultural areas, species that exploit the opportunities and resources provided by human activity are often persecuted (Cornell et al., 2012; Griffin & Boyce, 2009), but not all people will be involved in persecution. In these cases, fear of humans can allow individuals to avoid danger, but exhibiting an inappropriate fear response to all humans would prevent individuals from exploiting these habitats. The ability to learn to discriminate between threatening and non-threatening people may therefore be highly beneficial. For example, several urban bird species have demonstrated the ability to learn about dangerous people based on previous experience, and even incorporate subtle human cues such as gaze direction when assessing risk (Northern mockingbird *Mimus polyglottos,* Levey et al., 2009; Eurasian jackdaw *Corvus monedula,* Davidson, Clayton, & Thornton, 2015; von Bayern & Emery, 2009; American crow *Corvus brachyrhynchos,* Clucas, Marzluff, Mackovjak, & Palmquist, 2013; Marzluff, Walls, Cornell, Withey, & Craig, 2010; raven *Corvus corax,* Bugnyar, Stowe, & Heinrich, 2004; Eurasian magpie *Pica pica,* Lee, Lee, Choe, & Jablonski, 2011; green bee-eater *Merops orientalis,* Watve et al., 2002; European starling *Sturnus vulgaris,* Carter, Lyons, Cole, & Goldsmith, 2008). In this context, learning from the responses of conspecifics could be extremely valuable in allowing individuals to learn which humans are dangerous without the risk of a potentially fatal encounter. However, the potential for animals to use social learning to discriminate between dangerous and harmless people is poorly understood. Determining how social learning shapes responses to humans may provide an additional insight into how species and populations cope in a rapidly changing anthropogenic landscape (Sih, 2013; Sih et al., 2011).

A small number of studies raise the possibility that social information plays a key role in shaping how individuals learn to associate people with a dangerous place or event. For example, common myna (*Acridotheres tristis*) become warier in a location where they have previously seen an alarmed bird being captured by a human, relative to a control treatment where subjects were not given conspecific cues (Griffin & Boyce, 2009; Griffin & Haythorpe, 2011). A field study of American crows (*Corvus brachyrhynchos*) provides the most compelling evidence to date that information about dangerous humans is socially transmitted through populations (Cornell et al., 2012). Here, experimenters wearing masks when trapping crows were later mobbed by birds that were not present at the initial capture event, and offspring present during mobbing events involving parents later mobbed masks independently. This evidence is indicative of both horizontal and vertical transmission of social information, but the processes through which social learning might occur remain unclear as individuals' exposure to social information was not manipulated explicitly. Mobbing events, during which large groups of crows gathered and alarm-called for extended periods (up to 40 crows for up to 10 minutes) are likely to have created significant opportunities for social learning, but this possibility has yet to be tested experimentally. Moreover, for many animals such large-scale mobbing of dangerous people is likely to be infrequent because of the substantial costs (in terms of time, energy and risk; Dugatkin & Godin, 1992) associated with approaching a potential threat. More commonly, individuals will be exposed to a short-lived bout of conspecific alarm calling, often from a single individual who may be out of sight. If individuals are able to learn from acoustic cues alone, this could provide a powerful mechanism by which information about dangerous people could spread through populations without the need for involvement in costly mobbing events. I therefore tested whether exposure to alarm calls from a single conspecific is sufficient to change the responses of naïve wild birds towards unfamiliar humans.

I also examined whether learning was influenced by the characteristics of the signaller. Learning indiscriminately from others may be detrimental if information is irrelevant, erroneous or out of date (Kendal et al., 2005; Rendell et al., 2010), so individuals are expected to employ social learning strategies in deciding when, how and from whom to learn (Coussi-Korbel & Fragaszy, 1995; Laland, 2004). However, no studies have empirically investigated the social learning strategies employed in antipredator contexts (but see Griesser & Suzuki, 2016; Kavaliers, Colwell, & Choleris, 2005; Kern & Radford, 2016; Mateo & Holmes, 1997). This is surprising given that social dynamics may play a key role in shaping predator recognition: for example, when novel predators are encountered frequently or individual predators differ in their level of threat, prey may preferentially attend to information from familiar conspecifics who possess more locally relevant knowledge about danger (Coussi-Korbel & Fragaszy, 1995; Laland, 2004). To investigate this possibility, I used alarm calls from familiar and unfamiliar conspecifics to determine whether the familiarity of the caller influences subsequent responses to a potential threat.

I conducted experiments on wild jackdaws (*Corvus monedula*), highly social members of the corvid family that form long-term monogamous pair bonds and tend to nest in breeding colonies that are stable over time (Henderson et al., 2000; Salomons et al., 2007). They are commonly found in agricultural and urban areas across Europe, exploit anthropogenic resources (including food and breeding sites; Gregory & Marchant, 1996; Harris et al., 2018) and are targeted as pests (BirdLife International, 2018; Wildlife and Countryside Act, 1981). Like many corvids (Bugnyar et al., 2004; Clucas et al., 2013; Lee et al., 2011; Marzluff et al., 2010), jackdaws can learn to discriminate between individual people based on facial cues (Davidson et al., 2015; von Bayern & Emery, 2009). When presented with a person wearing a mask, jackdaws return to their nest more quickly if that mask has previously been worn during a nest intrusion, demonstrating that jackdaws learn to recognise individual people and associate them with prior events (Davidson et al., 2015). In order to test whether jackdaws use social learning during encounters with people, I presented breeding jackdaws with an unfamiliar person at their nest box, using playback of alarm calls from colony and non-colony members to provide social information about danger. If birds incorporated the social information from the playback into their behavioural response, I predicted that birds that heard alarm calls would subsequently show a higher fear response relative to a control group that heard playback of contact calls. As alarm calls from familiar conspecifics have previously been shown to increase collective responses to threats in jackdaws (Woods et al., 2018), I also predicted heightened fear responses among individuals that had heard the alarm calls of colony members rather than unfamiliar birds. Using a three-phase, within-subject paradigm previously employed in studies of socially acquired predator avoidance (Griffin & Boyce, 2009; McIvor et al., 2018), I was able to quantify changes in individual response according to playback treatment, without altering the nature of the encounter with the human. Thus, I was able to separate social learning from the effects of individual learning and ensure that the nature of the social learning experience was consistent between test subjects.

## 6.2. Methods

### 6.2.1. Study Population

This experiment was conducted during the 2017 breeding season using free-living nest box populations of jackdaws at three study sites in Cornwall, UK: a village churchyard (Stithians 50°11′26″N, 5°10′51″W; 33 nest boxes), an active farmyard (Pencoose Farm 50°11′56″N, 5°10′9″W; 35 nest boxes), and at the University of Exeter's Penryn campus (50º17'32"N; 5º11'96"W; 11 nest boxes). At these sites, jackdaws are captured in nest boxes or ladder traps and individually colour-ringed by the Cornish Jackdaw Project. Resident jackdaws at all three sites have experience of humans walking around the area on a regular basis without posing any threat. However, some persecution of corvids occurs in the area (*pers. obs.*) and fieldworkers monitor nests daily during the breeding season, eliciting alarm calling from resident jackdaws. Thus, discriminating between dangerous and harmless people is likely to be beneficial.

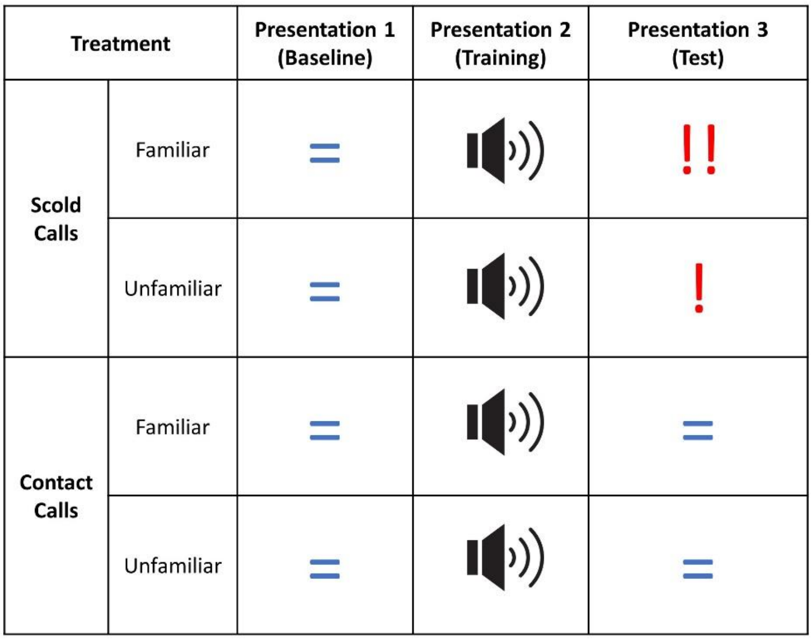
### 6.2.2. Experimental Design

Following protocols used in previous studies of socially acquired predator avoidance (Griffin & Boyce, 2009; McIvor et al., 2018), focal jackdaws underwent 3 trial phases (Figure 6.1):

1. Baseline phase: Subjects presented with a novel human stimulus (an experimenter wearing a mask) at their nest box.
2. Training phase: Subjects presented with the same human stimulus, paired with playback of conspecific calls to provide social information about the level of danger (see below).

3. Test phase: Subjects presented with the human stimulus a third time, to compare any changes in individual behaviour occurring as a result of the training.

In the training phase, scold calls were used to imply danger and contact calls were used as a control (Supplementary Figure S1). Scold calls are antipredator vocalisations given by jackdaws to recruit others to mob a predator (Woods et al., 2018), and contact calls are used in a range of contexts to advertise identity but are not associated with any specific event (McIvor et al., 2018). Contact calls and scold calls both encode information about the identity of the caller (Stowell et al., 2016; Woods et al., 2018), and are frequently heard in jackdaw colonies. To determine whether familiarity with the caller influences social learning, calls were presented from colony members and unfamiliar birds from a different breeding colony. Focal pairs were assigned to one of four treatments: familiar contact calls, unfamiliar contact calls, familiar scold calls or unfamiliar scold calls. If subjects incorporate social information from the training phase into their behavioural response, I expected an increase in fear behaviour in the test phase compared to the baseline phase, but only for birds in the scold call treatments (see Figure 6.1). If subjects preferentially attend to social information from familiar conspecifics, subjects that heard familiar scold calls in the training phase were predicted to show a greater change in fear response between the baseline and test phases, compared to subjects that heard unfamiliar scold calls. This design allowed the effects of social learning to be separated from individual learning: masked experimenters were unfamiliar to all test subjects during the baseline phase, and in the test phase all subjects had identical previous experience with the experimenter apart from the type of vocalisations heard in the playback phase.



| Treatment | | Presentation 1 (Baseline) | Presentation 2 (Training) | Presentation 3 (Test) |
|---|---|---|---|---|
| Scold Calls | Familiar | = | 🔊 | !! |
| | Unfamiliar | = | 🔊 | ! |
| Contact Calls | Familiar | = | 🔊 | = |
| | Unfamiliar | = | 🔊 | = |

**Figure 6.1:** Experimental design and predictions. Focal birds received 3 stimulus presentations at their nest box (baseline, training and test phase). In the training phase, subjects were presented with playbacks from one of four treatments (scold call/familiar; scold call/unfamiliar; contact call/familiar; contact call/unfamiliar). If jackdaws learn socially about dangerous people, I expected birds to increase their fear response to the human following association with scold calls (denoted by exclamation marks). If jackdaws engage in directed social learning in this context, I predicted that the strength of the effect would be greater for birds that heard familiar scold calls in the training (denoted by two exclamation marks).

### 6.2.3. Experimental stimuli: presentation of unfamiliar human

Experimenters wore full-head latex masks throughout all trials to ensure the novelty of the stimulus and avoid potential confounding effects of birds' familiarity with the experimenters (Supplementary Figure S2). Two different masks were worn at each site, one during scold call trials and the other during contact call trials. The mask-treatment combinations were counterbalanced between sites; the mask worn during scold call trials at one site was worn during contact call trials at another site and vice versa. As commercially available masks have lurid, unrealistic hair or lack hair, all masks were paired with a plain hat. Mask and hat pairings were kept constant at each site.

Two experimenters (V.E.L. and N.R.) carried out trials, with focal birds being presented with the same experimenter for all three trials. Both experimenters carried out trials in all treatment groups at all three sites, and wore both types of mask. Experimenters wore a large raincoat to disguise any body shape or gait cues and wore the same clothing during all trials.

### 6.2.4. Experimental stimuli: playback calls

*Audio Recordings*

Playback calls were extracted from recordings obtained during the 2014-2016 breeding seasons, and only calls of known individuals were used in the experiment. Contact calls were recorded using lapel mics (AKG-C417PP) installed inside nest boxes, and scold calls were recorded using a shotgun microphone (Sennheiser ME66) while nests were being visited by researchers. All calls were recorded using multitrack linear PCM recorders (Olympus LS-100 & Tascam DR-100MKII).

### *Call extraction*

Exemplars of contact calls and scold calls with minimal background noise were extracted from audio recordings and normalised for amplitude using Audacity (www.audacityteam.org). Extracted calls were arranged into playback files comprising either 5 contact calls or 5 scold calls from a single individual, occurring at 2s intervals to simulate natural calling (Supplementary Figure S1). Scold calls are longer in duration (median = 0.46s; Woods et al., 2018) than contact calls (median = 0.27s; Stowell et al., 2016), and short bouts of both types of vocalisation are frequently heard around jackdaw colonies (McIvor et al., 2018). Where possible, playback files contained 5 different calls from the same individual (contact calls: 3-11 calls from 30 individuals, mean 5 calls per individual; scold calls: 3-13 calls from 18 individuals, mean 4 calls per individual). For cases where fewer than 5 calls were available, the number of repeated calls was kept to a minimum, and order of calls was modified to ensure that test subjects would not hear repeated calls presented in the same order. There were also 2 cases where many high-quality calls were available for an individual, and multiple playback tracks were made (containing different calls from the same individual) to maximise the number of different playback tracks used across the experiment. In total, this produced contact call playback files from 30 individuals (15 males and 15 females, 3-11 calls available per individual) and scold call playback files for 18 individuals (9 males and 9 females, 3-13 calls available per individual, with one male and one female contributing 3 files each). All playbacks were played through FoxPro Fury remote-controlled loudspeakers, at a set volume level that simulated the natural amplitude of calls at a distance of 10m (McIvor et al., 2018; Woods et al., 2018).

*Allocation of playbacks*

Focal pairs were assigned to treatment groups as required to maintain a balanced design across the experiment. For ‘familiar’ treatment playbacks, near neighbours (birds nesting within 500m of the focal pair) were used wherever possible to maximise the likelihood that focal birds were familiar with the caller. However, I avoided using the calls of immediate neighbours (birds nesting within 200m of the focal pair), who were likely to have been in the vicinity during trials. For ‘unfamiliar’ treatment playbacks, focal pairs were played calls from non-colony members. Because of their close geographical proximity (1.2km) and the observed movement of birds between Stithians churchyard and Pencoose farm (*pers. obs.*), only calls obtained from birds at the Campus site (>5km) were used in the unfamiliar treatments at the Stithians and Pencoose sites (extensive observations suggest that birds do not move between Stithians/Pencoose and Campus sites). Both male and female callers were used for playbacks, allocated as required to balance the proportion of callers of both sexes within sites and across treatment groups. All callers were known to be alive and breeding in the colonies at the time of the experiment. Callers were also resident in the colony in the year prior to the experiment (except two individuals whose vocalisations were used in contact call playbacks).

### 6.2.5. Experimental Trials

In total, I carried out 102 trials at 34 focal nest boxes across the three study sites (15 nests at Stithians; 16 at Pencoose; 3 at Campus). Trials were conducted between 08:00 and 18:00. Trials at a single nest were carried out on consecutive days and at the same time of day (start times fell within 2 hours for all three trials), to ensure a broadly similar rest period between trials for each nest, and control for variation in feeding rate over the course of the day. Trials at a focal nest box began no earlier than 3 days after the first chick hatched (to minimise risk of nestling mortality or parental abandonment) and no later than 6 days post-hatching (to ensure provisioning was still frequent enough for parents to return within the trial period).

Prior to the experiment, the experimenter set up a chair and recording equipment 30m away from the nest box and directly facing the nest box entrance. Recording equipment comprised a tripod with a HD camera (Panasonic HC-X920) taking a close-up view of the nest box to identify colour rings of birds and record fine-scale behavioural measures at the nest. A small wide-angle camera (SJcam M10) was attached to the same tripod, to record experimenter behaviour and the behaviour of birds on approach to the nest box. For the training phase, a loudspeaker was deployed on the ground halfway between the experimenter and the nest box. After setting up equipment, the experimenter moved away to a concealed location to put on a mask and coat. The experimenter then returned to the area and approached the chair, keeping as far away from the nest box as possible. The experimenter set camera recordings and a stopwatch timer for the end of trial before sitting in the chair and remaining motionless for the duration of the trial, maintaining a constant gaze directly at the nest box throughout. At the end of the trial the experimenter would get up, collect recording equipment and leave the area, keeping the mask on until out of sight of the colony.

Trials for the baseline (1) and test (3) phase lasted for 30 minutes. In the training phase (2), trials lasted until the first visit to the nest box by any member of the focal pair (if birds did not return within 40 minutes, the trial was terminated). As the first bird made contact with the nest box, the experimenter activated the playback using a handheld remote control. The experimenter would remain seated for 2 minutes after the playback and then leave the area, to ensure temporal consistency between presentation of the playback calls (unconditioned stimulus) and presentation of the human (conditioned stimulus) in the training phase.

If individuals hearing scold calls in the playback phase show a higher fear response in the test phase, it is possible that this effect could be carried over from having heard conspecific scold calls on the previous day. To control for this, all birds were exposed to the same number of scold and contact calls on the second day of the experiment using control playbacks. These were carried out by playing the other type of call from a speaker deployed in the same location, while birds were visiting the box but without human presence in the area.

### 6.2.6. Behavioural Analysis

I recorded the frequency and duration of all behaviours exhibited at focal nest boxes using the open-source video coding software BORIS (Friard & Gamba, 2016). Birds included in the experiment were individually identifiable. The behaviour of both males and females was recorded from experimental footage, with analysis carried out at the level of the individual.

The close-up view of the nest box from the HD camcorder enabled identification of individuals and recording of behaviours occurring at the nest box. This footage was aligned to the wide-angle footage (using the built-in ‘offset’ function in BORIS) to allow individuals to be identified as they approached the box. I recorded the frequency and duration of all behaviours exhibited by either bird during the time the experimenter was sat motionless during the trial (setup times were excluded). Behaviours recorded from the close-up footage included landing on the nest box, entering the nest box, and scolding. From the wide-angle footage, I recorded when birds returned and left the area of the nest box (defined as landing within the view of the wide-angle camera).

