
A critical evaluation of neophobia in corvids: causes, consequences and conservation implications

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October 2016

This dissertation is submitted to the University of Cambridge for the degree of
Doctor of Philosophy

Preface

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except as detailed on the Declaration page and specified in the text. No part of this thesis has been submitted, or is being concurrently submitted, to any other university in application for a higher degree. The text does not exceed 60,000 words.

Summary

Neophobia, or the fear of novelty, is thought to restrict animals' ecological niches and hinder their propensity for innovation; two processes that should limit behavioural adjustment to human-induced changes in the environment. However, birds within the corvid family (*Corvidae*) defy this trend by being highly neophobic, yet highly successful alongside humans across diverse habitats. This thesis examines the causes and ecological consequences of neophobia to unravel corvids' puzzling neophobic tendencies. Throughout the thesis I find evidence that corvids are very neophobic, but that individuals differ in their level of novelty avoidance. Neophobia is not a fixed trait across time and towards all types of novelty. Neophobia levels differ depending on the type of novel stimuli being presented, and individuals can be inconsistent when environments change seasonally (Chapter Three). Although individual differences in neophobia are expected to be associated with fitness outcomes, I found no direct connections between neophobia, reproductive success or offspring stress hormone expression (Chapter Four). Moreover, if neophobia levels were defined by human presence, populations should differ in their novelty avoidance according to their proximity to humans. However, corvids show similar patterns of object neophobia between urban and rural areas (Chapter Five). The lack of connection between neophobia, fitness, and urbanization indicates that corvids might be able to circumvent individual differences in neophobia that might otherwise restrict behavioural adjustment. Accordingly, experience observing conspecifics consume novel foods and approach threatening objects encourages individual risk-taking, such that highly neophobic individuals could benefit from social information (Chapter Six). I therefore propose that corvids' flexibility and their success alongside humans may be due to their ability to overcome their fear through learning. How animals make decisions in the face of ecological novelty may predict whether they behaviourally adjust to human-altered habitats and is relevant in the wider context of species conservation.

Acknowledgments

To say that a PhD is a lonely journey is ludicrous. Over the course of the past three and a half years I have experienced the greatest outpouring of support and kindness that I have ever known. Nothing I say will truly be able to thank everyone who helped me along the way, but I might as well try.

I will begin where this journey began; over a shaky Skype connection with Alex Thornton on the line. I will never forget his first question when I told him I was calling from fieldwork in Hawaii. “Well, why on earth would you want to come to rainy England?”. I cannot say I entirely understand my decision (as it is currently pouring outside while I write this), but I am forever glad that I decided to come. I genuinely believe that the entire trajectory of my scientific career has been positively influenced by Alex’s support since that time. I thank him for having patience with my continued fumbling of words, topics, and tangential ideas, and for continually pushing me to explore the difficult questions.

Landing in Cambridge would have been a bewildering experience without a lab to call home. I am grateful that Nicky Clayton let me join hers. Nicky has taught me about navigating the academic world, and has been supportive of my forays into conservation. Her trust in me to get things done independently has meant a lot. From day one, Gabrielle Davidson was there to answer any question, lending advice and friendship. In guiding me through silly paperwork to serving as my partner in jackdaw fieldwork mayhem, I would not have survived those first couple of years without her help. Many others in the Comparative Cognition Lab, including Ljerka Ostojic, Edward Legg, Katharina Brecht, Natalie Williams, Laura Kelly, Rachael Miller, and Lucy Cheke have been hugely supportive throughout my time here. From reading drafts, providing feedback on ideas, to helping with analyses, and discussing figures over tea, lunches and long walks, the lab has been a loving science family.

However, as the odd field biologist in the Psychology department, I would have been lost if Alex had not encouraged me to weasel my way into the Zoology department and mingle with the lively behavioural ecology folks. I am so grateful that I was warmly received by Neeltje Boogert, Nick Davies, Alecia Carter, Hannah Rowland, and Corina Logan (whose advice helped me get through the Gates interview in the first place!). Without Neeltje reminding me that not all my work is terrible, without Nick Davies politely pointing out its flaws, and without Alecia being willing to debate them openly, I would not have found a balanced argument or sense of scientific self. As part of the Zoology bunch, I am especially grateful to Jolle Jolles. He was good enough to not laugh at me when I nearly fell off my first

ladder because I was paralysed with fear, and has stuck around ever since as a great collaborator, conference travel buddy, and friend.

I would not have been able to call myself a birder by any definition if Chris Thorne had not taken me under his wing. Whether we were bantering about running statistics during early morning ringing sessions at Wicken Fen, or talking about corvids on the sidelines after my races, I knew I had gained an unexpected ally. I could not have collected the field data I needed if Chris had not allowed me to drag him through forests full of barbed wire and nettles, and if he had not badgered others from the Wicken Fen group to join for the experience of seeing some “colour ringing”.

In the end, however, the wilds of Madingley were only part of PhD story. I feel doubly fortunate because I lucked into having two sets of science families, a Cambridge and a Cornish one. The fondness I feel for Cornwall is due in no small part to the immeasurable thoughtfulness of Chlöe Cyrus-Kent. She and Alex opened up their home with nightly dinners and welcoming smiles every time I walked through the door; even if me staying meant implanting ideas about cheese in their delightful boys’ heads. Fieldwork would not have been anywhere near as much fun without the cheery figure of Guill McIvor, who made me laugh until I cried, even after the biggest experimental disasters. I continue to be awe about the endless library of ring combinations, individual identities, and jackdaw anecdotes that he carries in his head. I probably would have starved during the last field season if not for the baking mastery and positivity of Lina Arenas and Sarah Paul. To the entire Cornish Jackdaw project, and all those inhabiting the basement at Tremough House, I am grateful you let a jackdaw-smelling Cambridge intruder join your ranks.

There are of course all of the wonderful people without whose logistical help the field and lab work of this thesis would not have been possible. I am grateful to Paul Gluyas, and the entire staff at Pencoose farm for never questioning my strange looking experiments, nor my funny accent. To the gardeners at Madingley who allowed me to romp around with long poles and a ladder, even through wedding receptions at the Hall. Huge thanks go to Andrew Szopa-Comley, and Christopher Smith for helping monitor the nest boxes. I am indebted to Karen Spencer and her lab group for hosting me in St. Andrews, and allowing me to masquerade as a molecular biologist. I am grateful for Stithians Parish Council and Joan Stevenson-Hinde for allowing me to put up feeding tables or ladder traps on their land.

Fieldwork aside, throughout my time in Cambridge I have been fortunate to be part of several communities that have made life richer, and helped me survive the darkest of PhD days. I am endless grateful to the Gates-Cambridge Trust, not only for funding my dream

PhD, but for creating a vibrant community within which I have felt honoured to be included. I would surely have lost my sanity along the way without the company and comradery of the Cambridge University Hare and Hounds along endless muddy miles. Dear friends within the King's community, including Jess Corsi, Katie Reinhart, Tobias Haeusermann, Nicholas Worth, Andrew Munro, Krishna Kumar, James Taylor and, Charlotte Houldcroft, are responsible for keeping me smiling over many a meal.

I would have struggled to make it to this finishing line without the help of Max Hewkin-Smith. He has brightened every step of the second half of this journey. From advising on coding, to proof-reading manuscripts, and supporting in me in all things non-PhD, he has helped me more than this page can do justice.

In all fairness, I would not have made it to even the starting line at Cambridge without the love and support of my family. My parents have always encouraged me to follow my passions, even if they took me to far-away places, doing very unconventional things. The fact that both of my parents, at one point or another, eagerly "volunteered" to come out in the field and help on ringing days is a testament to their support. I could not be more grateful.

Finally, my thanks would be incomplete if I did not acknowledge the birds themselves. I feel fortunate to have happened upon such a puzzling and wonderfully awe-inspiring study system. I will always have a special place in my heart for corvids.

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Declaration

The work of this thesis was carried out under the supervision of Dr Alex Thornton, and Professor Nicola Clayton, FRS. No part of this dissertation has previously been submitted for a qualification. All of the work was my own, apart from what is specified below:

Chapter Three: Jolle Jolles kindly let me use his data from a previous study (2010) to compare behaviour with the neophobia measures I collected during 2014. He, along with Natalie Williams, collected the dominance data that make up the 2014 dataset. Jolle provided feedback on a final stage of the draft that was submitted as a paper. Students Chantal Deininger, Katrin Herzhauser, Nadine Beck, Alice Li, and Adina Krik, acted as novel people. The study idea, design, analysis, and writing are my own.

Chapter Four: Masters student Ellis Langley collected and video coded portions of the neophobia trials from the Cornish sites, following the guidelines I developed. Katharina Brecht, Andrew Szopa-Comley, and Lily Moormon Dodd helped with inter-coder reliability on the Madingley videos. For Lily this formed part of her Part II project, which I supervised. Fellow PhD student, Gabrielle Davidson assisted with monitoring nests in Cambridge and the entire Cornish Jackdaw Project was responsible for monitoring nests in Cornwall. Guill McIvor conducted the PCR analysis to determine sex of the birds. Karen Spencer provided advice on CORT analysis and feedback on a final draft of the paper.

Chapter Five: A volunteer research assistant, Christopher Smith, helped code videos to contribute to intercoder reliability. Antony Fulford advised me on statistics, and Sinéad English confirmed his recommendations, Antony also offered comments on drafts of the manuscript.

Chapter Six: Guill McIvor helped with the initial setup of field logistics, coded videos for intercoder reliability. Guill also provided feedback on drafts of the paper.

Publication List¹

Chapters One, Two and Seven include material from: Greggor, A. L., Thornton, A., & Clayton, N. S. (2015). Neophobia is not only avoidance; improving neophobia tests by combining cognition and ecology. *Current Opinion in Behavioral Sciences*, 6, 82–89.

Chapter Three has been accepted for publication as: Greggor, A. L., Jolles, J. W., Thornton, A., Clayton, N. S. Seasonal changes in neophobia and its consistency in rooks: the effect of novelty type and dominance position. *Animal Behaviour*.

Chapter Four has been submitted for publication as: Greggor, A. L., Spencer, K. A., Clayton, N. S., Thornton, A. Variation in hormones and reproductive success in wild jackdaws (*Corvus monedula*) is connected to brood size and provisioning rate, but not to neophobia. *General and Comparative Endocrinology*.

Chapter Five has been published as: Greggor, A. L., Clayton, N. S., Fulford, A., Thornton, A. (2016). Street smart: faster approach towards litter in urban areas by highly neophobic corvids and less fearful birds. *Animal Behaviour*, 117, 123-133.

Chapter Six has been published as: Greggor, A. L., McIvor, G., Clayton, N. S., & Thornton, A. (2016). Contagious risk taking: social information and context influence wild jackdaws' responses to novelty and risk. *Scientific Reports*, 6, 27764.

Chapter Seven also includes material from: Greggor, A. L., Clayton, N. S., Phalan, B., & Thornton, A. (2014). Comparative cognition for conservationists. *Trends in Ecology & Evolution*, 29(9), 489–495.

Publications not included in this thesis

Greggor, A. L., Berger-Tal, O., Blumstein, D. T., Angeloni, L., Bessa-Gomes, C., Blackwell, B. F., ... Sutherland, W. J. (in review). Prioritising animal behaviour research to increase conservation efficacy. *Trends in Ecology and Evolution*.

Greggor, A.L., Laidre, M. E. (2016). Food fights: aggregations of marine hermit crabs (*Pagurus samuelis*) compete equally for food and shell related carrion. *Bulletin of Marine Science*, 92(3), 293-303.

Laidre, M. E., & Greggor, A. L. (2015). Swarms of swift scavengers : ecological role of marine intertidal hermit crabs in California. *Marine Biology*, 162, 969–977.

Greggor, A. L., Clayton, N. S., Phalan, B., & Thornton, A. (2014). Translating cognitive insights into effective conservation programs: Reply to Schakner et al. *Trends in Ecology and Evolution*, 29(12), 652–653.

¹ Since many of the chapters have been submitted for publication, there is repetition in portions of their methods sections, and the format of chapters differs slightly.

Chapter One

Introduction²



² The first four sections of this chapter have been adapted from: Greggor, A. L., Thornton, A., & Clayton, N. S. (2015). Neophobia is not only avoidance; improving neophobia tests by combining cognition and ecology. *Current Opinion in Behavioral Sciences*, 6, 82–89.

1.1 What is neophobia?

Many animals show an aversion to novelty; a behavior known as neophobia. In the wild, avoiding novel predators, foods, objects and locations shapes life history (Greenberg & Mettke-Hofmann, 2001) and influences how animals react to new environments (Sol, Griffin, Bartomeus, & Boyce, 2011). Neophobia was first studied by comparative psychologists in the 1950s (Berlyne, 1950) to quantify non-human fear, anxiety, curiosity, and memory, and is still commonly used in psychopharmacology and neurobiology for testing drugs and mapping brain circuitry (Hughes, 2007). Only more recently have behavioral ecologists studied neophobic behavior, focusing instead on the adaptive value, evolutionary trade-offs, and ecological consequences of variation in neophobia between species, populations and individuals (Greenberg & Mettke-Hofmann, 2001). Boosted by growing evidence that non-human animals exhibit stable individual differences in behavior (i.e. temperament, or personality; Réale, Reader, Sol, McDougall, & Dingemanse, 2007), neophobia tests have become a common way of comparing variation in personality with other traits. For example, neophobia levels have been reported to be negatively correlated with propensities for behavioral innovation (Greenberg, 2003), and with decreased physiological stress responses (Carere & van Oers, 2004); and to have implications for fitness (Ferrari, McCormick, Meekan, & Chivers, 2015; Smith & Blumstein, 2008). However, the testing protocols used to generate “neophobia scores” in these results vary considerably.

With so many potential implications, neophobia tests must be rigorous and valid. However, there is no consensus across disciplines on how to measure neophobia or interpret seemingly neophobic behavior. Similar tests—such as quantifying movement in a novel or aversive space—are interpreted variously as measures of context-specific exploration (e.g. spatial neophilia, Mettke-Hofmann, Lorentzen, Schlicht, Schneider, & Werner, 2009), of general “fearfulness” (Villalba, Manteca, & Provenza, 2009) or anxiety (Bourin & Hascoët, 2003). Conversely, very different methods are used to test neophobia: such as measuring how often animals inspect peep-holes to see novelty (File & Wardill, 1975), measuring latencies to approach novel feeding platforms (Rockwell, Gabriel, & Black, 2012) or consume novel foods (Villalba et al., 2009). Therefore, current testing methods may fall prey to both sides of the “jingle-jangle fallacy” (Carter, Feeney, Marshall, Cowlshaw, & Heinsohn, 2013; Gosling, 2001): of lumping together distinct behaviors, or of mislabeling the same trait as two separate attributes. Additionally, there has been little attention to potential differences between species in their perception and subsequent responses to the objects, spaces or foods

used for testing, and the choice of novel stimuli is rarely validated against known fearful or previously experienced stimuli. These oversights have led to a confusing body of conflicting results (see Appendix 1). For example, it is unclear how to compare a test that places a green hairbrush in a common myna's (*Acridotheres tristis*) home cage (e.g. Sol et al., 2011) with one that exposes a fallow deer (*Dama dama*) to a mirror in an experimental arena (e.g. Bergvall, Schäpers, Kjellander, & Weiss, 2011), particularly when they come to opposite conclusions about whether object neophobia correlates with a latency to eat novel food.

Despite utilizing tests developed by psychologists, behavioral ecologists often ignore the cognition underlying fear behavior, sometimes explicitly (e.g. Réale et al., 2007). Cognition encompasses the mental processes behind perception, learning, decision making and memory (*sensu* Shettleworth, 2010); processes that underlie most behaviour. Crucially, responding to something because of its novelty *per se* relies on classifying an encountered stimulus as novel. Therefore, behaviour during tests with novel objects or food may involve an additional cognitive process to other fear or explorative reactions and may not serve as the best measure of overall fearfulness (e.g. Villalba et al., 2009), or boldness (e.g. Kurvers et al., 2010). Individuals may differ in how easily they are aroused by fear-inducing stimuli, differ in their generalization and categorization abilities (i.e. whether they classify a stimulus as novel, and therefore fear-provoking), and differ in their experiences from which they define novelty. Neophobia tests that ignore cognition fail to address these distinct processes, and risk misinterpreting both the proximate mechanisms and ultimate function of avoidance behaviour, making apparent correlations between “neophobia” and other behaviors difficult to interpret. For example, albatrosses (*Thalassarche melanophrys*) differ in how aggressively they react when a pink volleyball approaches their nest (Patrick & Weimerskirch, 2014); an aggressive response being interpreted as high boldness and related to foraging patterns. However, it is unclear whether the “bolder” birds classify the object as a threat and the “shyer” birds do not, or whether the two groups genuinely differ in their neophobia; a crucial distinction for determining their response to novelty in non-threatening situations.

Meanwhile, despite measuring an ecologically important behavior, psychologists often ignore the adaptive context that favors attention towards and fear of novel stimuli. For example, novel stimuli are rarely vetted to ensure they do not incidentally target ecologically relevant cognitive biases towards certain colors, shapes or patterns. Since responses to novelty are commonly used as indicators of memory (Hughes, 2007), and stimuli that incidentally target biases may be attended to in higher frequencies than those that do not,

psychological tests can be skewed by object design. For example, depending on the species, an object that incorporates the color red may mimic dangerous aposematic prey (Roper & Cook, 1989) or an attractive, sexually selected signal (e.g. Karubian, 2002); thereby producing opposite patterns of avoidance or approach that may be resistant to fatigue, regardless of memory. Additionally, whether fear behaviors are specific to testing situations can be crucial to interpreting results, from the efficacy of drug treatments to the consistency of brain activity across contexts and species. Laboratory animal strains may differ, and even produce contradictory results in identical neophobia tests (Bert, Fink, Sohr, & Rex, 2001). Therefore animals' selective history and the stimuli's ecological relevance must be considered to enable accurate comparisons. Ultimately, testing neophobia consistently and accurately depends on integrating methods from both fields to better understand the proximate causes and ecological consequences of neophobia.

1.2 Problems with neophobia tests

Operationally, neophobia can be divided into the fear of novel objects, spaces, and foods, and is generally considered to be a separate process to neophilia, i.e. an attraction to novelty (Greenberg & Mettke-Hofmann, 2001; Greenberg, 2003). The fear of novel foods (i.e. dietary wariness) breaks down into two behaviours: fearing the appearance of food (a form of object neophobia) and hesitating to incorporate it regularly into the diet (i.e. dietary conservatism Marples & Kelly, 1999; see how to separate them, Chapter Six). There is disagreement over whether the types of neophobia correlate and measure the same underlying mechanism. Within the animal personality literature, all types of neophobia are often classified under the same umbrella of exploration-avoidance (Réale et al., 2007) and are used interchangeably to measure exploration (Verbeek, Boon, & Drent, 1996; Verbeek, 1994), and boldness (Atwell et al., 2012; Patrick & Weimerskirch, 2014). Using different types of neophobia to measure the same “personality” trait could be especially problematic if individuals' responses differ independently across novelty types and varying environmental conditions (Chapter Three).

Whether animals explore novelty depends on both their fear and their interest (i.e. neophilia) in interacting with it (Greenberg & Mettke-Hofmann, 2001; Hughes, 2007), both of which may change as the costs and benefits for exploration change. Neophobia can interfere with measures of exploration because the two motivations can in theory occur simultaneously to create ambiguous behaviour (Greenberg & Mettke-Hofmann, 2001).

Awareness of this issue is especially important in spatial exploration tests, where response measures gauge movement in a novel environment (NE), with higher movement interpreted as greater exploration (Verbeek, 1994). Although these tests have been proven repeatable (Quinn, Patrick, Bouwhuis, Wilkin, & Sheldon, 2009), and to correlate with other traits (Quinn, Cole, Bates, Payne, & Cresswell, 2012), they require different interpretations if movement stems from fear, curiosity or a combination of the two. For example, object neophobia was found to correlate positively with NE movement in jackdaws (*Corvus monedula*), suggesting that more fearful birds explored more (Schuett, Laaksonen, & Laaksonen, 2012); the opposite of what is expected if movement in NE tasks measure a lack of fear. Perhaps a better explanation is that jackdaws, like other corvids, often display fearfulness by hopping around (Heinrich, 1988); so movement may actually indicate spatial neophobia, not curiosity or exploration. Since greater movement in the NE predicted lower reproductive success in this study (Schuett et al., 2012), the cause of the movement is critical to understanding why individual differences influence jackdaw reproductive success.

Even if neophobia involves distinct processes across contexts, separating neophobia tests into strict categories is not always straightforward. For example, coyotes (*Canis latrans*) respond differently to novel objects in familiar or unfamiliar environments (Harris & Knowlton, 2001). Therefore it is unclear whether a novel object in a novel environment tests object neophobia, spatial neophobia, or some interaction of the two. Furthermore, how do we classify neophobia that is extended beyond the artificial objects, spaces, and foods to more ecologically valid stimuli, such as novel predators (e.g. Brown, Ferrari, Elvidge, Ramnarine, & Chivers, 2013)? The stimulus driven definitions of neophobia may seem simple, but risk being arbitrary if not connected to their ecological context and neurological underpinnings. The source of confusion over these definitions becomes clear when examining the cognitive steps that produce neophobic behaviour.

1.3 Combining the cognition and ecology of neophobia

Animals' subjective experience of fear is unobservable. However, perceiving fearful stimuli triggers measurable endocrine responses, generating observable physiological changes (e.g. increased heartrate and reduced salivation, Thomson, 1979) and avoidance, flight and withdrawal behaviours. The cascade of fear responses is prompted by a cognitive assessment of risk because the sympathetic nervous system will not respond to injury if the brain is experimentally disconnected or unconscious (Mayes, 1979).

Although current neurobiological evidence has not resolved whether separate types of neophobia involve disparate brain regions, assessing and reacting to novelty correlates with activity in several areas of the brain, suggesting that multiple cognitive processes are involved. Perceiving novelty activates brain regions associated with memory and decision making (Ranganath & Rainer, 2003). Areas within the prefrontal cortex and the hippocampus, along with activity of the neurotransmitter acetylcholine have been implicated experimentally in neophobic and exploratory responses, presumably because they process memory formation, retrieval, and decision making (Hughes, 2007; Løvstad et al., 2011; Ranganath & Rainer, 2003). Reacting negatively towards novelty activates brain regions associated with fear. For example, lesions to the amygdala and the administration of anxiolytic drugs tend to decrease neophobic behaviors, presumably by dampening fear responses (Hughes, 2007). The physiological effects of activating fear circuitry during neophobic as opposed to general fear behavior are largely unstudied. In linnets (*Acanthis cannabina*), an increased heartrate has been documented with encountering novelty (Gaßmann, 1991), and in great tits (*Parus major*), birds that were slower to explore a NE exhibited a faster and higher peak glucocorticoid stress hormone response after being handled (Baugh, van Oers, Naguib, & Hau, 2013). However, these hormone measures were taken during a fearful event that did not involve novel stimuli. Other work measuring corticosterone levels immediately after encountering novel objects has produced conflicting results (Mettke-Hofmann, Rowe, Hayden, & Canoine, 2006; Richard et al., 2008). Therefore more work is needed to determine how the cognitive appraisal of novelty leads to the physiological expression of neophobic behavior. Detecting physiological correlates of fear does not imply that behavioural responses stem from a fear of novelty *per se*; instead, they may result from the categorization of novelty as a known danger (see Figure 1.1).

Determining the cause of seemingly neophobic behavior has critical ecological implications. Whether animals respond aversively to all novelty or only to novelty that closely resembles a known danger, such as a predator, can greatly impact survival. For instance, in fathead minnows (*Pimephales promelas*) the more closely related a novel predator is to a known one, the more likely it will elicit anti-predator behaviour (Ferrari, Gonzalo, Messier, & Chivers, 2007). In this case, since avoidance reactions seem to depend on the categorisation of a predatory stimulus, neophobic behaviour may not play a major role in avoiding a novel, invading predator. However, in neophobic species, such as juvenile

whitetail damselfish, (*Pomacentrus chrysurus*) (Ferrari et al., 2015), broader avoidance may facilitate naïve individuals' escape from predators without a dangerous learning experience.

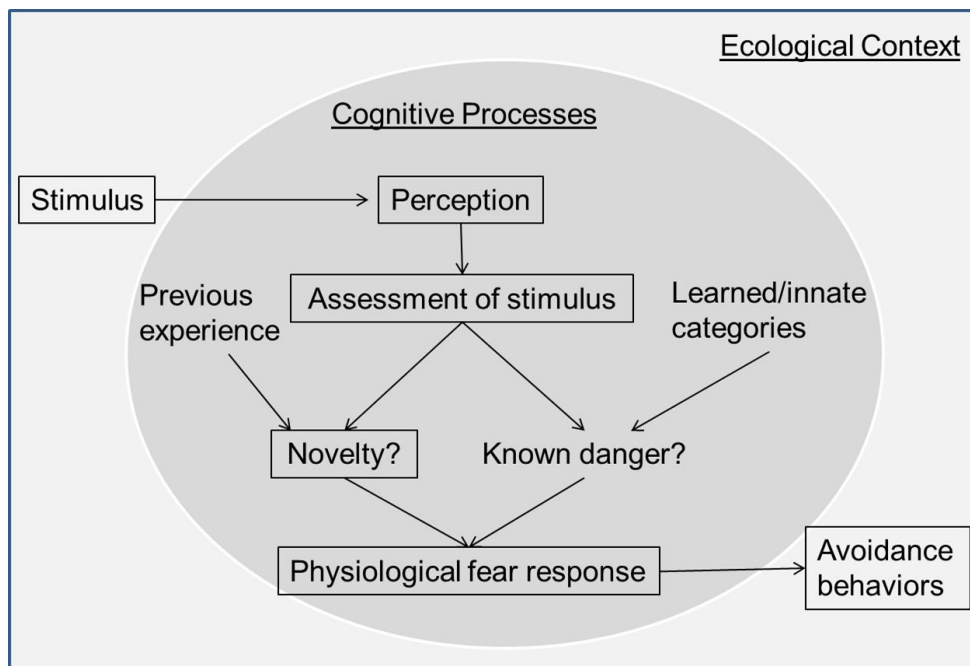


Figure 1.1 Combining the cognitive processes with ecological pressures in the expression of avoidance behaviour. Routes through which a stimulus can elicit avoidance behaviour; only the route with boxes is neophobia. Previous experience with similar types of novelty can influence the reaction towards subsequent encounters of novel things.

From an ecological perspective, each type of neophobia may be expected to evolve in response to different selective pressures (Greenberg & Mettke-Hofmann, 2001). For example, high predation pressure may favour object neophobia if avoiding new stimuli allows animals to escape (Brown, Chivers, Elvidge, Jackson, & Ferrari, 2013; Greenberg & Mettke-Hofmann, 2001). The need to exploit different habitats or migrate may promote low spatial neophobia (e.g. Mettke-Hofmann et al., 2009). Finally, a high prevalence of dangerous foods may favour dietary wariness to prevent poisoning (Thornton, 2008). It is often suggested that high levels of neophobia would be favoured in dangerous habitats where avoiding novelty would have a protective function (i.e. the Dangerous Niche Hypothesis, *sensu* Greenberg, 2003). However, the fitness consequences of neophobia are rarely tested in the wild (Chapter Four).