An independent coder who was blind to treatment analysed a subset of 15% of the videos. An intra-class correlation coefficient (Gamer et al., 2012) showed a high degree of agreement between coders for the time individuals spent in the nest box (ICC=0.998, p<0.001), latency to enter the nest box (ICC=1,p<0.001), and latency to land on the nest box (ICC=1, p<0.001) (data for females only, see below). The subset of videos for independent coding were selected at random; in some cases, it was initially difficult for inexperienced coders to accurately identify when females returned to the area prior to their first landing (e.g. if birds landed in barns or shaded areas before returning to the nest box). For this reason, the same independent coder analysed another subset of videos for this variable, with all nest boxes located in single trees (10% of the remaining videos, ICC= 0.96, p<0.001). Both coders also confirmed return times for all females in the original subset, once the returning bird had been pointed out by the original coder.

### 6.2.7. Statistical Analysis

Of the 34 focal pairs, only birds that heard the playback were included in analyses. Playbacks occurred after the first bird landed on the nest box in the second trial; this was the female of the pair in 24 cases and the male in 10 cases. However, in 13 cases the second member of the pair was close to the nest box when the first bird triggered the playback. This meant that in total, 18 males and 29 females heard the playback and could potentially respond to the experimental treatments.

There was substantial heterogeneity of variance between males and females for many of the behaviours recorded. Females were more variable than males in their latency to return to the nest on the first visit (females: median=26.4s, Q1=13.0s, Q3=118.8s; males: median=30.6s, Q1=7.9s, Q3=48.3s; Supplementary Figure S3). Females also spent more time in the box over the whole trial than males (females: median=527.4s, Q1=69.9s, Q3=983.4s; males: median=27.7s, Q1=0.95s, Q3=62.8s; Supplementary Figure S3), as would be expected given that females invest heavily in incubation at this stage in the breeding attempt. For these reasons, only data from females were analysed; for males, the smaller sample size and uneven distribution between treatment groups precluded formal analysis.

All analyses were carried out in R (R Core Team, 2017) using general linear mixed models (GLMMs) with a Gaussian error distribution, following box-cox transformation of response variables. All models included phase (baseline/test), call type (contact call/scold call) and caller familiarity (familiar/unfamiliar) as fixed effects with a three-way interaction, and individual ID as a random term. Models were constructed using the lme4 package (Bates et al., 2015). Model plots were examined to ensure that assumptions were met (homogeneity and normality of residuals) and model goodness-of-fit estimates (marginal and conditional $R^2$; Nakagawa & Schielzeth, 2013) were calculated using MuMIn (Barton, 2017). Models were compared using log-likelihood ratio tests. Sample sizes vary between models (see below), after excluding birds that did not hear the playback in phase 2, birds that did not exhibit the behaviour during the baseline (1) or test (3) trials, and cases where reliable measures could not be obtained (see below).

### *Time taken to approach nest box*

In a similar experiment, Davidson et al. (2015) found that jackdaws return to their nest box more quickly after learning that a person is dangerous, which is likely to reflect a motivation to defend the nest and monitor the threat. To investigate how quickly females approach the nest box when watched by a person previously associated with scold vs. contact calls, I calculated the time females spent near the box prior to landing on the box on their first visit. This model included data from 21 females (10 females in the contact call group; 11 in the scold call group). Of the original sample (n=34), five females were excluded as they were not present during the playback in Phase 2. Seven females did not land on the box during either the baseline (1) or test (3) trials, and due to poor lighting in one trial female return time was estimated in the video footage. This individual was subsequently excluded from the model after examination of Cook's distances confirmed that this estimate was inaccurate.

### *Latency to enter nest box*

To determine whether females spend more time on the nest box prior to entering when faced with a 'dangerous' person, I analysed female latency to enter the nest box after landing. This model included data from 23 females (12 in the contact call group, 11 in the scold call group). In five cases females did not hear the playback during phase 2, and six females did not land on and/or enter the nest box during the baseline (1) or test (3) phase.

*Time spent in nest box*

Finally, I investigated whether females spent less time in the nest box incubating and feeding chicks during presentations of a ‘dangerous’ person. This model included the total time spent in the nest box by females in each trial as the response variable. 20 females were included in this model (12 in the contact call group and 8 in the scold call group), after excluding females that did not hear the playback (n=5) and cases where trials were cut short or disturbed (n=9; although this was not relevant for the latency variables above, disturbance may have influenced the amount of time that females spent in the nest box over the trial as a whole). Females that did not enter the nest box over the course of a trial were given a score of zero.

## 6.3. Results

During the training phase (2), birds responded to playbacks as would be expected for genuine scold calls and contact calls. Upon hearing scold calls, birds always left the nest box immediately and several emitted scold calls in response. In contrast, birds did not leave the nest box in response to contact calls, instead remaining on the nest box during the playback or entering the nest box to feed chicks.

### 6.3.1. Time taken to approach nest box

Between the baseline phase (1) and the test phase (3), females altered the time taken to approach their nest box depending on the type of calls heard in the playback phase (2) (phase/playback type interaction: $X^2$=4.35, df=1, p=0.037; Table 6.1). Females were quicker to approach the nest box in the test phase compared to the baseline phase if they heard scold calls in the playback phase; females that heard contact calls took longer to approach the box in the test compared to their baseline (Figure 6.2, Table 6.1). For subjects in the scold call treatment, this equates to a 53% reduction in approach time on average between the baseline and the test phase, whereas subjects in the contact call treatment increased their approach time by 63% on average (Supplementary Table S4). Familiarity with the playback caller had no significant effect on the time taken to approach the nest box ($X^2$=0.68, df=1, p=0.411; Table 6.1).

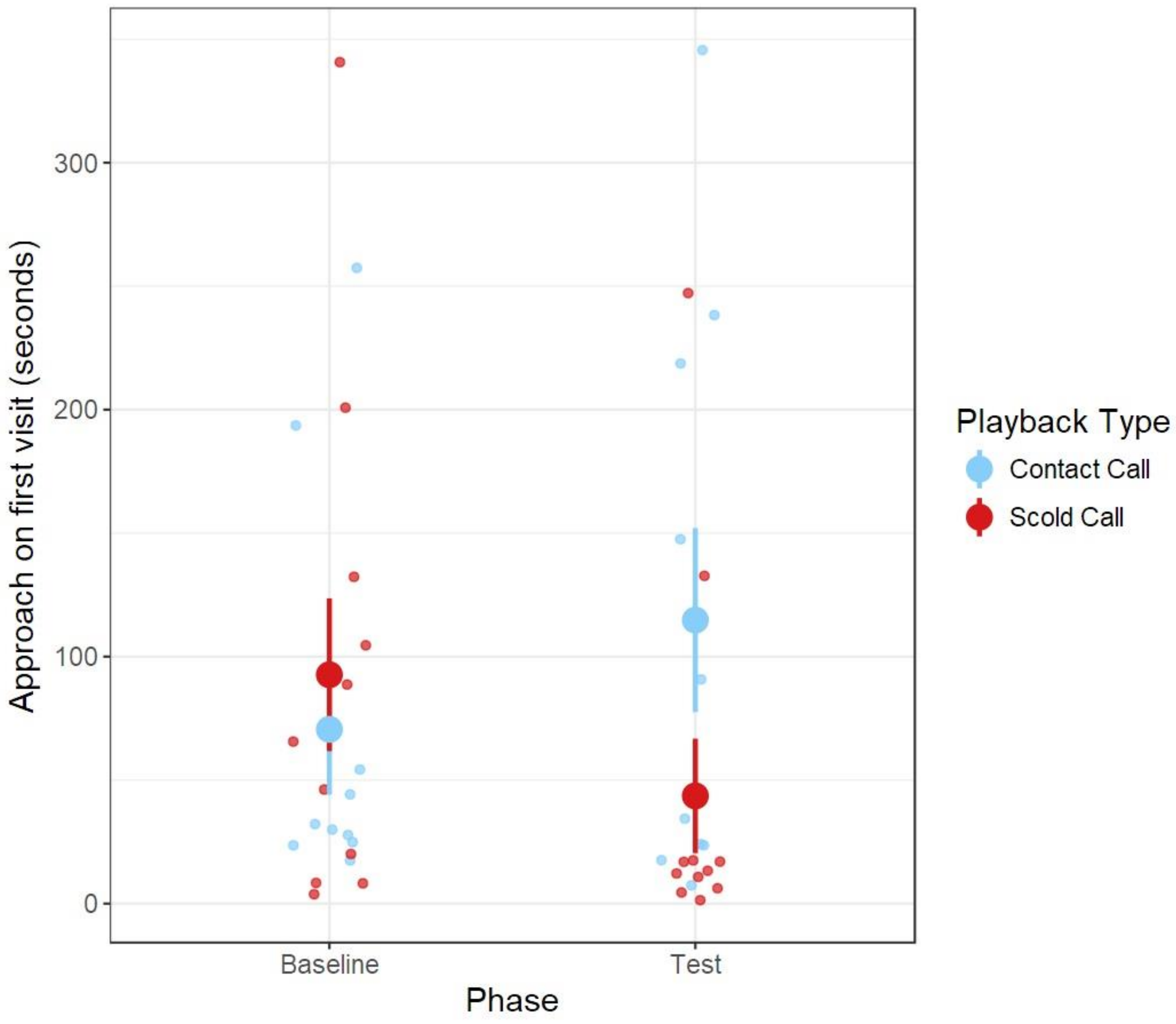


**Figure 6.2:** Time taken by females to land on the nest box following their return to the area. Females that heard scold call playbacks in trial 2 (training phase) were quicker to approach the nest in the test phase (trial 3) compared to their baseline (trial 1). Females that heard contact call playbacks in the training phase took longer to approach the nest on their first visit in the test phase (trial 3) compared to their baseline (trial 1). Points and whiskers denote mean and standard error, n=42 observations of 21 females.

### 6.3.2. Latency to enter nest box

The time taken by females to enter the nest box after first landing did not change significantly between the baseline and test phase ($X^2$=0.40, df=1, p=0.53). The type of call heard in the playback (scold calls/contact calls) and familiarity with the caller (familiar/unfamiliar) also had no significant effect on entry latency (playback type: $X^2$=0.54, df=1, p=0.46; familiarity: $X^2$=1.42, df=1, p=0.23; Table 6.1). In the baseline phase (1), females in the scold call group were quicker to enter the nest box than those in the contact call group (median entry latency±IQR: scold call group=6.5s±50.25; contact call group=21.8s±430.68), despite chicks being of the same age in both treatment groups. However, female entry latency showed no significant change between trials as a result of the playback (phase/call type interaction: $X^2$=0.60, df=1, p=0.44; Table 6.1; Figure 6.3).

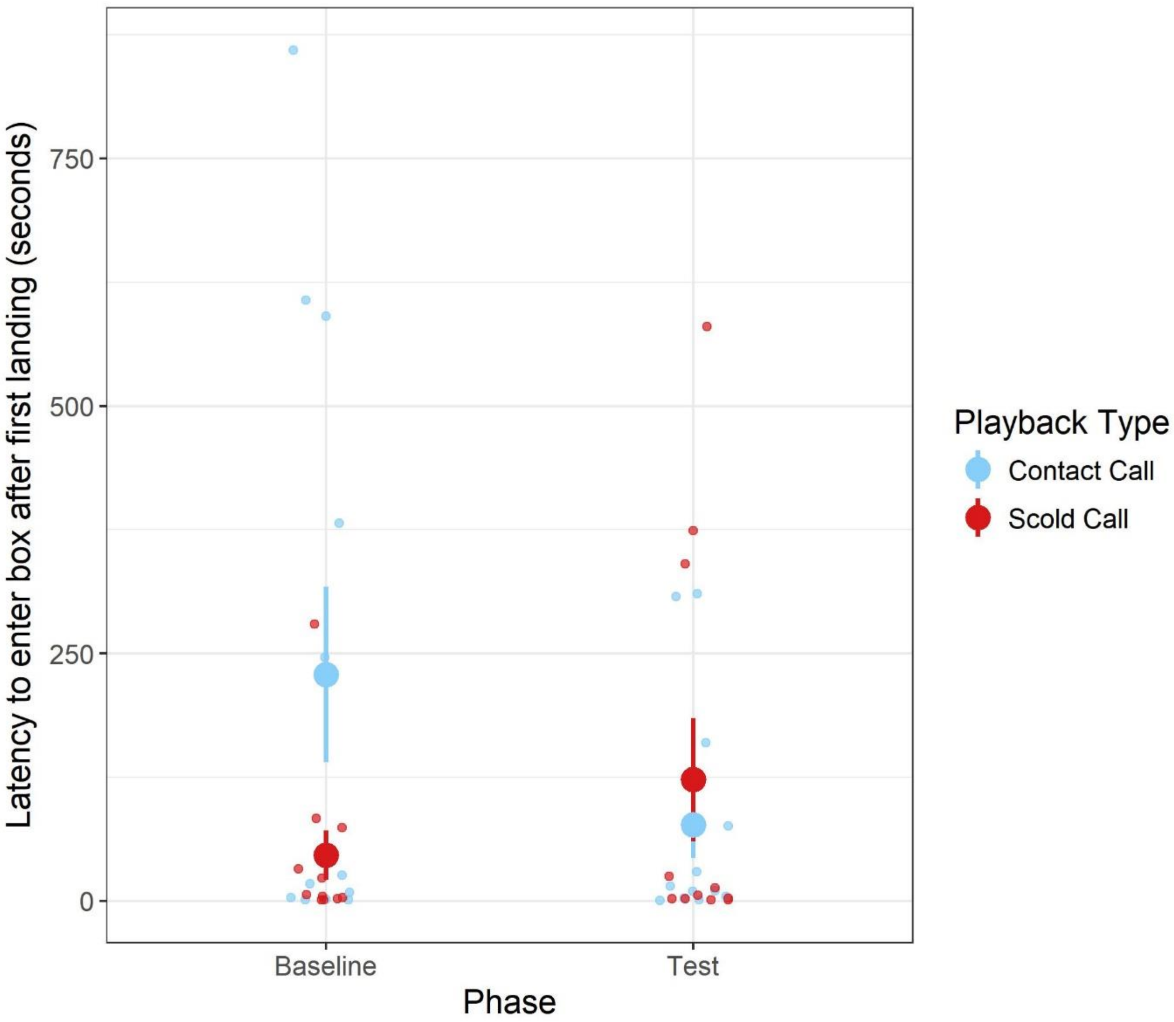


**Figure 6.3:** Female latency to enter after first landing on the nest box in the baseline (trial 1) and test phase (trial 3), according to playback type (scold calls/contact calls). Points and whiskers denote mean and standard error, n=46 observations from 23 females.

### 6.3.3. Time spent in nest box

Females spent a similar length of time inside the nest box during the baseline and test phase ($X^2$=0.02, df=1, p=0.89). This was not influenced by the type of call heard in the playback ($X^2$=1.20, df=1, p=0.27) or familiarity with the caller ($X^2$=0.01, df=1, p=0.94; Table 6.1; Figure 6.4).

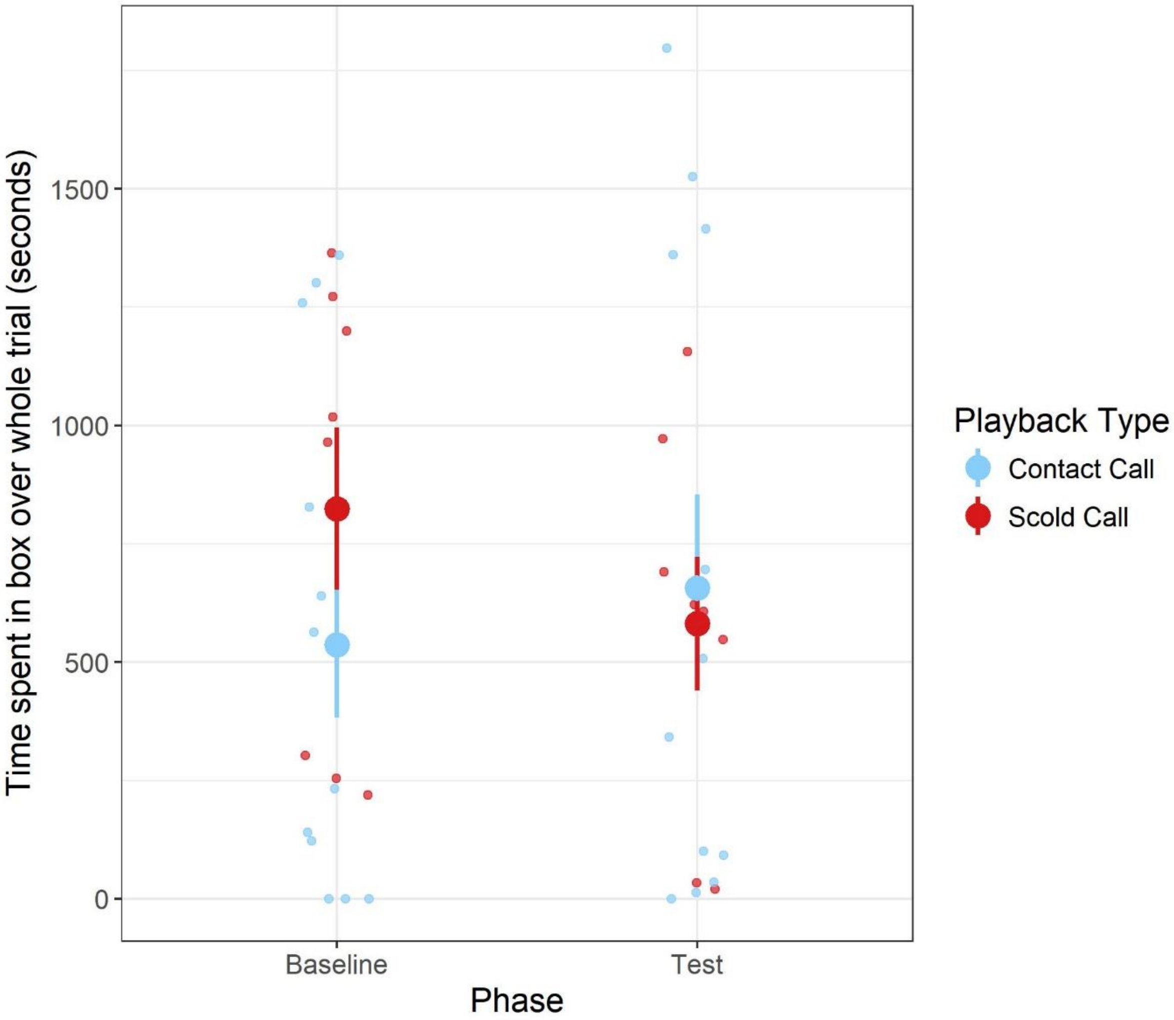


**Figure 6.4:** Time spent by females in the nest box during baseline (trial 1) and test phase (trial 3), according to playback type (scold calls/contact calls). Points and whiskers denote mean and standard error, n=40 observations from 20 females. Females that did not enter the nest box during the trial were given a score of zero.