Studies testing multiple, closely-related species on various types of neophobia provide evidence for differential selection on neophobia categories. For example, different rat species (*Rattus norvegicus*, *Rattus fuscipes*, and *Rattus villosissimus*) have similar levels of spatial

neophobia but the brown rat (*R. norvegicus*), which has an evolutionary history as a human commensal species that regularly encounters rat poison, expresses considerably higher levels of object neophobia (Cowan, 1977). However, the extent to which environmental pressures such as human presence, impact neophobia levels across a greater range of species is unknown (Chapter Five). Beyond within-family comparisons (e.g. Mettke-Hofmann, Winkler, & Leisler, 2002), we know very little about the greater phylogenetic constraints that influence the possible expression of neophobic behavior. Broad, interspecific comparisons are largely absent from the neophobia literature, apart from early studies that did not control for differences in animals' perceptual abilities (e.g. Glickman & Sroges, 1966), and therefore phylogenetically controlled analyses are not yet possible.

If behavioural ecologists are interested in animals' responses to novel predators, food, or locations they may benefit from targeting a specific category of neophobia to increase the ecological relevance of the test. Conversely, where the interest is in quantifying an individuals' propensity for overall risk taking, boldness, or general fear reactivity, then tests that avoid the confound of novelty might be more appropriate (Réale et al., 2007). While researchers should consider whether neophobia tests or measures of general fear behaviour are more appropriate for their research questions, they can take steps to increase the validity and accuracy of neophobia tests. I discuss these methods in detail in Chapter 2.

1.4 How should we test reactions to novelty?

Novelty is not inherent to any stimulus, but arises through an interaction of perception and memory (Hughes, 2007). In designing an object neophobia test, researchers would benefit from considering whether the properties of an object could fall into an individual's previously held or evolutionarily relevant categories. Species can differ in the manifestation of their fear behaviours (e.g. reacting with flight responses or tonic immobility; Archer, 1979) and may also possess differing cognitive biases as a result of their evolutionary history, predisposing them to find certain stimuli or situations more frightening than others (Carter et al., 2013). For instance, if animals find certain stimulus characteristics, such as aposematic colours (Roper & Cook, 1989) or spots similar to predator eyes (Vallin, Jakobsson, Lind, & Wiklund, 2005), intrinsically aversive, avoidance may not be due to novelty alone. Unfortunately, often little justification is given for choosing seemingly arbitrary objects in behavioural ecology (e.g. a pink plastic key chain, Fox, Ladage, Roth, & Pravosudov, 2009; a

battery, Martins, Roberts, Giblin, Huxham, & Evans, 2007), and in psychology (e.g. an aluminium painted cube, Cowan, 1977; see Appendix Table 1).

Reactions to novelty may combine fear, interest, and indifference. Several methodological details can help tease apart fear from exploration interest (i.e. neophilia). For example, tests that measure animals' hesitations to venture outside a familiar space may differ critically from those in which animals are forced into novel environments, where activity may be better explained by motivation to escape (Carter et al., 2013; Hughes, 1997). Both fearfulness and curiosity can be assessed by combining these two types of tests: measuring animals' latencies to enter (neophobia), and their subsequent exploration of a novel space (e.g. Mettke-Hofmann et al., 2009). Similarly, neophobia can be measured through tests that compare approach latencies towards a reward such as food with latencies towards food next to a novel object (e.g. Greenberg, 1992; Chapters Three, Five). Conversely, tests measure exploration when the only motivation for approaching an object is to gain information about the object itself (e.g. Mettke-Hofmann, 2007). These two tests do not always correlate (Mettke-Hofmann et al., 2002). Additionally, behaviour in a neophobia test might be confounded by reactions to testing stressors other than the novelty presented. For example, if spatial exploration negatively correlates with object neophobia (e.g. Cole & Quinn, 2014)—the opposite relationship to that reported with jackdaws (Schuett et al., 2012)—it could mean that individuals classified as most explorative may be faster to recover and resume normal behaviour following a general stressor (e.g. Baugh et al., 2013), such as being handled. In the absence of a control measurement of normal behaviour, (e.g. activity around a familiar object), it is harder to determine whether avoidance behaviour is neophobia (Fox et al., 2009), or movement is explorative.

Overall, controlled laboratory studies and ecologically relevant field experiments are equally important in moving the study of neophobia towards more informed tests. We need psychologists to ascertain the mechanisms, and behavioral ecologists to explain why neophobic behavior exists. With accurate neophobia tests, we can confirm whether neophobia should be separated into distinct categories and whether all categories need to be sampled to measure overall fearfulness. Making these distinctions will help determine why neophobia exists, and how its expression impacts individuals and species. Ultimately, however, assessing the ecological impact of neophobia depends on understanding how quickly novelty is no longer perceived as novel, and how animals learn to make adaptive choices after

neophobia subsides to continue avoiding danger or approach potential resources (Chapter Six).

1.5 Overcoming neophobia: the corvid paradox

If and how neophobic responses subside over time is of equal importance in ecological contexts to animals' initial fear reactions. The question of how animals overcome their neophobia is perhaps most complex and most pressing for animals that exhibit high levels of neophobia and neophilia. Birds of the crow family, Corvidae, are suggested to fall within this category (Greenberg & Mettke-Hofmann, 2001). Corvids are ranked as the most innovative of birds, based on their frequency of foraging innovations (Nicolakakis & Lefebvre, 2000), yet also are very neophobic (Greenberg & Mettke-Hofmann, 2001; Heinrich, 1988). Such a combination appears paradoxical because neophobia is often suggested to inhibit innovation (Benson-Amram & Holekamp, 2012; Greenberg, 2003), and be associated with narrow ecological niches (Greenberg, 1990b). However, the corvid family is arguably one of the most successful bird groups. They have a nearly worldwide distribution (Figure 1.2), and occupy a diversity of niches, and habitat types. How this puzzling contradiction between high levels of fear, and high levels of innovation functions to influence the success of this family is unclear.

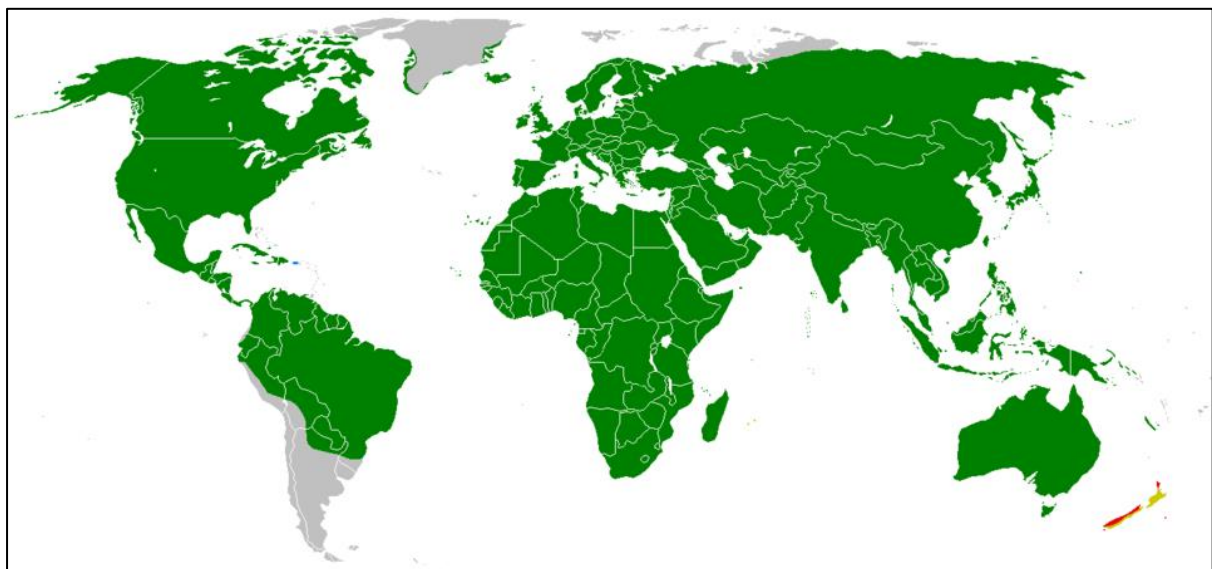


Figure 1.2 Worldwide distribution of the Corvidae family. Colours: green, native range; blue, recently extinct (post 1500), Hawaii, Malta, Puerto Rico; red, historically extinct (pre 1500), Hawaii, New Zealand; yellow, introduced range, New Zealand, Mauritius, Réunion. Distribution data gathered from (Goodwin, 1986; Madge & Burn, 1993). Photo accessed from Wikipedia Commons under a Creative Commons license, author: MPF.

Corvid species often polarize public opinion because they are revered for their intelligence, yet they are equally disliked for their supposed cunning and mischievousness (Marzluff & Tony, 2005). Corvids have a long history of being hunted by people (F. Coombs, 1978), and are often persecuted as farm pests (e.g. in the UK; Henderson, 2002) and for frequenting refuse dumps (Baglione & Canestrari, 2009; Baxter & Robinson, 2007). Seven of the eight species of UK corvid—the exception being the red-billed chough (*Pyrrhocorax pyrrhocorax*)—are widespread across Britain despite the large anthropogenic changes that characterize the UK landscape. The level of conflict they have with humans may help explain their levels of neophobia. If corvids occupy a particularly dangerous niche because of the levels of persecution they experience, increased neophobia could be essential to corvid survival (i.e. Greenberg, 2003). Therefore, studying neophobia in corvids offers an opportunity to investigate the costs and benefits of fear-related behaviour in a set of successful species that experience high levels of conflict with humans.

This thesis highlights the importance of considering the cognitive processes and ecological contexts underlying neophobic behavior, by examining the sources of individual and population level variation, the fitness consequences of such variation, and potential routes for overcoming neophobic behaviours in corvids. In Chapter Two I discuss the general methods of this thesis, i.e. the field logistics that allowed these investigations to be ecologically valid and some of the methods employed to account for sensory biases in designing novel stimuli. Since individual consistency is crucial to predicting the impact of any long term costs or benefits for being neophobic, Chapter Three examines how consistent individuals are in their neophobia across seasons and assesses the relationship between object neophobia and a fear of novel people. Such types of experiments question the assumption that neophobia is an individually stable trait, and that all types of novelty evoke the same responses.

With evidence supporting consistency within seasons (Chapter Three), Chapter Four investigates what reproductive costs and benefits such individual variation may incur. Individually stable traits that represent responses to stressors are often assumed to be associated with fitness outcomes (Dall, Houston, & McNamara, 2004). Neophobia is no exception (Réale et al., 2007), but the fitness consequences of neophobia are rarely tested in the wild. Should neophobia provide a protective function for corvids, we would expect higher neophobia to correlate with higher fitness and survival.

If human contact is the driver of corvid neophobia, then we would expect there to be higher occurrences of neophobia where conflict with humans is greatest. Whether or not neophobia expression differs between populations that may experience different ecological consequences for interacting with humans, such as across urban and rural gradients, will be examined in Chapter Five. Moreover, since corvids' neophobia has not been compared in the wild simultaneously to other species' Chapter Five also examines how these urban gradients impact the neophobia of birds outside of the corvid family.

After assessing the stability of neophobia, its fitness consequences, and natural variation across populations, I investigate a potential route through which corvids could overcome their neophobia in Chapter Six. The mere persistence of conspecifics has been suggested to encourage object exploration in the wild (Miller, Schiestl, Whiten, Schwab, & Bugnyar, 2014), but social facilitation does not reduce neophobia in all species (Greenberg, 1987). Chapter Six investigates the extent to which social influences encourage novel food consumption and approaching a startling object over seasons where the motivation may differ. Whether or not social learning is the key to corvid success despite such high neophobia is highly relevant to other socially learning species that face novelty in their environment.

As humans are increasingly altering habitats, investigating what behaviours and potential learning mechanisms facilitate behavioural adjustment to environmental change is increasingly important. Corvid success in light of their high neophobia is therefore related to understanding how species can cope with anthropogenic change. The potential that neophobia research has to influence species conservation is a running theme throughout this thesis and is considered in detail in Chapter Seven alongside a discussion of how ecologists and psychologists can continue to improve neophobia research.

Chapter Two

General methods³



³ The section of this chapter on neophobia tests has been published in Greggor, A. L., Thornton, A., & Clayton, N. S. (2015). Neophobia is not only avoidance; improving neophobia tests by combining cognition and ecology. *Current Opinion in Behavioral Sciences*, 6, 82–89.

2.1 Assessing neophobia as a field psychologist

As outlined in Chapter One, neophobia is an ecologically relevant fear behaviour that arises through a cognitive assessment of novel stimuli. Designing tests that account for both the ecology and psychology of neophobic behaviours is required if the proximate causes and ecological consequences of neophobia are to be explored. Since I investigated these dynamics in the corvid family, this Chapter explains what methods were used to study neophobia in wild corvids and how I aimed to design valid neophobia tests.

Several chapters of this thesis (Chapters Four, Six) focus specifically on the Eurasian jackdaw, *Corvus monedula*. Chapter Three instead focuses on captive rooks *Corvus frugilegus*, and Chapter Five on several corvid and non-corvid species. Both of these chapters employ the object design and neophobia test techniques detailed below. Specific housing details of the captive rooks are listed in the methods section of Chapter Three.

2.2 The Eurasian jackdaw

Wild jackdaws are an excellent corvid species for linking individual variation in physiological and cognitive traits to reproductive success within an ecologically relevant context. Since jackdaws are a cavity breeding species that will readily nest in man-made nest boxes (Henderson & Hart, 1993), during the breeding season pairs and their offspring can be carefully examined and manipulated. There are several aspects of jackdaws' life history, social system, and ecological niche that are important for this thesis.

The Eurasian jackdaw is widespread throughout Europe and is not a species of conservation concern. Jackdaws commonly inhabit farmland, villages and deciduous forest (Robinson, 2016). They are the most common corvid in UK gardens, and one of the most frequently seen UK garden birds (Robinson, Marchant, et al., 2015). In winter they form large interspecific foraging flocks with rooks, and gather in the thousands at night to roost (Coombs, 1961). They sometimes travel 8km between roosting and daily foraging sites, and the catchment areas for roosts can be upwards of 250 sq. miles (Coombs, 1961). Roosting and daily foraging sites can differ in their levels of human disturbance (personal observation). Meanwhile, during the breeding season (April – June), jackdaws remain local to a smaller area, and form dominance hierarchies between other birds in their nesting colony (Röell, 1978). The majority of UK jackdaws are residents, but some are known to migrate to northern Europe for breeding (Robinson, Leech, & Clark, 2015). While some individuals

breed in similar locations to where they hatched, colour ringed birds from the field sites have been reported by the public via ringing recoveries to have dispersed as far as 90 km away. The dispersal patterns and daily movements of some individuals indicate that jackdaws are likely to experience habitats that require different feeding and anti-predator techniques, especially given the fragmented landscape of the UK.

Jackdaws are dietary generalists, and often rely on food produced by humans, such as via agriculture and refuse dumps (Baxter & Robinson, 2007; Holyoak, 1968; Lockie, 1956). Their historical prevalence alongside farms has led to the perceived (but not necessarily proven) belief that they are pests, and to their subsequent designation as vermin in the UK (Wildlife and Countryside Act 1981). Whether or not this designation actually helps farmland is debatable because evidence from Cyprus suggests that the presence of corvids could benefit agriculture when they eat crop damaging insects (Hadjisterkotis, 2003). Jackdaws are often found foraging with rooks out in open fields (Lockie, 1956), and even in heavily degraded habitats such as landfills (Baglione & Canestrari, 2009). Foraging flocks in suburban areas tend to be smaller than those on rural farmland (Jadczyk, 2009).

Jackdaws form long term pairs-bonds that usually last for multiple seasons (Röell, 1978). They have so few extra pair copulations that they are considered to be genetically monogamous (Henderson, Hart, & Burke, 2000; Liebers & Peter, 1998). Females do the majority of incubating, but both parents provision their young (Henderson & Hart, 1993; Holyoak, 1968; Röell, 1978) and actively defend their nests (Henderson & Hart, 1993; Röell, 1978).

Although jackdaws historically use tree holes and cliff faces for nesting, in suburban and urban areas they often use chimneys and man-made structures for nest sites (Röell, 1978; Salvati, 2002). Jackdaws produce a single clutch per season that usually contains between 4-5 eggs (Henderson & Hart, 1993; Robinson, Marchant, et al., 2015). The brood hatches asynchronously, and full clutches very rarely survive (Henderson & Hart, 1993; only 40% of all chicks survive in the study sites). Parents' ability to provide food for their offspring is the biggest predictor of hatchling survival (Henderson & Hart, 1993, Chapter Four); accordingly, starvation is the biggest cause of hatchling death, while predation plays a relatively minor role (D. G. Wingfield, 1987). The laying and hatching season is temporally constrained, such that all nests within each of the study sites hatch within about two and a half weeks (mean 17.3 ± 3.5 days) in early May.

2.3 Study sites

The field data for this thesis (Chapters Four-Six) primarily comes from two study sites within the UK: one in Madingley, Cambridgeshire, the other near Penryn, Cornwall (see Figure 2.1). In both areas, boxes were placed on trees 4-5m off the ground, such that chicks could be accessed via a large extendable ladder. Feeding tables are scattered throughout both sites (see Figure 2.2). Regular baiting at these tables is used to attract birds to experiments there, such as Chapters Five and Six.

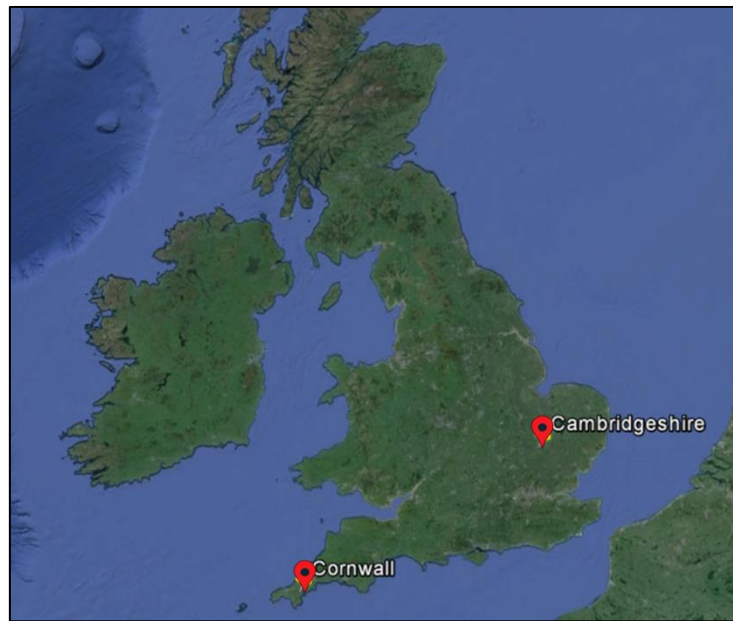


Figure 2.1 Location of field sites within the UK. Map generated with Google Earth.

The Cambridgeshire site is situated on University owned land in the village of Madingley and was set up by Alex Thornton in 2010. The site consists of 118 nest boxes suitable for jackdaws, arranged in clusters around woods and farmland. The boxes centre around a historical roosting site, to which rooks and jackdaws flock in the thousands every winter evening (Harrison, 1932). Eurasian jays (*Garrulus glandarius*), carrion crows (*Corvus corone*), and Eurasian magpies (*Pica pica*) also frequent the area throughout the year. Some of the jackdaws that roost in Madingley have been observed travelling to the city of Cambridge during the day, and nesting in the city during the spring and summer months (e.g. individual 389; personal observation).



Figure 2.2 Map of the field sites. The site in the East of England is located in Madingley (A) and the sites in the Southwest of the country are located around Penryn (B, C, D). Light blue patches indicate areas where nest boxes are set up, yellow pins indicate regularly baited feeding tables. B is located in the village of Stithians, C spans the city centre of Penryn and the adjacent University of Exeter Cornwall campus, and D is located on a farm one mile from Stithians. Maps generated with Google Earth, accessed in March 2016.

The Cornish site was set up by Alex Thornton as part of the Cornish Jackdaw Project in 2012. Over 100 nest boxes were erected across a variety of habitat types that range from rural farmland to a busy churchyard and the University of Exeter's Penryn campus (see Figure 2.2). In comparison to Madingley, the Cornish site is much more heterogeneous in its levels of human disturbance and habitat type. The greater heterogeneity in these sites is reflected in the birds' greater tolerance of human disturbance (see Chapter Four and Appendix 2). Despite corvids appearing more tolerant of humans around the Cornish site, corvid culling is known to occur in the rural areas near each site, both historically (Kempson, 1912), and within the study period of this thesis (Figure 2.3).



Figure 2.3 A rook shot dead while provisioning its chicks at its nest in Stithians. The rook colony in question was repeatedly attacked because the owner of the trees disliked the noise of the breeding birds and the amount of faeces falling into his garden.

Across both sites, adult corvids are caught using ladder traps (see Figure 2.4) and ringed with a unique combination of three colour rings and one metal ring inscribed with a unique number provided by the British Trust for Ornithology (see Figure 2.5a). Every breeding season chicks are ringed in their nests on the 25th day post-hatching for the oldest chick within a nest. At ringing, birds' wing length was measured with a wing ruler, tarsus length measured using callipers (to the nearest 0.1mm) and weight recorded (to the nearest 0.1g using an electronic balance). A blood sample was also taken to later determine sex. When blood was needed for other purposes, such as sampling for stress hormones, a different procedure was used, as detailed in Chapter Four. Table 2.1 shows the number of corvids that had been ringed at each site per year. From mid-way through the 2013 breeding season, all ringed jackdaws were also fitted with an RFID tag.

	Madingley			Cornwall					
	JD Adult	JD Chick	Jay	JD Adult	JD Chick	Rook	Crow	Jay	Magpie
2010	1	6	0	NA	NA	NA	NA	NA	NA
2011	16	9	0	NA	NA	NA	NA	NA	NA
2012	41	47	0	NA	NA	NA	NA	NA	NA
2013	0	103	3	411	51	65	6	6	4
2014	0	106	0	176	96	15	2	0	2
2015	NA	NA	NA	62	167	17	0	0	0

Table 2.1 Corvids ringed at both field sites. JD Adult is the total of all birds ringed outside of their nests, regardless of age beyond fledging. JD Chick covers only birds that were ringed in their nests. Fledgling totals also include chicks ringed in natural nests, not just ones located in nest boxes.



Figure 2.4 Ladder trap. The traps were baited with bread during the breeding season and summer months for catching free-flying jackdaws and other corvids. Traps were left open through the removal of a side panel to train birds to enter. When the trap was closed, birds would close their wings to enter through the rungs in the “ladder” on the top of the trap, and then be unable to fly out with closed wings. Closed traps were monitored every 30 minutes.

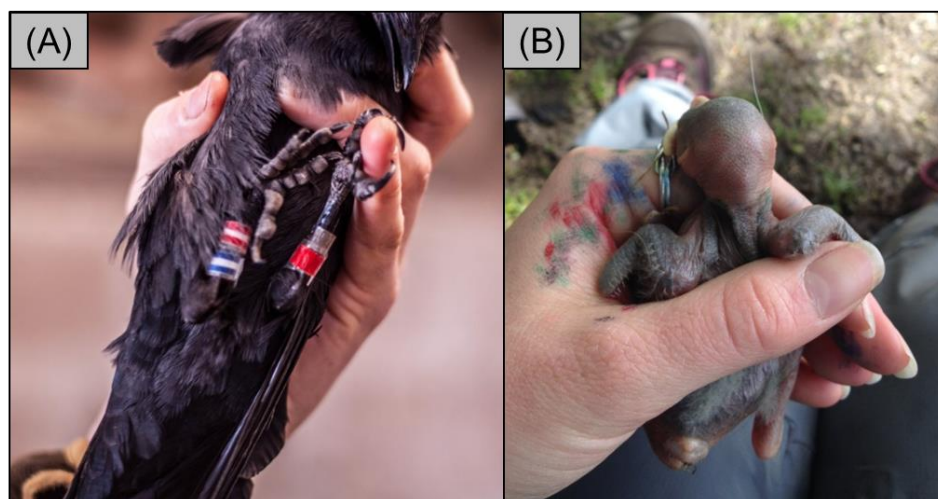


Figure 2.5 Marking methods. Colour ringing (A): each bird received three plastic colour rings and a metal ring issued by the BTO. Chick marking and weighing (B): chicks were marked with non-toxic sharpie pens, the colours assigned based on hatching order.

The breeding success of each site was tracked from its founding, with the exception of the Madingley site in 2015. Nest checks were conducted with a ladder, a camera on the end of an extendable pole, or an internally mounted nest camera. Nests were checked daily from late nest building stages until the clutches appeared complete. Once eggs were laid, nests were checked several times per week and then daily when they neared the end of the incubation period (i.e. day 18). Once chicks had hatched they were checked three times a week, and then every day as fledging approached (i.e. day 30). The weight trajectories and

survival of individual chicks were measured every two to three days in all nests in the Cornish site, and a select number of nests in the Madingley site. In these nests individual chicks were distinguished with coloured marker, reapplied at every check (see Figure 2.4b).

2.3.1 Nest Success

Body condition was calculated differently for within versus between site comparisons. Within sites, body condition was calculated based on chicks' residual deviation from the nestling population's regression of weight against tarsus (e.g. Chapter Four, Verhulst and Salomons, 2004), such that birds with a larger body weight than expected by their tarsus length were judged to be in relatively good condition. However, since measures of tarsus can be unreliable when measured by different people, cross site comparisons instead use nestling mass. The data on nest success within and between the two study sites can be found in Appendix 3, to help provide background to the two chapters that conduct cross site comparisons in behaviour (Chapter Four, Five).

2.3.2 Ethical statement

All studies conducted at the two field sites fall under the Home Office project license given to Alex Thornton (80/2371), and under the Home Office personal licenses given to Alex (70/25311), and myself (70/24971) to allow for blood sampling. Ringing was conducted under British Trust for Ornithology licenses (no. C6079, C5752, C5746). Nest disturbance was approved by Natural England License (20130067).

2.4 Novel object tests

Three of the chapters from this thesis employ object neophobia tests (Chapters Three-Five). In each of these chapters the following rationale was used in the design of objects and testing protocols (summarized in Table 2.2). New sets of novel objects were constructed for each experiment that conducted object neophobia tests. Records have been kept of all experiments run at both study sites on corvids, so that novel testing apparatus were known to be novel. Testing stimuli was designed to not inadvertently mimic known fear-related stimuli, such as black flapping material that could look like a dead conspecific from a distance (described anecdotally in Lorenz, 1952). The distinctiveness of object materials was verified through spectral analyses (details below). Additionally, since the complexity of a novel object (e.g. patterning, textures and shape) can influence how much animals interact with it (Berlyne, 1950; Greenberg & Mettke-Hofmann, 2001; Jones, Larkins, & Hughes, 1996;

Mettke-Hofmann et al., 2006), all objects were built with similar levels of complexity. Objects were constructed out of at least four bright materials of contrasting colours and textures. No object contained any element that could look like eyes.