**Table 6.1:** Model output for GLMMs investigating (a) the time taken by females to approach the nest box on their first visit; (b) the latency for females to enter the nest box after first landing; (c) the time spent by females inside the nest box over the whole trial. Models investigated the change in response between trials (trial 1/3) according to playback type (scold calls/contact calls) and caller familiarity (familiar/unfamiliar). Values are taken from full models, with significant effects given in italics. Marginal $R^2$ ($R^2_m$) estimates the proportion of variance explained by the fixed effects, and conditional $R^2$ ($R^2_c$) estimates the proportion of variance explained by both the fixed and random effects.

| **Model** | **N** | **Subjects** | **$R^2_m$** | **$R^2_c$** | **Fixed and random effects** | **β ± SE** | **t-value** | **Variance ± SD** |
|---|---|---|---|---|---|---|---|---|
| (a) Approach time | 42 | 21 | 0.29 | 0.55 | Intercept | 4.14 ± 0.45 | 9.23 | |
| | | | | | *Phase* | *-0.13 ± 0.51* | *-0.26* | |
| | | | | | *Playback Type* | *0.33 ± 0.69* | *0.48* | |
| | | | | | Familiarity | -0.47 ± 1.00 | -0.47 | |
| | | | | | *Phase x Playback Type* | *-0.85 ± 0.77* | *-1.10* | |
| | | | | | Phase x Familiarity | 2.37 ± 1.13 | 2.09 | |
| | | | | | Playback Type x Familiarity | -0.44 ± 1.26 | -0.35 | |
| | | | | | Phase x Playback Type x Familiarity | -2.79 ± 1.43 | -1.96 | |
| | | | | | Subject | | | 0.58 ± 0.76 |
| | | | | | Residual | | | 1.02 ± 1.01 |

**Table 6.1 (continued):**

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| (b) Entry latency | 46 | 23 | 0.10 | 0.61 | Intercept | 2.60 ± 0.55 | 4.75 | |
| | | | | | Phase | -0.65 ± 0.51 | -1.28 | |
| | | | | | Playback Type | -0.58 ± 0.87 | -0.67 | |
| | | | | | Familiarity | 0.56 ± 1.10 | 0.51 | |
| | | | | | Phase x Playback Type | 0.09 ± 0.80 | 0.11 | |
| | | | | | Phase x Familiarity | 0.74 ± 1.02 | 0.73 | |
| | | | | | Playback Type x Familiarity | -0.57 ± 1.48 | -0.38 | |
| | | | | | Phase x Playback Type x Familiarity | 0.62 ± 1.37 | 0.45 | |
| | | | | | Subject | | | 1.54 ± 1.24 |
| | | | | | Residual | | | 1.16 ± 1.08 |
| (c) Time in box | 40 | 20 | 0.10 | 0.66 | Intercept | 16.45 ± 3.87 | 4.25 | |
| | | | | | Phase | 2.85 ± 3.35 | 0.85 | |
| | | | | | Playback Type | 6.81 ± 6.00 | 1.13 | |
| | | | | | Familiarity | -1.47 ± 6.00 | -0.25 | |
| | | | | | Phase x Playback Type | -9.03 ± 5.19 | -1.74 | |
| | | | | | Phase x Familiarity | -1.30 ± 5.20 | -0.25 | |
| | | | | | Playback Type x Familiarity | 3.01 ± 10.00 | 0.31 | |
| | | | | | Phase x Playback Type x Familiarity | 6.59 ± 8.30 | 0.80 | |
| | | | | | Subject | | | 65.79 ± 8.11 |
| | | | | | Residual | | | 39.29 ± 6.27 |

### 6.3.4. Frequency of scolding

There were 8 trials where females responded by scolding the experimenter (Supplementary Table S5). Five females scolded in the baseline phase (trial 1) and three females scolded in the test phase (trial 3). One female scolded in both the baseline and test phases; four birds scolded in the baseline phase but not in the test phase, and two birds scolded in the test phase but not in the baseline phase (one after hearing contact calls and one after hearing scold calls in the playback phase). Females that scolded gave a median of 5.5 calls (range 2-11 calls per bird).

## 6.4. Discussion

I predicted that if jackdaws use social learning to inform their response to unfamiliar people, subjects would show a heightened response to a human watching their nest box after seeing that person associated with conspecific scold calls. I found evidence to support this hypothesis, as females that heard scold call playbacks in the training phase (trial 2) spent less time in the area before landing on the nest box in the test phase (trial 3) compared to the baseline phase (trial 1). In contrast, females that heard contact call playbacks during the training phase (2) spent longer near their nest box before landing in the test phase (3) compared to their baseline (1). Playback treatment (contact calls/scold calls) did not influence the latency of females to enter the nest box after first landing, or the time spent in the nest box overall.

The finding that subjects in the scold call group returned to the nest more quickly than subjects in the contact call group may reflect parents' motivation to monitor the perceived threat and defend the nest box, and concurs with findings of similar studies in this species (Davidson et al., 2015). Returning to the nest may also allow individuals to gather more information before deciding to recruit others to mob the potential ‘predator’. Indeed, when field researchers at my study sites visit nests to monitor breeding progress and/or weigh chicks, adult jackdaws commonly respond by returning to the area to monitor and scold the person (*pers. obs.*). If jackdaws preferentially attend to social information from familiar individuals, I predicted that changes in response between the baseline (1) and test (3) phases would be highest for birds that were trained using familiar scold calls (2). I found no evidence to support this, as familiarity with the caller had no significant effect on any of the behavioural responses measured. This may be because for breeding birds hearing scold calls near the nest box is a highly salient stimulus and thus always elicits a strong response. This explanation is supported by the fact that during the playback phase, all birds responded to the scold call playbacks immediately by leaving the nest box and/or giving responsive scolds, whereas subjects that heard contact calls remained on the nest box during the playback. In contrast to the scold call group, females in the contact call group showed an increase in latency to approach the nest between the baseline (1) and test (3) phase. This may be because, in the absence of information that the person near the nest box is dangerous, birds show reduced motivation to return quickly to the nest as the chicks grow and can be left alone for longer periods of time.

Individual test subjects also varied in their behavioural responses during experimental trials, with individual identity explaining a substantial proportion of the variance in the data (see Table 6.1). This may partly explain the modest overall effect size seen for the interaction between phase (baseline/test) and playback type (scold calls/contact calls) on the time taken by females to approach the nest box (Table 6.1). Taken together, my findings suggest that there is an element of social learning involved in refining jackdaws' responses to unfamiliar people, but there is a considerable amount of individual variation in how these responses are manifested (see also McIvor et al., 2018). Therefore, although jackdaws appear to use social learning to identify a 'dangerous' person, individuals vary in how they respond during subsequent encounters with that person. Individual variation in behaviour is often controlled for but rarely discussed explicitly in experiments of this kind, and is likely to be critical to our understanding of animal cognition (Boogert et al., 2018; Cauchoix et al., 2018).

This study provides direct evidence that individual animals alter their responses to individual people via social learning. My findings complement those of Davidson et al. (2015) who demonstrated that jackdaws' personal experience with individual people informs their subsequent behavioural response in a similar way. The current study extends this work, suggesting that jackdaws may not need to directly experience an unpleasant event to identify a human as 'dangerous' and can use social cues to learn about dangers associated with specific people. My results also contribute to a wider body of work on socially acquired predator avoidance. Although this area has received relatively little attention compared to other aspects of social learning (Griffin, 2004), previous studies have shown that social cues play an important role in learning to avoid novel predators (Curio et al., 1978a, 1978b; Suboski et al., 1990), novel parasites (Davies & Wellbergen, 2009; Feeney & Langmore, 2013) and dangerous locations (Griffin & Boyce, 2009). To date, only one other study has investigated socially acquired predator avoidance in the wild, providing compelling circumstantial evidence for social transmission of information about dangerous people from informed to naïve American crows (Cornell et al., 2012).

My experiment builds on this by showing that a single short-lived, commonly-occurring alarm calling event may be sufficient to alter individual behaviour in response to specific people, by reducing latency to return to the nest. These types of social learning events are likely to be important for organisms that exploit human-dominated habitats where individual people represent varying levels of threat, especially for species such as corvids that are often persecuted as pests.

Understanding how social learning shapes antipredator responses is vital to predicting and mitigating the effects of human activity, and provides valuable insights into how cognitive abilities influence adaptation to changing environments. However, socially acquired predator avoidance has received surprisingly little attention given its importance for individual fitness. Despite being limited in number, studies to date have provided some compelling insights into how animals learn socially about danger; further research is urgently needed to investigate how social environments facilitate antipredator learning, particularly under natural conditions. Studying a wide range of species is also essential to identify factors underlying success in anthropogenic habitats, which could subsequently be applied to effectively manage pest species and conserve declining populations.

# Supplementary Material for Chapter 6: Jackdaws learn socially about dangerous people

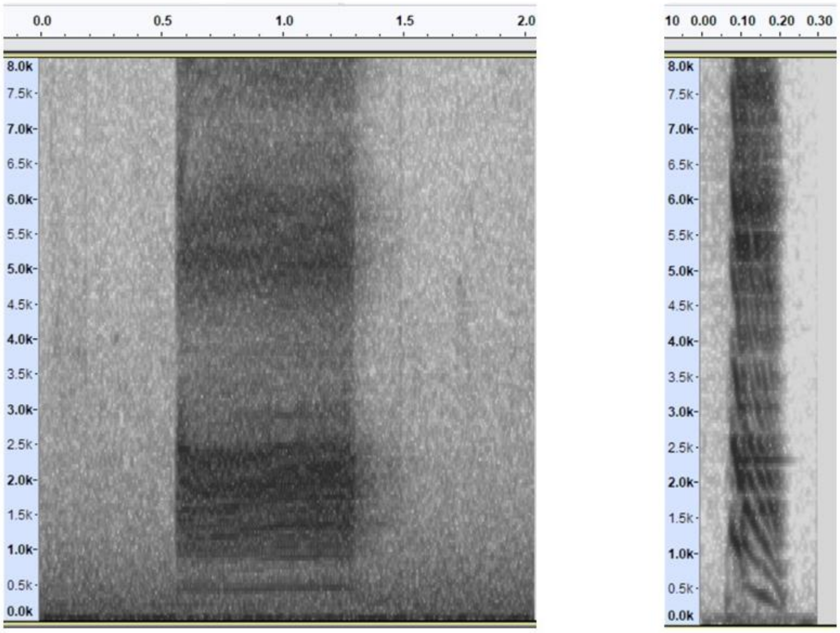


**Figure S1:** Spectrogram of a jackdaw scold call (left) and a jackdaw contact call (right). Playbacks were comprised of 5 calls from the same individual separated by an inter-call interval of 2 seconds to simulate natural call rates.

**Figure S2:** Masks used by experimenters during trials. Each focal jackdaw pair was given three presentations of the same experimenter wearing the same mask. Masks were paired with a plain hat and the same clothing was worn by experimenters throughout the trials. Each mask was allocated to a consistent playback treatment (scold calls/contact calls) at a given field site, and mask-treatment allocations were counterbalanced between sites.

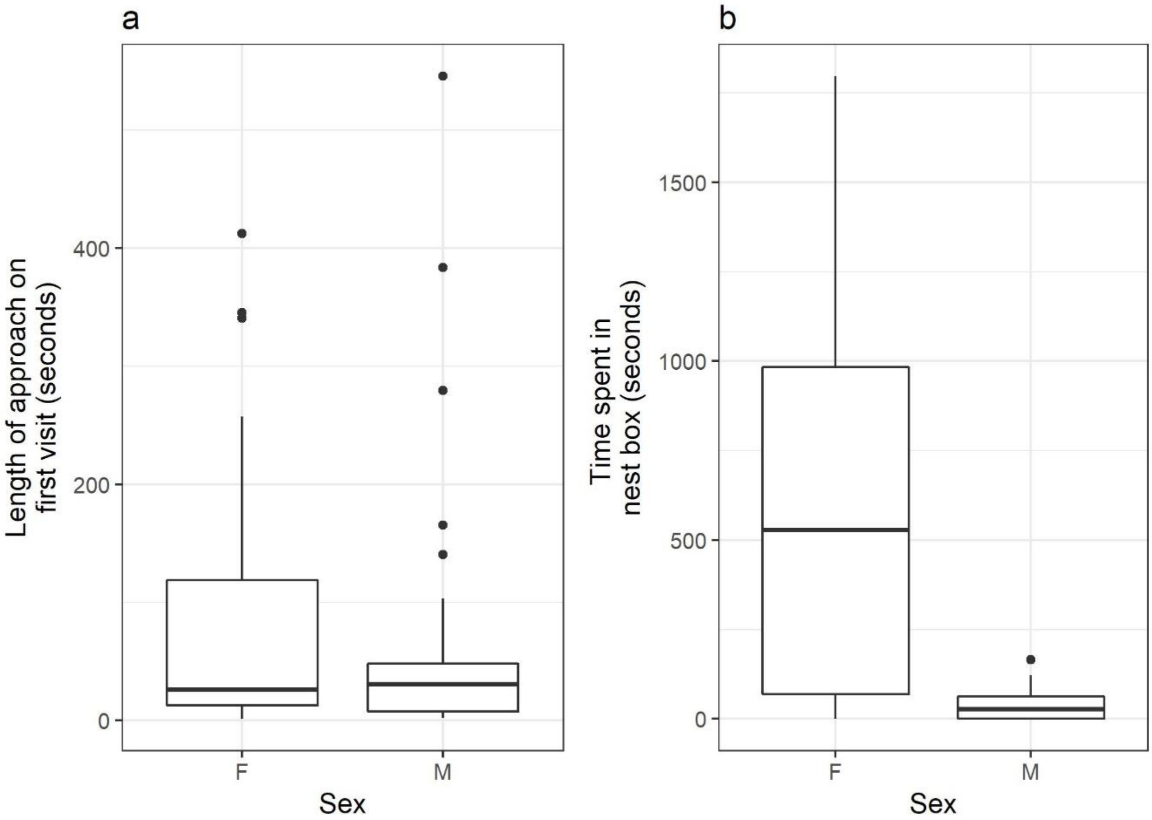


**Figure S3:** Heterogeneity of variance between sexes for key behavioural responses. a) Females were more variable than males in their latency to approach the nest box on the first visit; b) Females spent more time in the nest over the course of the trials, as expected at this stage in the breeding attempt.

**Table S4:** Summary statistics for female approach times on their first visit to the box in the baseline and test phases, by treatment group.

| | **Scold Calls** | | **Contact Calls** | |
|---|---|---|---|---|
| | Baseline | Test | Baseline | Test |
| n | 11 | 11 | 10 | 10 |
| Mean±SE | 92.7s ± 31.0 | 43.6s ± 23.2 | 70.6s ± 26.5 | 114.8s ± 37.2 |
| Median±IQR | 65.6s ± 104.2 | 13.3s ± 8.8 | 31.1s ± 26.2 | 62.6s ± 177.2 |

**Table S5:** Proportion of females scolding in each experimental treatment (infrequent scolding precluded formal analysis of this response). Excludes individuals that were not present during the playback presentation in the training phase.

| Proportion of females scolding | **Baseline** | **Test** |
|---|---|---|
| **Contact calls** | 4/16 | 2/16 |
| **Scold calls** | 1/13 | 1/13 |

# Chapter 7

# Individual differences shape behavioural responses of wild jackdaws during encounters with people

## Abstract

Tolerance of human presence plays a key role in allowing wildlife to adapt to human-altered environments. Among-individual differences in responses to human disturbance may have a profound effect on individual survival and reproductive success by influencing foraging efficiency and provision of parental care. However, only a handful of studies have quantified within-individual consistency in response to human disturbance, and fewer still have investigated the fitness consequences associated with these individual differences. Here, I present the first study to investigate links between individual differences in tolerance of human presence and reproductive success. In two experiments where wild jackdaws were exposed to an unfamiliar person near their nest, individuals differed consistently in their risk-taking behaviour, with some birds spending more time at the nest than others. However, I found no evidence that the length of time individuals spent at the nest in the presence of a person predicted their subsequent reproductive success.  My results highlight the importance of individual differences in shaping behaviour during human-wildlife encounters, and provide insights into how individual variation in behaviour may contribute to success in a rapidly changing world.

## **7.1. Introduction**

Humans have drastically altered almost every habitat on Earth, exerting strong selection pressures on other species (Darimont et al., 2009; Palumbi, 2001). Species vary in their responses to this human-induced rapid environmental change (HIREC): while some show severe population declines, others appear to thrive in anthropogenic habitats (Sih, 2013; Sih et al., 2012, 2011). Predicting how animal species will respond to human-altered habitats is vital in order to identify potentially adaptive traits, mitigate impacts and conserve declining species (Greggor et al., 2014; Sih, 2013; Sih et al., 2011; Sol, Lapiedra, & González-Lagos, 2013). A number of traits are predicted to facilitate success in novel environments, including habitat generalism (Cassey, Blackburn, Sol, Duncan, & Lockwood, 2004; Sol et al., 2005), innovation propensity (Sol et al., 2005) and behavioural flexibility (Sol et al., 2013). In addition to these factors, consistent inter-individual differences in behaviour (‘personality’) are widespread across the animal kingdom (Bell, Hankison, & Laskowski, 2009) and are likely to play an important role in influencing how organisms respond to environmental change (Dingemanse et al., 2004; Sih et al., 2012, 2011). Risk-taking behaviour, in particular, is likely to influence the ability of animals to inhabit areas dominated by human activity (Lapiedra et al., 2017). For example, individual differences in risk aversion may influence tendencies to exploit novel resources or habitats (Breck et al., 2019; Kozlovsky et al., 2017; Lapiedra et al., 2017; Sol et al., 2011; Thompson et al., 2018); responses to encounters with predators and humans (Evans et al., 2010; Schoener et al., 2018; Short & Petren, 2008); and responses to competitors (Duckworth & Badyaev, 2007; Evans et al., 2010; Hardman & Dalesman, 2018). In many cases, risk-related behaviours are correlated across contexts in a behavioural syndrome

(Adriaenssens & Johnsson, 2013; Dingemanse et al., 2004; Schoener et al., 2018; Sih et al., 2004). Much research effort has been devoted to identifying the causes and consequences of personality variation (e.g. Ballew, Mittelbach, & Scribner, 2017; Santos et al., 2015; see Dingemanse & Wolf, 2010; Réale, Dingemanse, Kazem, & Wright, 2010; Smith & Blumstein, 2008 for reviews), including the adaptive value of different personality types under varying ecological conditions (Both, Dingemanse, Drent, & Tinbergen, 2005; Dingemanse et al., 2004; Réale & Festa-Bianchet, 2003; Schoener et al., 2018). How individual differences in behaviour influence success in human-dominated habitats has become an increasing focus for empirical research, but remains poorly understood (Lapiedra et al., 2017; Short & Petren, 2008; Sih et al., 2012; Sol et al., 2011). In particular, individual variation in response to human disturbance has received surprisingly little attention.