Table 2.2 What to consider when designing a neophobia test.

Test	Things to consider	Why
Object Neophobia	Careful selection of objects	Ecologically relevant stimuli can trigger innate fear responses. Novelty increases with stimulus complexity (patterns, colours, textures).
	Conduct at least 2 replicates each with a new object	Many animals show repeatability, but can respond to objects differently. Responses to novelty will decrease with repeated presentations
	Does test measure exploration or fear?	Hesitancy to approach novelty alongside a reward shows fear responses. Exploration is best measured as an attraction to novelty without other rewarding stimuli present.
	Is neophobic behaviour compared to normal behaviour?	Without a control measure behaviour may not be due to the novel situation
Spatial exploration	Is the animal forced to enter a novel space?	Forced entry can lead to fear, not exploratory behaviour
	Was the animal handled beforehand?	Minimize other fearful stimuli where possible
	Is it compared to a measure of activity in a familiar area?	Movement in novel space could otherwise reflect activity
Food Neophobia	Distinguish between neophobia of the food and dietary conservatism	Dietary wariness is made up of two separate processes
General Neophobia	Consider species-specific fear responses	Species differ in their cognitive biases
	If research questions are specific to one type of neophobia, specifically target that type	Testing one type alone may be more ecologically relevant
	Pair neophobia tests with other types of tests to tease apart mechanisms	Pair with a general fearfulness and an information-processing test

Despite the potential variation in responses towards different objects (Greenberg, 1983; Heinrich, 1995; Heyser & Chemero, 2012), relying on a single neophobia test is not advisable because at least two measures of a temperament trait are needed to verify its reliability within individuals (Réale et al., 2007). Therefore neophobia tests were repeated with a range of objects—not repeats of the same object (e.g. Cole & Quinn, 2014; Patrick & Weimerskirch, 2014), which are no longer novel on subsequent presentations—to create a more accurate measure of general novelty responses. Moreover, experiments that aim to test an individual's novelty categories (such as Chapter Five) presented objects that were designed to differ in distinct ways to help define which aspects of a stimulus contribute to its novelty. Finally, all object neophobia tests were paired with a control trial to ensure that responses were to novelty and not to other stressors created by the testing situation.

2.5 Colour analysis

A colour analysis was conducted to ensure that the novel objects and foods used in this thesis were as distinctive to the birds as they were to human eyes. The spectral qualities of the novel foods and materials used for object construction were analysed using an Ocean Optics USB2000 spectrometer, with illumination provided by a PX-2 pulsed Xenon lamp. The probe tip was housed in a hollow sheath so that samples were measured at 45 degrees to normal, and I used a Spectralon 99% white reflectance standard (Labsphere) and a dark current reading to standardize scans. A sample of each colour was measured three times, each at a different location. Colour distances between food or material types were calculated using the coldist function of the pavo package in R (Maia, Eliason, Bitton, Doucet, & Shawkey, 2013), using starlings (*Sturnus vulgaris*) as the visual model, and are reported in units of just noticeable differences (JNDs). In chapters where colour analysis was most heavily used (Chapter Five, Six), the visual distinctiveness of the spectral reflectance of the analysed materials was plotted in two dimensional and three dimensional projection plots that use the avian tetrahedral visual space (see respective chapters for plots).

2.6 Statistical Analysis

All data was analysed in the open-source software, R version 3.2.2 (2015). Unless otherwise specified, behavioural data were analysed using linear mixed models (LMMs) and generalized linear mixed models (GLMM). Depending on the distribution of the data either the lme4 (Bates, Maechler, Bolker, & Walker, 2013), or the glmmADMB (Fournier et al., 2012) package was used based on which one best supported analysis of that distribution.

Such flexible analyses allow for the control of inherently noisy field data that often defies the normal distribution and contains non-random variation caused by factors such as geographic proximity, repeated measures, and relatedness (Bolker et al., 2009). Model selection was based on backwards step-wise elimination techniques (Zuur, Ieno, Walker, Saveliev, & Smith, 2009) that began with a maximal model containing all possible terms and their interactions. Terms were dropped if their exclusion did not increase the models' Akaike Information Criterion (AIC), i.e. the relative measure of model quality, by more than 2.0. Once final models were determined, effect sizes, and P-values were calculated. Any factor with a P-value <0.05 was deemed to be significant, but its predictive value was judged by its effect size relative to other terms in the model. Model assumptions were validated through inspection of diagnostic plots.

Chapter Three

Seasonal changes in neophobia and its consistency in rooks: the effect of novelty type and dominance position⁴



Photo of captive rooks in this study, taken by Julia Leijola

⁴ A version of this chapter has been accepted for publication at *Animal Behaviour* as: Greggor, A. L., Jolles, J. W., Thornton, A., Clayton, N. S. Seasonal changes in neophobia and its consistency in rooks: the effect of novelty type and dominance position.

3.1 Abstract

Neophobia, or the fear of novelty, may offer benefits to animals by limiting their exposure to unknown danger, but can also impose costs by preventing the exploration of potential resources. The costs and benefits of neophobia may vary throughout the year if predation pressure, resource distribution and conspecific competition change seasonally. However, despite such variation, neophobia levels are often assumed to be temporally and individually stable. Whether or not neophobia expression changes seasonally and fluctuates equally for all individuals is crucial to understanding the drivers, consequences and plasticity of novelty avoidance. I investigated seasonal differences and individual consistency in the motivation and novelty responses of a captive group of rooks (*Corvus frugilegus*), a seasonally breeding, colonial species of corvid that is known for being neophobic. I considered differences in dominance that could influence the social risk of approaching unknown stimuli, and tested the group around novel objects and novel people to determine whether responses generalized across novelty types. I found that the group's level of object neophobia was stable year round, but their avoidance of novel people decreased during the breeding season. Additionally, although subordinate birds were more likely to challenge dominants during the breeding season, this social risk-taking did not translate to greater novelty approach. Individuals were not consistent between seasons in their object neophobia but were consistent in their avoidance of novel people, despite demonstrating within-season consistency for both measures. Since seasonal variation and individual consistency varied differently towards each novelty type, responses towards novel objects and people seem to be governed by different mechanisms. Such a degree of fluctuation has consequences for other individually consistent behaviours often measured within the non-human personality literature.

3.2 Introduction

When animals express neophobia, or the fear of novelty, they show an aversion to an unknown risk (Greenberg & Mettke-Hofmann, 2001). Since species have been shaped over evolutionary time to avoid unknown risks, neophobia is often thought to drive species-level traits such as niche breadth, home range size, or dietary generalism (Greenberg & Mettke-Hofmann, 2001; Greenberg, 1989, 1990a, 1992). For example, high levels of neophobia may be favoured by selection in habitats where increased wariness is beneficial for survival and reproduction, for example in predator-rich environments (Ferrari et al., 2015). However, elevated neophobia may also carry potential costs if increased fear inhibits innovation

(Benson-Amram & Holekamp, 2012; Greenberg, 2003), or limits defences, for instance, against nest predators (Vrublevska et al., 2015). These costs and benefits of risk-taking are likely to vary over time and contexts in a way that could alter the expression of neophobia. For example, it could be beneficial to adjust neophobia levels when environmental opportunities or dangers change, such as food availability or predation pressure (e.g. Brown et al. 2013). Therefore animals may have evolved species-typical patterns of plasticity in neophobia if environments vary in predictable ways.

Every year environments undergo predictable seasonal cycles that trigger changes in animals' metabolism and thermoregulatory processes (Thomas, Bieber, Arnold, & Millesi, 2012). Therefore just as seasonal change impacts behaviour related to physiological processes, neophobia levels may also change in response to the changing risks and rewards of the time of year. The extent to which species mediate their neophobia seasonally is unclear, and the handful of studies conducted on birds to date have generated conflicting and inconsistent findings (Apfelbeck & Raess, 2008; Mettke-Hofmann, 2000, 2007; Shephard, Lea, & Hempel de Ibarra, 2014). Moreover, it is unknown whether or not all individuals respond similarly to seasonal influences.

Individuals are commonly assumed to vary consistently in their neophobia (e.g. Bebus et al. 2016). In fact, neophobia is often used as a marker of non-human personality or temperament, because it is considered a stable response to challenges or risks across times or situations (Dall et al., 2004). However, it is unclear if all individuals similarly mediate their neophobic behaviours under changing conditions. Such individual variation begs the question of why certain behaviours remain rigid and why others show variable plasticity (Carter, Goldizen, & Heinsohn, 2012).

Several proximate and ultimate explanations for neophobic behaviour suggest species' neophobia levels should vary seasonally, and that not all individuals may be consistent in these changes. Firstly, changes in motivation and hormone levels throughout the year could have a powerful influence on neophobia and other types of risk-taking. For example, many bird species undergo physiological and behavioural changes during breeding (Pdulka, Rohrbaugh, & Bonney, 2004) altering hunger and activity levels, which could contribute to changes in neophobic behaviours. Levels of stress hormones, such as corticosterone (CORT), that are thought to influence neophobic responses, vary by season (Romero, 2002), and often lack consistency within individuals beyond seasons (Ouyang, Hau, & Bonier, 2011). In line

with these patterns, over short periods of time, neophobia measures have been shown to be highly repeatable (e.g. Jolles et al. 2013, although see Miller et al. 2015) , while over longer timeframes, such as years, it can lack such consistency (e.g. Klun & Brommer 2013).

Secondly, seasonal changes to animals' social systems could influence the risks and rewards of approaching novelty. For example, the presence of dominant individuals can alter the costs of neophobia or exploration if approaching novelty allows subordinates to circumvent competition for favoured resources, but this can depend on the species in question. In some corvid social systems, such as those of carrion crows (*Corvus corone*), dominants are more likely to take risks by approaching novelty, and subordinates benefit, at least in family groups (Chiarati, Canestrari, Vera, & Baglione, 2012). However, in other species, such as common ravens (*Corvus corax*), subordinates are less neophobic, at least around novel food, potentially approaching novelty to avoid competition with dominants (Heinrich, Marzluff, & Adams, 1995). If seasonal changes in social structure and hormone levels increase the frequency of contact and aggression between subordinates and dominants, then the risks and rewards for approaching novelty might also vary, but would do so differently depending on individuals' dominance rank. Additionally, the presence of conspecifics can influence levels of novelty approach (Miller et al., 2015), and the extent to which conspecific social cues influence behaviour can vary seasonally (Chapter Six). Therefore efforts to determine the factors that influence neophobia must also consider the social context of risk-taking and the dominance of the individual, especially since the social context can influence levels of novelty approach (Miller et al., 2015). By measuring neophobia within social settings that would be common in the wild (Dall & Griffith, 2014), tests are more likely to capture natural interactions between dominance, neophobia, and seasonal changes to the social system.

Finally, not all types of novel stimuli evoke the same reactions, and different types of novelty may be more threatening at certain times of year. Individual measures of neophobia towards different types of novelty, such as objects and locations, do not always correlate (e.g. Boogert et al. 2006; Fox et al. 2009), and neophobia is not always predictive of wariness towards other threatening stimuli such as predators (e.g. Carter et al. 2012b). Similar to what has been proposed for other behaviours considered to be stable across time and/or contexts (Dall & Griffith, 2014), understanding the mechanisms behind neophobic behaviour, requires examining it when contextual changes occur that may influence its expression. Several underlying mechanisms can contribute to the expression of neophobic behaviour, such as

novelty categorization, and physiological fear responses (Chapter One). Individual fluctuation in these mechanisms could help explain the existence and maintenance of individually varying behavioural reaction norms (e.g. Dingemanse et al. 2010). However, without an understanding of how neophobia naturally varies throughout the year, it is difficult to assess to what extent individuals might vary in their level and stability of neophobia.

I measured the risk-taking behaviour of a social group of captive rooks (*Corvus frugilegus*) towards novel objects and novel people to measure the seasonal effects and individual stability of neophobia. Tests and their control conditions were run over a full year within a social group to gauge the potential effect of social rank on neophobia over time. While novel object tests are the most common measure of neophobia (Chapter One), examining reactions to novel people allowed me to verify whether seasonal change influences novelty responses *per se*, or influences more ecologically relevant fear behaviours such as predatory wariness. Rooks are an excellent model species to test these dynamics because they experience seasonal changes in behaviour while breeding, are known to be very neophobic (Chapter Five; Jolles et al. 2013), and are likely able to discriminate between human faces, as other corvids do (Davidson, Clayton, & Thornton, 2015; Lee, Lee, Choe, & Jablonski, 2011; Marzluff, Walls, Cornell, Withey, & Craig, 2010). Moreover, since I tested a group from which data had previously been collected on neophobia and dominance in the context of social feeding tactics (Jolles et al., 2013), I was also able to compare select behaviours across a four year period.

The experimental setup led to a set of four predictions. I predicted that (1) the rooks would be more likely to approach novel objects and people during the breeding season, because hunger and feeding rates increase at that time (Feare, Dunnet, & Patterson, 1974), which can increase risk-taking (Damsgard & Dill, 1998). Additionally, I predicted (2) that subordinates would demonstrate lower neophobia to avoid competition with dominants (i.e. a similar situation to ravens, Heinrich et al. 1995), but expected this effect to depend on the season, as subordinates might be more willing to risk competing with dominant individuals during breeding season. I also predicted that (3) individual consistency across seasons would differ depending on the type of novelty. Despite both stimuli being novel, reactions towards novel people also may evoke reactions of predatory wariness, which does not always correlate with neophobia (Carter, Marshall, et al., 2012), and could be subject to different seasonal pressures. Finally, I predicted that (4) individuals may not be consistent in their responses towards the different types of novelty because avoidance towards objects versus

people could involve different cognitive mechanisms and ecological biases whose response strength may vary independently between individuals.

3.3 Methods

3.3.1 Subjects and housing

The group of adult rooks was housed in an outdoor aviary at the University of Cambridge's Sub-Department of Animal Behaviour, Madingley, U.K. where they experienced ambient light and temperature fluctuations throughout the year. The birds were collected as chicks under English Nature Permit 20030108 from two Cambridgeshire colonies in 2003 and were hand-raised. The birds were given sticks for nest building during breeding season, and they formed pairs and laid eggs. During this time they were highly active in maintaining and defending their nests, since the group had a fixed amount of high quality sticks. Eggs were pricked upon discovery (in accordance with Home Office animal welfare regulations) so that no birds were actively rearing young. The group consisted of 19 birds when initial data on dominance and object neophobia were collected in the 2010 breeding season by Jolles et al. (2013). After this, three changes in the group occurred: two birds died in 2013 (group $N = 17$); and during 2014, the data collection for the main seasonal comparison in this study, one bird died in the summer (group $N = 16$); and two new birds were added in the autumn (group $N = 18$) from a similar aviary on the premises.

The aviary (8 x 20m and 3m high) was constructed of wood and mesh with gravel floor, and had several perches and platforms at different heights, and three feeding tables 1.1m off the ground. Birds were given colour leg rings to enable individual identification. Birds had ad libitum access to water and food except during the experimental procedures when the group was deprived for up to four hours. The experiments were conducted in accordance with the University of Cambridge's animal welfare guidelines as non-regulated procedures under the U.K. Home Office project license PPL 80/1975 and adhere to the standards set forth by the ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching (2012).

3.3.2 Experimental procedure

Experimental trials took place at one of 6 locations within the aviary; 3 on the ground, and 3 on a feeding table. All locations were used on each testing day, and their order was randomly determined beforehand. Since birds preferred to occupy different parts of the

aviary, testing in multiple locations gave the greatest number of birds a chance to participate. The group was deprived of food for at least 90 minutes (101 ± 5 min) prior to the start of that day's experiments. Each testing day was randomly assigned to 6 novelty response trials or 6 motivational control trials (detailed below). Although this type of control is sometimes used to validate neophobia tests (e.g. Cole & Quinn 2014), it also serves as a measure of motivation, and therefore helps determine whether changes to motivation could explain any seasonal changes in neophobia that might occur.

All experiments were filmed with a Panasonic HDC-SD90 camcorder from outside the aviary, and later video coded. Birds were deemed to approach if they came within 1 m of the food; a distance that a person, conspecific, or threatening object (if it were to move), could easily travel. Each bird's approach time and food consumption was noted for each trial. Birds' approach latency was used as an indicator of avoidance, and the number of worms consumed indicated their ability to gain access to resources in that context. Birds that did not approach were given a maximum time equal to the length of the trial. Intercoder reliability on approach times and food consumption was assessed by re-coding a random subset of videos (31% of trials). Reliability was deemed to be very high (approach times; ICC (1) = 0.93, CI = 0.92-0.94, food consumption; ICC (1) = 0.92, CI = 0.91-0.93).

3.3.3 Novelty response tests

3.3.3.1 Novel object tests

Object neophobia was assessed similarly to previous protocols used with the same group of birds (Jolles et al., 2013). The experimenter placed a familiar food bowl containing 8 wax moth larvae (a preferred food) and the novel object in the aviary, 10cm apart, and left the aviary. After 5 minutes the experimenter returned and removed the object and food bowl, even if the food had not been consumed. The experimenter then conducted another trial with a new object until all 6 locations had been tested. Novel objects were constructed out of bright, artificial materials, that differed in colour, texture, and shape, contained at least one shiny element, all of the primary colours, and did not contain any parts that could look like eyes. A new novel object was used for every trial. Non-object, motivational control trials were run in the same manner as the novel object trials, but with food presented only. Throughout 2014, a total of 42 object neophobia trials and 36 control trials were run over the course of 13 days.

3.3.3.2 *Novel people tests*

Over the years, many anecdotes have accumulated indicating that the rook groups at the study site were highly wary of novel people despite having been hand raised. New experimenters had to spend several months with the group before the majority of birds would approach and feed near them. Furthermore, there appeared to be substantial individual variation in how long birds took to take food from the hand of a new experimenter, with some birds never hand-feeding despite years of interactions with an experimenter.

In order to quantify these tendencies and determine the extent to which they related to variation in novel object responses, 6 novel female experimenters each conducted a set of 6 feeding latency trials over the course of 2014. The birds had never seen the novel experimenters prior to the day of the trial. Each experimenter approached the aviary unaccompanied (i.e. without the presence of a known experimenter), walked to one of the 6 predetermined locations within the aviary, tossed five wax moth larvae 2-3m in front of her, and remained staring at the worms. She tossed five instead of eight worms—the number presented in the novel object trial—because pilot trials indicated that five were easier to monitor on the gravel floor. The experimenter then waited until all five worms were eaten and then tossed an additional five. She continued doing this for a total of 10 minutes. If no bird approached during that time, she left the initial five worms and exited the aviary. She repeated the trial until all six locations had been tested. In order to control for differences in hunger motivation over the course of the year, control trials were run with the same protocols by a familiar female experimenter who had been working with the group consistently since the spring of 2013.

3.3.4 *Dominance*

Dominance hierarchies were measured via *ad libitum* (Altmann, 1974) behavioural observations of the group. Observations were used from a previous study (Jolles et al., 2013) from summer 2010, and were collected at three additional time points: (1) breeding season 2014, (2) summer 2014, and (3) winter 2014. Behavioural observations were carried out in person from 10m outside the aviary as well as from video recordings of morning feedings. A total of 1753 agonistic interactions were recorded throughout the year. Aggressive interactions included behaviours such as displacing, threatening or chasing other individuals, and pecking or feather pulling (for full ethogram see Jolles et al. 2013). The identity of both the aggressor and the aggressed individual were noted. Aggressive interactions at nest

locations were not included since birds might be expected to defend their nest even against dominant individuals.

All dominance interactions were organized in a sociometric matrix. To test for linearity I calculated Landau's index h and the index of linearity h' using the DyaDA package (Leiva, Solanas, & Kenny, 2010). Both indices vary from 0 (complete absence of linearity) to 1 (complete linearity). The index h' is based on h and takes into account the existence of unknown relationships. Statistical significance of h' is provided by a resampling procedure using 10,000 randomizations (de Vries, 1995). When linearity of the dominance was observed, individuals' ranks were calculated such that their rank order minimized the number of inconsistencies and then minimized the total strength of inconsistencies (de Vries, 1998).

Additionally, in order to determine whether the levels of aggression within the group varied seasonally, the number of aggressive behaviours that occurred around the food bowl was recorded for all non-object control trials and compared across seasons. Non-object controls were used instead of the familiar person controls because a standardized amount of food was presented in these trials, thereby providing identical opportunities for aggression, and hence a more accurate measure of whether or not subordinates' experienced different social costs for approaching between seasons.

3.3.5 Analysis

All data were analysed in R (R Core Team, 2015). In the few cases where bird identity could not reliably be determined from the video, that trial was removed from analysis (7.5% of trials had at least one uncertain bird, but this was spread evenly throughout the year).

3.3.5.1 Seasonal variation in behaviour

I assessed seasonal variation in behaviour by analysing birds' raw approach times and the amount of food they consumed. Firstly, I analysed the probability that any bird would approach over time using a Cox proportional hazards regression model (e.g. Bókonyi et al. 2012) on the raw approach time data. Survival analyses avoid censoring the data, thereby allowing for the assumption that birds assigned to maximum times may have approached had the trials run longer. I primarily investigated the effects of experimental condition, sex, dominance, season and any interactions between them. The potentially confounding covariates of trial order, and aviary location were included in the model. Data were clustered

around bird identity and trial to account for dependence in the data. I used the ‘survival’ package in R (Therneau, 2015).

Secondly, I analysed the raw data on the number of worms consumed by each bird with Generalized Linear Mixed Models (GLMMs) with a negative binomial error structure and the same effects and covariates as the survival analysis. Bird identity and trial were included as random effects to account for repeated measures. Models were run with the *glmmadmb* package (Fournier et al., 2012), and the final model determined through backwards stepwise elimination (Zuur et al., 2009). Effects were retained if their exclusion increased AIC values by at least 2. Once the final model was established, P-values and effect sizes were calculated. Any analysis that found seasonal effects was repeated without the three individuals that either left or entered the group over the year to ensure changes in group composition could not explain any seasonal variation found. The results section only reports this extra analysis when it produced different results.

Finally, the total counts of aggression for the control object trials were compared across seasons with a Chi square test.

3.3.5.2 Behavioural consistency

I assessed how consistent individuals were within seasons in their approach times in the presence of novelty and during motivational controls. The distribution of raw approach times was non-normal and highly skewed by birds that did not approach. Therefore I assessed individuals’ within-season behavioural consistency by calculating intraclass correlation coefficients (ICC; Nakagawa & Schielzeth 2010) using the ‘irr’ package (Gamer, Lemon, Fellows, & Singh, 2010), for each condition and stimuli type.

Additionally, I assessed how consistent individuals were between seasons and years in their dominance by using their approach ranks in control and test conditions. Raw approach times were transformed into individual approach ranks for control and test conditions and compared with Spearman’s rank correlation tests. Approach ranks were calculated for each trial based on the order in which individuals approached the food cup. Overall ranks were determined by averaging trial ranks separately for each condition and season, accounting for the number of trials in which each bird was present. Any birds that did not approach during a given trial were given the same lowest approach rank.

Additionally, to compare birds' rankings in novel object tests and dominance status in breeding season across years, I combined my data with that from a previous study of the same group (Jolles et al., 2013). Individual rankings for this comparison were based on the number approaches individuals made towards novel objects or the control food bowl and only birds found in both time periods of interest were used in comparisons.

Finally, I compared birds' consistency in their ranking between stimuli types (object and people tests) and between motivational controls within seasons with Spearman's rank correlation tests. Only birds present in both time periods being compared were used ($n = 17$ between years, $n = 16$ between seasons). Since rank measures were used in multiple comparisons (between seasons, between years, and within seasons against different stimuli types), all reported P-values were adjusted through Holm's method (Shaffer, 1995).

3.4 Results

3.4.1 Seasonal variation in behaviour

3.4.1.1 Novel object tests

Birds were less likely to approach the food bowl when a novel object was present compared to when one was not (Cox proportional hazards model, $n = 1303$ observations, 253 events: $z = -4.29$, $P < 0.001$), but in contradiction to prediction (1), neophobia persisted regardless of season ($z = 0.25$, $P = 0.801$). There was an interaction between season and dominance that held for both test and control conditions, thus going against prediction (2). All birds were equally likely to approach the food bowl in the breeding season, but dominant birds were more likely than subordinate birds to approach outside of the breeding season ($z = 3.46$, $P < 0.001$; see Figure 3.1). To ensure this seasonal effect was not due to changes in group composition, the same tests were conducted on the data from birds only present in all time periods. Although this interaction was no longer significant with this restricted dataset ($z = 1.64$, $P = 0.102$), the smaller dataset showed the same non-breeding season trends, both before and after the addition of two birds (see Supplementary Materials, Figure 3.S2). Birds were faster to approach an object on the floor than on a feeding table ($z = -3.70$, $P < 0.001$); but there was no effect of sex, or any of the other covariates on birds' approach (see Table 3.1). In addition to approaching less, birds also ate less food when a novel object was present, compared to when it was not (GLMM, $n = 1303$, Est = -0.54 ± 0.22 , $z = -2.46$, $P = 0.014$). Food consumption did not differ by season, dominance rank or any other factor (see Table

3.S1). Meanwhile a higher number of aggressive behaviours occurred during non-object control trials in breeding season than outside of breeding season (31 during 18 trials vs 6 during 18 trials, $\chi^2 = 7.97$, $df = 1$, $P = 0.005$).

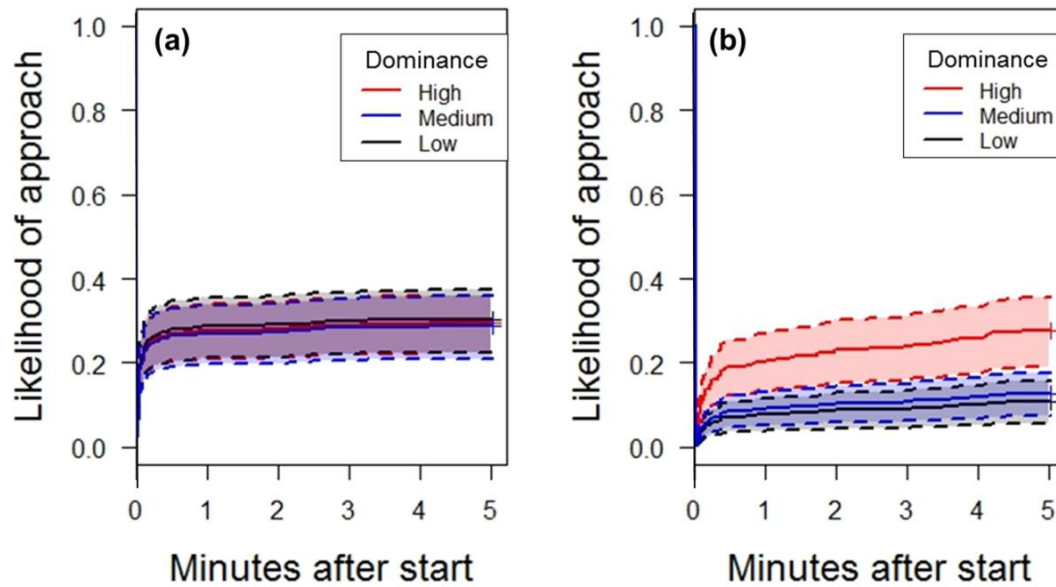


Figure 3.1 Food bowl approach. Inverted survival curves showing the likelihood that birds of different dominance ranks approach the food bowl in both object and non-object conditions over time in the (a) breeding and (b) non-breeding season. Dotted lines show confidence intervals. Dominance ranks were grouped evenly into categories of “high”, “medium” and “low” for graphical representation, but were analysed as a continuous variable.