For many animals that frequently encounter humans, escape decisions may be subject to a trade-off. Fear of humans might be beneficial in allowing individuals to avoid potential danger (Bremner-Harrison et al., 2004); on the other hand, fleeing in response to benign human presence may entail unnecessary time and energy costs, reducing foraging efficiency (Smith, Wang, & Wilmers, 2015; Thomas, Kvitek, & Bretz, 2002) and provision of parental care (Fernández & Azkona, 1993; Verhulst et al., 2001). Given these fitness implications, individual differences in response to human disturbance may have far-reaching consequences for population dynamics, community composition and species persistence (Pelletier & Garant, 2012; Pirotta et al., 2018; Schlesinger, Manley, & Holyoak, 2008; Sih et al., 2011; Smith et al., 2015; Stankowich & Blumstein, 2005; Tuomainen & Candolin, 2011). Moreover, understanding how individuals may differ in their tolerance of people can help to inform conservation management and mitigate human-wildlife conflict (Breck et al., 2019; Greggor et al., 2014; Smith et al., 2015). A number of studies show that animals living in urban areas alter their activity patterns to minimise encounters with people (Beckmann & Berger, 2003; Duarte et al., 2011; Rodriguez-Prieto, Fernández-Juricic, Martín, & Regis, 2009; Samia et al., 2015; Wheat & Wilmers, 2016). However, few studies have investigated between-individual differences in response to human disturbance, and the consistency of these responses over time. Notable exceptions include studies by Carrete & Tella (2010, 2013) which found that individual burrowing owls (*Athene cunicularia*) differ in their flight initiation distance (FID) when approached; these individual differences are highly consistent both within and across years. In roe deer (*Capreolus capreolus*), inter-individual differences in responses to risk influence tendency to use open habitat during periods of higher human disturbance (Bonnot et al., 2015). In another study, chipmunks (*Tamias striatus*) captured in areas of higher human disturbance were more exploratory when introduced to a novel environment, and were more docile during handling (Martin & Réale, 2008). Finally, Runyan & Blumstein (2004) found that although individual marmots (*Marmota flaviventris*) varied in their responses to human approach, individuals differed in the rate at which they habituated to this disturbance. Nevertheless, despite identifying consistent differences in how individuals respond to human presence, very few studies have investigated how these inter-individual differences influence fitness under natural conditions (see Ciuti et al., 2012; Greenberg & Holekamp, 2017), particularly with regards to reproductive success.

Here, I aim to address these research gaps by quantifying individual differences in response to human disturbance in wild jackdaws (*Corvus monedula*) and determine whether these individual differences relate to reproductive success. Jackdaws are highly social corvids that thrive in human-dominated habitats by utilising anthropogenic resources such as food and breeding sites (Gregory & Marchant, 1996; Harris et al., 2018). Reflecting a history of persecution, jackdaws show remarkable discrimination and learning abilities when identifying anthropogenic threats (Davidson, Clayton, & Thornton, 2015; von Bayern & Emery, 2009; see also Chapter 6), much like other corvids (Bugnyar et al., 2004; Clucas et al., 2013; Lee et al., 2011; Marzluff et al., 2010). Individuals also form long-term pair bonds and provide biparental care essential to offspring survival (Henderson & Hart, 1993; Röell, 1978). In this study, I quantified individual differences in jackdaws' responses to an unfamiliar person sitting outside their nest box. To do this, I used behavioural data collected during two field experiments designed to test discrimination and learning of anthropogenic threats (Chapter 5 and Chapter 6). Both experiments involved repeatedly presenting breeding pairs of jackdaws with a human wearing a mask, to investigate whether jackdaws use objects being carried by people as cues during risk assessment (Chapter 5) and whether jackdaws learn about 'dangerous' people via social learning (Chapter 6). All experimental trials were similar in the sense that birds were presented with people sitting outside their nest box whilst wearing a mask, although the exact nature of stimuli differed depending on experimental treatment. The length of time that individual birds spent in the nest box during experimental trials was broadly similar over time and across experimental treatments. As cavity-nesting birds, entering the nest box is a behaviour that may be risk-sensitive for jackdaws: although birds may be relatively safe from attack when inside the nest box, entering the nest box involves losing sight of the potential threat (when disturbed, jackdaws usually leave the nest to obtain more information about the threat; *pers. obs*., see also Schneider & Griesser, 2013). Consistently failing to provision offspring in the presence of people may result in fitness losses, especially for individuals nesting in areas of frequent human disturbance (Fernández & Azkona, 1993; Verhulst et al., 2001). If individuals consistently differ in their tendency to take risks when humans are nearby, this may influence their ability to exploit anthropogenic habitats. I therefore predicted that, in my study colonies (where human disturbance is relatively frequent, see 7.2.1), individuals that spent more time inside the nest box in the presence of a person would have higher reproductive success.

## 7.2. Methods

### 7.2.1. Study population

Behavioural data for this study were obtained from two field experiments conducted in 2016 and 2017, during the jackdaw breeding season (Chapter 5-6). Test subjects were members of nest box populations managed by the Cornish Jackdaw Project in Cornwall, UK. Nest boxes at the Pencoose site (50°11′56″N, 5°10′9″W) are centred around an active farmyard, and the Stithians site (50°11′26″N, 5°10′51″W) is located in a village churchyard and surrounding fields. While most pedestrians are typically ignored by resident jackdaws, some people are perceived as a threat: corvids are occasionally shot by hunters in and around the study sites (*pers. obs.*). Jackdaws also regularly encounter field researchers who monitor breeding progress, remove chicks from nest boxes for weighing, trap and ring adult birds and conduct experiments at nest boxes and feeding tables. Adult jackdaws respond to these activities by monitoring researchers from a safe distance and giving alarm calls, a typical anti-predator response (McIvor et al., 2018; Woods et al., 2018).

### 7.2.2. Behavioural data

#### *7.2.2.1. Time spent in nest box as a measure of risk-taking*

When encountering a potential threat at the nest, including human disturbance, jackdaws often respond by returning to the vicinity of the nest to monitor the predator (Davidson et al., 2015; see also Chapter 6), and may give alarm calls to recruit others to form a mob (Woods et al., 2018). However, entering the nest whilst being watched by a predator is potentially risk-sensitive for jackdaws: as cavity nesters, entering the nest to provision chicks involves losing sight of the predator. For example, when jackdaws detect disturbance whilst inside the nest, birds typically look out of the nest entrance to gain more information about the potential threat (*pers. obs*., see also Schneider & Griesser, 2013). On the other hand, consistently failing to enter the nest or feed chicks in the presence of non-threatening people may result in fitness losses, particularly for jackdaws and other species that nest in busy urban and agricultural settings with high levels of human disturbance (Blumstein et al., 2005; Fernández & Azkona, 1993; Pirotta et al., 2018; Tuomainen & Candolin, 2011; Verhulst et al., 2001).

In this study, I investigated whether individual jackdaws differ consistently in their risk-taking propensity when faced with an unfamiliar person outside their nest. To do this, I quantified the length of time jackdaws spent in their nest box in the presence of an unfamiliar human (as a measure of risk-taking) and calculated the within-individual repeatability of this behaviour over time. Data derive from two experiments conducted over two years, where birds were repeatedly presented with an unfamiliar person sitting outside their nest box.

Although these experiments were originally designed to address different questions regarding discrimination and learning of anthropogenic threats (see below), the data derived from these experiments also provide opportunities to investigate the extent, consistency and potential consequences of individual variation in response to human disturbance. The results of the original experiments demonstrated that subject identity explained a substantial proportion of the variance in birds' responses to experimental trials, suggesting that individuals may differ in their behaviour towards unfamiliar people (see Chapters 5-6). Here, I quantify these individual differences in tolerance to human presence explicitly and investigate the potential fitness consequences of individual variation in risk aversion in this context. Experiments were conducted at 51 focal nest boxes in total (17 nests in Experiment 1; 34 nests in Experiment 2), with 12 jackdaw pairs taking part in both experiments.

#### *7.2.2.2. Presentations of unfamiliar people*

*Experiment 1: Using anthropogenic objects to infer risk (Chapter 5)*

In 2016, I conducted an experiment to investigate whether jackdaws infer risk from humans based on objects being carried by people (Chapter 5). Specifically, I compared birds' responses to an unfamiliar person sitting outside their nest box holding either a gun ('dangerous' object) or a wooden stick (a similar but non-threatening object). In a fully crossed design, 17 jackdaw pairs were each given four 30-minute presentations of the same unfamiliar person holding a gun across the lap; pointing a gun at the nest box; holding a wooden stick across the lap and pointing a wooden stick at the nest box. Trials at a given nest box occurred on consecutive days (c. 24 hours between presentations), beginning 4-6 days following hatching of the first chick. The order in which objects were presented was counterbalanced across nest boxes (see Chapter 5 for detailed methods). The object carried by the experimenter (gun/stick) and the orientation of the object (pointing/lap) had no significant influence on the behaviour of test subjects (in terms of tendency to return and enter the nest box, and latency to do so; length of time spent in the nest box, and length of time spent vigilant in the vicinity of the nest box). In some cases, subjects showed habituation to experimental trials over time (see Chapter 5 for detailed results).

*Experiment 2: Social learning about dangerous people (Chapter 6)*

The following year, I conducted a second experiment to determine whether jackdaws use social learning to inform their response to unfamiliar people. For this experiment, 34 jackdaw pairs were given three presentations involving an unfamiliar person sitting outside their nest box. Birds were given a baseline trial (an unfamiliar person sitting outside the nest box for 30 minutes), followed by a training trial (presentation of the same person combined with alarm call playbacks to denote danger, or contact call playbacks as a control) and a test trial (another 30-minute presentation of the person). This was designed to investigate whether the type of call heard in the training phase influenced birds' subsequent behaviour in the test phase. Unlike Experiment 1, this experiment followed a nested design, with each pair assigned to one of two treatment groups (alarm call playback or contact call playback). Presentations occurred on consecutive days beginning 3-5 days following hatching of the first chick (c. 24 hours between trials; see Chapter 6 for detailed methods). When comparing changes in subjects' behaviour between the baseline and test phases, playback type (alarm calls/contact calls) influenced the time taken for females to land on the nest box after returning to the area on their first visit; however, there was no significant effect of treatment on subjects' latency to enter the nest box after first landing or the length of time spent in the nest box during a trial (see Chapter 6 for detailed results).

### 7.2.3. Fitness data

All nest boxes at both study sites were monitored daily for signs of hatching, starting 18 days after the first egg was laid. Chicks were weighed and individually colour-marked on the day of hatching (using non-toxic marker pens), and then every three days following hatching of the last chick in the brood. Any chick mortality was also recorded throughout the breeding attempt. All chicks were individually colour-ringed 26 days after hatching of the first chick in the nest. Biometric data were also taken for all chicks at ringing (including tarsus length, wing length and body mass), along with a small blood sample (<1ml) for molecular sexing purposes. After ringing, nests were monitored daily to obtain exact fledging dates for all chicks.

### 7.2.4. Statistical analysis

All analyses were carried out in R with models created using *lme4* (Bates et al., 2015). Models were simplified using log-likelihood ratio tests after verifying that model assumptions were met (normality and homogeneity of residuals). Repeatability estimates were calculated using the *rptR* package (Stoffel, Nakagawa, & Schielzeth, 2017).

#### *7.2.4.1. Repeatability of risk-taking*

Risk-taking measures from Experiment 1 and Experiment 2 were analysed separately, due to differences in variance partitioning between the two study designs. Experiment 1 used a fully crossed design, whereas in Experiment 2, test subjects were nested within experimental treatments (resulting in the interaction variance being pooled with the random-effect variance). Therefore, whilst it was possible to quantify individual repeatability within each experiment, repeatability could not be calculated using data pooled across both experiments (Schielzeth & Nakagawa, 2013). For this reason, it was not possible to investigate whether repeatability of risk-taking correlated across experiments for the 12 pairs that took part in both experiments. From each experiment, data were obtained on the total time each individual member of the pair spent inside the box during each 30-minute trial. For cases where females were already inside the nest box at the beginning of the trial, time spent in the box was calculated following female trial start time (the time at which the female first saw the experimenter). Analyses were carried out at the level of the individual, and sexes were analysed separately due to heterogeneity of variance between males and females in the total length of time spent in the nest box: this is to be expected at this stage in the breeding attempt, as females are primarily occupied with incubating young chicks (see Supplementary Figure S1). Data were included from all trials in Experiment 1, and from the baseline and test trials in Experiment 2 (exact sample sizes vary according to whether reliable data were obtained during a given trial; see below). Repeatability measures were adjusted to account for any effect of experimental treatment or presentation order; confidence estimates were obtained via parametric bootstrapping (n=1,000) and significance testing was carried out using log-likelihood ratio tests and permutation of residuals (n=1,000; Stoffel et al., 2017).

### *Experiment 1: Using anthropogenic objects to infer risk*

To estimate the repeatability of behaviour, it is necessary to control for any potential effects of experimental treatment. To control for the potential effects of object type (gun/stick) and orientation (pointing/lap) on the length of time subjects spent inside the nest box across trials, I firstly created two linear mixed models with Gaussian error distributions (one for each sex). The total length of time spent inside the nest box during a trial was included as the response variable in both models, following Box-Cox transformation. Fixed effects included the object held by the experimenter (gun/stick), the orientation of the object (pointing/lap) and trial number (1-4). Subject ID was included as the random term. Models included all trials in which an individual spent at least some time inside the nest box: the model for females comprised 41 observations from 11 individuals (3-4 trials per female); the model for males comprised 37 observations from 12 individuals (2-4 trials per male). Repeatability estimates were subsequently derived from minimal models, after I confirmed that the fixed effects had no significant influence on the responses of either males or females (see *Results*).

### *Experiment 2: Social learning about dangerous people*

To estimate individual repeatability while controlling for the potential effects of playback treatment (alarm calls/contact calls) on the consistency of subjects' time spent inside the nest box during Experiment 2, I first created a Gaussian linear mixed model for each sex. Again, total length of time spent inside the nest box during a trial was included as the response variable in both models following Box-Cox transformation. Experimental phase (baseline/test) and playback type (contact/alarm calls) were included as fixed effects, along with an interaction between phase and playback type. Subject ID was included as a random effect. Only individuals that entered the box during both trials were included in the analysis. The model for females comprised 54 observations from 27 individuals: repeatability estimates were calculated from the minimal model (no fixed effects had any significant effect on the response, see *Results*). The model for males comprised 42 observations from 21 individuals, and repeatability estimates were adjusted to account for the significant effect of phase (baseline/test) on the length of time males spent inside the nest box (see *Results*).

#### *7.2.4.2. Linking risk-taking to reproductive success*

In order to determine whether parents that spent more time feeding chicks in the presence of people had higher reproductive success, I investigated whether time spent in the nest box during trials predicted (i) the total number of chicks fledged and (ii) the body condition of chicks at ringing (at 26 days post-hatching; calculated as average residual weight of chicks in the nest after accounting for tarsus length; Greggor, Spencer, Clayton, & Thornton, 2017; Labocha & Hayes, 2012; Verhulst & Salomons, 2004). The time spent in the nest box by parents during experimental trials may also depend on the mass of chicks in the nest: females in particular may be less motivated to return to the nest and incubate chicks that are heavier and better able to regulate their own body temperature. To control for this, total brood mass on the first day of the experiment was calculated for each nest box and included as a covariate in models. For chicks weighed on the day of the experiment, exact weights were used; for broods that were not weighed on the day of the experiment, brood mass on the first day of the experiment was estimated based on data obtained before and after the experiment started (±1-3 days). For one nest box in Experiment 1, chicks were not weighed prior to the experiment and were weighed for the first time on the day after the experiment started (day 4 post-hatching). For this nest, data obtained on this day were taken to be representative of brood mass during the experiment.

*Experiment 1: Using anthropogenic objects to infer risk*

To investigate whether the length of time spent in the nest box during trials in Experiment 1 predicted reproductive success, I created four linear models (two for each sex). Average body condition of chicks at ringing (residual weight after controlling for tarsus length) was included as the response variable in a linear model with a Gaussian error distribution, and the number of chicks fledged was included as the response variable in a poisson GLM. All models contained two fixed effects: brood mass on the first day of the experiment (exact or inferred) and the mean time spent inside the nest box across all experimental trials (Box-Cox transformed). The two models for females comprised of 11 observations from 11 individuals, and the two models for males comprised 12 observations from 12 individuals.

*Experiment 2: Social learning about dangerous people*

Four linear models (two for each sex) were similarly constructed to determine whether time spent in the nest box in Experiment 2 predicted reproductive success. As for Experiment 1, response variables included average body condition of chicks at ringing (Gaussian linear model) and number of chicks fledged (poisson GLM). Brood mass on the first day of the experiment (exact or inferred) and mean time spent inside the nest box across trials (Box-Cox transformed) were included as fixed effects. Models for females comprised 27 observations from 27 individuals, and models for males comprised 21 observations from 21 males.

## 7.3 Results

### 7.3.1. Repeatability of risk-taking

*Experiment 1: Using anthropogenic objects to infer risk*

When faced with consecutive presentations of a person holding a gun or a wooden stick near their nest box, both male and female jackdaws showed significant individual consistency in the length of time spent inside the nest box (Figure 7.1; Figure 7.2; Table 7.1). In addition, models confirm the results of the original analyses (Chapter 5). For females, the type of object held by the experimenter (gun/stick), the orientation of the object (pointing/lap) and trial number (1-4) did not influence the length of time spent inside the nest box (object: $X^2$=0.14, df=1, p=0.71; orientation: $X^2$=0.50, df=1, p=0.48; trial number: $X^2$=0.91, df=1, p=0.34; Supplementary Table S2). For males, the type and orientation of the object held by the experimenter did not influence the length of time spent inside the nest box during experimental trials (object: $X^2$<0.001, df=1, p=0.99; orientation: $X^2$=0.70, df=1, p=0.40; Supplementary Table S2). Trial number had a marginally non-significant effect on the length of time males spent in the nest box ($X^2$=3.65, df=1, p=0.056; Supplementary Table S2), and so the more conservative repeatability estimate (excluding trial number) is presented here (Stoffel et al., 2017).

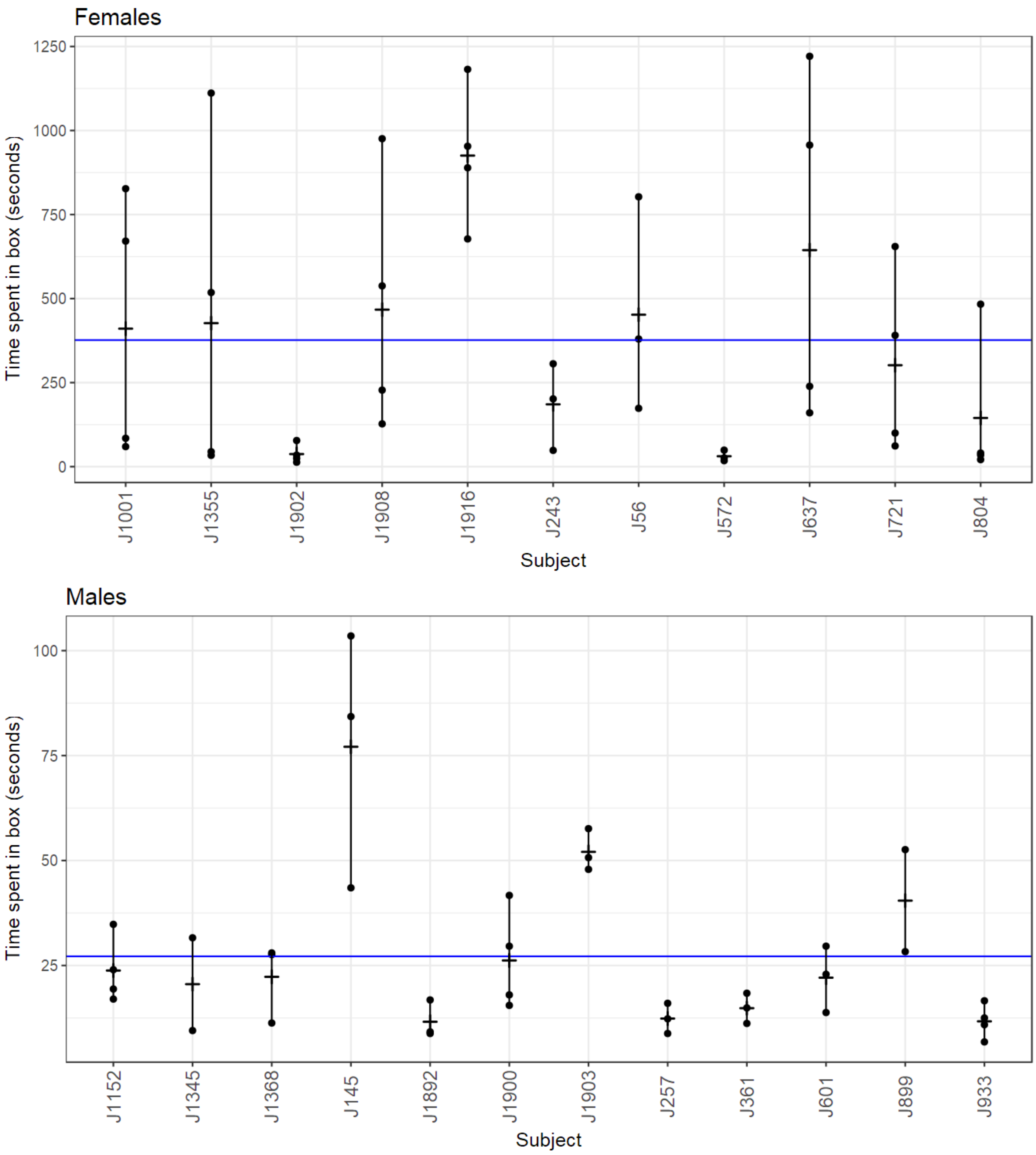
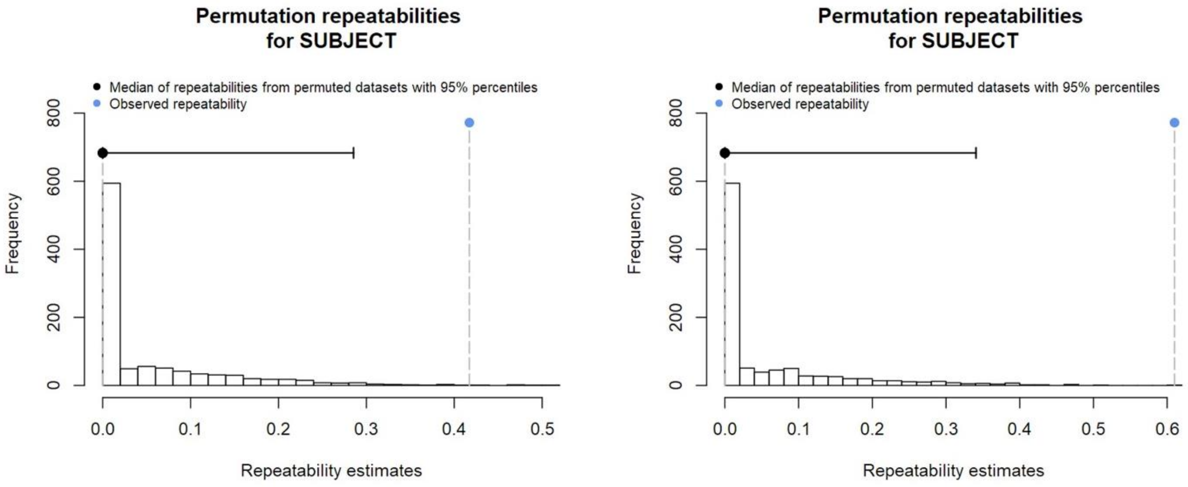


**Figure 7.1:** Repeatability in the length of time spent inside the nest box during trials in Experiment 1, by (a) females (11 subjects; 3-4 measures per individual) and (b) males (12 subjects; 2-4 measures per individual). Points represent raw data, black horizontal lines indicate mean value for each individual, and blue line shows mean value for all birds included in the model.



a) Females

b) Males

**Figure 7.2:** Results of permutation tests calculating significance of repeatability estimates for the length of time spent in the nest box by (a) females and (b) males during trials in Experiment 1.

*Experiment 2: Social learning about dangerous people*

In the second experiment, females and males again showed high individual consistency in the length of time spent inside the nest box when faced with an unfamiliar person (Figure 7.3; Figure 7.4; Table 7.1). As for Experiment 1, this analysis also confirmed the results of the original experiment (Chapter 6). Females spent a similar length of time inside the nest box regardless of experimental phase (baseline/test) and the type of calls heard during the training phase (phase: $X^2$=0.55, df=1, p=0.46; playback type: $X^2$=0.47, df=1, p=0.50; phase x playback interaction: $X^2$=1.63, df=1, p=0.20; Supplementary Table S2). Likewise, the length of time that males spent in the nest box did not differ between experimental treatments (playback type: $X^2$=2.39, df=1, p=0.12; phase x playback interaction: $X^2$=0.54, df=1, p=0.46; Supplementary Table S2). Males showed a significant decrease in time spent in the nest box between the baseline and test phase ($X^2$=7.14, df=1, p=0.008; Supplementary Table S2; Supplementary Figure S3), and repeatability estimates are adjusted to reflect this (estimates derive from a model including trial number as a single fixed effect; Stoffel et al., 2017).

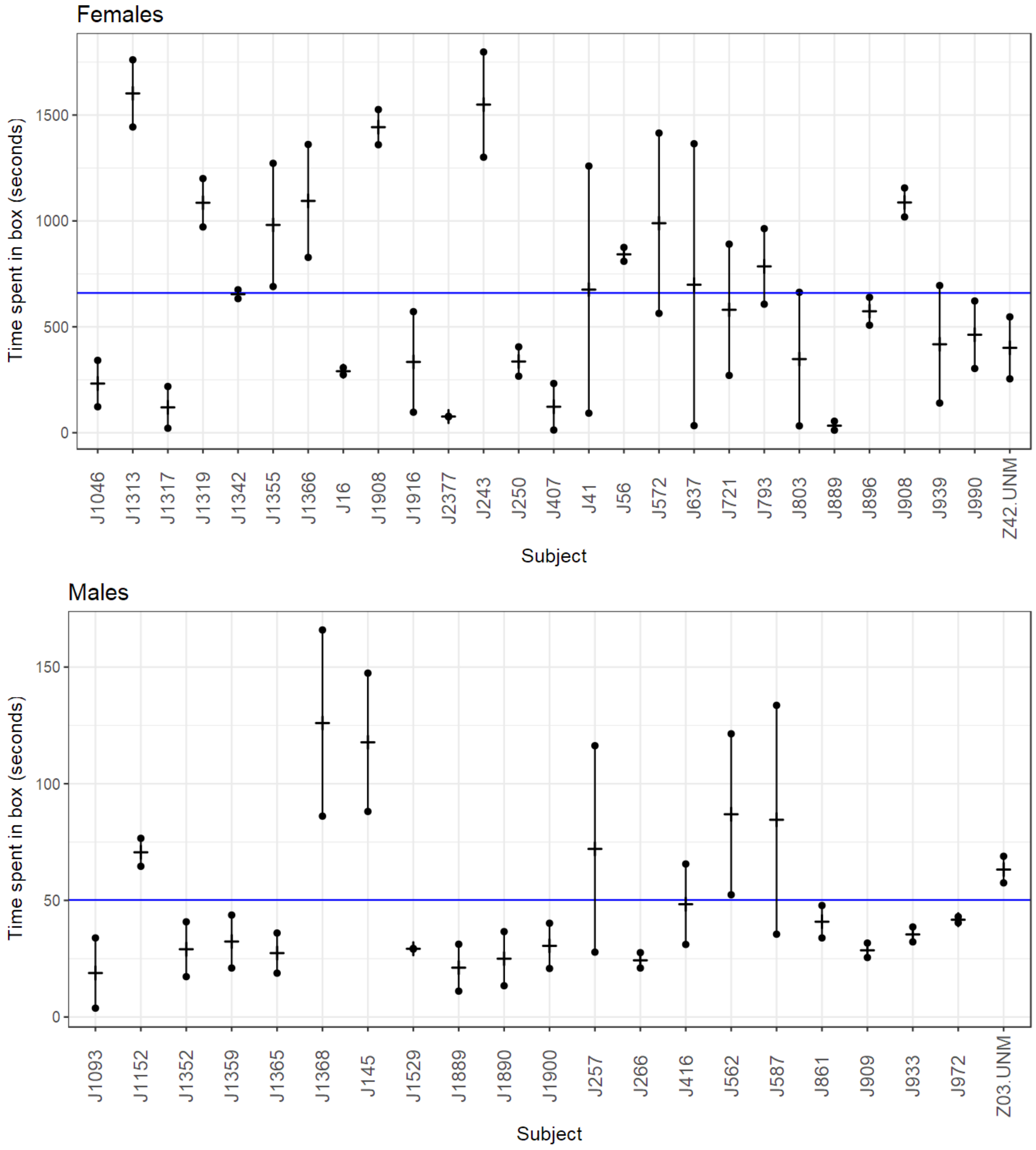


**Figure 7.3:** Repeatability in the length of time spent inside the nest box during trials in Experiment 2, by (a) females (27 subjects; 2 measures per individual) and (b) males (21 subjects; 2 measures per individual). Points represent raw data, black horizontal lines indicate mean value for each individual, and blue line shows mean value for all birds included in the model.

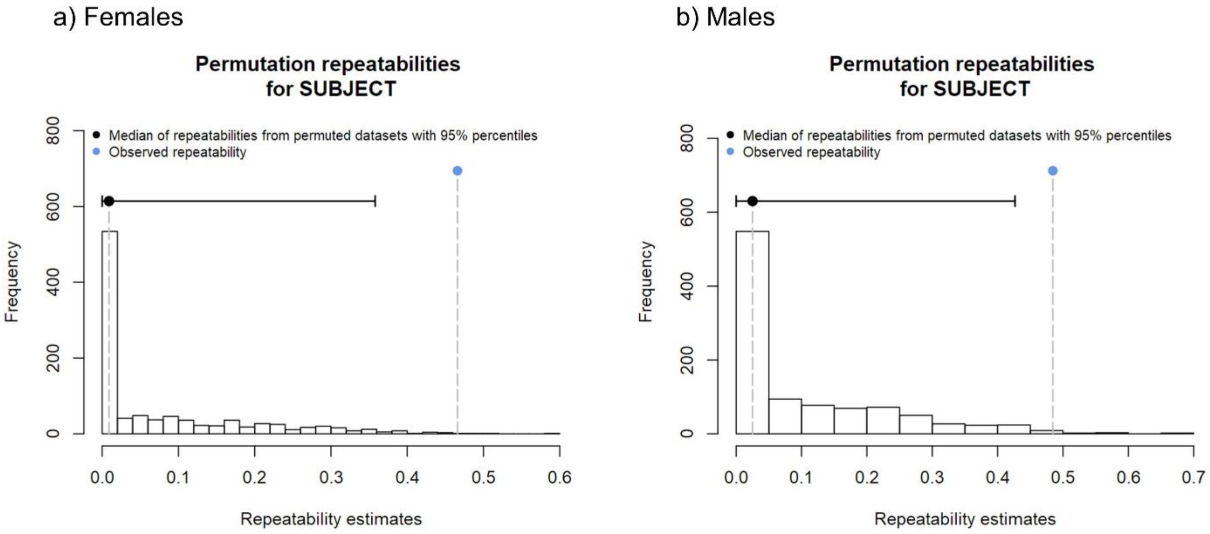


**Figure 7.4:** Results of permutation tests calculating significance of repeatability estimates for the length of time spent in the nest box by (a) females and (b) males during trials in Experiment 2.

**Table 7.1:** Repeatability estimates for the length of time birds spent inside the box during experimental trials. In Experiment 2, repeatability estimates were adjusted to account for the significant effect of experimental phase (baseline/test) on male behaviour. Low R scores (0) indicate low repeatability with high within-individual variance and high R scores (1) indicate high repeatability with low within-individual variance.

| | **Sex** | **R** | **SE** | **95% CI (lower, upper)** | **P-value** |
|---|---|---|---|---|---|
| **Experiment 1** | Females | 0.42 | 0.17 | 0.03, 0.68 | 0.005 |
| | Males | 0.61 | 0.16 | 0.23, 0.82 | <0.001 |
| **Experiment 2** | Females | 0.47 | 0.15 | 0.11, 0.70 | 0.007 |
| | Males | 0.49 | 0.17 | 0.11, 0.78 | 0.009 |

### 7.3.2. Linking risk-taking behaviour to reproductive success

*Experiment 1: Do jackdaws use anthropogenic objects to infer risk?*

For females, the average length of time spent in the nest box during trials in Experiment 1 did not predict offspring quality or quantity (average body condition of chicks: $F_{1,8}$=2.26, p=0.171; number of chicks fledged: $X^2_{1,8}$=0.88, p=0.348; Table 7.2). Brood mass on the first day of Experiment 1 did not predict body condition of chicks at ringing ($F_{1,9}$=0.48, p=0.507; Table 7.2); and although females whose broods were heavier during the experiment fledged more chicks ($X^2_{1,9}$=4.40, p=0.036; Table 7.2), this effect disappeared after excluding two nests where chicks died between ringing and fledging ($X^2_{1,7}$=1.10, p=0.294; see Supplementary Figure S4).

For males, the length of time spent in the nest box during trials did not predict the body condition of chicks at ringing ($F_{1,9}$=0.24, p=0.638) or the number of chicks fledged from the nest ($X^2_{1,9}$=2.62, p=0.106; Table 7.2). Similarly, brood mass during the experiment did not predict offspring body condition at ringing ($F_{1,10}$=0.04, p=0.845; Table 7.2). There was also a trend for males with heavier broods during the experiment to fledge a higher number of chicks ($X^2_{1,10}$=3.25, p=0.071; Supplementary Figure S5).

**Table 7.2:** Output of GLMs investigating the relationship between risk-taking (mean length of time spent in the nest box) during trials in Experiment 1 and two measures of reproductive success. Total brood mass on the first day of Experiment 1 was included as an additional fixed effect; values derive from full models.

| | Sex | Response | Fixed effects | β ± SE | z- or t-value | p-value |
|---|---|---|---|---|---|---|
| Experiment 1 | Females | Average body condition of chicks (Day 26) | Intercept | 13.36 ± 17.59 | 0.76 | 0.47 |
| | | | Risk-taking during experiment | -0.46 ± 0.30 | -1.50 | 0.17 |
| | | | Brood mass at experiment start | 0.03 ± 0.08 | 0.40 | 0.70 |
| | | Number of chicks fledged | Intercept | 0.21 ± 0.74 | 0.28 | 0.78 |
| | | | Risk-taking during experiment | -0.01 ± 0.01 | -0.94 | 0.35 |
| | | | *Brood mass at experiment start* | *0.01 ± 0.00* | *2.00* | *0.05* |
| | Males | Average body condition of chicks (Day 26) | Intercept | -40.85 ± 87.57 | -0.47 | 0.65 |
| | | | Risk-taking during experiment | 28.67 ± 58.81 | 0.49 | 0.64 |
| | | | Brood mass at experiment start | 0.01 ± 0.10 | 0.15 | 0.89 |
| | | Number of chicks fledged | Intercept | 4.75 ± 3.25 | 1.46 | 0.14 |
| | | | Risk-taking during experiment | -3.52 ± 2.23 | -1.58 | 0.11 |
| | | | Brood mass at experiment start | 0.01 ± 0.00 | 1.96 | 0.05 |

*Experiment 2: Do jackdaws learn socially about dangerous people?*

In Experiment 2, the length of time spent in the nest box by females during trials did not predict offspring condition at ringing or the number of chicks fledged (average chick body condition: $F_{1,24}$=0.78, p=0.386; chicks fledged: $X^2_{1,25}$=0.20, p=0.657; Table 7.3). Brood mass on the first day of Experiment 2 did not predict the number of chicks fledged ($X^2_{1,24}$=0.42, p=0.516); but showed a marginally significant trend with body condition at ringing ($F_{1,25}$=4.18, p=0.052; Table 7.3). Females with heavier broods during the experiment tended to have chicks in lower body condition than expected for their body size at 26 days of age (Table 7.3; Supplementary Figure S6).

Among males, the length of time spent in the nest box during trials did not predict the average body condition of chicks at ringing, or the number of chicks fledged (body condition: $F_{1,18}$=0.79, p=0.387; chicks fledged: $X^2_{1,19}$=0.68, p=0.408). The total mass of the brood at the start of Experiment 2 did not predict the number of chicks fledged ($X^2_{1,18}$=0.01, p=0.919). However, as for females, males with heavier broods during the experiment had chicks with lower body mass than expected at ringing ($F_{1,19}$=13.24, p=0.002; Table 7.3; Supplementary Figure S6).