Table 3.1 Survival models for latency to approach the food bowl. Interactions are denoted with an asterisk and variable level listed within parentheses, SE, standard error. Effects retained in the minimal model are in bold; their values were calculated when all non-significant terms were dropped. The highest ranking bird was assigned a dominance of 1.

<u>Variable</u>	<u>B</u>	<u>SE</u>	<u>z</u>	<u>P</u>
Trial number	0.033	1.03	0.86	0.388
Season (Breed)	-0.207	0.29	-0.73	0.468
Sex (Male)	0.054	0.20	0.28	0.783
Aviary location (Table)	-0.480	0.13	-3.70	< 0.001
Dominance	-0.108	0.02	-4.42	<0.001
Condition (Novel Object)	-0.548	0.13	-4.29	<0.001
Condition * Sex	-0.145	0.30	-0.48	0.632
Condition * Season	0.069	0.27	0.25	0.801
Season * Dominance	0.103	0.03	3.46	< 0.001

3.4.1.2 Novel people tests

In line with prediction (1), birds approached novel and familiar experimenters similarly in the breeding season, but were slower to arrive around novel people in the non-breeding season (Cox proportional hazards model, $n = 928$ observations, 299 events, Condition*Season interaction, $z = 2.73$, $P = 0.006$; see Figure 3.2). However, in contradiction to prediction (2) dominant birds were more likely to approach the experimenter ($z = -2.42$, $P = 0.016$), regardless of whether the person was novel, or the time of year, however the magnitude of the effect was comparatively small. Sex, aviary location, and trial order did not have an effect (see Table 3.2). A greater percentage of the food was eaten by dominant compared to subordinate birds (GLMM, $n = 928$, Est = -0.13 ± 0.03 , $z = -4.00$, $P < 0.001$), regardless of season or condition. No other covariates influenced food consumption (see Table 3.S2).

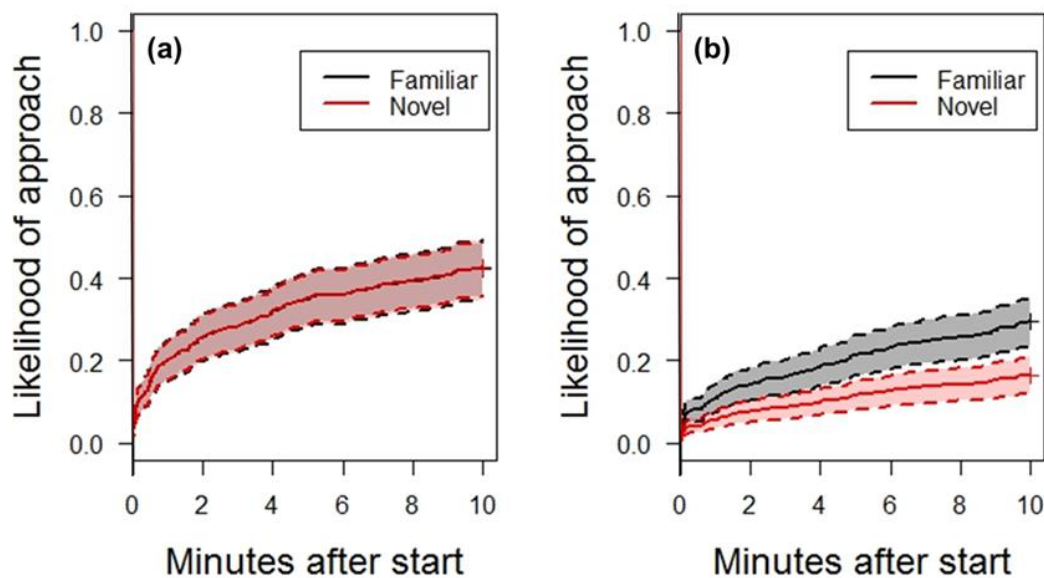


Figure 3.2 Novel and familiar people approach. Inverted survival curves showing the increasing probability that birds approach the experimenter over time, broken down by condition in (a) breeding and (b) non-breeding season. Dotted lines denote confidence intervals.

3.4.2 Behavioural consistency

3.4.2.1 Dominance

The dominance hierarchy was linear during the 2010 breeding season ($h = 0.57$, $h' = 0.61$, $P < 0.001$) as well as in both seasons in 2014 (breeding: $h = 0.32$, $h' = 0.39$, $P < 0.001$,

nonbreeding: $h = 0.47$, $h' = 0.51$, $P < 0.001$). Breeding season ranks between 2010 and 2014 for birds present in both time periods were highly correlated ($r = 0.77$, $CI = 0.45-0.91$, $P < 0.001$). However, the dominance hierarchies between the breeding and non-breeding season of 2014 were not significantly correlated ($r = 0.42$, $CI = -0.10-0.76$, $P = 0.110$).

Table 3.2 Survival models for latency to approach experimenter. Interactions are denoted with * and variable level listed within parentheses, SE, standard error. Effects retained in minimal models are in bold; their values calculated when all non-significant terms were dropped. The highest ranking bird was assigned a dominance of 1.

<u>Variable</u>	<u>B</u>	<u>SE</u>	<u>Z</u>	<u>P</u>
Trial number	-0.004	0.03	-0.13	0.895
Aviary location	-0.144	0.12	-1.22	0.223
Dominance	-0.070	0.01	-5.59	< 0.001
Condition (Novel Person)	-0.655	0.18	-3.54	< 0.001
Season (Breeding)	0.020	0.36	0.06	0.956
Sex (Male)	0.299	0.23	1.31	0.191
Season * Sex	0.554	0.28	1.94	0.052
Condition * Sex	-0.046	0.28	-0.16	0.870
Condition * Dominance	-0.014	0.03	-0.46	0.646
Condition * Season	0.661	0.24	2.75	0.006
Season * Dominance	0.030	0.03	0.96	0.339

3.4.2.2 Novel object tests

Birds were consistent in their tendency to approach the food bowl during the novel object trials within the breeding season ($ICC(1) = 0.28$, 95% Confidence Interval (CI) = 0.16-0.49, $P < 0.001$) and within the non-breeding season ($ICC(1) = 0.15$, $CI = 0.06-0.34$, $P < 0.001$). Birds were also consistent in their tendency to approach during the non-object control trials in breeding season ($ICC(1) = 0.23$, $CI = 0.12-0.442$, $P < 0.001$), but had a very low measure of consistency during non-breeding season ($ICC(1) = 0.06$, $CI = 0.01-0.19$, $P = 0.007$). Individual approach rankings between the breeding and the non-breeding season of 2014 were not consistent for novel object trials ($r = 0.49$, $CI = -0.01-0.79$, $P = 0.105$, see Figure 3A), but were consistent for non-object controls ($r = 0.53$, $CI = 0.05-0.82$, $P = 0.042$, see Figure 3.3B). In contrast, across breeding seasons in different years (2010 vs. 2014) birds' approach ranks were marginally non-significantly correlated during novel object trials

($r = 0.48$, $CI = 0.00-0.78$, $P = 0.053$, see Figure 3.3C), and significantly correlated during controls ($r = 0.50$, $CI = 0.02-0.79$, $P = 0.042$ see Figure 3.3D).

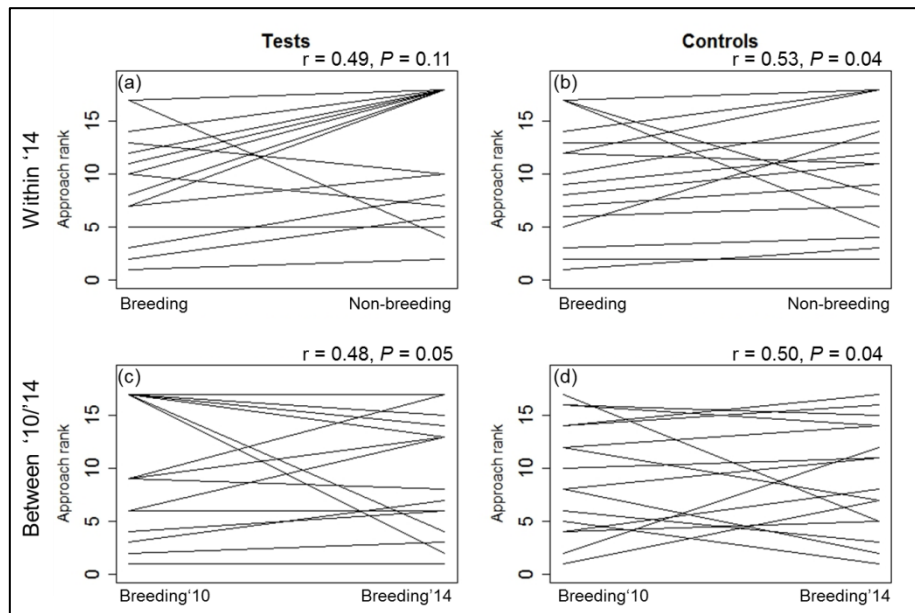


Figure 3.3 Approach rankings across time, and experimental condition. Comparisons of (a) novel object test and (b) non-object control rankings between seasons of 2014 and of (c) test and (d) control between breeding seasons of 2010 vs 2014. Correlations and P values noted. Tied ranks occurred when individuals showed identical approach behaviour over the season.

3.4.2.3 Novel people tests

Birds were consistent in approaching novel experimenters within the breeding season ($ICC(1) = 0.16$, $CI = 0.06-0.36$, $P < 0.001$), but not consistent within the non-breeding season ($ICC(1) = 0.00$, $CI = 0.00-0.07$, $P = 0.533$). Similarly, birds approached consistently during the breeding season in control trials with the familiar experimenter ($ICC(1) = 0.24$, $CI = 0.11-0.46$, $P < 0.001$), but showed very low, but significant levels of consistency within the non-breeding season ($ICC(1) = 0.08$, $CI = 0.01-0.23$, $P = 0.008$). Birds were consistent in their approach rank between seasons during novel conditions ($r = 0.55$, $CI = 0.07-0.82$, $P = 0.028$), but were not consistent during control conditions ($r = 0.42$, $CI = -0.09-0.76$, $P = 0.105$); the opposite pattern to novel object conditions, thereby supporting prediction (3).

3.4.2.4 Correlations between novelty responses

The relationship between responses towards novel objects and novel people changed throughout the year, thus supporting prediction (4). During the breeding season, individuals' ranks on the two novelty responses were correlated ($r = 0.76$, $CI = 0.44-0.91$, $P = 0.001$, see

Figure 3.4A), but outside the breeding season they were not ($r = 0.36$, $CI = -0.13-0.71$, $P = 0.144$; see Figure 3.4B). Meanwhile, birds were consistent in their approach across both types of motivational controls (non-object, and familiar person) during both the breeding season ($r = 0.70$, $CI = 0.32-0.88$, $P = 0.006$, see Figure 3.4C) and the non-breeding season ($r = 0.75$, $CI = 0.43-0.90$, $P < 0.001$, see Figure 3.4D).

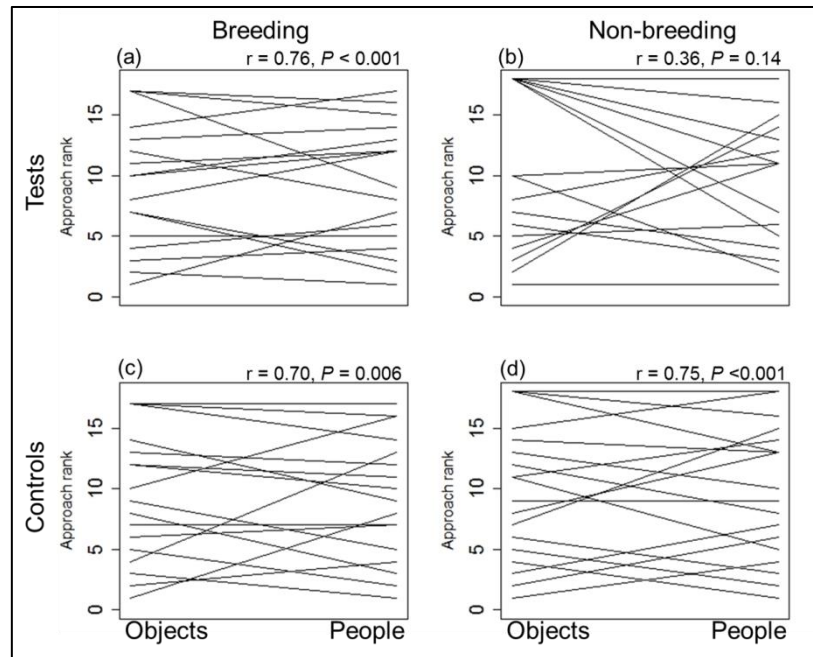


Figure 3.4 Approach rankings within seasons and across types of stimuli. Comparisons of (a) breeding and (b) non-breeding season test rankings, and of (c) breeding and (d) non-breeding season control ranks. Correlations noted, adjusted P-values listed. Tied ranks occurred if individuals approached or did not approach in the same frequencies.

3.5 Discussion

Little is known about the extent to which neophobia levels vary seasonally, and whether or not all individuals respond similarly as environmental conditions change. I investigated seasonal changes in motivation and responses to novelty within a social group of rooks and determined how consistent individuals were across time and contexts. The level and consistency of individuals' risk-taking varied depending on the season, birds' dominance ranks and the type of novel stimuli used. The group was more likely to approach novel people during the breeding season, as expected, but was equally wary of novel objects in both seasons, going against prediction (1). Thus, the breeding season effect on novelty approach depended on the type of stimuli being presented. Additionally, although subordinate birds were more likely to approach a highly contested food bowl around dominants during breeding season, they did not approach novelty more than dominants, allowing for the

rejection of prediction (2). Finally, whether or not all individuals responded similarly to these seasonal changes depended on the type of stimuli; individuals were not consistent between seasons in their novel object approach, but were consistent in their novel people approach, supporting predictions (3) and (4). Overall, the season greatly impacted both the motivation and novelty responses of individuals, but did not always impact them equally.

The differences in motivation and neophobia that I found could stem from several seasonal changes that birds undergo, including: increased hunger, altered responses to predators, and/or stress hormone changes. For example, the increased energetic costs of breeding and maintaining a nest could cause decreases in neophobia because hunger stimulates risk-taking (Damsgard & Dill, 1998). Accordingly, rooks are more likely to take risks while foraging in the wild during the breeding season (Green 1981), and those who take risks are more likely to be in poorer body condition (Patterson, Dunnet, & Goodbody, 1988). Moreover, baseline levels of glucocorticoid (GC) stress hormones are known to be higher during breeding season in a range of bird species (Romero, 2002) and the extent of these changes can vary depending on dominance status (Kotrschal, Hirschenhauser, & Mostl, 1998), or sex (J. C. Wingfield, Smith, & Farner, 1982). I found evidence that subordinate birds were more motivated for food during the breeding season, because they were more willing to compete with dominants, despite the seasonally higher levels of aggression they suffered when approaching the food bowl in object neophobia tests and controls. However, unlike other studies that have found differences in neophobia by dominance status in corvids (Chiarati et al., 2012; Heinrich et al., 1995), subordinate rooks competed equally around dominants regardless of whether it was a novel object or control trial, and therefore any increases in motivation did not translate to increases in novelty approach. Subordinates' greater approach of the food bowl in breeding season did not translate to any differences in food consumption because only 8 worms were available throughout the trial, and these were highly contested regardless of season.

Since increases in the main avian GC hormone corticosterone (CORT) has been linked to reductions in boldness and increases in neophobia in previous studies (Baugh et al., 2013; Richard et al., 2008), it would be expected that hormonal changes would contribute to increases novelty approach. However, the breeding season only promoted higher risk-taking around novel people—when birds were equally quick to approach familiar and novel experimenters. In contrast, season did not have an impact on novel object approach. Hunger levels should have been similar at the beginning of both types of tests because individuals

were consistent when compared across both types of motivational food controls. Therefore the contrasting relationship between seasonal change and stimuli type cannot be attributed solely to hunger or hormone levels. Thus although hunger or hormones may play a role in changing animals' motivations during the season, it is clear that predicting what risks animals are willing to take depends on the context of risk and the type of stimulus under question.

Reactions to novel objects and novel people may involve different cognitive mechanisms, despite sharing a component of novelty (Chapter One). The novelty of an unknown person is conflated by the fact that they are also a potential predator (Frid & Dill, 2002), and birds may be primed to take more risks around predators during the breeding season because they have nests to defend. Therefore the rooks might have also been primed to take more risks around novel people, and this would explain why they treated novel people similarly to familiar people during the breeding season. In contrast, unlike predation pressure that can reliably vary by season (Post & Götmark, 2006), it might be harder to predict the threat of a novel object and therefore object neophobia may not be influenced by seasonal biases in risk-taking. Moreover, if rooks of all dominance ranks share these cognitive biases, it could explain why subordinate and dominant birds did not differ in how they responded seasonally to either type of novelty.

In addition to the seasonal changes to motivation and novelty approach, I also found that individuals' levels of consistency differed across time and context. Birds were consistent within seasons in both novelty responses, but they were only consistent between seasons in their responses towards novel people. Therefore there may be greater constraints on individual plasticity towards stimuli that may resemble predators. Comparing behaviours that do and do not remain consistent offers insight into the costs and benefits of consistency (Carter, Goldizen, et al., 2012; Dall et al., 2004). The lack of consistency in object neophobia cannot be explained by fluctuations in motivation because birds' food motivation ranks remained stable between seasons. Instead perhaps, object neophobia levels respond much more to the social and environmental context than is often suggested in the non-human personality literature where traits such as neophobia or other forms of risk-taking are stable (e.g. Bell et al. 2009). Evidence is accumulating that temporary changes in the environment, such as changes in the recent or current social context, can influence the levels of otherwise stable risk-taking (Jolles et al., 2014; Jolles, Aaron Taylor, & Manica, 2016), and the characteristics of individuals that innovate (Duffield, Wilson, & Thornton, 2015). Therefore inter-individual differences in behaviour are not always maintained over time (Carter,

Goldizen, et al., 2012; Klueen & Brommer, 2013). This would not be the first time that individual consistency in neophobia has been found only during short time periods, and its variability has been deemed a result of individual differences in reaction norms across contexts (Klueen & Brommer, 2013). However, the fact that individual consistency varied in a different manner towards each of the types of novelty, shows that individuals can express contrasting reaction norms for different types of avoidance behaviours. Further examination of the social and environmental influences on these norms and other types of personality traits helps to shape our understanding of the trade-offs and state-dependent nature of stable individual behaviours (Dall & Griffith, 2014).

Overall, the extent of seasonal change and inconsistency I observed in this study implies that caution should be taken when using neophobia as a sole measure of personality across time, and that variation in consistency across seasons should not be dismissed as noise. Critically, these results show that had either season been tested alone, I would have come to entirely different conclusions about the connections between neophobia, risk-taking, and dominance. For example, during the breeding season individual approach ranks towards both types of novel stimuli were correlated, but outside the breeding season they were not. The seasonal difference in correlation between both stimuli types may help explain why some studies have found links between types of neophobia (Bergvall et al., 2011; Verbeek, Drent, Piet, & Wiepkema, 1994), while others have not (e.g. Boogert et al. 2006; Fox et al. 2009). Glossing over such variability risks mis-categorizing traits, and masking the drivers and consequences of novelty avoidance. Instead, neophobia might be better studied with the expectation that individuals will differ in how consistent they are across situations (e.g. Stamps et al. 2012). Therefore although researchers may be able to assess meaningful variation via a neophobia test at a single time-point, over longer periods, such a measure may not reflect maintained differences between individuals.

This study demonstrates that seasonal changes in novelty responses depend on the season, type of novelty, and the social consequences of novelty approach. Continued research into the mechanisms underlying such variation in neophobia is needed considering that novelty avoidance has ecological consequences, and is often used in the personality literature. In particular, studies examining hormonal mechanisms and individual reaction norms could prove useful in disentangling individual variation from seasonal trends. However, it is critical that this variation is assessed in social settings for social animals, rather than on isolated

individuals (Dall & Griffith, 2014). Such efforts will help determine when, where and why we should expect to see stable individual difference in behaviour.

3.6 Supplementary materials

Table 3.S1 Model selection for food consumption in novel object tests and controls.

<u>Number of worms eaten GLMM, n=1303</u>	<u>ΔAIC</u>
No. eaten ~ Condition + Season + Sex + Sex*Condition + Season*Condition+ + Dominance + Dominance*Season + Table_Location + Trial_No. + Dominance*Condition	0.0
No. eaten ~ Condition + Season + Sex + Sex*Condition + Season*Condition+ + Dominance + Dominance*Season + Table_Location + Trial_No.	-2.0
No. eaten ~ Condition + Season + Sex + Sex*Condition + Season*Condition+ + Dominance + Dominance*Season + Table_Location	- 1.9
No. eaten ~ Condition + Season + Sex + Sex*Condition + Season*Condition+ + Dominance + Dominance*Season	- 1.5
No. eaten ~ Condition + Season + Sex + Sex*Condition + Season*Condition+ + Dominance	- 1.3
No. eaten ~ Condition + Season + Sex + Sex*Condition + Season*Condition	- 0.9
No. eaten ~ Condition + Season + Sex + Sex*Condition	- 0.4
No. eaten ~ Condition + Season + Sex	+ 0.7
No. eaten ~ Condition + Season	- 1.5
No. eaten ~ Condition	+ 0.9

Determining what factors influenced the number of worms individuals consumed during novel object tests and their controls. Terms were dropped if their exclusion increased the AIC value by 2.0 or more. The bold model is the final model.

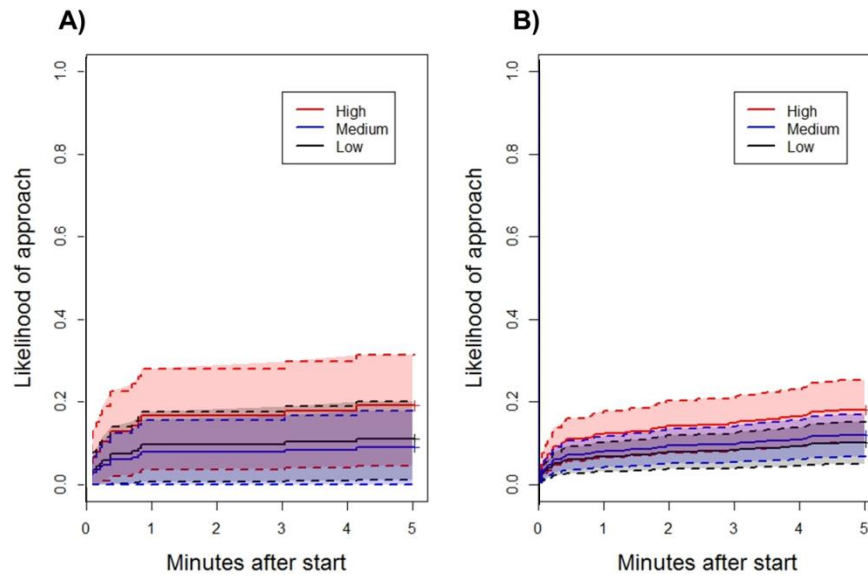


Figure 3.S1 Food bowl approach by dominance in two periods of non-breeding season. Inverted survival curves on the restricted dataset containing birds present in both seasons; likelihood that birds of different dominance rank approach the food bowl in both conditions in the A) Summer of 2014 before two individuals were added and B) Autumn of 2014 after two individuals were added. Dotted lines show confidence intervals. Dominance ranks were grouped evenly into categories of “high”, “medium” and “low” for graphical representation, but were analysed as a continuous variable. Both non-breeding season plots show a similar pattern (with birds of high dominance being more likely to approach), to the non-breeding season panel of Figure 3.1, that included all birds.

Table 3.S2 Model selection on food consumption during novel people tests and controls.

<u>Percentage of available worms eaten GLMM, n=928</u>	<u>ΔAIC</u>
Perct_eaten ~ Dominance + Sex + Condition + Season + Season*Condition + Trial_No. + Dominance*Season + Table_Location + Sex*Condition + Dominance*Condition	0.0
Perct_eaten ~ Dominance + Sex + Condition + Season + Season*Condition + Trial_No. + Dominance*Season + Table_Location + Sex*Condition	-2.0
Perct_eaten ~ Dominance + Sex + Condition + Season + Season*Condition + Trial_No. + Dominance*Season + Table_Location	- 2.0
Perct_eaten ~ Dominance + Sex + Condition + Season + Season*Condition + Trial_No. + Dominance*Season	- 1.9
Perct_eaten ~ Dominance + Sex + Condition + Season + Season*Condition + Trial_No.	- 1.8
Perct_eaten ~ Dominance + Sex + Condition + Season + Season*Condition	- 0.1
Perct_eaten ~ Dominance + Sex + Condition + Season	+ 0.2
Perct_eaten ~ Dominance + Sex + Condition	+ 0.5
Perct_eaten ~ Dominance + Sex	+ 0.2
Perct_eaten ~ Dominance	+ 1.7

Determining what factors influenced the percentage of available food that individuals consumed during novel people tests and their controls. Terms were dropped if their exclusion increased the AIC value by 2.0 or more. The bold model is the final model.

Chapter Four

Variation in stress hormones and reproductive success in wild jackdaws is connected to brood size and provisioning rate, not to neophobia⁵



⁵ A version of this chapter has been submitted for publication in *General and Comparative Endocrinology*: Greggor, A. L., Spencer, K. A., Clayton, N. S., Thornton, A. Variation in hormones and reproductive success in wild jackdaws (*Corvus monedula*) is connected to brood size and provisioning rate, but not to neophobia.

4.1 Abstract

Many species show individual variation in neophobia and stress hormones, but the causes and consequences of this variation in the wild are unclear. Variation in neophobia levels could determine the number of offspring animals produce, and more subtly influence the rearing environment and offspring development. Nutritional deficits during development can elevate levels of stress hormones that trigger long-term effects on learning, memory, and survival. Therefore measuring offspring stress hormone levels, such as corticosterone (CORT), helps determine if parental neophobia impacts the condition and developmental trajectory of young. Being highly neophobic, jackdaws (*Corvus monedula*) are an excellent species for exploring the potential effects of parental neophobia on developing offspring. I investigated if neophobic responses, alongside known drivers of fitness, influence nest success and offspring hormone responses in wild breeding jackdaws. Despite its consistency across the breeding season, and its suggested importance for survival, parental neophobia did not predict nest success, provisioning rates or offspring hormone levels. Instead, sibling competition and poor parental care contributed to the natural variation in stress responses I recorded. Parents with lower provisioning rates fledged fewer chicks, chicks from larger broods had elevated baseline CORT levels, and chicks with later hatching dates showed higher stress-induced CORT levels. Since CORT levels may influence the expression of adult neophobia, variation in juvenile stress responses could explain the development and maintenance of neophobic variation within the adult population.

4.2 Introduction

Neophobia, or the fear of novelty, allows animals to avoid unknown danger, but it may prevent the exploitation of new resources (Greenberg & Mettke-Hofmann, 2001). Individuals who express elevated neophobia may be more likely to survive when predation pressure is high (Ferrari et al., 2015), but they may be at a disadvantage when gathering resources in variable environments, as high neophobia can inhibit behavioural innovation (Benson-Amram & Holekamp, 2012; Greenberg, 2003). Although many species are thought to show consistent individual variation in neophobia (Réale et al., 2007), the consequences of this variation in the wild are poorly understood. Behaviours such as neophobia that can be classified as consistent responses to stressors, are proposed to have important consequences for individual fitness (Dall et al., 2004). Meta-analyses reveal that less fearful, or “bolder” individuals typically have higher reproductive success (Smith & Blumstein, 2008). However,

the majority of evidence for connections between object neophobia and fitness come from studies in which behavioural measures and/or subsequent reproductive success were assessed in captivity (Bremner-Harrison, Prodohl, & Elwood, 2004; Janczak, Pedersen, Rydhmer, & Bakken, 2003; Korhonen, Jauhiainen, & Rekila, 2002; Korhonen, Niemela, & Siirila, 2001; Korhonen & Niemela, 1996). To my knowledge, only one study has found correlations between neophobia and reproductive output in the wild, reporting that neophobic great tits (*Parus major*) had higher occurrences of nest failure than their less fearful conspecifics (Vrublevska et al., 2015). Direct measures of the impact of neophobia in the wild are rare (although see Schuett et al., 2012). Moreover, even if parental neophobia levels do not impact the gross number of offspring produced, they could more subtly influence the rearing environment and the later development of offspring if they prevent the parent from providing adequate or predictable food sources. However, connections between neophobia, foraging ability, and their impact on offspring quality have yet to be tested.

If neophobia levels impact parents' ability to forage for their young, then parental neophobia would be expected to influence measures of developmental stress and offspring quality. Although stress can be caused by numerous factors, such as food deprivation (Pravosudov & Kitaysky, 2006), disrupted maternal care (Banerjee, Arterbery, Fergus, & Adkins-Regan, 2012), and acute stressful events (Jacobson-Pick & Richter-Levin, 2010), elevated stress hormones are a common mechanism by which stress impacts a growing organism (Romero, 2004). One stress hormone, corticosterone (CORT) naturally circulates at a baseline level in the blood, regulating physiological processes such as animals' circadian rhythm. CORT levels also increase dramatically after a stressful event to prime animals for a "fight or flight" response (Romero, 2004; Sapolsky, Romero, & Munck, 2000). Therefore elevated levels of baseline CORT can serve as a marker of ongoing or developmental stress, and exaggerated levels of CORT during stressful events can indicate an individual's magnitude of fear response (Romero, 2004).

Experiencing chronically elevated levels of CORT during development can have long-term effects ranging from impairments in brain structure (Welberg & Seckl, 2001), to reductions in life expectancy (Monaghan, Heidinger, D'Alba, Evans, & Spencer, 2012), and implications for immune function (Kriengwatana, Wada, Macmillan, & MacDougall-Shackleton, 2013). Long term stress can also decrease the sensitivity of glucocorticoid receptors present in the brain (Banerjee et al., 2012; Hodgson et al., 2007) which potentially modifies the negative feedback loops of stress hormone expression (Romero, 2004; Zimmer,

Boogert, & Spencer, 2013), and determines how individuals cope with future stressors. Therefore responses to stress and levels of CORT expression are often considered stable traits (Evans et al., 2006; Jenkins et al., 2014; Kralj-Fišer et al., 2007; although see Ouyang et al., 2011), and have been suggested to drive individual differences in avian temperament (Baugh et al., 2012; Cockrem, 2007; Moretz, Martins, & Robison, 2007). Although many species show individual variation in stress hormone expression (e.g. Cockrem and Silverin, 2002; Grunst et al., 2014), the factors driving this variation differ depending on the species (e.g. food deprivation in western scrub jays, *Aphelocoma californica*, Pravosudov and Kitaysky, 2006; sibling competition in barn swallows, *Hirundo rustica*, Saino et al., 2003). Therefore the drivers of stress hormone variation are not well understood, despite their potentially far-reaching consequences for development and behaviour.

One species that could help disentangle the relationship between neophobia, fitness and offspring rearing environment is the jackdaw (*Corvus monedula*). Like other members of the corvid family, jackdaws are known for having high levels of neophobia in comparison to other species (Chapter Five; Greenberg and Mettke-Hofmann, 2001). Individual variation in neophobia and other forms of wariness have been documented in jackdaws (Chapter Three, Five, Six; Schuett et al., 2012), but the consequences of their comparatively high neophobia are still unclear. Although a previous study on jackdaws found no relationship between a single object neophobia measure and the number of chicks produced in one season (Schuett et al., 2012), it is unclear if the neophobia measure was repeatable within the season. Also, it is unclear whether or not neophobia would have correlated with nest success had feeding rate—the principal driver of variation in jackdaw reproductive success (Henderson and Hart, 1993)—been accounted for. Even if neophobia does not impact the gross number of chicks produced per season, it is unknown whether variation in neophobia more broadly impacts the quality of the rearing environment and the subsequent physiological stress responses of offspring. Such influences are critical to determining the potential costs and benefits of neophobic behaviour because the effects of developmental impairment could occur after chicks fledge.

I examined the connections between parental neophobia levels, provisioning rates, and breeding success in two populations of wild breeding jackdaws. I then looked at a subset of nests to assess whether these factors influenced chicks' baseline and stress-induced CORT expression, when other potential influences on CORT such as brood size (Saino et al., 2003) were considered. I predicted that the impact of individual variation in neophobia would not

be captured by a measure of fledgling number, as has been shown before (Schuett et al., 2012). Instead neophobic variation could influence offspring in other, less direct ways by reducing provisioning rates to an extent that impacts fledgling chicks' body condition or alters baseline circulating CORT and juveniles' propensity to mount a stress-induced hormone response. Therefore even if parents' neophobia does not directly impact chicks' survival in the nest, it could have other long-term impacts on offspring development that would explain selection for or against neophobic behaviour.

4.3 Methods

4.3.1 Study sites

The two study sites were situated in the UK: one in Madingley Village, Cambridgeshire, and the other in areas surrounding Penryn, Cornwall. During the breeding season of 2013 68 and 14 jackdaw nest boxes were tested on neophobia, from each site, respectively, and measured CORT levels in 58 chicks from 34 boxes in the Cambridgeshire site. Boxes are clustered into colonies within each study site (see Chapter Two).

Both sites were monitored throughout the breeding season. Laying and hatch dates were determined by daily nest checks. Since jackdaw nests hatch asynchronously, nests continued to be checked daily until all eggs hatched or until several days had lapsed with no new chicks emerging. After all viable eggs hatched, boxes were monitored at least three times a week through to fledging to provide information on nestling mortality and nest failure. All nest disturbances were conducted under a Natural England License (20130067 to A.L.G.), blood sampling under Home Office permits (PIL 70/24971 to A.L.G, PPL to A.T. 80/2371) and ringing under British Trust for Ornithology license (no. C6079, C5752, C5746).

4.3.2 Experimental protocol and blood sampling

Identical neophobia tests were run at both sites. Three novel objects were constructed out of bright, man-made materials, without elements that resembled eyes, or an animal shape (see Figure 4.S1). Exact replicas of each object were constructed to allow for concurrent testing across sites. Each nest box was tested with two objects over the course of the study. No box received the same object more than once. Each object contained the same large clip to attach it to the nest-box's platform via an extendable pole while minimizing disturbance (see Figure 4.S2). Each box was tested twice, an improvement over a previous jackdaw study in which it was only measured once (e.g. Schuett et al., 2012). Boxes were tested once during

the first half (6.17 ± 0.22 days since hatching) and once during the second half of hatchling development (20.22 ± 0.36 days since hatching), each time paired with a control trial that occurred either the prior or following day. Tests involved setting up the video camera, presenting the object at the hole of the box to ensure the female left the box, placing the object onto the platform with the extendable pole, and leaving the vicinity of the nest site. Control trials were set up identically to tests, except that no object was placed on the pole when I made the same motions at the box that occurred during a test to ensure the female left the box. The order of control vs. test trials, and the specific object used were determined using a random number generator prior to the beginning of the study. No two boxes in the same cluster of boxes were tested concurrently. Each trial lasted 90 minutes and was video recorded from a camouflaged tripod.

Blood sampling of all chicks in each box took place in conjunction with nestling ringing on the 25th day of life of each box's oldest chick. Boxes were approached quietly to avoid disturbing the chicks ahead of sampling. All sampling was conducted at least 2 hours after sunrise, and 2 hours before sunset. Baseline samples (100ul) for all chicks within the nest were collected within or as close to three minutes as possible (Romero & Reed, 2005) of the ladder touching the tree of the nest box (mean 2.34 ± 0.59 minutes). Stress-induced samples were collected for each individual 10 minutes after their baseline sampling time. Sample collection times were noted to the nearest second. Between samples, chicks' wing and tarsus length were measured using callipers (to the nearest 0.1mm) and weight was recorded (to the nearest 0.1g using an electronic balance). The chicks were returned to their nest after they had been processed. The blood was immediately put on ice, and spun in a centrifuge within 3 hours of collection. The plasma was separated from the rest of the blood sample and frozen at -80C until it was analysed. The remaining red blood cells were diluted with 1ml of ethanol and used for molecular sexing analysis with PCR.

CORT hormone concentrations were determined from plasma samples through direct radio-immunoassay (see Spencer et al., 2009). Aliquots of jackdaw plasma (20ul) and three sets of standard chicken plasma with known CORT concentration were combined with 25ul of radiolabelled CORT and left to rest for 1hr. The samples were extracted with 1ml ether, and reconstituted with 300ul assay buffer. Samples were then divided to be run in duplicates, combined with primary antibody AB-ine880 (sourced from Antibodies Online), with an extra 100ul of radiolabelled CORT, and left in the refrigerator overnight. A dextran coated charcoal suspension was then added to the mixture and the mixture centrifuged. The

remaining supernatant was analysed in a gamma counter. Their values were compared to a standard curve, prepared through a serial dilution of known CORT values. Calculations of hormone concentrations were corrected for variation in initial aliquot volume and individual recoveries. Samples were run between three assays, and samples from siblings and the clusters of nest boxes were randomized across assays. Individuals' baseline and stress-induced measures were always run in the same assay. As the chicken plasma used for validating sample measures ended up being highly variable, potentially due to issues with plasma quality, intra (5.0%, 5.2%, 2.3%) and inter-assay (21.4%) variation was calculated by comparing three random points along the standard curve. The estimated detection limit was 0.08 ng/ml.

4.3.3 Behavioural data

Neophobia was measured from video recordings, and defined as the time elapsed from the beginning of the trial to when the first bird entered the nest (e.g. Schuett et al., 2012). The initial entrance time was similarly noted for control trials, as was the number of entrances that occurred during the remainder of the 90 min control trial. Neophobia and control scores were determined by averaging both tests or both control entrance times, or by the single time if the nest failed before the second test was conducted. Feeding rate was determined based on the number of additional entrances during control trials, divided by the minutes from the first entrance to the end of the trial. Each of these measures capture behaviour at the level of the pair because individuals could not always be identified (as was done in Shephard et al., 2014). Testing at the pair, as opposed to individual level is justified, given that both parents care for the nestlings (Röell, 1978), and both must provide adequate food in order for nestlings to survive (Henderson & Hart, 1993). Therefore any impacts to fitness would be visible at the level of the pair.

A subset (16%) of trials were video coded by two people, and intercoder reliability was deemed to be excellent ($ICC(1) = 0.959$, $P < 0.001$).

We quantified breeding success in two ways: (1) the proportion of hatchlings that fledged in each nest, and (2) for nests that fledged chicks, I analysed the average body condition of chicks within the brood at ringing. Body condition was calculated based on chicks' residual deviation from the nestling population's regression of weight against tarsus (e.g. Verhulst and Salomons, 2004), such that birds with a larger body weight than expected by their tarsus length were judged to be in relatively good condition. Chicks' condition was

compared only to others within its nest site, such that the quality of the Madingley and Cornish chick were calculated separately. The proportion of hatchlings that survive and chick quality reflect the success of the pair's foraging and nest defence efforts instead of their fertility. Also, since jackdaws have close to zero extra pair copulations (Henderson et al., 2000; Liebers & Peter, 1998) the chicks were assumed to belong to both parents.

4.3.4 Statistical Analysis

I determined how consistent boxes were in their neophobia test entrance time, control entrance time, and provisioning rate across the two sampling periods with an Intra-Class Correlation (ICC) analysis (Nakagawa & Schielzeth, 2010). To assess whether or not control entrance times were related to object test entrances, I ran a Pearson's product moment correlation test on the mean control and mean neophobia test times. In addition, I used a Cox proportional hazards regression model to determine what factors influenced birds' nest entrance times during the tests and controls. This survival analysis examined the extent to which experimental condition, provisioning rate, test number (first or second test), order of conditions, time of day, age of oldest chick, hatch date, and all biologically meaningful interactions between these terms predicted entrance times. Each nest's hatch date was defined in reference to the number of days since the first egg hatched within the population. Observations were clustered around box and around box colony to account for the non-independence of observations.

I constructed models to assess the factors that contributed to each of the two measures of nest success (i.e. proportion of surviving chicks, and average nestling body condition), and the factors that influenced each hormone measure (i.e. baseline and stress-induced). All models used the lme4 package (Bates et al., 2013) in R (R Core Team, 2015). The proportion of surviving chicks (no. fledged/no. hatched) was analysed with a Generalized Linear Mixed Model (GLMM) that had a binomial error structure and a logit link function. The mean body condition of chicks per nest was analysed with a Linear Mixed Model (LMM). Both of these nest success models investigated the influence of hatch date, neophobia score, mean control latency, and provisioning rate, taking box colony into account as a random effect. The model on average nestling body condition also included the brood size as a fixed effect. Hormone concentrations were log-transformed to create normal distributions before being analysed with LMMs. Baseline hormone analyses assessed the impact of brood size, hatch date, provisioning rate, sex, weight in relation to siblings, and mean neophobia scores, controlling for the time of day, exact time of sampling from initial

disturbance, body condition, and assigning nest box and nest box group as random effects. Stress-induced analyses contained the same set of variables, but also included baseline level as a covariate. All models were simplified through backwards stepwise elimination, based on changes in AIC values. Effects were retained if their exclusion increased AIC values by 2 or more. Once the final model was established, P-values and effect sizes were calculated to be included in the text.

4.4 Results

4.4.1 Population nest success

Within the Madingley site, 53 of the 118 boxes successfully fledged young, (1.94 ± 0.63 fledglings per nest), out of the 72 that hatched chicks. Of the nineteen nests that failed during the 2013 season, 15 were tested for parental neophobia at least once prior to failure. In Cornwall, 17 of the 37 viable nests failed, 3 of which were tested once before failure, one of which was tested twice before failing (see Appendix Three for comparisons of nest success between sites).

4.4.2 Individual consistency

Pairs were consistent in their entrance times during object test conditions ($n = 54$, $ICC(1) = 0.581$, $P < 0.001$, $CI = 0.38-0.74$). Although this effect was strongly biased by the birds that did not return in either neophobia test—because removing them eliminated the effect of consistency ($n = 39$, $ICC(1) = 0.187$, $P = 0.122$, $CI = -0.13-0.47$)—the fact that all birds returned for at least one of their two control trials indicates these non-returners were consistent in being particularly fearful of the object. In contrast, birds' entrance times were not consistent during control conditions ($n = 59$, $ICC(1) = 0.192$, $P = 0.07$, $CI = -0.06-0.43$), even though nest provisioning rate was consistent within pairs ($n = 57$, $ICC(1) = 0.368$, $P = 0.002$, $CI = 0.12-0.57$). Additionally, the mean control and mean object test entrance times were correlated within nests ($t = 2.84$, $df = 77$, $r = 0.308$, $CI = 0.09-0.50$, $P = 0.005$), even when the boxes that did not return within 90 minutes were excluded ($t = 2.67$, $df = 45$, $CI = 0.09-0.60$, $p = 0.011$).

4.4.3 Entrance times during experiments

Birds were slower to enter their nests when a novel object was present (Cox proportional hazards regression, $n = 274$ observations, 209 events, $B = -1.76 \pm 0.16$, $z = -11.48$, $P < 0.001$; see Figure 4.1) and birds with later hatch dates were slower to return to their nests, regardless of experimental condition ($B = -0.08 \pm 0.03$, $z = -2.50$, $P = 0.012$) as there was no significant condition, hatch day effect. Additionally, birds with lower feeding rates took longer to return to their nest ($B = -0.07 \pm 0.02$, $z = 2.87$, $P = 0.004$), but this effect was not specific to neophobia tests or control trials since there was no interaction between feeding rate and experimental condition. Also, Madingley birds were slower to return to their nests than Cornish birds, regardless of experimental condition ($B = -0.42 \pm 0.18$, $z = -2.13$, $P = 0.033$).

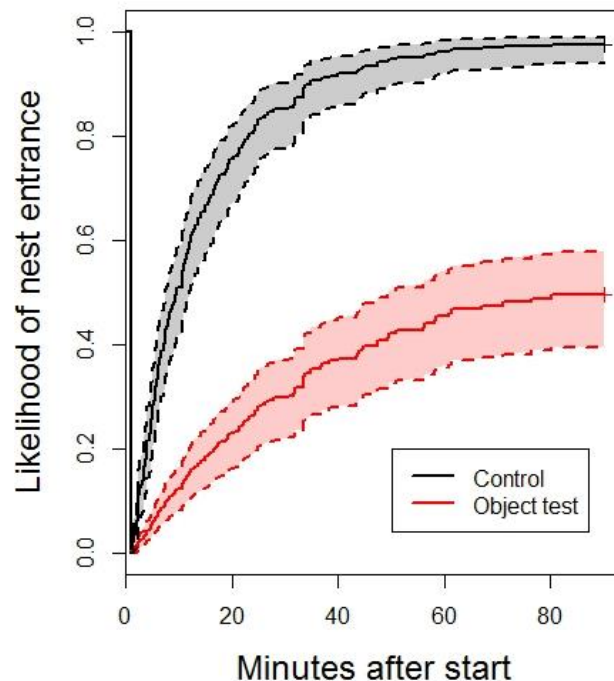


Figure 4.1 Likelihood of entering the nest. Inverted survival curves showing the likelihood over time that birds return to their nest boxes from the beginning of the trial. Dotted lines show confidence intervals.

4.4.4 Individual nest success

Parents who had higher provisioning rates raised a greater proportion of their hatching young to fledging age (GLMM, $n = 82$ nests, $\text{Est} = 0.10 \pm 0.04$, $z = 2.68$, $P = 0.007$; see Supplementary Table 4.S1). Although larger broods had chicks that were of lesser quality on average (LMM, $n = 63$, $\text{Est} = -10.89 \pm 5.04$, $z = -2.16$, $P = 0.031$), none of the other variables I

measured, including parental neophobia scores, predicted the average body condition of chicks (Table 4.S2).

4.4.5 Hormone levels

Baseline CORT values were higher for chicks with a greater number of siblings on ringing day (LMM, $n = 57$, $\text{Est} = 0.392 \pm 0.15$, $z = 2.63$, $P = 0.009$; see Figure 4.2, Table 4.S3), but body condition, sex, parents' neophobia score, and all other explanatory factors tested did not have an impact. Although baseline concentrations influenced individuals' stress-induced levels of CORT (LMM, $n = 55$, $\text{Est} = 0.062 \pm 0.02$, $z = 2.70$, $P = 0.007$) stress-induced values were not influenced by brood size. Instead, stress-induced levels were higher in chicks whose nest started later in the season ($\text{Est.} = 0.092 \pm 0.04$, $z = 2.122$, $P = 0.034$; see Figure 4.3, Table 4.S4).

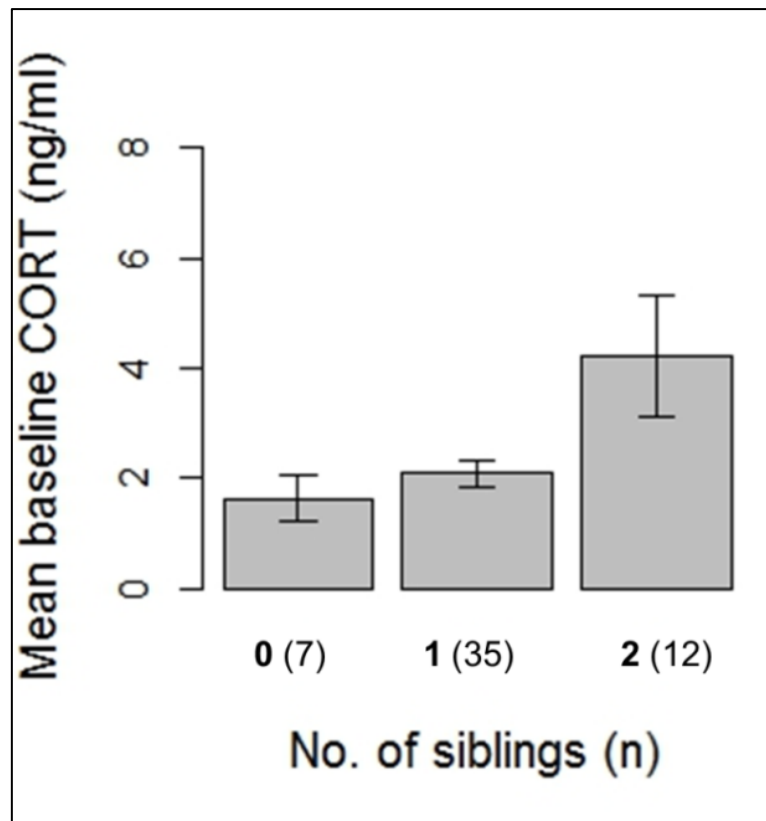


Figure 4.2 Baseline CORT by brood size. Means of raw baseline CORT levels for chicks within nests that have zero, one or two siblings present at the time of sampling. Error bars represent standard errors (SE's) and numbers in parentheses indicate the number of individuals sampled from each brood size.

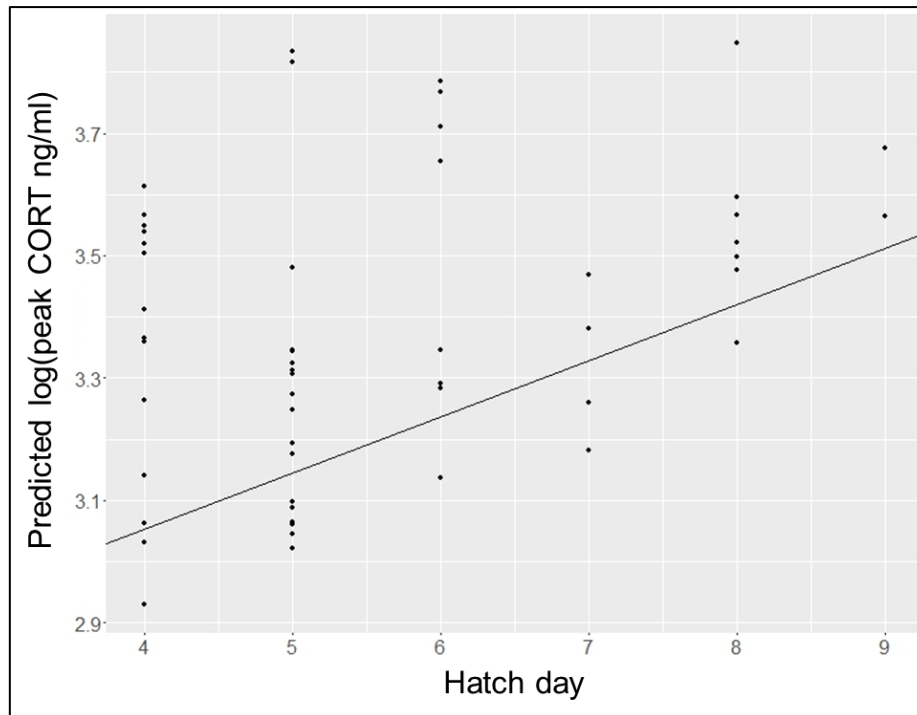


Figure 4.3 Predicted stress-induced CORT by hatch day. Predicted values were based on the output of an LMM, with stress-induced CORT on the logarithmic scale. Est. = 0.092 ± 0.04 , $z = 2.122$, $P = 0.034$

4.5 Discussion

Contrary to my predictions that parental neophobia levels would impact provisioning rates and the levels of developmental stress offspring experience, I did not find correlations between neophobia, feeding rate, or offspring hormone levels. Although parents' provisioning rate was the main predictor of chicks' survival, thereby confirming previous studies (Henderson & Hart, 1993), provisioning rate was not correlated with parental neophobia scores, nor directly related to chicks' body condition. However, certain aspects of the rearing environment did have important influences on chicks' stress hormone levels. For example, nests with larger broods had higher baseline CORT levels (Saino et al., 2003), and later hatching nests showed an exaggerated CORT response to handling stress, irrespective of chicks' body condition. Since parents from later hatching nests also were slower to return in both experimental conditions, such a response may indicate that either these parents were more sensitive to nest disturbance, independent of novelty responses, or that they spent less time at their nests generally. Overall, the results reveal the importance of sibling competition and hatching date in contributing to natural variation in stress responses, but suggest that parents' neophobia has no detectable influence on their reproductive success. Figure 4.4

provides a graphical illustration of the relationships between parental traits, rearing environments and offspring traits.