**Table 7.3:** Output of GLMs investigating the relationship between risk-taking (mean length of time spent in the nest box) during trials in Experiment 2 and two measures of reproductive success. Total brood mass on the first day of Experiment 2 was included as an additional fixed effect. Values derived from full models, with significant effect shown in italics.

| | **Sex** | **Response** | **Fixed effects** | **β ± SE** | **z- or t-value** | **p-value** |
|---|---|---|---|---|---|---|
| Experiment 2 | Females | Average body condition of chicks (Day 26) | Intercept | 35.52 ± 16.12 | 2.20 | 0.04 |
| | | | Risk-taking during experiment | -0.20 ± 0.23 | -0.88 | 0.39 |
| | | | Brood mass at experiment start | -0.31 ± 0.15 | -2.05 | 0.05 |
| | | Number of chicks fledged | Intercept | 0.60 ± 0.58 | 1.04 | 0.30 |
| | | | Risk-taking during experiment | 0.00 ± 0.01 | -0.43 | 0.67 |
| | | | Brood mass at experiment start | 0.00 ± 0.01 | 0.65 | 0.51 |
| | Males | Average body condition of chicks (Day 26) | Intercept | 29.29 ± 17.70 | 1.66 | 0.12 |
| | | | Risk-taking during experiment | 0.76 ± 0.85 | 0.89 | 0.39 |
| | | | *Brood mass at experiment start* | *-0.43 ± 0.14* | *-3.10* | *0.01* |
| | | Number of chicks fledged | Intercept | 1.02 ± 0.90 | 1.14 | 0.26 |
| | | | Risk-taking during experiment | -0.03 ± 0.05 | -0.72 | 0.47 |
| | | | Brood mass at experiment start | 0.00 ± 0.01 | 0.10 | 0.92 |

## 7.4. Discussion

When presented with an unfamiliar person sitting outside their nest box, individual birds were highly repeatable in the length of time they spent in the nest box feeding and/or incubating chicks. Individual identity explained 42%-61% of the observed variation across two different experiments, indicating that both male and female jackdaws exhibit consistent individual differences in this aspect of risk-taking behaviour during encounters with people (Bell et al., 2009). Entering the nest box to care for chicks in the presence of a potential threat is risk-sensitive for jackdaws, as it involves losing sight of the potential ‘predator’ (cavity-nesting birds tend to leave the nest in response to a potential threat; e.g. Schneider & Griesser, 2013). These results suggest that individuals differ consistently in their risk aversion and response to human disturbance, with some birds being more ‘risk-averse’ while others are more ‘risk-prone’ (frequently referred to as ‘boldness’; Reale, Reader, Sol, McDougall, & Dingemanse, 2007). Whilst it cannot be ruled out that individual jackdaws differ in the length of time they spend inside the nest box in general, at this stage in the breeding season, parents (and particularly females) should be strongly motivated to spend long periods of time caring for dependent chicks. It is therefore more likely that these results reflect variation in tolerance of human disturbance: variation which may impact reproductive success. A tendency to be overly risk-prone may result in fitness losses if individuals experience high levels of human disturbance, yet consistently fail to provide adequate parental care (Fernández & Azkona, 1993; Sih et al., 2011; Smith et al., 2015; Thomas et al., 2002; Verhulst et al., 2001). However, I found no evidence that individuals’ risk-taking behaviour during either experiment influenced their subsequent reproductive success, in terms of either offspring quantity or quality.

Instead, I found that nests with heavier broods during experimental trials (<1 week post-hatching) tended to have offspring in poorer body condition close to fledging (26 days post-hatching). This corroborates the results of a previous study in this species, which found that nestlings from larger broods were in poorer body condition on average and exhibited higher baseline stress hormone levels (Greggor, Spencer, et al., 2017). Interestingly, this relationship was only observed in Experiment 2 and not in Experiment 1, which may be due to sample size differences or may reflect variation in environmental conditions (e.g. food availability) between years. Although parental risk-taking behaviour within the context of these experiments does not appear to correlate with the number and condition of offspring, this remains the first study to investigate links between individual differences in response to human presence and reproductive success in the wild.

These findings highlight the importance of considering inter-individual variation when quantifying responses to human disturbance (Pelletier & Garant, 2012; Sih et al., 2012). For many species today, humans present a threat greater than or equivalent to natural predators, contributing to widespread population declines (Lima & Dill, 1990; Sih et al., 2012, 2011). However, some species – including many corvids (Gregory & Marchant, 1996; Harris et al., 2018) – appear to thrive in human-dominated habitats by taking advantage of the abundant resources provided by people. As well as identifying the causes of population declines, understanding the behavioural and cognitive processes that facilitate adaptation to anthropogenic environments is essential to predicting and mitigating the effects of human-induced environmental change (Sih et al., 2012, 2011; Tuomainen & Candolin, 2011). The results presented here indicate that individual differences in risk-taking tendencies play an important role in influencing how jackdaws respond during encounters with people, similarly to other species that exploit human-altered habitats (e.g. burrowing owls *Athene cunicularia*, Carrete & Tella, 2010, 2013; lizards *Anolis sagrei,* Lapiedra et al., 2017; roe deer *Capreolus capreolus*, Bonnot et al., 2015; eastern chipmunks *Tamias striatus*, Martin & Réale, 2008; yellow-bellied marmots *Marmota flaviventris*, Runyan & Blumstein, 2004). Although the original experiments were not specifically designed to quantify individual differences in behaviour, birds nevertheless showed high repeatability across treatments in two experiments that were functionally similar (Cauchoix et al., 2018). Having measured repeatability in a single behaviour in a single context in this case, it is not currently possible to identify whether 'risk aversion' extends to other aspects of behaviour in jackdaws. A promising avenue for future research would be to identify whether individual risk-taking behaviour in the presence of people correlates with risk-taking behaviour in other fitness-relevant contexts, such as the tendency to enter traps (Carter, Heinsohn, Goldizen, & Biro, 2012) or exploit novel resources (Lapiedra et al., 2017). If risk-taking behaviour correlates across contexts, representing a 'behavioural syndrome' (Dingemanse et al., 2004), it raises the possibility that some jackdaws may be better suited to life in urban or agricultural habitats than others.

To date, only two studies have quantified the fitness outcomes of individual behavioural differences during human encounters with wild animals: work on spotted hyaenas (*Crocuta crocuta;* Greenberg & Holekamp, 2017) and elk (*Cervus elaphus;* Ciuti et al., 2012) show that individuals that are bolder in the presence of humans have a lower probability of survival. However, this is the first study to investigate how individual differences in response to human disturbance influence reproductive success in the wild. I found no evidence that my measure of risk-taking behaviour predicted reproductive success in this context. As there are multiple factors that likely influence reproductive success in jackdaws, it may be that the effects of parental risk-taking propensity on reproductive success are only apparent when other factors are controlled for (e.g. parental condition or offspring provisioning rate). Similarly, it may be that variation in tolerance of human disturbance influences other aspects of lifetime fitness not examined here, such as long-term offspring survival. If individual risk-taking behaviour does influence the success of jackdaws breeding in areas frequented by people, this raises the question: what maintains the observed variation in tolerance of human disturbance? Firstly, it has been suggested that that personality variation may be valuable in itself, by increasing the range of ecological conditions that the population is able to cope with over longer timescales (Réale et al., 2010; Sih et al., 2012). For example, it may be that the costs and benefits of ‘risk-prone’ and ‘risk-averse’ behavioural strategies vary depending on environmental conditions, such as the availability of food and the level of threat posed by people (Dingemanse et al., 2004; Réale & Festa-Bianchet, 2003; Schoener et al., 2018; Smith & Blumstein, 2008). Furthermore, the benefits of being risk-prone may depend on the trade-offs associated with exhibiting this behaviour, which may be context dependent: for example, being risk-prone may be beneficial during encounters with humans, but costly when encountering a natural predator (Sih et al., 2004; Smith & Blumstein, 2008). Alternatively, the fitness outcomes of individual risk-taking behaviour, in terms of reproductive success, may partly depend on the personality of a breeding partner (Both et al., 2005). In order to determine the fitness consequences of individual differences in response to human encounters, further work is needed to quantify the consistency of these responses over longer timescales and under a range of environmental and socio-ecological conditions; this information could then be used to investigate fitness outcomes over the lifetime of an individual. This would then help to ascertain whether individuals that thrive in human-altered habitats do so by altering their behaviour in response to human disturbance (e.g. via learning), whether individuals with particular personality types are more likely to colonise these habitats in the first place, or whether natural selection favours some personality types over others (Sol et al., 2013).

Although there is increasing interest in determining how animal personalities influence success in a human-dominated world, how these individual differences shape behaviour during human-wildlife encounters remains poorly understood. Only a handful of studies have quantified individual differences in response to human disturbance (Bonnot et al., 2015; Carrete & Tella, 2010, 2013; Martin & Réale, 2008; Runyan & Blumstein, 2004), and fewer still have investigated the associated fitness implications (Ciuti et al., 2012; Greenberg & Holekamp, 2017). Further study is urgently needed to determine how individual differences in response to human encounters influence survival and reproductive success, and how prior experience with people shapes individual personalities. This requires robust tests of risk aversion, conducted using known individuals under a range of environmental conditions. Long-term studies of wildlife populations are vital to achieving these goals, where known individuals can be tested repeatedly in a range of contexts, and where fitness can be quantified over an individual’s lifetime under natural conditions. Given that animal personalities have profound consequences for habitat use (Bonnot et al., 2015), social structure (Aplin, Farine, et al., 2013) and population dynamics (Pelletier & Garant, 2012), understanding how personality influences responses during human encounters is central to predicting and mitigating the effects of human-induced environmental change (Barrett et al., 2018; Sih et al., 2012).

# Supplementary Material for Chapter 7: Individual differences shape behavioural responses of wild jackdaws during encounters with people

## Repeatability of risk-taking

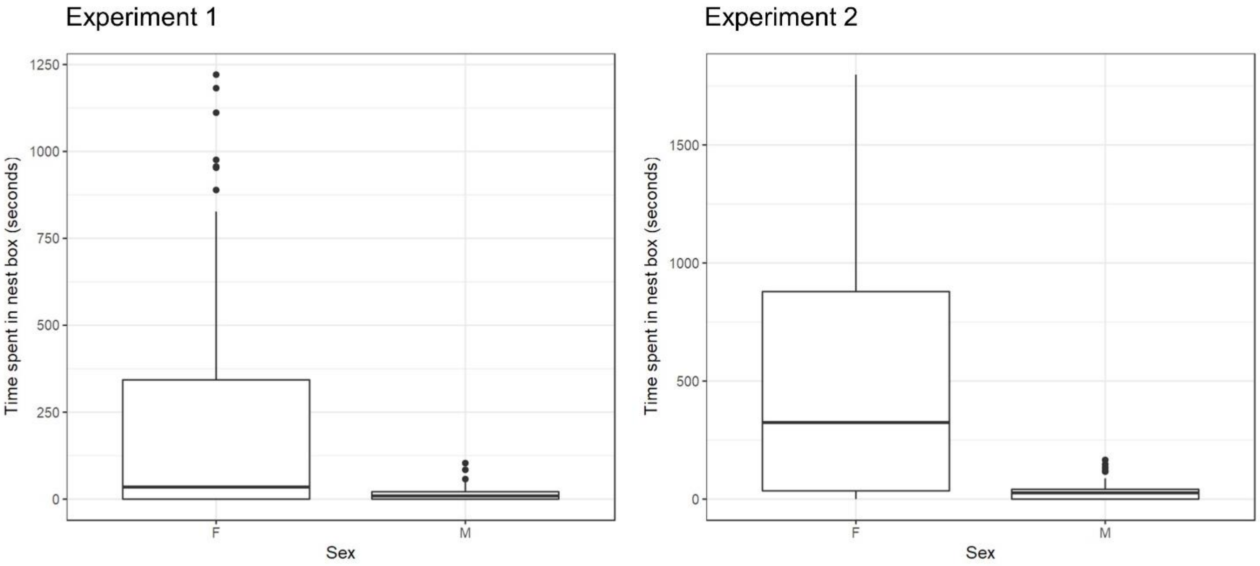


**Figure S1:** Heterogeneity of variance between males and females in the length of time spent in the nest box during (a) Experiment 1 and (b) Experiment 2. Given the division of labour within jackdaw pairs, with females primarily occupied with incubation, this is to be expected at this stage in the breeding attempt.

| Model | N | Subjects | Fixed effects | | β ± SE | t-value |
|---|---|---|---|---|---|---|
| Experiment 1 (Females) | 41 | 11 | Intercept | | 7.08 ± 0.87 | 8.14 |
| | | | Object | Gun | (reference) | |
| | | | | Stick | 0.19 ± 0.54 | 0.35 |
| | | | Orientation | Lap | (reference) | |
| | | | | Pointing | 0.39 ± 0.55 | 0.71 |
| | | | Trial number | | -0.26 ± 0.25 | -1.06 |
| Experiment 1 (Males) | 37 | 12 | Intercept | | 1.85 ± 0.10 | 18.69 |
| | | | Object | Gun | (reference) | |
| | | | | Stick | 0.00 ± 0.05 | 0.00 |
| | | | Orientation | Lap | (reference) | |
| | | | | Pointing | -0.04 ± 0.05 | -0.85 |
| | | | Trial number | | 0.05 ± 0.03 | 2.13 |
| Experiment 2 (Females) | 54 | 27 | Intercept | | 33.18 ± 4.40 | 7.54 |
| | | | Phase | Baseline | (reference) | |
| | | | | Test | 1.56 ± 4.51 | 0.35 |
| | | | Playback type | Contact calls | (reference) | |
| | | | | Alarm calls | 7.94 ± 6.34 | 1.25 |
| | | | Phase x playback type | | -8.41 ± 6.49 | -1.30 |
| Experiment 2 (Males) | 42 | 21 | Intercept | | 5.24 ± 0.32 | 16.25 |
| | | | *Phase* | *Baseline* | *(reference)* | |
| | | | | *Test* | *-0.51 ± 0.34* | *-1.50* |
| | | | Playback type | Contact calls | (reference) | |
| | | | | Alarm calls | -0.43 ± 0.46 | -0.97 |
| | | | Phase x playback type | | -0.35 ± 0.47 | -0.74 |

**Table S2:** Outputs of GLMMs investigating effects of experimental treatments on the length of time subjects spent in the nest box during trials. Values derived from full models with significant effects shown in italics.

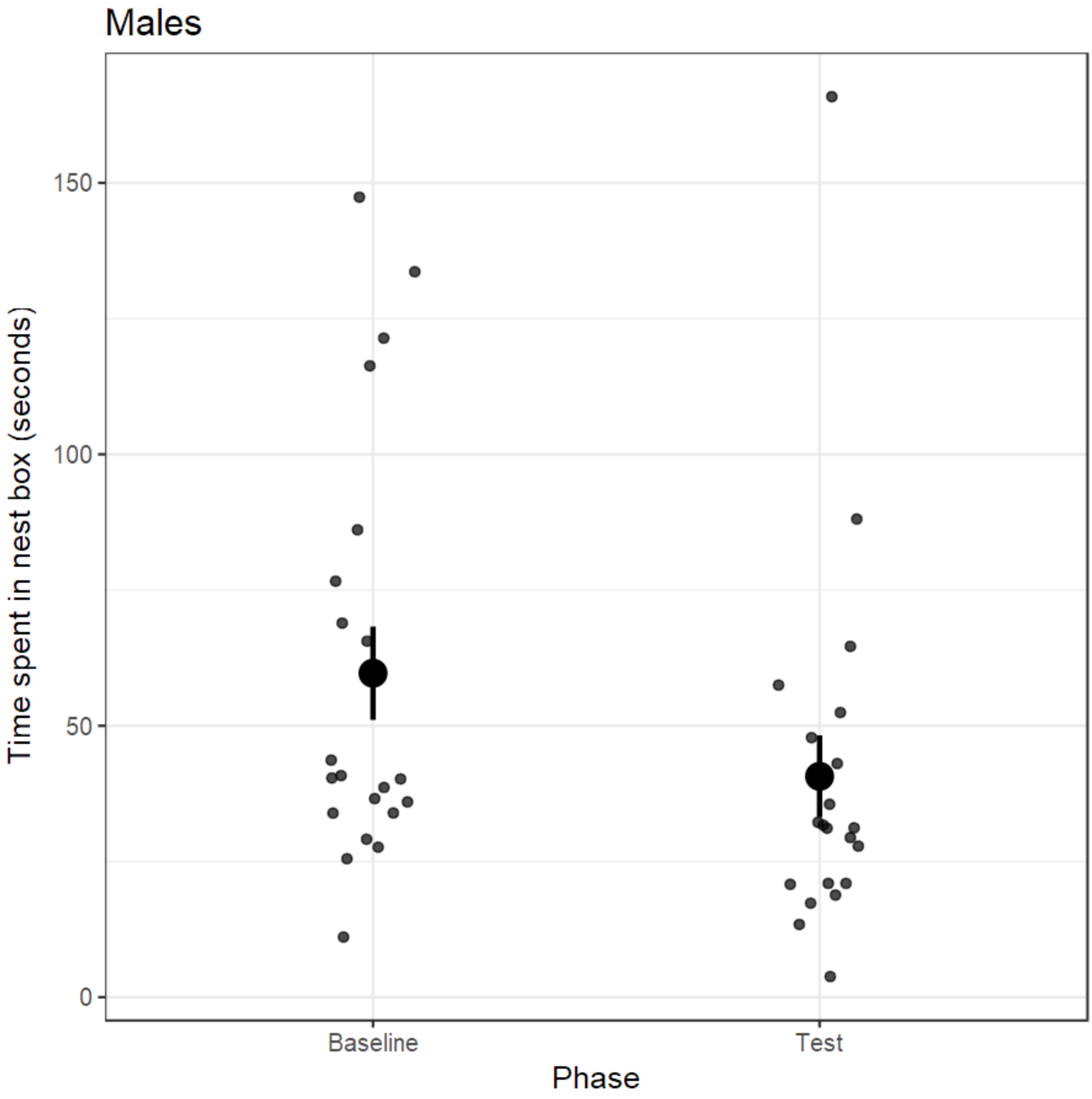


**Figure S3:** In Experiment 2, the length of time that males spent in the nest box decreased significantly between the baseline and test phase. Repeatability estimates were adjusted to account for the significant effect of phase.