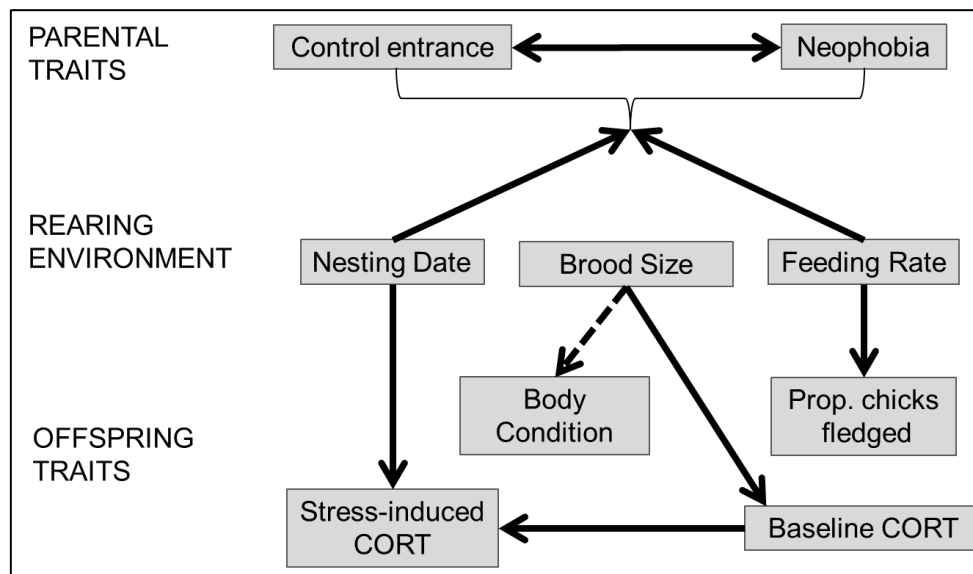


Figure 4.4 Summary of results. All boxes connected by arrows were statistically linked. Arrow type indicates the direction of the relationship: solid lines are positively correlated, dashed lines are negatively correlated. Boxes without arrows were not significantly related. Arrow direction does not imply causality, but the arrows point to the response variable in the analysis. Control entrance is the time at which birds entered their nests during controls, neophobia is the same measure during object neophobia trials.

Although parents' neophobia scores did not correlate with either the number or condition of their chicks, the scores themselves cannot be dismissed as noise. Neophobia scores and provisioning rate measures were consistent across the season, with similar repeatability to that reported in studies on other species that have presented novel objects at nest boxes (Cole & Quinn, 2014). Given that individual variation across cognitive responses and traits may have important effects on fitness (Thornton & Lukas, 2012), one might expect this variation to have impacts on reproductive success. However, I found no impact of neophobia on either the percentage of hatching chicks that fledged per nest (similar to what has been shown before Schuett et al., 2012), or the body condition of chicks. Given that jackdaws are known to be more neophobic than other passerine species, such as great tits (Chapter Five), it may seem puzzling at first that I found no obvious costs or benefits to this distinctive trait.

Neophobia levels are suggested to impact fitness by increasing wariness and thus survival alongside predators and by helping with foraging among potentially dangerous resources (e.g. the dangerous niche hypothesis, Greenberg, 2003). This hypothesis relies on

there being a high prevalence of predators, or poisonous prey. However, the same environmental conditions may impact the optimal level of neophobia differently depending on animals' life stage. For instance, high neophobia increases survival in juvenile, predator naïve reef fish (Ferrari et al., 2015). Meanwhile higher parental neophobia is correlated with lower nest survival in great tits, supposedly because more neophobic individuals were less likely to challenge predators and defend their nests (Vrublevska et al., 2015). In this way, the same level of neophobia could have different costs and benefits depending on the life stage and the dangers of the environment, such that neophobia might be beneficial for juveniles who can flee predators but costly for adults when fleeing predators leaves their nests defenceless. Potentially, therefore, neophobia could impact jackdaw survival at a different life stage or time of year than what my breeding success measures capture.

One reason why neophobia did not impact reproductive success is because neophobia levels were not connected to pairs' combined provisioning rate. Since neophobic behaviour involves the psychological appraisal of novelty (Chapter One), neophobia would only aid in acquiring variable food if variability involved novel, not just patchy resources, or if food were often found near novel objects. Therefore reactions towards a novel object in a foraging context might be more relevant for fitness consequences than reactions in a nesting context. While object neophobia is generally repeatable when tested in the same context and time of year (Chapter Three; Jolles et al., 2013), the consistency of individuals in the wild toward object neophobia tests in different contexts is rarely studied. Moreover, very little is known about how individual variation in object neophobia impacts natural feeding choices in the wild. Since I was unable to measure the extent to which single parents contributed towards the neophobia score and overall provisioning rate, it is possible that partners could compensate if one member of the pair was particularly neophobic, and therefore mask pair-level connections between neophobia and provisioning. However, as the reproductive output that we measured stemmed from pair-level success, the birds' combined effort, and hence their combined neophobia, would have the greatest bearing on fitness.

Regardless of whether compensation was occurring, overall feeding rate did not predict either baseline or stress-induced CORT levels. This null result is surprising because nutritional deficits have been shown to impact CORT hormone levels in other corvids (Pravosudov & Kitaysky, 2006). Since higher feeding rates were associated with increased brood size (see Figure 4.4), and increased brood size predicted elevated baseline CORT levels, the way food was allocated within the nest may explain why feeding rate did not

impact CORT. The predictability of a food source, not just the total amount of food available can influence CORT expression (Buchanan, Spencer, Goldsmith, & Catchpole, 2003). Having more siblings could decrease the predictability with which any one individual was fed. This effect seemed to impact all chicks within the brood similarly because I found no direct connection between baseline or stress-induced hormone levels and nestling body condition. An independence between baseline hormone levels and body condition contrasts with findings from studies of other birds (Müller, Jenni-Eiermann, & Jenni, 2010; Rensel, Wilcoxon, & Schoech, 2011).

Since elevated baseline CORT encourages chicks to beg more often, such long term increases may act as an adaptive response to sibling competition, despite the costs that these hormones incur, such as later impacts on spatial memory (Kitaysky, Kitaishkaia, Piatt, & Wingfield, 2003) and immune responses (Loiseau, Sorci, Dano, & Chastel, 2008). Although higher levels of baseline CORT have been documented in experimentally enlarged clutches in other species (Saino et al., 2003) not all studies with brood manipulations or natural brood variation have found such an effect (Bize, Stocker, Jenni-Eiermann, Gasparini, & Roulin, 2010; Brewer, O'Reilly, & Buck, 2010; Müller et al., 2010). These differences between species in the effect of brood size on CORT cannot be explained by differences in hatching asynchrony. Even though it is unclear why larger broods of jackdaws have higher baseline CORT when other species may not, there are likely to be long-term effects of such sibling competition on individuals from larger broods.

Rearing conditions also influenced chicks' stress-induced hormone levels, as later hatching nests had higher stress-induced CORT values. There are two potential explanations for this effect, namely that late season chicks may have had worse parents that were prone to higher fear reactivity, or may have experienced a different surrounding environment than early breeders. I found that parents from later season nests were slower to return in both control and object test conditions, which could mean that later season parents were more sensitive to disturbances such as a trial setup, or that they generally visited less often. Although nests that were slower to return in test and control conditions were also more likely to have lower provisioning rates, provisioning rate itself did not directly predict stress-induced hormone levels. Instead, later season jackdaws' reluctance to return to the nest might have been indicative of lower levels of nest attendance. Reductions in nest attendance have been shown to alter stress hormone physiology in Florida scrub-jays (*Aphelocoma coerulescens*), which has been suggested to be the result of the social stress of separation

from the mother (Rensel, Wilcoxon, & Schoech, 2010). Therefore the parenting of late breeders' might be to blame for the increases in stress-induced CORT I found.

Alternatively, the hormonal difference might not be due to the characteristics of late breeding parents, but to some type of external stress that impacts late nests disproportionately. Overall, later breeding individuals in many species produce smaller or poorer quality clutches (e.g. Hochachka, 1990; Winkler and Allen, 1996), but whether their poor performance is a result of individual quality is unclear because timing and quality are often intertwined (Verhulst & Nilsson, 2008). Although later nests fledged a similar number and quality of chicks, their elevated stress-induced hormone levels could indicate that late hatching individuals might be on a different developmental trajectory that predisposes them to be more responsive to acute stressors.

Although I found no impact of parental neophobia on offspring CORT levels, the variation in baseline and stress-induced CORT that I detected among nestlings could potentially contribute to downstream variation in adult stress responses. Since elevated levels of CORT during development may modify the negative feedback loops of stress hormone expression (Romero, 2004; Zimmer et al., 2013), the impact of sibling competition and later hatch date may determine how individuals cope with future stressors. Moreover, since the expression of neophobia and CORT are thought to be linked within individuals (Bebus, Jones, Elderbrock, Small, & Schoech, 2015), and there is evidence that experimentally administering CORT during development increases neophobia later in life, at least in males, (Spencer & Verhulst, 2007), differences in the rearing environment might also contribute to adult variation in neophobia. Testing whether or not, for example, chicks in larger broods show differing levels of neophobia as adults could help determine the long term consequences of early life stress and help explain why there is variation in neophobia without clear fitness consequences.

Investigating the development of individual differences in stress physiology helps explain some of the variation in cognitive traits, and stress responses seen in the wild. Neophobia, provisioning rates and CORT were not connected in this study. If this disconnect is true for a number of species, then perhaps we need to re-examine under what ecological conditions neophobia should be favoured. Future research needs to determine whether neophobia is not predictive of the quality of rearing environment across a greater diversity of environmental conditions when food is scarce and innovation could be helpful. Also,

assessing the fitness consequences of neophobia at other times of year could help inform where neophobia might benefit individuals. Without such assessments the ecological consequences of individual variation in traits such as neophobia will remain elusive.

4.6 Supplementary materials

Figure 4.S1 Objects used on nest boxes.

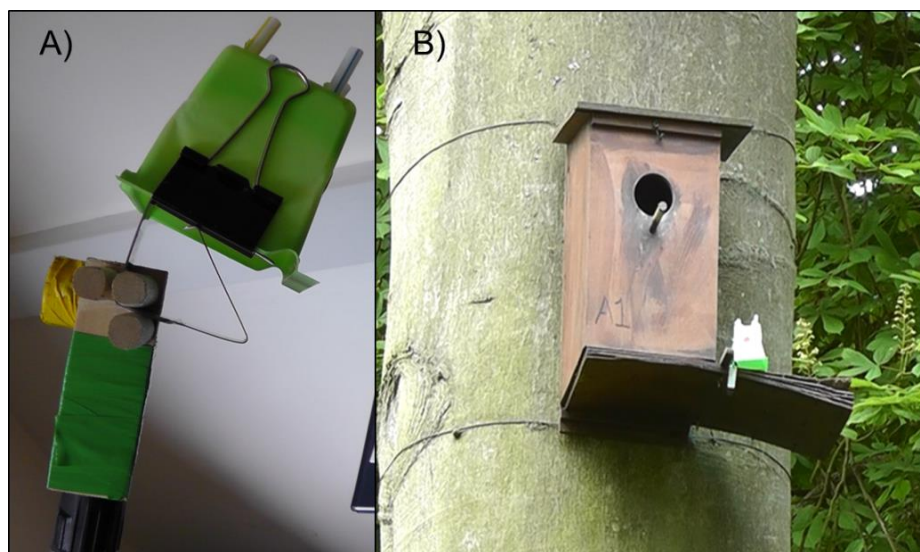
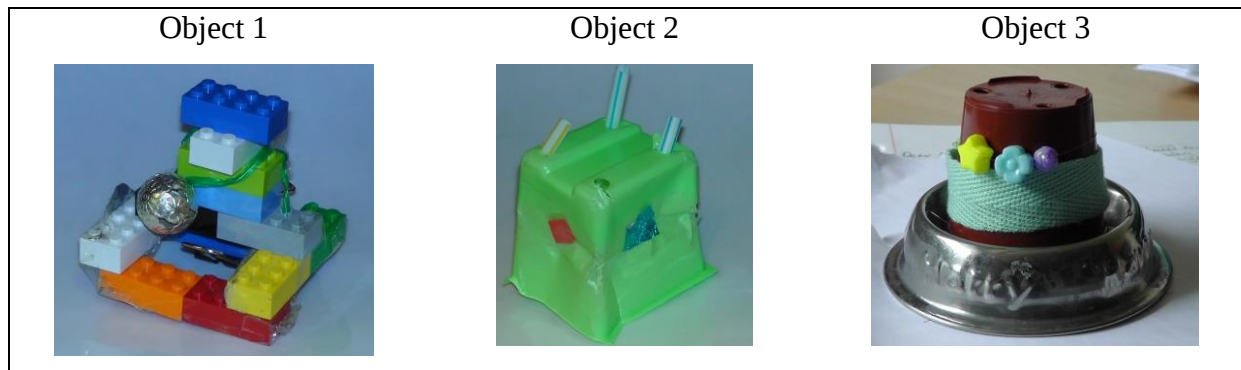


Figure 4.S2 Experimental setup. An extendable pole with an attachment (A) was used to place objects on box platforms (B).

Table 4.S1 Factors impacting proportion of chicks fledged. Box colony was included as a random effect. Terms were dropped if their exclusion increased the AIC value by less than two. The bold model is the minimal model.

<u>Proportion of chicks surviving GLMM, n=68</u>	<u>ΔAIC</u>
Num_fledge/Num_hatch~ Feed_Rate+ Control + Hatch_day + Test + + Feed_Rate:Hatch_day + Test:Hatch_day	0.0
Num_fledge/Num_hatch~ Feed_Rate+ Control + Hatch_day + Test + + Feed_Rate:Hatch_day	- 0.6
Num_fledge/Num_hatch~ Feed_Rate+ Control + Hatch_day + Test	- 1.1
Num_fledge/Num_hatch~ Feed_Rate+ Control + Hatch_day	- 1.7
Num_fledge/Num_hatch~ Feed_Rate + Control	- 1.0
Num_fledge/Num_hatch~ Feed_Rate	- 0.0
Num_fledge/Num_hatch~ 1	+ 3.0

Table 4.S2. Factors impacting mean body condition of fledging chicks per nest.

Individual body condition was determined based on their deviation from the regression of weight against tarsus. Box colony was included as a random effect. Terms were dropped if their exclusion increased the AIC value by less than two. The bold model is the minimal model.

<u>Mean body condition of nest GLMM, n=53</u>	<u>ΔAIC</u>
Condition~ Num_fledge + Test +Feed_Rate + Num_fledge:Feed_Rate + Hatch_day + Test:Hatch_day + Control	0.0
Condition~ Num_fledge + Test +Feed_Rate + Num_fledge:Feed_Rate + Hatch_day + Test:Hatch_day	- 1.8
Condition~ Num_fledge + Test +Feed_Rate + Num_fledge:Feed_Rate + Hatch_day	- 1.2
Condition~ Num_fledge + Test +Feed_Rate + Num_fledge:Feed_Rate	- 1.3
Condition~ Num_fledge + Test +Feed_Rate	+ 0.9
Condition~ Num_fledge + Test	- 1.5
Condition~ Num_fledge	- 0.6
Condition~ 1	+ 2.0

Table 4.S3 Factors influencing baseline CORT levels. Box colony and box ID were included as random effects. Interactions are denoted with a “:”. The bold model is the minimal model.

<u>LMM, n=57</u>	<u>ΔAIC</u>
log(Baseline)~ Brood_size + Blood_sample_time + Chick_quality + Brood_size:Chick_quality + Hatch_day + Feed_rate + Neophobia_score + Time_of_day + Sex + Comparative_weight + Control_score	0.0
log(Baseline)~ Brood_size + Blood_sample_time + Chick_quality + Brood_size:Chick_quality + Hatch_day + Feed_rate + Neophobia_score + Time_of_day + Sex + Comparative_weight	- 2.0
log(Baseline)~ Brood_size + Blood_sample_time + Chick_quality + Brood_size:Chick_quality + Hatch_day + Feed_rate + Neophobia_score + Time_of_day + Sex	- 2.0
log(Baseline)~ Brood_size + Blood_sample_time + Chick_quality + Brood_size:Chick_quality + Hatch_day + Feed_rate + Neophobia_score + Time_of_day	- 1.9
log(Baseline)~ Brood_size + Blood_sample_time + Chick_quality + Brood_size:Chick_quality + Hatch_day + Feed_rate + Neophobia_score	- 1.9
log(Baseline)~ Brood_size + Blood_sample_time + Chick_quality + Brood_size:Chick_quality + Hatch_day + Feed_rate	- 1.6
log(Baseline)~ Brood_size + Blood_sample_time + Chick_quality + Brood_size:Chick_quality + Hatch_day	- 1.8
log(Baseline)~ Brood_size + Blood_sample_time + Chick_quality + Brood_size:Chick_quality	- 0.7
log(Baseline)~ Brood_size + Blood_sample_time + Chick_quality	- 0.1
log(Baseline)~ Brood_size + Blood_sample_time	- 1.8
log(Baseline)~ Brood_size	- 1.0
log(Baseline)~ 1	+ 4.7

Table 4.S4 Factors influencing peak CORT levels. Box colony and box ID were included as random effects. Interactions are denoted with a “:”. The bold model is the minimal model.

<u>LMM, n=56</u>	<u>ΔAIC</u>
log(Peak)~ Baseline + Hatch_day + Feed_rate + Control_score + Neophobia_score + Chick_quality + Comparative_weight + Time_of_day + Brood_size + Sex + Blood_sample_time	0.0
log(Peak)~ Baseline + Hatch_day + Feed_rate + Control_score + Neophobia_score + Chick_quality + Comparative_weight + Time_of_day + Brood_size + Sex	- 2.0
log(Peak)~ Baseline + Hatch_day + Feed_rate + Control_score + Neophobia_score + Chick_quality + Comparative_weight + Time_of_day + Brood_size	- 2.0
log(Peak)~ Baseline + Hatch_day + Feed_rate + Control_score + Neophobia_score + Chick_quality + Comparative_weight + Time_of_day	- 1.3
log(Peak)~ Baseline + Hatch_day + Feed_rate + Control_score + Neophobia_score + Chick_quality + Comparative_weight	- 1.6
log(Peak)~ Baseline + Hatch_day + Feed_rate + Control_score + Neophobia_score + Chick_quality	- 0.3
log(Peak)~ Baseline + Hatch_day + Feed_rate + Control_score + Neophobia_score +	- 2.0
log(Peak)~ Baseline + Hatch_day + Feed_rate + Control_score	- 0.1
log(Peak)~ Baseline + Hatch_day + Feed_rate	- 1.4
log(Peak)~ Baseline + Hatch_day	- 0.4
log(Peak)~ Baseline	+ 2.5

Chapter Five

Faster approach towards litter in urban areas by highly neophobic corvids and less fearful birds⁶



⁶ A version of this chapter has been published as: Greggor, A. L., Clayton, N. S., Fulford, A., & Thornton, A. (2016). Street smart: faster approach towards litter in urban areas by highly neophobic corvids and less fearful birds. *Animal Behaviour*, 117, 123-133.

5.1 Abstract

The extent to which animals respond fearfully to novel stimuli may critically influence their ability to survive alongside humans. However, it is unclear whether the fear of novel objects, object neophobia, consistently varies in response to human disturbance. Where variation has been documented, it is unclear whether this variation is due to a change in fear towards specific novel stimuli, or whether it is symptomatic of a general change in fear behaviour. I measured levels of object neophobia in free-flying birds across urban and rural habitats, comparing corvids—a family known for being behaviourally flexible and innovative—with other urban adapting bird species. Neophobic responses were measured in the presence of different types of objects that varied in their novelty, and were compared to behaviour during a baited control. Corvids were more neophobic than non-corvid species towards all object types, but their hesitancy abated after conspecifics approached in experimental conditions where objects resembled items they may have experienced previously. Both sets of species were faster to approach objects made from human litter in urban than rural areas, potentially reflecting a category-specific reduction in fear based on experience. These results highlight species similarities in behavioural responses to human-dominated environments despite large differences in baseline neophobia.

5.2 Introduction

Animals' responses to novel stimuli may influence their survival as humans drastically alter habitats (Robertson, Rehage, & Sih, 2013). The extent to which animals respond fearfully to novelty (i.e. demonstrate neophobia) may help or hinder their success, depending on the dangers and benefits associated with novelty. For example, high levels of object neophobia may help animals avoid danger should the objects harbour predators or toxins, but reduced neophobia allows animals to approach and exploit potentially advantageous novel resources (Greenberg & Mettke-Hofmann, 2001). Since human-dominated habitats offer combinations of food, dangers, and habitat types that differ substantially from less undisturbed environments, examining how animals respond behaviourally to novelty is important in understanding how they adjust to man-made changes in the environment (Chapter Seven).

Urban areas exert strong selection pressures that often reduce species richness for vertebrate and invertebrate groups (McKinney, 2008). Although some bird species thrive in urban areas, no single defining trait predicts a species' urban presence (Croci, Butet, &

Clergeau, 2008; Kark, Iwaniuk, Schalmitzek, & Banker, 2007; Anders Pape Møller, 2014; Shochat, Warren, Faeth, McIntyre, & Hope, 2006). Instead, success in urban environments may depend on species' ability to adjust to the demands of a new habitat by modifying behaviour, such as foraging strategies or the timing of breeding attempts (Kark et al., 2007; Shochat et al., 2006; Sol, Timmermans, & Lefebvre, 2002). Behavioural flexibility may be crucial in allowing animals to reduce costly and unnecessary fear responses, or to increase them to deal with new dangers. For example, some urban birds are able to avoid investing in unnecessary anti-predator responses by selectively responding to specific threatening humans (Davidson et al., 2015; Lee et al., 2011; Levey et al., 2009). However, it is unclear whether areas of human disturbance also favour selective reductions in fear towards other stimuli, such as potentially dangerous objects.

There is no consensus about the optimal level of object neophobia in urban environments because opposing hypotheses predict benefits for high or for low neophobia. Some studies suggest that less neophobic individuals are faster to interact with and solve novel foraging tasks (Benson-Amram & Holekamp, 2012; Biondi, Bó, & Vassallo, 2010; Boogert, Reader, Hoppitt, & Laland, 2008; Griffin & Guez, 2014). Since human litter provides opportunities for foraging that requires the manipulation of novel objects, such as food packaging, reduced neophobia may make animals more likely to innovate with novel food or objects when invading novel habitats (Greenberg & Mettke-Hofmann, 2001; Greenberg, 2003; L. B. Martin & Fitzgerald, 2005). Accordingly, urban common mynas (*Acridotheres tristis*) have been shown to be less neophobic than suburban conspecifics (Sol et al., 2011), and urban groups of house sparrows (*Passer domesticus*) solve tasks more quickly than rural ones (Liker & Bókony, 2009). Such reductions towards fear-related stimuli in urban environments has been documented in other behaviours such as flight initiation distance (Clucas & Marzluff, 2012; McCleery, 2009; A. P. Møller, 2010; Anders Pape Møller, 2008), a dampened corticosterone stress response (Grunst et al., 2014), or both (Atwell et al., 2012) (though note that these stress hormone patterns are not universal, see Bonier, 2012).

In contrast, increased neophobia may be favoured in potentially dangerous locations where exploration may expose animals to threats such as generalist predators or poisons (G. E. Brown, Ferrari, et al., 2013; Greenberg, 2003). Urban areas typically contain more of these threats (Evans, Newson, & Gaston, 2009; Sims, Evans, Newson, Tratalos, & Gaston, 2008; Sorace & Gustin, 2009; Sorace, 2002). Laboratory manipulations of predation pressure in fish show that individuals' predator neophobia can plastically respond to the dangers of the

environment (G. E. Brown, Ferrari, et al., 2013), and that experience with these pressures can increase survival upon reintroduction into the wild (Ferrari et al., 2015). Additionally, urban environments may select for increased neophobia over time. Human commensal species of wild rats, for example, show higher levels of object neophobia than laboratory and feral strains that do not have a history of surviving alongside a rat poison (Cowan, 1977). Similarly, elevated levels of object avoidance have been documented in house sparrows and shiny cowbirds (*Molothrus bonariensis*) in urban compared to rural habitats (Echeverría & Vassallo, 2008).

Studies may have found conflicting relationships between neophobia and urban areas for several reasons. Firstly, different species may respond in divergent ways to urban selection pressures. Interspecies comparisons between and within environments are crucial to explaining human impact on temperament traits, such as neophobia, but they are rarely conducted in the wild (Archard & Braithwaite, 2010; Réale et al., 2007). Secondly, studies often measure neophobia in subtly different ways. Tests must present objects that accurately represent either known or novel stimuli because avoidance should only be interpreted as neophobia if it reflects a response to novelty, rather than a generalised fear response (Chapter One). Thirdly, neophobia tests are classically conducted on isolated individuals (e.g. Greenberg 1990), yet the presence of foraging conspecifics is likely to influence novelty approach in groups in the wild. Therefore to assess wild birds' responses towards novelty and objects characteristic of urban and rural spaces, I compared behavioural responses of foraging groups towards several types of objects across a range of bird species.

I presented free-flying bird communities with an object made from either natural items that mirrored natural stimuli, litter items that mimicked anthropogenic foraging opportunities in urban areas, or entirely artificial objects designed not to resemble any familiar stimulus. I examined the responses of 12 species of urban exploiting birds that ranged in size, foraging ecology, and evolutionary history. Five of these species were corvids (Corvidae), a family often described as very neophobic (Greenberg & Mettke-Hofmann, 2001; Heinrich et al., 1995; Marzluff & Heinrich, 1991) yet highly innovative and skilled at exploiting novel opportunities (Emery & Clayton, 2004; Nicolakakis & Lefebvre, 2000); a seemingly paradoxical combination considering that neophobia is commonly thought to inhibit innovation (Greenberg, 2003; Griffin & Guez, 2014). To my knowledge corvid object neophobia has not been tested across urban gradients before, nor has their reputed high level of neophobia been verified through comparison with other wild species. I compared their

neophobic responses to those of the other seven participating species to determine how universal urban neophobia changes might be. Both sets of species could, in theory, benefit equally from reduced neophobia in urban areas if it allowed for increased feeding opportunities around human-created packaging and waste. Corvids in urban areas have been reported to consume more human refuse than rural conspecifics (Rowley & Vestjens, 1973), and other bird species have been known to rely on anthropogenic food sources, especially during the winter (Orell, 1989). However, both sets of species also encounter potential dangers associated with the novelty they encounter, such as urban predators, including cats (Evans et al., 2009; Sims et al., 2008; Sorace & Gustin, 2009; Sorace, 2002). Therefore selectively avoiding certain types of objects, without having to relax their overall defences would allow urban birds to take advantage of beneficial types of novelty. Additionally, since both the corvid and non-corvid groups contained social foraging species, known to make foraging decisions based on the behaviour of conspecifics (e.g. Chiarati et al. 2012; Aplin et al. 2012), the presence of conspecifics could help birds distinguish beneficial from dangerous novelty.

I predicted that: 1) corvids would show higher neophobia than non-corvids towards novel objects within habitats; 2) both sets of species would reduce their neophobic behaviour in urban areas towards objects that would be less novel there, such as litter; and that 3) foraging birds would be more likely to approach objects after a conspecific visited.