## Linking risk-taking behaviour with reproductive success

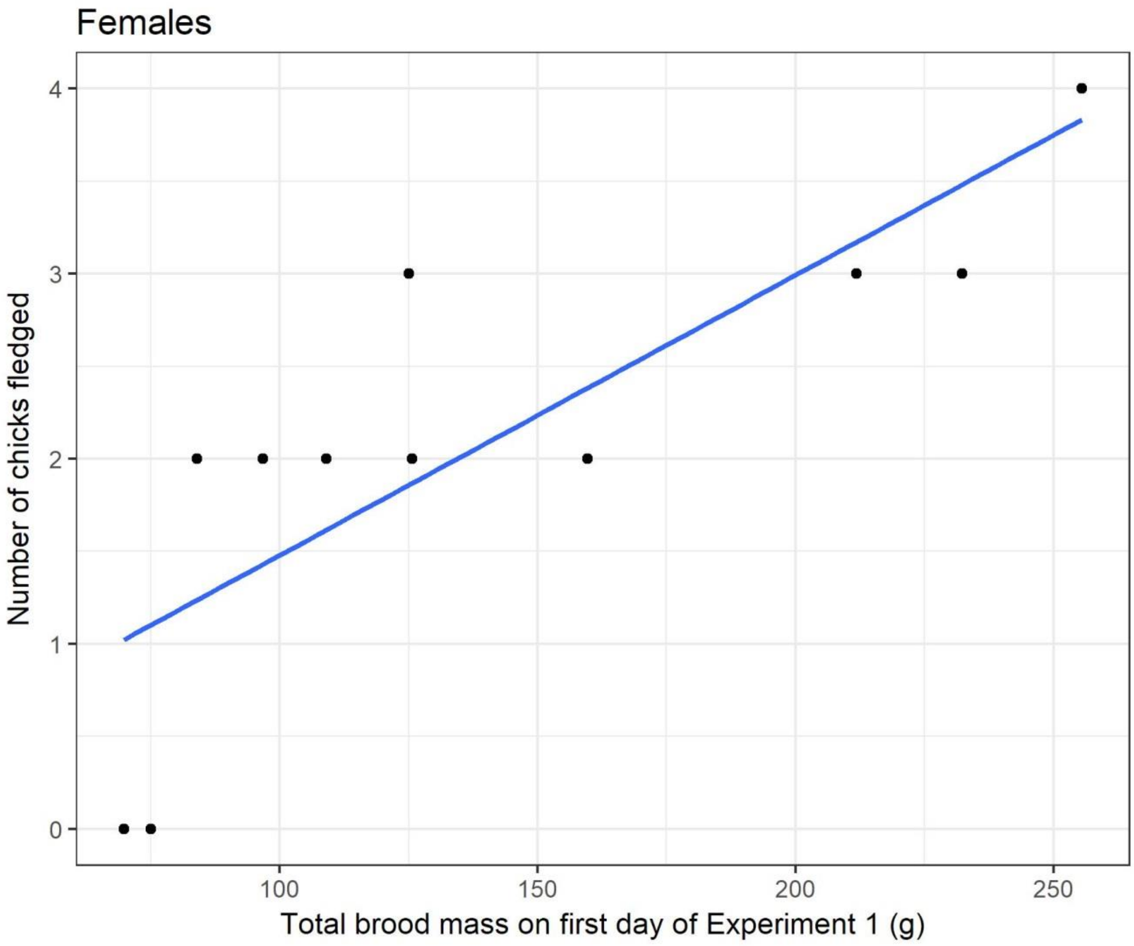


**Figure S4:** Females whose broods were heavier on the first day of Experiment 1 fledged a significantly higher number of chicks, although the strength of this relationship diminished after excluding two females whose chicks died between ringing and fledging.

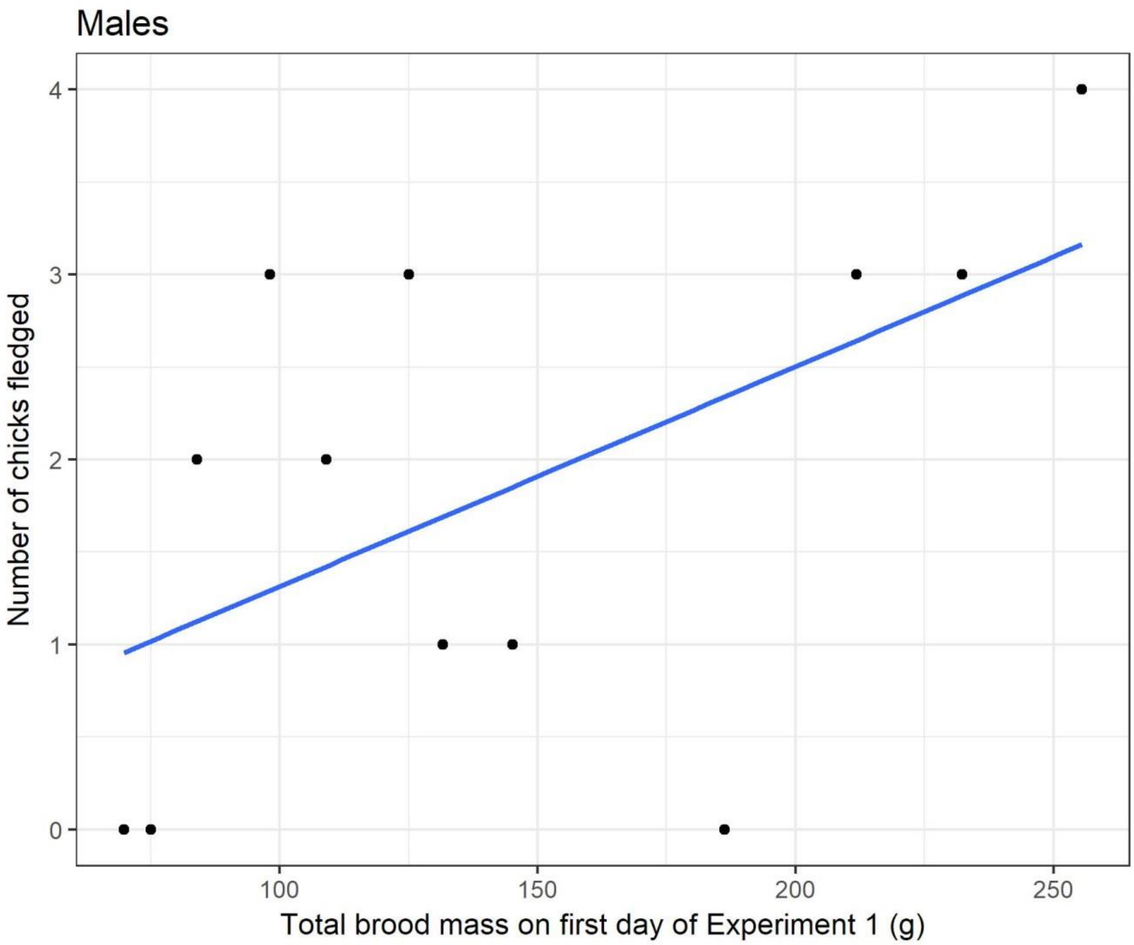


**Figure S5:** Non-significant positive trend between brood mass during Experiment 1 and the number of chicks fledged by males.

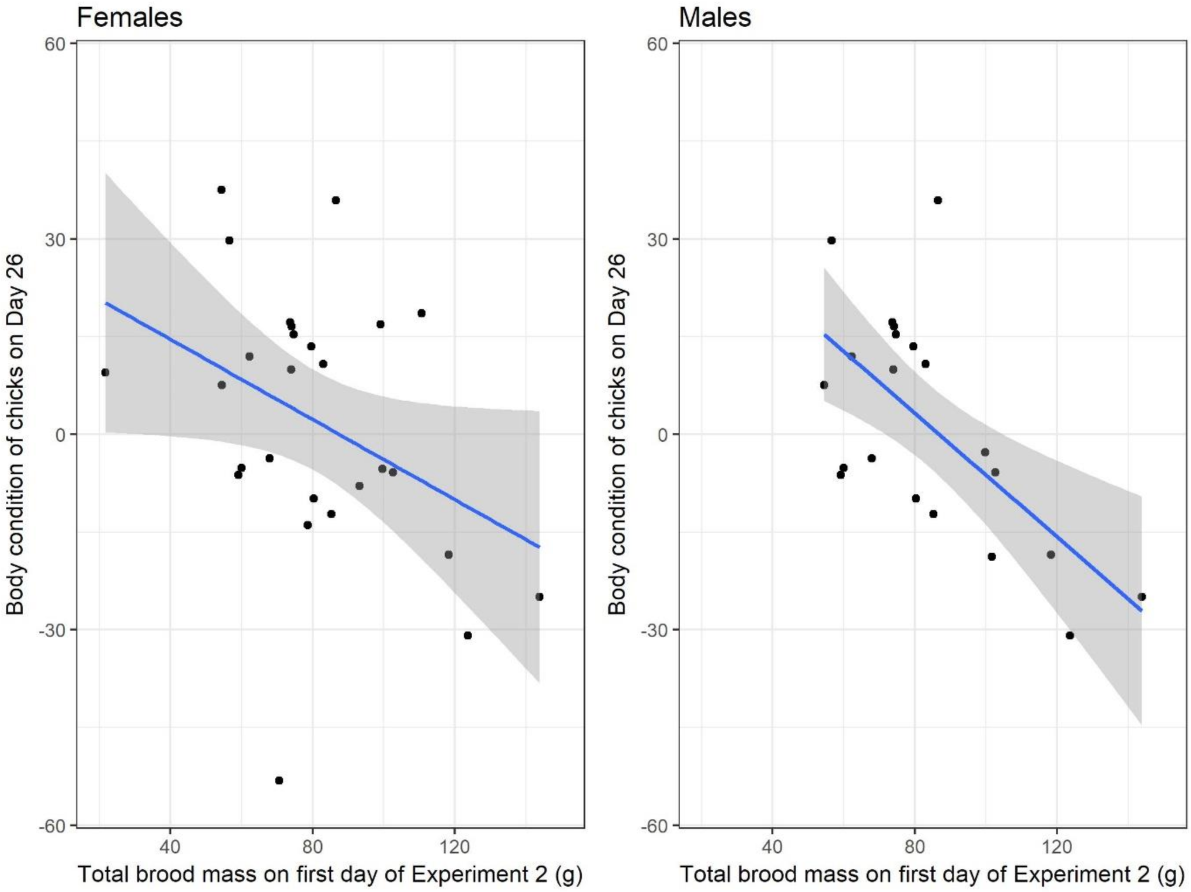


**Figure S6:** Parents with heavier broods during Experiment 2 also had chicks that were lighter than expected at ringing. Relationship statistically significant for males (p=0.002) and marginally significant for females (p=0.052).

# Chapter 8

# General Discussion

*This chapter contains material adapted from: Lee, V. E., Greggor, A. L., Thornton A. Social learning in birds. In: The Cambridge Handbook of Animal Cognition (eds. Kaufman, A., Call, J., Kaufman, J.). In review.*

Explaining variation in animals' responses to human-induced rapid environmental change (HIREC) is a major challenge facing behavioural ecologists (Sih, 2013). In many cases, behaviour can act as an initial, rapid response to HIREC: animals that are able to gather information from their environment, and flexibly adjust their behaviour accordingly, may be more successful when conditions change (Sih et al., 2011). Identifying the cognitive processes underpinning these behavioural adjustments provides important insights as to how and why species vary in their ability to cope with environmental change, but is currently poorly understood. In this thesis, I investigated how the behaviour and cognitive abilities of jackdaws (*C. monedula*) allow them to cope with the challenges of a rapidly changing world. As members of the corvid family, jackdaws appear to be thriving in habitats altered by human activity (Gregory & Marchant, 1996; Harris et al., 2018). Whilst their high degree of ecological generalism is likely to contribute to their ability to exploit a wide range of habitats (Holyoak, 1968; Lockie, 1956), their behavioural flexibility and their cognitive abilities may also play an important role (Emery & Clayton, 2004; Sol et al., 2005).

In the first part of this thesis, I explored how socio-cognitive abilities allow jackdaws to track their changing social environment. I provided the first evidence for individual recognition in wild corvids (Chapter 3) and presented one of the first field experiments testing relationship recognition in a non-primate in the wild (Chapter 4). In Chapter 5 and 6, I then investigated how jackdaws' remarkable discrimination and learning abilities facilitate risk assessment during encounters with people. In Chapter 5, I tested the widely cited anecdote that corvids use shotguns being carried by hunters to infer risk, discriminating shotguns from similar objects such as walking sticks (Creagh, 2011; Forgrave, 2015; Marzluff & Angell, 2005, 2012). In Chapter 6, in the most controlled field experiment of its kind to date, I tested whether jackdaws learn socially about dangerous people and identify the mechanism by which information about anthropogenic threats is spread through populations, minimising the need for costly direct encounters. A common thread throughout these field experiments is that test subjects differed considerably in their behavioural responses to stimuli, particularly during presentations of unfamiliar people. In Chapter 7 I therefore explored this inter-individual variation explicitly, to determine how differences in risk-taking tendencies influence responses to human disturbance. I also considered how individual differences in risk-taking behaviour influences the breeding success of jackdaws in habitats dominated by human activity.

In this chapter, I summarise the findings of these studies and discuss how jackdaws' behavioural flexibility and cognitive abilities assist in coping with the challenge of human-induced rapid environmental change. I highlight how these findings emphasise the importance of fundamental cognitive and behavioural research in predicting and mitigating the effects of HIREC, and conclude by highlighting key avenues for future research.

## 8.1. Social cognition in a changing world

The demands of tracking a rapidly changing social environment are hypothesised to exert selective pressure on cognitive abilities (the Social Intelligence Hypothesis; Dunbar, 1998; Humphrey, 1976). For group-living species, cognitive processes such as discrimination, learning and memory govern how individuals acquire, store and utilise information about social companions (Shettleworth, 2010). Although acquiring and applying this information is likely to be cognitively demanding (Cheney & Seyfarth, 2008; Clayton & Emery, 2007; Dunbar & Shultz, 2007), social knowledge may be useful in structured societies that exhibit persistent social relationships, allowing individuals to recognise others, track prevailing social relationships and maintain valuable social bonds (Dunbar & Shultz, 2007; Holekamp et al., 2007). For instance, among birds, it has been suggested that the need to maintain long-term, monogamous pair bonds requires individuals to retain a large amount of information about these highly valuable relationships (the Relationship Intelligence Hypothesis; Emery, Seed, von Bayern, & Clayton, 2007; Shultz & Dunbar, 2010). A few studies suggest that individuals that form stronger social ties gain fitness benefits as a result (Cameron et al., 2009; Campbell et al., 2018; Silk et al., 2003). For example, increased numbers of social partners and/or stronger social bonds is positively associated with overwinter survival in Barbary macaques (*Macaca sylvanus*; Campbell et al., 2018), infant survival in yellow baboons (*Papio cynocephalus*; Silk et al., 2003) and birth rates and foal survival in feral horses (Cameron et al., 2009). Longer pair bond durations have also been linked to increased reproductive success in several monogamous bird species (Black, 2001; Sánchez-Macouzet, Rodríguez, & Drummond, 2014; van de Pol, Heg, Bruinzeel, Kuijper, & Verhulst, 2006), although the mechanisms by which social bonding enhances fitness in the wild are still unclear in many cases. Moreover, our understanding of how socio-cognitive abilities contribute to the formation and maintenance of these important social bonds remains limited (Wascher et al., 2018). Support for the Social Intelligence Hypothesis has generally been sought through comparative studies linking brain size and other aspects of neural architecture with measures of social structure, with mixed results (Ashton, Thornton, et al., 2018;

DeCasien et al., 2017; Healy & Rowe, 2013; Holekamp, 2007; Sayol et al., 2016). Meanwhile, direct empirical evidence for relationship intelligence remains scant (e.g. Emery et al., 2007; Scheiber et al., 2008; Shettleworth, 2010), although some comparative evidence suggests that birds forming long-term pair bonds tend to have larger brains (Emery et al., 2007; Shultz & Dunbar, 2007; but see Sayol et al., 2016). Consequently, we still know little about the specific cognitive demands of social bonding and how socio-cognitive abilities confer benefits in a changing social world.

Maintaining social bonds first requires individuals to recognise their social companions. In Chapter 3, I used a playback experiment to investigate whether female jackdaws discriminate between conspecific contact calls under natural conditions. I demonstrated that female jackdaws recognise the contact calls of their breeding partner via ‘true’ individual recognition, as opposed to discrimination based on category-level information (Tibbetts & Dale, 2007; Tibbetts et al., 2008; Yorzinski, 2017). Because individual recognition involves integrating identity cues with unique information gained from previous interactions with the signaller, it is considered to be a cognitively demanding process (Tibbetts & Dale, 2007; Wiley, 2013). Despite the associated costs, specific mechanisms of partner recognition are likely to be vital for jackdaws, allowing individuals to identify and keep track of each other in large flocks (Jolles, King, et al., 2013; Ling et al., 2019) or foraging groups (Valletta et al., 2017) and coordinate the energetically demanding parental care necessary to successfully raise offspring (Henderson et al., 2000; Röell, 1978). As well as providing the first evidence for individual recognition in wild corvids, these results provide important insights into the cognitive demands involved in maintaining a long-term pair bonds (Emery et al., 2007). Whilst my findings here do not provide empirical evidence for the Relationship Intelligence Hypothesis directly, recognition of a breeding partner is likely to be a fundamental prerequisite for relationship intelligence in monogamous species living in structured societies. In this context, less specific mechanisms of partner recognition based on category-level discrimination (e.g. familiar versus unfamiliar individuals, kin versus non-kin) may be unlikely to suffice when individuals must identify a breeding partner among several other familiar conspecifics. Whether individual recognition extends beyond the pair bond in jackdaws is currently unclear, as females did not appear to distinguish between the contact calls of familiar neighbours and unfamiliar birds. However, I could not rule out that this may have been due to a lack of motivation to respond to call playbacks rather than an inability to discriminate between familiar and unfamiliar callers *per se* (for detailed discussion, see Chapter 3). Further work to determine the extent of individual recognition in this species would be useful to elucidate the cognitive demands of jackdaw social life. Do jackdaws identify other conspecifics, in addition to their breeding partner, via individual recognition? Do jackdaws individually recognise a small number of social companions with whom they share a strong bond, or are they capable of recognising a number of colony members (and possibly even non-colony members, as has been demonstrated for ravens; Massen, Pašukonis, Schmidt, & Bugnyar, 2014)? Addressing these questions will require controlled experiments, ideally in subjects’ natural environments, using cues from known individuals to assess recognition capabilities.

As well as recognising social companions, the ability to track relationships is likely to be beneficial for animals living in stable social groups. In Chapter 4, I investigated the ability of jackdaws to track changes in their own social relationships and the relationships of other birds within the colony. Using playbacks of male copulation calls to simulate infidelity events, I found no evidence that female jackdaws used these infidelity simulations to track changes in social relationships. However, this does not necessarily imply that jackdaws are incapable of third-party relationship representation; subjects may have simply failed to respond to information about infidelity in this experimental context. This may be because there is no fitness benefit to females in responding to information about male infidelity, or because aspects of the experimental setup were incongruent with naturally occurring extra-pair copulation events (see Chapter 4 for detailed discussion). It therefore remains unclear whether jackdaws recognise third-party relationships under natural conditions. Given that dominance hierarchies exist within jackdaw societies (Salomons et al., 2007), it seems likely that third-party relationship recognition would be useful in allowing individuals to navigate potential conflicts (Bergman et al., 2003; Borgeaud et al., 2013; Massen, Pašukonis, et al., 2014; Wittig et al., 2014). Further studies of jackdaws and other species living in stable, long-term social groups are required to determine the extent of third-party relationship recognition across species in the wild. Given that third-party relationship representation was once considered to be unique to primates (Tomasello, 1998; Tomasello & Call, 1997), determining how other highly social animals cognitively represent their social environment will shed important light on the cognitive demands of living in complex societies. The results of Chapter 4 also highlight an important issue in cognitive research: when a study fails to find evidence for a particular cognitive ability or process, it is very difficult to ascertain whether subjects are incapable of demonstrating this ability, or whether the chosen study design simply failed to detect it. The experiments conducted as part of this thesis, including the study presented in Chapter 4, were carried out using small sample sizes which may have reduced statistical power. The logistical challenges inherent in studying animal cognition often constrains sample sizes (Thornton & Lukas, 2012) and, whilst sample sizes should be maximised as far as possible, publishing null results is also crucial to increase reproducibility and develop robust experimental designs (van Assen, van Aert, Nuijten, & Wicherts, 2014). Similarly, studying the same cognitive ability in multiple experimental contexts can improve the reliability of results and provide valuable insights into how cognition influences behaviour (e.g. Cauchoix et al., 2018).

Just as human activity damages animals' physical environments, it also has the potential to severely disrupt social environments (Blumstein, 2012; Firth & Sheldon, 2015). Sudden changes to the social environment may place additional cognitive demands on animals, if tracking their social environment is cognitively demanding. My finding that jackdaws individually recognise their breeding partner contributes to a growing body of work aiming to identify the cognitive demands of living in stable social groups (reviewed in Ashton et al., 2018). The results of Chapter 3 imply that changes in social structure may induce cognitive challenges when animals are required to form and maintain new social bonds, learn to recognise new individuals or learn their new position in a dominance hierarchy (though the overall structure of social networks may be robust to these perturbations; see Boucherie et al., 2017). The structure of social groups also has a profound influence on social learning dynamics (Aplin, Farine, Morand-Ferron, & Sheldon, 2012; Firth, Sheldon, & Farine, 2016). Given that social learning may be involved in the acquisition and transmission of novel behaviours (e.g. Aplin et al., 2015), this may play an important role in shaping responses to HIREC (see Section 8.2 below). However, as we understand relatively little about how animals cognitively represent their social environments, it is difficult to foresee the effects of social disruption caused by anthropogenic activity (e.g. Shannon et al., 2013).

Fundamental research into how social knowledge is obtained and used to make behavioural decisions is therefore urgently needed. As a starting point, we require a better understanding of how social cognition is linked to social structure. Animal societies differ widely in their structure, and sophisticated socio-cognitive abilities may not be required in all cases; on the other hand, some species may possess more sophisticated socio-cognitive abilities than traditionally assumed (Coolen et al., 2005; Wilkinson, Kuenstner, Mueller, & Huber, 2010). Individuals within these societies may also differ in their social knowledge: for example, matriarchs act as repositories for cultural knowledge in African elephant (*Loxodonta africana*) and killer whale (*Orcinus orca*) groups (Brent et al., 2015; McComb et al., 2001). As a result of this uneven distribution of social knowledge, not all individuals will be affected in the same way when social conditions change. Similarly, the loss of these keystone individuals may have a profound impact on group persistence and functioning, with potentially disastrous long-term consequences (McComb et al., 2001). For example, culling or translocation of African elephants is associated with impaired social skills in individuals that experienced this social disruption, even decades after the event (Shannon et al., 2013). Whilst this may represent an extreme example, this highlights the urgent need to improve our understanding of how different socio-cognitive abilities are favoured to different extents in different social systems, in order to predict and mitigate the impacts of anthropogenic activity.

## 8.2. Identifying anthropogenic threats

As well as disrupting social systems, humans pose a direct threat to harvested animals and those that conflict with human interests. The presence of people may also have extensive non-lethal effects on wildlife by disturbing foraging and breeding activities (Frid & Dill, 2002). Life in human-altered habitats may favour the ability to assess risk during encounters with humans to avoid dangerous people and habituate to benign disturbance (Frid & Dill, 2002; Sih et al., 2011). This may favour particular cognitive abilities, such as learning and memory, that allow individuals to gather information and apply previous experience during future encounters (Sih et al., 2011). However, we know little about how organisms assess risk during encounters with humans (see Davidson, Clayton, & Thornton, 2015; Goumas, Burns, Kelley, & Boogert, 2019; Marzluff, Walls, Cornell, Withey, & Craig, 2010), which may be particularly important for those species that must discriminate between individual humans and generalise previous information to novel scenarios.

In Chapter 5, I investigated whether jackdaws use specific stimuli, the objects being carried by people, to infer risk during encounters with unfamiliar humans. It is often reported that corvids flee more readily from a person holding a shotgun than a person holding a similar object, such as a walking stick (Creagh, 2011; Forgrave, 2015; Marzluff & Angell, 2005, 2012); this appears to be a commonly held preconception, despite never having been tested explicitly. Using two field experiments, I found no evidence that jackdaws use the objects being carried by unfamiliar people (guns/wooden sticks) to inform their escape decisions or their behaviour near their nest. This may be an issue of ecological relevance in this case, rather than an inability to discriminate or learn about anthropogenic objects. Although jackdaws are often targeted in the area where the experiments were conducted, it may be that birds have insufficient prior experience with hunters to consider people carrying guns as a threat (see Chapter 5 for a detailed discussion). My results suggest that, although some corvids may well use anthropogenic objects to infer risk during encounters with people, not all populations will respond in the same way. This highlights the need for robust experiments to test whether commonly held cultural perceptions about wildlife are supported by empirical evidence.

Although jackdaws do not appear to assess risk from people based on objects being carried, at least within the context of the experiments outlined in Chapter 5, jackdaws do appear to use social information to refine their responses to unfamiliar people. In Chapter 6, I showed how a short-lived, commonly occurring alarm calling event is sufficient for jackdaws to alter their behaviour during future encounters with a ‘dangerous’ person. This study provides the first evidence that individual animals alter their responses to individual people via social learning, supporting the compelling circumstantial evidence previously gleaned from studies of American crows (*Corvus brachyrhynchos;* Cornell, Marzluff, & Pecoraro, 2012). Learning socially about individual people allows jackdaws to identify potential danger without the need for costly direct encounters, and also provides a powerful mechanism by which information about dangerous people can be transmitted through groups in the wild. Contrary to expectations, I found no evidence that jackdaws preferentially attend to the alarm calls of familiar over unfamiliar conspecifics. This may be due to the high salience of the social stimulus, where any alarm calls are treated as a reliable indication of danger (see Chapter 6 for a detailed discussion). These results highlight the value of social learning in allowing individuals to rapidly learn about novel threats, which may be particularly useful in human-altered habitats where individual people differ in the level of threat they pose. Alongside the results of a previous study in this species, which found that jackdaws are more likely to consume novel foods after seeing a conspecific do so (Greggor et al., 2016), my results demonstrate how jackdaws' use of social information may allow them to exploit anthropogenic habitats whilst avoiding potential danger.

The finding that jackdaws identify dangerous people via social learning demonstrates the benefits of sociality in adapting to human-induced environmental change. Learning from others allows more rapid acquisition and transmission of behaviours than individual learning (Laland, 2004; Mesoudi, Whiten, & Laland, 2004). Social learning also promotes the spread of information through groups, and may lead to the emergence of culture if these socially acquired behaviours persist over the long term (Laland & Hoppitt, 2003; Mesoudi et al., 2016). Although examples of animal culture have been identified in a range of taxa and behavioural contexts (see Whiten, Caldwell, & Mesoudi, 2016 for a review) whether and how these culturally acquired behaviours enhance individual fitness in the wild is yet to be identified (Aplin, 2018). Having said that, it is likely that culture confers some adaptive value given that culturally acquired behaviours are often found in fitness-relevant contexts and can make up a large proportion of a species' behavioural repertoire (Whiten, 2017).

Cultural traits evolve over time via mechanisms similar to biological evolution (Mesoudi et al., 2004) and consequently, animal cultures have important implications for other evolutionary processes including speciation (Catchpole & Slater, 2008; Grant & Grant, 2009; Lachlan & Servedio, 2004), adaptation (Greggor et al., 2014; Keith & Bull, 2017) and genetic evolution  (Rendell, Fogarty, & Laland, 2011). In particular, there is growing interest in the role of social learning and culture in facilitating adaptation to HIREC (Brakes et al., 2019; Greggor et al., 2014; Keith & Bull, 2017). Although this is an exciting and emergent field, how culturally-acquired behaviours enhance individual fitness in the wild remains an open and important question (Aplin, 2018). Despite this, evidence is accumulating as to how the loss of cultural knowledge, whether that be through population declines or loss of keystone individuals, has the potential to adversely affect species persistence (McComb et al., 2001). For instance, reductions in song complexity and diversity in Hawaiian honeycreepers has been linked to population declines over last several decades, which may present barriers to species recovery (Paxton et al., 2019). An understanding of social learning and cultural dynamics can also be used to meet conservation goals (Greggor et al., 2014; Greggor, Thornton, et al., 2017): although few in number (Berger-Tal et al., 2015), there are some cases where social learning has been successfully applied to manage endangered species. For example, conservation practitioners used ultralight aircraft to train captive-bred whooping cranes (*Grus americana*) to follow migration routes on reintroduction (Mueller, O’Hara, Converse, Urbanek, & Fagan, 2013; Urbanek, Fondow, Zimorski, Wellington, & Nipper, 2010).

On the other hand, social learning may not always yield adaptive behaviour and may instead lead to the spread of suboptimal behaviours if social information is inaccurate or out of date (Dall et al., 2005; Donaldson et al., 2012; Giraldeau, Valone, & Templeton, 2002). As a result of a trade-off between social and individual learning, organisms may employ social learning strategies in deciding when and from whom to learn (Laland, 2004; Rendell, Fogarty, Hoppitt, et al., 2011). For example, individuals are predicted to favour social learning over individual learning when environmental conditions fluctuate to the extent that learning is beneficial, but not so frequently that information quickly becomes outdated (Boyd & Richerson, 1988; Laland, 2004). Individuals may also preferentially attend to information from particular social companions, such as those who are high-ranking or more successful (Horner, Proctor, Bonnie, Whiten, & de Waal, 2010; Jones, Aplin, Devost, & Morand-Ferron, 2017; Kavaliers et al., 2005; Nicol & Pope, 1994; van de Waal, Renevey, Favre, & Bshary, 2010). Considerable intraspecific variation in social learning tendencies may also arise from learning biases, irrespective of the relative payoffs of social and individual learning (Greggor, Thornton, et al., 2017). For example, stress in early life influences subsequent learning propensity in Japanese quail (*Coturnix japonica;* Boogert, Zimmer, & Spencer, 2013), and choice of song tutor in zebrafinches (*Taeniopygia guttata;* Farine, Spencer, & Boogert, 2015). Differences in social learning dynamics have also been linked to other factors including personality variation (reviewed in Mesoudi et al., 2016) and previous experience (e.g. Leadbeater & Chittka, 2009). In turn, the influence of these learning biases may vary within and between individuals according to season, ecological context and developmental stage (Greggor, Thornton, et al., 2017; Mesoudi et al., 2016). In order to gain an understanding of how social environments and social learning influence adaptation to HIREC, it is therefore important to identify not only the adaptive value of social learning, but also how social learning strategies and biases generate differences in individuals’ ability to adapt to HIREC.

## 8.3. The importance of individual differences

Whilst differences in cognitive abilities are likely to influence how individuals gather and apply information from their environment, personality variation may also have an important influence on behaviour. For example, differences in boldness or exploratory tendencies may influence the stimuli individuals encounter, influencing how they subsequently learn about these stimuli (Sih & Del Giudice, 2012). In recent years, the field of animal cognition has seen a shift towards quantifying intraspecific variation in cognitive performance, and the role of personality in contributing to this variation, rather than treating individual differences simply as ‘noise’ to be controlled for (Ashton, Thornton, et al., 2018; Boogert et al., 2018; Dougherty & Guillette, 2018). However, as this is an emerging field, the effects of personality variation on individual behaviour during cognitive experiments are currently poorly understood (Dougherty & Guillette, 2018). Furthermore, personality variation may influence how individuals respond to ecological change (Dingemanse et al., 2004; Sih et al., 2012, 2011), in terms of exploiting novel resources or habitats (Breck et al., 2019; Kozlovsky et al., 2017; Lapiedra et al., 2017; Sol et al., 2011; Thompson et al., 2018) and managing risk (Evans et al., 2010; Schoener et al., 2018; Short & Petren, 2008). In particular, individual differences in tolerance of human disturbance may influence ability to exploit anthropogenic habitats and learn about the dangers associated with people.

Throughout this thesis, a considerable amount of the variation in responses to experimental stimuli could be attributed to the individual (Chapters 4-6); in particular, I found substantial variation in how jackdaws respond to a person sitting outside their nest box (Chapters 5 and 6). Given that tolerance of human disturbance may influence the ability of jackdaws to forage efficiently (Smith, Wang, & Wilmers, 2015; Thomas, Kvitek, & Bretz, 2002) and provide adequate parental care (Fernández & Azkona, 1993; Verhulst et al., 2001), understanding how individuals vary in their responses to people is key to explaining the success of these birds in exploiting human-altered habitats. Using data gathered during presentations of unfamiliar people (Chapters 5 and 6), I quantified individual variation in risk-taking behaviour in Chapter 7. I found that birds consistently differed in their risk-taking behaviour during these experiments, with some individuals spending more time inside the nest box than others (a risk-sensitive behaviour; see Chapters 5-6 and Schneider & Griesser, 2013). As time spent incubating and provisioning offspring is likely to impact individual fitness, I also investigated whether individual differences in tolerance of human disturbance predicted subsequent reproductive success. Contrary to predictions, I found that the length of time individuals spent inside the nest box in the presence of a person did not influence their reproductive success in terms of the quality or quantity of offspring. Nevertheless, this work represents one of the first studies investigating how inter-individual differences in responses to human disturbance influences fitness in the wild (Ciuti et al., 2012; Greenberg & Holekamp, 2017), and the first study to investigate the implications of this individual variation for reproductive success. The results of Chapter 7 suggest that individual differences play an important role in shaping behaviour during human-wildlife encounters, and emphasises the need to consider how personality variation influences performance in cognitive studies.

That individual jackdaws differ consistently in their responses to human disturbance raises the possibility that some individuals may be better suited to life in urban or agricultural areas than others; although more data is required before conclusions can be drawn in this case. Further study is needed to determine whether differences in jackdaws' risk-taking tendencies correlate across contexts, and with other aspects of behaviour (Dingemanse et al., 2004). Longer-term data could also yield valuable information as to the within-individual consistency of risk-taking behaviours over longer timescales, as well as the costs and benefits of different risk-taking strategies. For example, it may be that the benefits of being risk-prone or risk-averse vary depending on the behavioural context, or socio-ecological conditions (Both, Dingemanse, Drent, & Tinbergen, 2005; Dingemanse et al., 2004; Smith & Blumstein, 2008).

Understanding how personality variation influences success in anthropogenic habitats can help us to predict whether certain behavioural types will be favoured as human activity continues to expand (Sih et al., 2012). Firstly, it may be that personality variation is useful in itself, by increasing the range of conditions a population is able to cope with: in rapidly changing environments, high inter-individual variation in behaviour may therefore be favoured (Réale et al., 2010; Sih et al., 2012). On the other hand, if the rapid fluctuations brought about by human activity favour a particular personality type (e.g. bolder or more exploratory individuals), this may reduce personality variation at the population level (Sih et al., 2012; Sol et al., 2013). This behavioural homogenisation could occur via natural selection, selective colonisation of these habitats by individuals with a certain personality type, or resulting from individual changes on behaviour via learning (Sol et al., 2013). Further work is needed to quantify how individual differences in response to human disturbance influence survival and reproductive success over individual lifetimes and under a range of different environmental conditions. Studies are also needed to investigate how encounters with people shape animal personalities over time, and whether individuals that learn to tolerate human presence reap subsequent fitness rewards.

## 8.4. Cognition in a changing world: future directions

Taken together, the findings of this thesis demonstrate how the cognitive abilities of jackdaws allow them to learn about novel threats and navigate a dynamic social environment. These cognitive abilities are likely to be useful for jackdaws, allowing them to gather detailed information during their interactions with other jackdaws (Chapters 3-4), and during their encounters with people (Chapters 5-6). The experiments conducted as part of this thesis demonstrate how this information is then applied to behavioural decision-making during subsequent encounters. My findings also highlight the importance of sociality in influencing jackdaws' responses to unfamiliar stimuli, by creating opportunities for social learning in situations where individual learning may be costly (Chapter 6). From these experiments, it is also clear that individual differences in behaviour play an important role in shaping responses to cues, particularly during encounters with people, highlighting the importance of the interplay between personality and cognition (Chapter 7).

Understanding how cognition shapes behaviour is key to predicting how animals will cope with impacts of human activity (Greggor et al., 2014; Sih et al., 2011). For social animals, social environments may play a key role in shaping responses to ecological change by favouring the evolution of cognitive abilities allowing individuals to navigate their social environment (Dunbar & Shultz, 2007), and by providing opportunities for social learning (Brakes et al., 2019; Greggor et al., 2014). However, not all individuals will respond to socio-ecological stimuli in the same way: individual differences in behaviour and cognitive ability may have a profound influence on how animals respond to HIREC (Sih et al., 2012). There is an urgent need to improve our understanding of the socio-cognitive processes underpinning responses to HIREC, in order that this information may be used to predict and mitigate the impacts of human activity on different species and social systems. Firstly, how does social knowledge influence success when social environments change? Addressing this question requires an understanding of the fundamentals of social cognition: how do animals cognitively represent their social world? What are the specific cognitive demands associated with life in different social environments? How and why do species and individuals differ in their ability to navigate their social environments, and what are the individual- and population-level consequences of this variation? Secondly, how do social learning dynamics influence adaptation to HIREC? Addressing this question requires an in-depth knowledge of how social information about ecological change is gathered and applied in different contexts, and results in behavioural change. For example, how do individuals and species differ in their tendency to learn socially about anthropogenic change? How do factors such as social learning strategies, learning biases and personality govern social learning dynamics (Greggor, Thornton, et al., 2017; Laland, 2004)? Whilst quantifying variation in social learning tendencies and identifying the underlying causes of this variation is important, it is also vital to understand the consequences for individual fitness. A key priority is to identify how socially acquired behaviours influence individual fitness in the wild (Aplin, 2018), and how this influences population-level adaptation to human-induced rapid environmental change.

Tackling these questions is an ambitious task, requiring in-depth study of a range of taxa and social systems. As well as explaining why some species fail to adapt to HIREC, identifying the traits that allow some species to thrive in anthropogenic habitats is also vitally important (Barrett et al., 2018). Whilst comparative studies are useful in terms of explaining species differences, comparisons between individuals of the same species are also vital to discover how intraspecific differences in behaviour and cognitive processing influence responses to HIREC. Furthermore, studies of wild animals are required to elucidate how these process operate under natural conditions, where behaviour is more reflective of real-world cognitive ability (Pritchard et al., 2016; Thornton & Lukas, 2012). Long-term behavioural studies are especially valuable in this regard, where marked individuals can be followed throughout their lives. This allows researchers to gain in-depth knowledge of individuals' social relationships, quantify cognitive and behavioural differences over time and across contexts, and analyse fitness outcomes over the lifetime of study subjects. Studies of this kind also allow detailed monitoring of population dynamics, providing vital insights into how species and populations adapt to human-induced rapid environmental change.

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