5.3 Methods

Twelve feeding tables were set up across human population gradients in distinct geographical regions of the east and southwest of England (Cambridgeshire, eight tables; Cornwall, four). I estimated the extent of human presence in the vicinity of each table based on the amount of impervious surface cover, such as tarmac and rooftops, in the 1km² surrounding the site. Surface cover area was calculated by manually drawing polygons on satellite images using the land area calculator in Google Earth Pro. All table locations with surface cover higher than 20% were classified as high human impact zones (mean 45.6% $\pm$ 7.2%), less than 6% as low impact zones (mean 3.7% $\pm$ 0.5%; see Table 1). For clarity I refer to these areas as urban and rural, but acknowledge the areas with the highest impervious surface area are closer to the range commonly reported for suburban measures of cover (20-50%) (Marzluff, 2001; McKinney, 2002, 2008). Rural sites were on large plots of private land where litter was almost completely absent, while urban sites were located in public

spaces or small gardens adjacent to busy streets. The two urban/rural gradients were located 430km apart; ensuring that distinct communities of birds were surveyed. Corvids were colour-ringed in these areas as part of related study sites (Cambridgeshire: 323 jackdaws, three jays, *Garrulus glandarius*; Cornwall: 734 jackdaws, 79 rooks, *Corvus frugilegus*, eight crows, *Corvus corone*; six jays; six magpies, *Pica pica*). Data were collected on these ringed individuals, on all other unringed corvids and on the unringed individuals of seven species outside of the corvid family (blue tits, *Cyanistes caeruleus*; great tits, *Parus major*; European robins, *Erithacus rubecula*; common blackbirds, *Turdus merula*; common wood pigeons, *Columba palumbus*; common chaffinches, *Fringilla coelebs*; house sparrows, *Passer domesticus*) that foraged during the trials. Although all of the species that participated are known to live in both rural and urban areas, not all of them visited both urban and rural tables (see Table 5.S1)

Table 5.1 Calculating human density. Percentage of impervious surface area within the 1km² grid surrounding the feeding table. Calculated with Google Earth Pro.

<u>Feeding Table ID</u>	<u>Region</u>	<u>Classification</u>	<u>Impervious Surface Area</u>
PH-S, PH-D	Cornwall	Urban	55.25%
J	Cambridgeshire	Urban	51.14%
SC	Cornwall	Urban	20.87%
M, H	Cambridgeshire	Rural	5.7%
PF	Cornwall	Rural	3.56%
I, K, N	Cambridgeshire	Rural	2.15%
B, D	Cambridgeshire	Rural	4.1 %

In the weeks leading up to the study, feeding tables were regularly baited between the hours of 08:00 and 14:00 with one cup of peanuts, to ensure that birds in the surrounding areas foraged readily at the tables. Tables were deemed ready for the experiment if a corvid and a non-corvid species took food from the table within 90 minutes of baiting for at least three days in a row. A total of 77 trials were run from late January through March during the winters of 2013 and 2014 (See Table 5.S2). The Cambridgeshire gradient was sampled in both 2013 and 2014, the Cornish gradient in 2014 only. The trials fell outside the breeding season for all participating species, except for the rook, which commences breeding in March, but all participating birds were known to be independently foraging adults since trials took place before juvenile rooks fledged.

Three separate classes of objects were used to assess the specificity of birds' fear responses within environments; i.e. to test whether they would respond neophobically to any new object placed on the feeding table, or respond less fearfully towards objects common in the surrounding habitat. *Novel* objects were built out of colourful, shiny, artificial materials

that did not resemble any naturally occurring shape or animal, and did not have any parts that could resemble eyes. Materials used for novel object construction were determined to be distinctive to the birds via spectral analyses in the avian visual space (see Figure 5.S1) No two materials that were separated by less than one just noticeable difference (JNDs; values less than one JND are indistinguishable, Vorobyev & Osorio 1998) were used in the same object. *Litter* objects were made from man-made food wrappers and containers, (e.g. crisp bags, jam jars, and Styrofoam fast-food containers) and were designed to mirror stimuli commonly found in urban areas. *Natural* objects consisted of rocks, leaves and sticks found in the local area (see Figure 5.1 for examples of object types). The objects from all conditions were of similar size; about half of the volume of a jay, the smallest corvid in this study. No object was repeated at any one table, but the same objects were used in urban and rural tables so any comparisons between the populations would be towards the same objects. Although few ringed individuals were seen at multiple tables ($n = 12$), no individual was seen at multiple tables when the same object was presented. In order to ensure I reliably measured fear, as opposed to exploration or food motivation, I compared neophobic behaviour to a control in which there was food but no object on the table (Chapter Two, Mettke-Hofmann, Winkler, Hamel, & Greenberg, 2013).

Figure 5.1 Examples of objects for each test condition



In all object conditions, an object was placed on the same corner of the table, and one cup of peanuts placed in the centre. In the control condition, food was placed on the table alone. One cup contained about 320 peanuts; several times more than what a single individual of the largest participating species could consume. Trials lasted 90 minutes, or until all of the food was consumed, whichever came first. All four conditions (Novel, Litter, Natural, and Control) took place on consecutive days, at the same time of day. The order of conditions was determined for each table with an online random number generator. In attempts to create an even number of trials across regions, several tables had additional sets of trials on following

days and were given a different time of day for each set. Trials were video recorded using a Panasonic HDC-SD90 camcorder, wrapped in camouflage tape, from a tripod located approximately 10 meters away and from the same location at each table for all trials.

Videos were subsequently analysed with Observer XT (Version 7.0, Noldus Information Technology, Wageningen, The Netherlands), to record the timing of each bird's visit, the amount of food it ate, its species and, where applicable, its colour ring combination. Fourteen full trials were coded by two people, one of whom was blind to the experimental questions.

5.3.1 Ethical note

This work was carried out under Home Office license (PIL 70/25311, PPL to AT 80/2371) and in accordance with the ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching (2012). Birds were ringed under license from the British Trust for Ornithology (no. C6079, C5752, C5746), either as nestlings in previous years (all jackdaw nestlings in the population are ringed) or as adults using ladder traps and nest-box trap doors.

5.3.2 Analysis

I analysed four response variables, clustered into two sets of analyses. The first set allowed me to test whether or not corvids were more neophobic than the other set of species, and whether or not urban and rural populations of these groups differed. Specifically I tested these hypotheses by investigating the behaviour of the least neophobic bird of each species by measuring (1) whether any member of that species (either ringed or unringed) appeared at the table during the trial, and (2) their latency of arrival from the time of table baiting. The second set focused on a restricted dataset, excluding bird species that did not appear more than once over the course of the trial, to analyse if birds behave differently towards the types of objects after a conspecific had visited the table. Therefore I investigated the (1) feeding rate and (2) visitation rate of birds after the first conspecific had foraged. Each set of analyses investigated the influence of the following main explanatory terms: experimental condition (Control, Natural, Litter, or Novel), habitat (Urban or Rural), species group, and interactions between these factors. They all controlled for the potential confounding variables of date, region (Cambridgeshire or Cornwall), time of day, year of experiment, and the presence of

other bird species where necessary (i.e. adding a binary variable that denoted whether another bird from their species group had arrived before them).

5.3.2.1 *Least neophobic individuals: appearance at tables*

In contrast to laboratory studies that can force interactions with novelty, wild animals can respond by avoiding novelty entirely (Greenberg, 2003). To determine the factors influencing whether or not birds appeared at tables, I ran a GLMM with a binomial error structure (Appeared=1, Did not appear=0). Only the first observation of each species was used, with each species at a single trial counting as one data point. All potentially confounding variables (date, region, time of day, year) were included as covariates. Feeding table and experimental trial were assigned as random factors to account for repeated measures from the same table and from the same 90 minute trial. Additionally, species was included as a random factor to control for differences between species within each species group (Corvids; non-Corvids). Species that were never observed during any trial at a given table, nor seen in the surrounding habitat during field observations were removed from analysis at that table. Analysis started with a maximal model, which was simplified through backwards stepwise elimination. Terms were kept if their exclusion increased the model's AIC value by at least two. Model selection is detailed in Table 5.S3. Once a minimal model was determined, P-values and effect sizes were calculated for each remaining covariate, and listed in the text (Zuur et al., 2009). Model assumptions were validated through inspection of diagnostic plots.

5.3.2.2 *Least neophobic individuals: approach latency*

Since approach latency is a commonly used measure of neophobia (Mettke-Hofmann et al., 2006), I examined how long it took for the first individual of each species to arrive at the table following baiting. To account for the fact some species may have arrived if given more time, I ran a Cox proportional hazards regression model (c.f. Bókony et al. 2012), on the same variables of interest, and potential confounding covariates as the GLMM. I clustered the observations around Trial, Species and Table, to account for interdependence in the data. The potential influence of other bird species on arrival time was accounted for by adding two binary terms: one denoted whether a corvid had arrived before the current observation; the other noting whether a non-corvid had arrived beforehand.

5.3.2.3 Group responses: feeding and visitation rate

Many individuals had the opportunity to forage after potential conspecific social cues were available because trials offered hundreds of peanuts. I analysed each species' feeding rate, and visitation rate to assess whether birds continued to avoid objects after a conspecific had foraged at the table. Each peanut picked up from the table counted as one food piece. A visit was defined as a bird touching the feeding table. Total numbers of food and visits were calculated from the behaviour of the second bird through to the end of the trial. Both rates were calculated by dividing the food and visit totals by the number of minutes from the first visitor to the end of the trial. Both food and visitation rate data were non-normal, so were log transformed and analysed with separate LMMs, using the same explanatory variables, random effects, and model selection methods as the appearance at tables GLMM.

All statistics were conducted in R (R Core Team, 2015), and models were created using the lme4 or survival package (Bates et al., 2013; Therneau, 2015).

5.4 Results

In total I recorded 4,300 visits and the consumption of 15,245 pieces of food across the 77 trials. Five species of corvid and seven species from other bird families participated in the experiment, with considerable variation in the species assemblages and visit numbers at each table (Table 5.S2). Overall the presence of corvids at the tables did not deter the other bird species from foraging, as corvid visits were often very short (<2 seconds), allowing plenty of time within the 90 minutes for other bird species to visit.

Inter-coder reliability was perfect for species appearance (Cohen's kappa = 1.0), and extremely high for arrival time (One-way Intraclass Correlation Coefficient: ICC = 0.99), visit number (ICC = 0.99), and the amount of food eaten (ICC = 0.96). All results reported below are derived from data that included all birds, regardless of whether or not they were ringed. The subset of data containing only ringed corvids indicates that the main appearance and arrival time results below do not depend on the behaviour of just a few individuals (see Supplementary Materials). Additionally, the effects discussed below were also present when analyses were conducted only on data from the two species from each group that visited the most (jackdaws/rooks and blue tits/great tits; Table 5.S5).

5.4.1 Table appearance

Corvids and non-corvids responded differently to the experimental conditions in their probability of appearing at the tables. Overall, there was an interaction between species group and response toward the objects: corvids were less likely to appear at tables when any type of object was present compared to controls when no object was present, while I found no evidence that non-corvid species differed in appearance across any condition (see Figure 5.2 for interaction details). Additionally, all birds were statistically more likely to appear as the date progressed, but the effect size was very small (GLMM: $n = 399$ observations, $\text{Est} + \text{SE} = 0.02 + 0.01$, $z = 2.54$, $P = 0.011$). Birds were equally likely to appear at tables in urban and rural areas, and none of the other potential confounding variables were retained in the final model (see Table 5.S4).

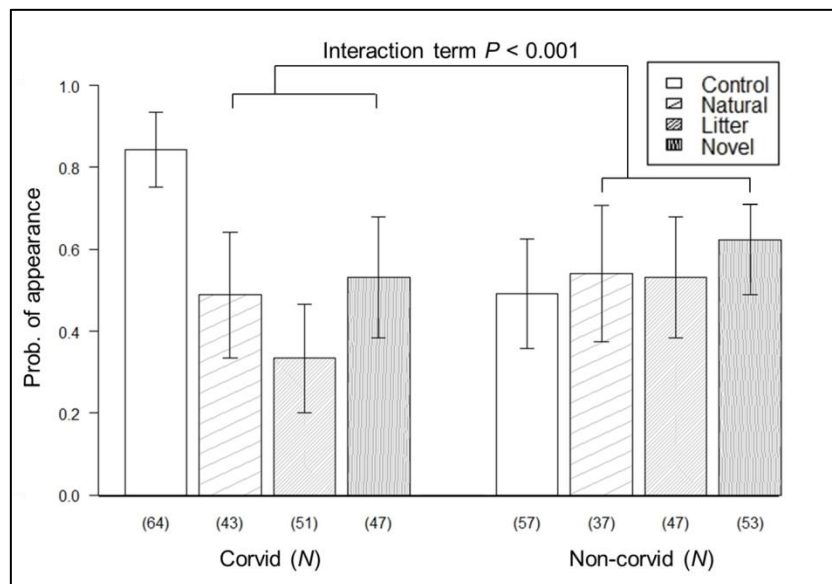


Figure 5.2 Interaction between species group (Corvid vs Non-corvid) and conditions. In each object condition corvids responded differently to the control than non-corvids did in their probability of appearing at tables. The control condition served as the reference category for all object conditions, and non-corvids for species group. GLMM: $n = 399$ observations, Corvid*Natural, $\text{Est} + \text{SE} = -2.67 + 0.80$, $z = -3.34$, $P < 0.001$; Corvid*Litter, $\text{Est} + \text{SE} = -3.79 + 0.79$, $z = -4.78$, $P < 0.001$; Corvid*Novel, $\text{Est} + \text{SE} = -3.00 + 0.77$, $z = -3.89$, $P < 0.001$. Bars show means from raw data $\pm$ SE. Sample sizes reflect number of observations; each species at each trial is one observation.

5.4.2 Arrival latency

Birds arrived faster in urban than rural areas, but only in Litter conditions (see Figure 5.3C). Additionally, corvids arrived more slowly than non-corvids ($\rho = 0.170$, $\chi^2 = 8.75$, $P = 0.003$). Finally, birds in Cornwall arrived slightly slower than in Cambridgeshire ($\rho =$

0.116, $\chi^2 = 5.412$, $P = 0.020$, see Table 5.2, Table 5.S5), and earlier in the morning birds arrived slightly faster than later in the day ($\rho = -0.126$, $\chi^2 = 3.92$, $P = 0.048$; see Table 5.2).

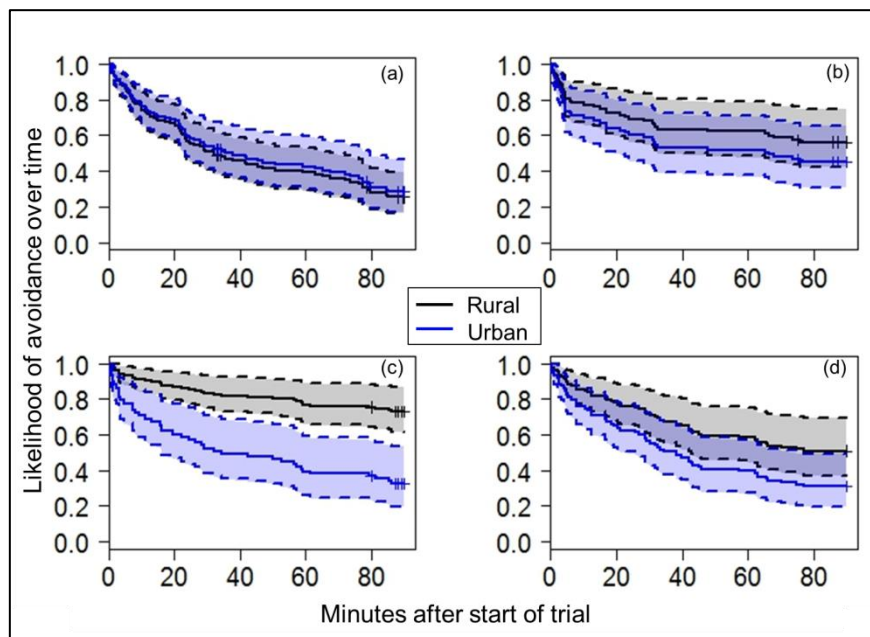


Figure 5.3 Table avoidance over time. Survival curves showing the probability of not arriving over time, broken down by habitat and condition: (a) control, (b) natural, (c) litter, (d) novel. Urban and rural populations only differ in litter object conditions. Cox proportional hazards regression: $n = 399$ observations, Urban*Natural, $\rho = 0.018$, $\chi^2 = 0.112$, $P = 0.738$; Urban*Litter, $\rho = -0.236$, $\chi^2 = 17.40$, $P < 0.001$; Urban*Novel, $\rho = -0.097$, $\chi^2 = 1.84$, $P = 0.175$. The control condition served as the reference category for object comparisons, and rural areas for the urban gradient.

Table 5.2 Cox proportional hazards models for latency to arrive at tables. Corv_before denoted whether a corvid species had arrived beforehand. Significant p values ($P < 0.05$) highlighted in bold. The control condition was the reference category for all object conditions, rural areas for the urban gradient, and Cambridgeshire for the region.

Variable	Minimal model		
	ρ	χ^2	P
Condition			
Litter	0.076	1.150	0.284
Natural	-0.157	8.760	0.003
Novel	0.073	0.911	0.340
Species Group (Corvid)	0.170	8.750	0.003
Habitat (Urban)	-0.002	0.001	0.979
Region (Cornwall)	0.116	5.412	0.020
Corv_before	0.256	16.900	< 0.001
Time	-0.126	3.920	0.048
Condition*Habitat			
Litter*Urban	-0.236	17.400	< 0.001
Natural*Urban	0.018	0.112	0.738
Novel*Urban	-0.097	1.840	0.175

5.4.3 Group responses: feeding and visitation rate

Both the food consumption and visitation rate models showed a similar interaction between species group and condition. Corvid species had lower feeding and visitation rates in novel object trials compared to control trials, while non-corvid species fed and visited at similar rates across all conditions after a conspecific had foraged (see Figures 5.4 and 5.5). Additionally all species showed increasing visit and feeding rates as the dates progressed, but the effect sizes were very small (Feeding, Est +SE = 0.01+0.005, $z = 2.67$, $P = 0.008$; Visit, Est +SE = 0.01+0.005, $z = 2.67$, $P = 0.008$). Feeding and visit rates were similar across urban and rural habitats, and no other factors had significant effects in the model (see Table 5.S3).

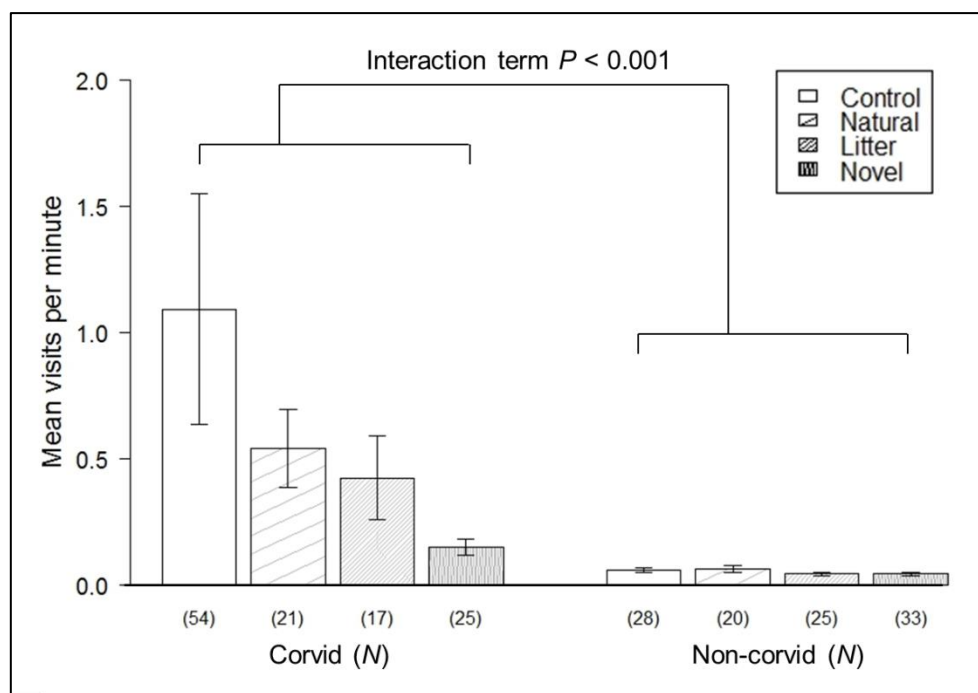


Figure 5.4 Visit rates. Interaction between species group (Corvid vs Non-corvid) and novel object condition in visitation rates. Corvids and non-corvids only differed in the relationship between their controls and the novel condition. The control condition served as the reference category for all object conditions, and non-corvids for species group. LMM, $n = 176$, Corvid*Natural, Est +SE = 0.02+0.43, $z = 0.04$, $P = 0.967$; Corvid*Litter, Est +SE = -0.58+0.43, $z = -1.33$, $P = 0.183$; Corvid*Novel, Est +SE = 1.18+0.43, $z = -2.72$, $P = 0.007$. Bars show means from raw data $\pm$ S.E.

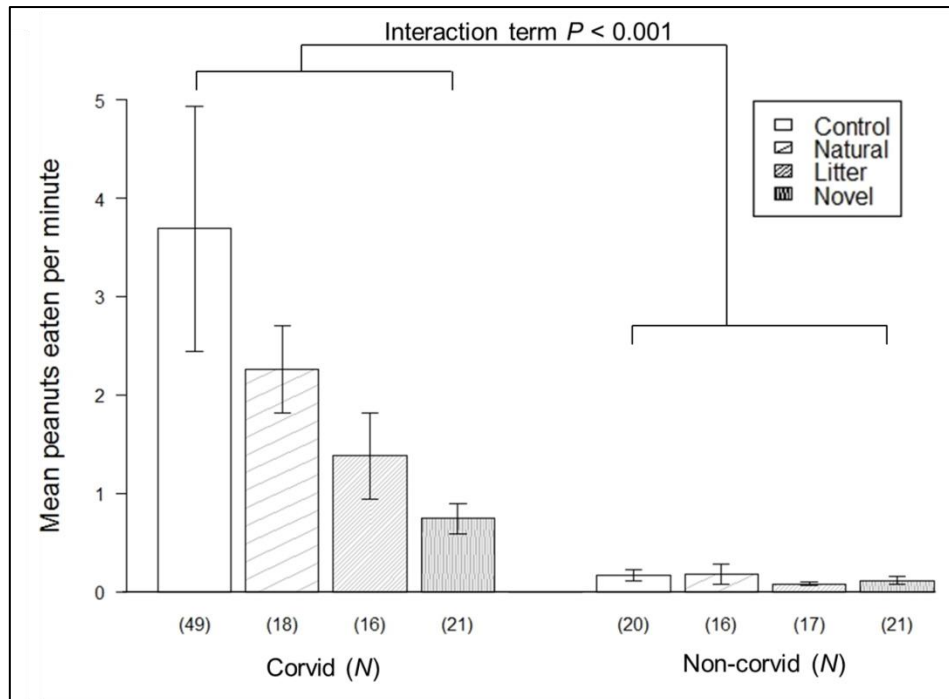


Figure 5.5 Feeding rates. Interaction between species group (Corvid vs Non-corvid) and Novel object condition in feeding rates. The control condition served as the reference category for all object conditions, and non-corvids for species group. LMM, $n = 178$, Corvid*Natural, Est +SE = $0.15+0.46$, $z = 0.32$, $P = 0.750$; Corvid*Litter, Est +SE = $-0.46+0.47$, $z = -0.98$, $P = 0.325$; Corvid*Novel, Est +SE = $-1.36+0.40$, $z = -3.40$, $P < 0.001$. Bars show means from raw data $\pm$ S.E.

5.5 Discussion

Although behavioural plasticity is commonly considered to be vital in allowing some species to survive in novel environments (Sol et al., 2002), it is unclear whether plasticity in fear around novelty is due to a general or specific modification of fear. In contrast to some previous studies (Bókonyi et al., 2012; Sol et al., 2011), I did not find reduced neophobia in urban birds, as responses towards novel objects were similar across habitats. However, as both species groups arrived faster around litter objects in urban than rural areas, their behaviour potentially reflects a specific reduction in fear towards a commonly occurring type of object. These patterns emerged despite the fact that corvid and non-corvid species differed in their neophobic responses and in their behaviour after the first individual foraged. Corvids appeared markedly more neophobic than other species in avoiding tables with any type of object, but were selective in how they responded to object types after a conspecific had foraged; only eating and visiting less around novel objects. Therefore these results indicate that both sets of species adjusted to urban areas by reducing fear towards regularly encountered objects despite both expressing different levels of fear.

Urban bird populations arrived faster compared to rural populations when the litter objects were present on tables. This result indicates that instead of showing generalized, population-level reductions in neophobia, urban birds expressed a lower level of fear only towards specific, potentially rewarding objects. Such specific differentiation between litter and novel objects would be unlikely to have arisen through genetic change alone because the two types of objects share many perceptual features. Therefore the population differences more likely reflect learned categorization as a result of different experience. Through repeated exposure to anthropogenic objects, birds may have been able to better distinguish between them and other types of novelty because as exposure to stimuli increases so does the ability to differentiate their details (Hall & Honey, 1989; Shettleworth, 2010). Better abilities to differentiate man-made objects, and continued rewards around objects made of litter would encourage birds to form a category of litter objects that shared some common stimuli. Whether birds' flexibility in mediating fear towards litter vs other types of objects is simply due to an increased exposure to stimuli (e.g. Lee et al. (2011) in differentiating humans), or whether urban and rural birds differ in their bias to flexibly classify stimuli may be important in determining whether success of urban exploiting species is a result of behavioural adjustments.

While corvids and non-corvids responded similarly to litter objects, corvids were overall more neophobic than other bird species. Corvids appeared at tables less often during all object conditions in comparison to controls, while other bird species were not deterred by the presence of objects, confirming suggestions that corvids are neophobic as adults (Greenberg & Mettke-Hofmann, 2001; Heinrich, 1988). Indeed, corvids' sensitivity to novelty was so pronounced that the presence of new objects on familiar feeding tables—even when those objects were natural materials that they likely encounter every day—reduced their probability of visiting tables relative to controls. Although the link between object neophobia and predatory wariness is unclear (Carter, Marshall, et al., 2012), I speculate that human behaviour towards the species groups in this study may differ in ways that may help explain the comparatively high levels of corvid fear. Human discouragement in the form of chasing, shooting, or threatening unpopular species has been shown to increase the fear responses of targeted birds towards humans (Clucas & Marzluff, 2012). In the UK humans actively encourage smaller songbirds to forage in their gardens, as 60% of households with gardens provide food for wild birds (Department of the Environment, 2002). In contrast, corvid species are listed as some of the least liked visitors to UK gardens (Cox & Gaston, 2015), and

often face persecution by people because they are classified as vermin under UK law (Wildlife and Countryside Act 1941).

Despite their persecution, corvids' high level of neophobia may be seen as paradoxical because they are also known for their high rates of behavioural innovation (Emery & Clayton, 2004; Nicolakakis & Lefebvre, 2000); two traits that do not normally correlate (Greenberg, 2003). The mechanism through which their neophobia subsides to allow them to manipulate objects and solve problems is unknown, but potentially they are able to rapidly learn to categorize novelty as “safe” or “unsafe”, similarly to how they can categorize other specific threatening stimuli, such as dangerous humans (Davidson et al., 2015; Lee et al., 2011; Marzluff et al., 2010), or known versus unknown predators (Marzluff, Delap, & Haycock, 2015). Whereas corvids fed and visited at equal rates to the control condition when social cues were available around natural and litter objects, these rates were significantly reduced around novel objects. This suggests that corvids may have classified objects according to their degree of novelty with the aid of social cues, with “less novel” treated as “safer”. This type of flexibility in responding to object types may explain how corvids can be so neophobic, but also highly innovative around objects with which they may have prior experience. However, this ability is clearly not unique to corvids, as the other bird species that participated in this study also showed differentiation between certain types of objects in responding less fearfully towards litter than novel objects in urban populations. The extent to which novelty categories and social cues influence corvids' neophobic behaviour deserves future research if their behavioural adaptation to human-altered environments is to be better understood. Specifically, it is yet to be established whether or not species with greater opportunities for social learning due to their social system are more likely to use social cues around novelty (see Chapter 6).

As part of the suite of behaviours that can change with human disturbance, understanding where and why neophobia levels differ could be of great importance in conservation and wildlife management contexts (Chapter Seven). I demonstrated that species respond similarly to experience in areas of human disturbance, despite exhibiting different levels of neophobia. However, it remains unclear how much exposure to objects is needed before animals no longer categorize stimuli as novel and thus fear-inducing. Future work is needed to reveal how population-specific patterns of object avoidance emerge in urban areas. Studies that examine the ontogeny of neophobic behaviours in urban vs rural areas could be particularly informative in investigating the role of individual experience in driving

neophobia and other behaviours. Additionally, research testing how animals learn to distinguish “safe” vs “unsafe” object categories may help us understand the processes behind behavioural adjustments to urban areas. Together these investigations may explain why certain species and not others are able to behaviourally adjust and thrive in human-dominated environments.

5.6 Supplementary materials

Table 5.S1 Number of trials per condition and table.

Region	Condition						
		Table	Control	Rubbish	Natural	Novel	Total
Cambridgeshire	Rural	B	1	2	1	1	5
		D	1	1	1	1	4
		H	3	1	1	1	6
		I	2	1	1	1	5
		K	1	1	1	1	4
		M	2	2	1	1	6
		N	1	1	1	1	4
	Urban	J	3	2	3	2	10
Cornwall	Rural	PF	2	2	1	3	8
	Urban	PHD	3	2	3	3	11
		PHS	1	1	1	1	4
		SC	3	2	2	3	10
Total			22	17	17	19	77

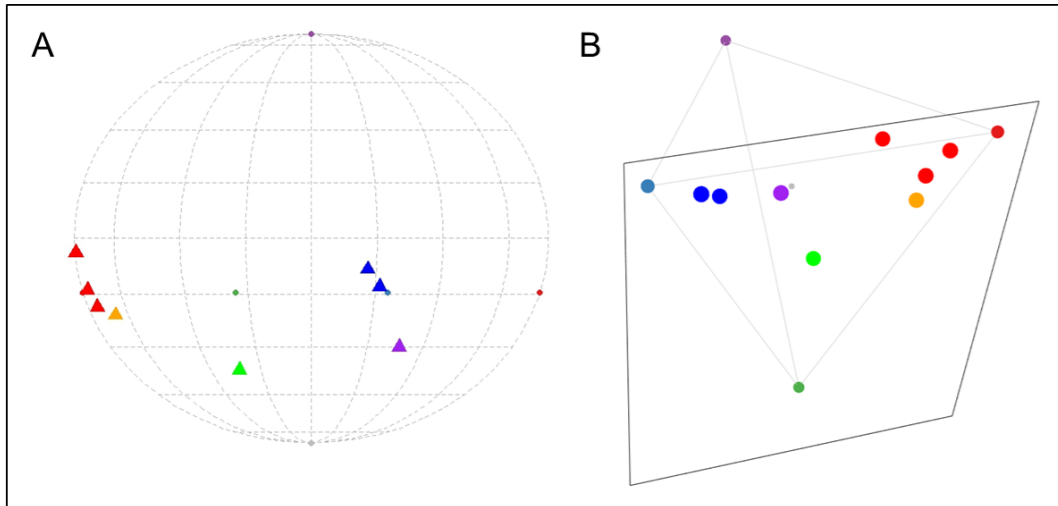


Figure 5.S1 Colour plots. Two dimensional (a) and three dimensional (b) projection plot of materials used for novel objects, plotted in the avian tetrahedral visual space. Both plots show the range of material colours that were used. Material colours are represented by triangles in (a), by central points in (b). Circles in (a) and triangle vertices in (b) provide reference points to the limit of visible wavelength for each receptor type. Only materials that occupied different visual spaces (such as the red and green triangles in (a)) were used in the same novel object.

Table 5.S2 Species participation at feeding tables.

		Cambridge							Cornwall				
		Rural							Urban	Rural	Urban		
		B	D	H	I	K	M	N	J	PF	PHD	PHS	SC
Corvid	Carrion crow (<i>Corvus corone</i>)	5	1	13	22		2						
	Eurasian jay (<i>Garrulus glandarius</i>)	38	115	7	130	105	110	82					69
	Eurasian magpie (<i>Pica pica</i>)	1					9	1			7		
	Jackdaw (<i>Corvus monedula</i>)	40	31	173	138	20	44		238	1161	82	26	968
	Rook (<i>Corvus frugilegus</i>)	1		54	11	3	1						206
	Blue tit (<i>Cyanistes caeruleus</i>)	4	17		23	1	6		56		20	5	38
	Common blackbird (<i>Turdus merula</i>)									1		5	14
	Common chaffinch (<i>Fringilla coelebs</i>)	1								26			5
	Common woodpigeon (<i>Columba palumbus</i>)								22				
	European Robin (<i>Erithacus rubecula</i>)									21			22
Non-Corvid	Great tit (<i>Parus major</i>)	11	2	12	28		1		1	10		4	35
	House sparrow (<i>Passer domesticus</i>)									13			

Numbers indicate their number of visits at each table across all conditions

5.6.1 Ringed birds analyses

A total of 76 ringed individuals (67 jackdaws, 8 rooks, 1 jay) participated alongside the many unringed birds, and I analysed the behaviour of this subset of the data. This dataset was biased (e.g. a large majority of ringed birds were in Cornwall, only one urban table was sampled, and only 23 trials saw ringed visitors), so results must be interpreted with caution. Nevertheless, I ran a similar model to the one in the main text on individuals' appearance during trials, with individual as an additional random effect. I found support for the main conclusion that corvids are neophobic, as individuals were less likely to appear at tables when there was a novel object on the table (GLMM, $N = 522$, Est +SE = $-2.62+1.03$, $z = -2.54$, $P = 0.011$). Moreover, survival analyses confirmed that the birds were quicker to arrive around litter in urban areas (Cox Proportional Hazards model, $N = 522$ observations, 109 events, $\rho = -0.233$, $\chi^2 = 5.87$, $P = 0.015$). I was unable to run formal models on individuals' visitation and feeding rates because there were so few individuals who visited more than once during a given trial ($N = 31$), and therefore models would have been over-parametrised, with the 4 random effects and even one main effect of experimental condition.

In addition to these analyses, I also looked at the relationship between ringed and unringed visitors to determine how well ringed corvids represented unringed ones. In the areas where there were ringed populations, I could identify a statistically similar percentage of visitors during all conditions (Chi-square test, no. visits by ringed birds vs no. visits by unringed birds: $\chi^2 = 6.3065$, $df = 3$, $P = 0.098$). Therefore the ratios of ringed to unringed birds were stable across conditions, and ringed bird behaviour likely predicted unringed bird behaviour. This means that the objects were as likely to be novel for unringed birds as they are for ringed individuals. Additionally, it is unlikely that a small number of unringed birds determined all of the results, otherwise we would have seen particular ringed individuals biasing the results too.

Table 5.S3 GLMM and LMM model selection based on ΔAIC values.

<u>Appearance at tables GLMM, n=399</u>	<u>ΔAIC</u>
Appears ~ Condition + Corvid + Corvid*Condition + Date + Time + Urban + Condition*Urban + Region + Year	0.0
Appears ~ Condition + Corvid + Corvid*Condition + Date + Time + Urban + Condition*Urban + Region	-0.5
Appears ~ Condition + Corvid + Corvid*Condition + Date + Time + Urban + Condition*Urban	-0.9
Appears ~ Condition + Corvid + Corvid*Condition + Date + Time + Urban	-1.2
Appears ~ Condition + Corvid + Corvid*Condition + Date + Time	-1.9
Appears ~ Condition + Corvid + Corvid*Condition + Date	+1.4
<u>Feeding rate, LMM, n=176</u>	<u>ΔAIC</u>
log(Feed.rate) ~ Condition + Corvid + Corvid*Condition + Date + Year + Urban + Condition*Urban + Time + Region	0.0
log(Feed.rate) ~ Condition + Corvid + Corvid*Condition + Date + Year + Urban + Condition*Urban + Time	-1.91
log(Feed.rate) ~ Condition + Corvid + Corvid*Condition + Date + Year + Urban + Condition*Urban	-1.97
log(Feed.rate) ~ Condition + Corvid + Corvid*Condition + Date + Year + Urban	-3.91
log(Feed.rate) ~ Condition + Corvid + Corvid*Condition + Date + Year	-0.02
log(Feed.rate) ~ Condition + Corvid + Corvid*Condition + Date	+0.86
<u>Visitation rate, LMM, n=178</u>	<u>ΔAIC</u>
log(Visit.rate) ~ Condition + Corvid + Corvid*Condition + Date + Year + Urban + Condition*Urban + Time + Region	0.0
log(Visit.rate) ~ Condition + Corvid + Corvid*Condition + Date + Year + Urban + Condition*Urban + Time	-0.91
log(Visit.rate) ~ Condition + Corvid + Corvid*Condition + Date + Year + Urban + Condition*Urban	-0.0
log(Visit.rate) ~ Condition + Corvid + Corvid*Condition + Date + Year + Urban	-4.13
log(Visit.rate) ~ Condition + Corvid + Corvid*Condition + Date + Year	+1.24
log(Visit.rate) ~ Condition + Corvid + Corvid*Condition + Date	+0.97

All models include Trial, Species, and Table as random effects. Final models are marked in bold. Dropping any terms listed in final models results in an > 2 increase in AIC. * denotes an interaction term

Table 5.S4 Final GLMM and LMM models for the restricted dataset.

Appearance at tables GLMM, <i>N</i> = 225			
	<u>Est.±SE</u>	<u>Z</u>	<u>P</u>
Corvid	2.81±1.16	2.41	0.016
Date	0.03±0.01	3.13	0.002
Litter*Corvid	-3.97±1.06	-3.73	< 0.001
Natural*Corvid	-2.71±1.07	-2.54	0.011
Novel*Corvid	-2.61±1.04	-2.51	0.012
Visitation rate LMM, <i>N</i> = 114			
	<u>Est.±SE</u>	<u>Z</u>	<u>P</u>
Corvid	2.25±0.46	4.88	< 0.001
Date	0.01±0.01	2.67	0.008
Litter*Corvid	-0.58±0.44	-1.33	0.183
Natural*Corvid	0.018±0.43	0.04	0.967
Novel*Corvid	-1.36±0.40	-3.40	< 0.001
Feeding rate LMM, <i>N</i> = 114			
	<u>Est.±SE</u>	<u>Z</u>	<u>P</u>
Corvid	3.06±0.41	7.44	< 0.001
Litter*Corvid	-0.37±0.46	-0.80	0.423
Natural*Corvid	0.19±0.46	0.41	0.684
Novel*Corvid	-1.13±0.43	-2.63	0.008

Data contained only the two species from each group that visited the most (jackdaws/rooks and blue tits/great tits). The control condition served as the reference category for all object conditions, non-corvids for species group, and rural areas for habitat type. * denotes an interaction term

Table 5.S5 Cox proportional hazards model on arrival times for the restricted dataset.

	<u>rho</u>	<u>χ²</u>	<u>P</u>
Corvid	0.195	6.30	0.012
Corv_before	0.174	7.61	0.006
Litter*Corvid	-0.188	5.69	0.017
Natural*Corvid	-0.071	1.56	0.211
Novel*Corvid	0.010	0.01	0.910
Litter*Urban	-0.232	9.05	0.003
Novel*Urban	0.019	0.118	0.731

Cox proportional hazards model, *N* = 225 observations, 140 events. Data contained only the two species from each group that visited the most (jackdaws/rooks and blue tits/great tits). The control condition served as the reference category for all object conditions, non-corvids for species group, and rural areas for habitat type. * denotes an interaction term

Table 5.S6 Cox proportional hazards models for latency to arrive at tables.

<u>Variable</u>	<u>Full model</u>			<u>Minimal model</u>		
	<u>rho</u>	<u>χ^2</u>	<u>P</u>	<u>rho</u>	<u>χ^2</u>	<u>P</u>
Date	-0.014	0.073	0.787			
Noncorv_before	-0.106	3.659	0.058			
Year	-0.094	3.284	0.070			
Condition*Species group						
<i>Litter*Corvid</i>	-0.061	0.947	0.330			
<i>Natural*Corvid</i>	-0.066	1.682	0.195			
<i>Novel*Corvid</i>	-0.021	0.084	0.771			
Condition						
<i>Litter</i>	0.026	0.172	0.679	0.065	0.817	0.366
<i>Natural</i>	-0.112	5.889	0.015	-0.167	9.891	0.002
<i>Novel</i>	0.029	0.157	0.692	0.028	0.143	0.705
Corvid	0.214	9.477	0.002	0.192	12.546	< 0.001
Urban	-0.048	0.544	0.461	-0.085	2.085	0.149
Cornwall	0.103	4.346	0.037	0.116	5.412	0.020
Corv_before	0.176	8.068	0.005	0.256	16.900	< 0.001
Time	-0.195	12.357	< 0.001	-0.168	7.607	0.006
Condition*Habitat						
Litter*Urban	-0.215	16.422	< 0.001	-0.243	21.609	< 0.001
Natural*Urban	0.068	2.158	0.142	0.045	0.703	0.402
Novel*Urban	-0.067	1.070	0.301	-0.055	0.637	0.425

Noncorv_before is a measure of whether a non-corvid species arrived before the current observation. Corv_before denoted whether a corvid species had arrived beforehand.

Significant p values ($p < 0.05$) highlighted in bold. The control condition was the reference category for all object conditions, rural areas for the urban gradient, and Cambridgeshire for the region.

Chapter Six

Social information and context influence wild jackdaws' responses to novelty and risk⁷



⁷ A version of this chapter has been published as: Greggor, A. L., McIvor, G., Clayton, N. S., & Thornton, A. (2016). Contagious risk taking: social information and context influence wild jackdaws' responses to novelty and risk. *Scientific Reports*, 6, 27764.

6.1 Abstract

Although wild animals increasingly encounter human-produced food and objects, it is unknown how they learn to discriminate beneficial from dangerous novelty. Since social learning allows animals to capitalize on the risk-taking of others, and avoid endangering themselves, social learning should be used around novel and unpredictable stimuli. However, it is unclear whether animals use social cues equally around all types of novelty and at all times of year. I assessed whether wild, individually marked jackdaws—a highly neophobic, yet adaptable species—are equally influenced by social cues to consume novel, palatable foods and to approach a startling object. I conducted these tests across two seasons, and found that in both seasons observers were more likely to consume novel foods after seeing a demonstrator do so. In contrast, observers only followed the demonstrator in foraging next to the object during breeding season. Throughout the year more birds were wary of consuming novel foods than wary of approaching the object, potentially leading to jackdaws' greater reliance on social information about food. Jackdaws' dynamic social cue usage demonstrates the importance of context in predicting how social information is used around novelty, and potentially indicates the conditions that facilitate animals' adjustment to anthropogenic disturbance.

6.2 Introduction

As humans drastically alter habitats worldwide we create novel stimuli, such as foods and objects. How animals respond to human-created novelty, and whether they learn to distinguish dangerous from beneficial stimuli, may crucially influence their survival and reproductive success (Chapter Seven; Robertson, Rehage, & Sih, 2013). Yet these stimuli often overlap in ways that make assessing their risk difficult. For example, while animals might be expected to approach certain combinations of novel food and man-made objects (e.g. crisps in a shiny packet on the pavement), people equally expect them to avoid other combinations of food and objects (e.g. reflective crop deterrents in a field). Although making incorrect assessments of these stimuli combinations can have serious consequences (e.g. promoting ecological traps; Gilroy & Sutherland, 2007), little is known about how animals learn about the novelty humans create.

Social cue usage is favoured when animals are uncertain, or when asocial learning is costly (Rendell et al., 2011); both of which are characteristic of encountering anthropogenic novelty. Even though theoretical models propose that using social cues helps animals adjust

to changing habitats (Brown, 2012; D. J. van der Post & Hogeweg, 2009), it is unclear how well these predictions apply to wild systems. Firstly, the motivation to approach novelty can vary with state (Reader & Laland, 2003), age (Miller et al., 2015), or season (Mettke-Hofmann, 2000). For example, birds go through dramatic physiological, and hormonal (Romero, 2002) changes in preparation for breeding, and often show changes in territoriality, social system, activity levels and caloric demands (Pdulka et al., 2004). Although these factors are likely to have substantial impacts on risk taking, and therefore social cue usage, studies rarely address these seasonal differences in ecology and behaviour (Marra, Cohen, Loss, Rutter, & Tonra, 2015). Moreover, while seasonal variation in exploration and object neophobia has been documented, its effects and directions are inconsistent (e.g. Apfelbeck & Raess, 2008; Klueen & Brommer, 2013; Mettke-Hofmann, 2000; Chapter Three), and it is unknown how this variation may impact social cue usage.

Secondly, it is unclear whether social information would be favoured to the same extent around different types of risk. Theoretical and empirical studies suggest that animals should rely on social cues both before consuming novel foods (Galef, 2009), and when deciding whether to approach potentially threatening objects (Griffin, 2004). However, avoidance of these different stimuli types does not always correlate within individuals (Marples & Mappes, 2011). Additionally, the same strategies may not be utilized in approaching novel versus threatening stimuli because different cognitive processes underlie novelty perception and risk assessment (Chapter One). For example, the hesitancy that animals may exhibit in approaching novel foods does not always correlate with measures of predatory wariness (e.g. Carter, Marshall, Heinsohn, & Cowlshaw, 2012; Chapter Three), thereby implying that different levels of risk may be involved in approaching novel versus known threats, or that responses stem from divergent processes such as taste sensitivity versus fear. Therefore, to understand how animals learn to distinguish beneficial from dangerous stimuli, it is critical we examine situations in which wild animals approach and learn about novelty that co-occurs with other forms of risk.

I investigated the influence of social cues on wild birds' foraging choices in populations where individuals regularly encounter beneficial and dangerous man-made stimuli. Like other birds of the corvid family, jackdaws (*Corvus monedula*) are highly neophobic (Greenberg & Mettke-Hofmann, 2001; Chapter Five) and highly innovative (Emery & Clayton, 2004; Nicolakakis & Lefebvre, 2000); a seemingly paradoxical combination since neophobia is thought to inhibit innovation (Greenberg, 2003; Griffin &

Guez, 2014). Jackdaws commonly utilize human resources (e.g. foods and nesting sites), but are legally classified as vermin (Wildlife & Countryside Act 1981) and are targeted by deterrents and active persecution (Henderson, 2002). Consequently, jackdaws provide an excellent system to assess how information about novelty is acquired around risk because their responses towards dangerous and beneficial novelty can determine their survival around humans. This is especially true in the village and farmland sites where I conducted this study, because corvids are culled in the surrounding area as a result of perceived conflict with humans (Chapter Two).

I measured the responses of individually marked, free-flying jackdaws towards novel coloured versus familiar food, in locations closer or farther from a startling camera that flashed when it detected motion. I ensured that food was perceived as novel, and reactions were not due to aversions toward a particular colour, by training different wild jackdaw groups in a series of experimental stages (see Figure 6.1). I measured the impact of social information on risk taking by comparing birds' choices between foraging bouts where other conspecifics (termed “demonstrators”) made risky choices to bouts where demonstrators chose the relatively safer food or location option.

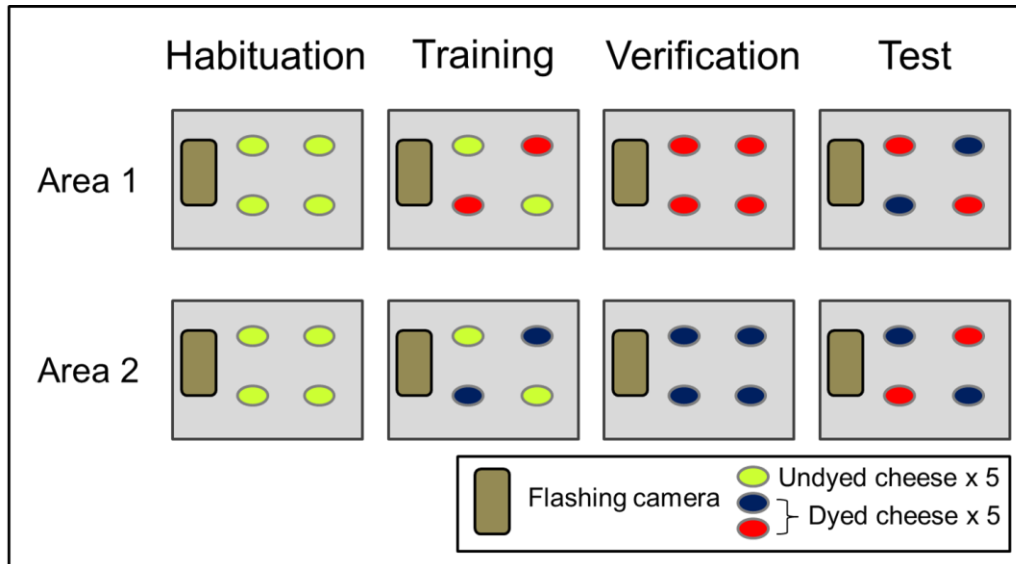


Figure 6.1 Experimental setup and stages. The habituation stage contained only known, yellow cheese. Training trials contained yellow cheese and a dyed training cheese to allow for a separation of the fear of approaching the food (neophobia) from the fear of consuming it (dietary conservatism). Verification trials ensured birds would forage without the presence of previously known cheese. Test trials determined that responses to each colour were not based on innate avoidance of a particular colour. Each table progressed to the next stage if cheese reliably disappeared from the table for at least three trials in a row. Area 1 and Area 2 were separated by 1.5km

As novel foods and a startling object both pose potential risks, I predicted that jackdaws would rely on social information in guiding their food and foraging location choices. Since jackdaws' forage in large flocks during winter and forage alongside their mate and members of their breeding colony during the breeding season (Röell, 1978), they have access to social foraging cues all year. However, I anticipated the effects of social information would change across the year as seasonal influences on motivation and risk aversion would influence social information use. Given that corvids often have increased caloric requirements during the breeding season (Feare et al., 1974), and hunger can stimulate risk taking (Damsgard & Dill, 1998), one may expect that breeding jackdaws would be more willing to take risks, and therefore less reliant on social information in the breeding vs nonbreeding season. Since social cues would theoretically be more useful in contexts of higher risk, I expected that fewer birds would take risks in approaching either stimulus type at times of year where social information use was highest.

6.3 Results

6.3.1 Influence of social information

I found that jackdaws were more likely to eat a novel food if a demonstrator had just done so, and this effect was strongest during the *training* stage of the experiment (GLMM, $n = 212$ visits by 44 individuals, interaction term, $\text{Est} = 3.13 \pm 1.27$, $z = 2.46$, $P = 0.014$; Figure 6.2). Additionally, observers were more likely to eat the novel food when more trials had been run at each table ($\text{Est} = 0.23 \pm 0.11$, $z = 2.07$, $P = 0.038$), and observers that landed on the risky side of the table were less likely to eat novel food ($\text{Est} = -1.21 \pm 0.59$, $z = -2.06$, $P = 0.040$). Season did not have an impact on social cue usage about food, nor did sex, age, or the demonstrator's proximity to the camera (see Supplemental Table 6.S1).

In contrast, the presence of a demonstrator near the camera only encouraged observers to land on the risky side of the table during breeding season (GLMM, $n = 516$ visits by 85 birds, interaction term, $\text{Est} = 0.86 \pm 0.42$, $z = 2.06$, $P = 0.039$; Figure 6.3). Although birds were more likely to land near the camera during the *training* stage, than the *habituation* stage ($\text{Est} = 0.76 \pm 0.22$, $z = 3.29$, $P < 0.001$), the experimental stage did not impact social cue usage. Similarly to the food choice model, the observer's location predicted their food choice, such that birds which chose the risky side of the table were less likely to eat the novel cheese ($\text{Est} = -0.96 \pm 0.30$, $z = -3.16$, $P = 0.002$). Additionally, sex, age, and trial number, did not impact the observer's likelihood of landing on the risky side of the table, nor did it impact their use of social information (see Supplemental Table 6.S2).

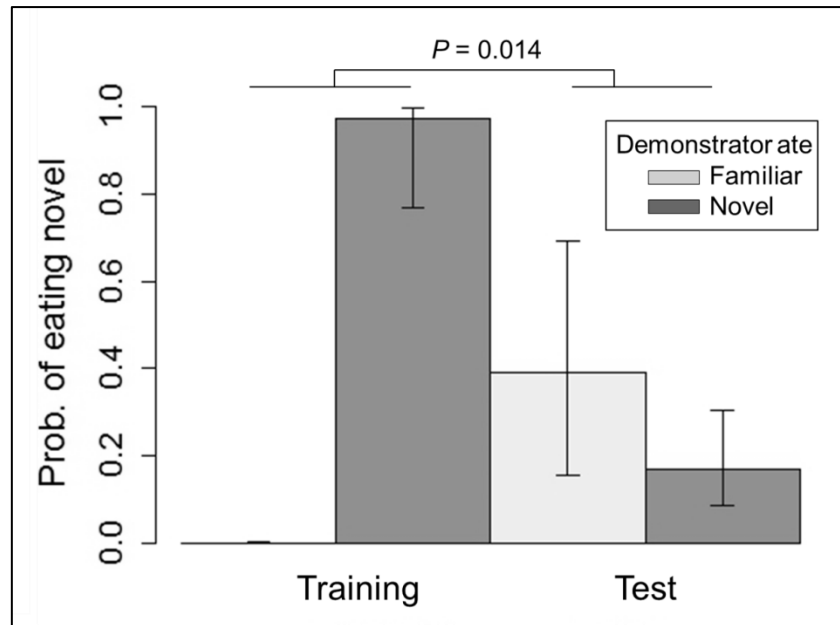


Figure 6.2 Novel food consumption. Predicted likelihood of the observer consuming the novel food depending on the demonstrator's food choice and the stage of experiment. GLMM, $n = 212$ visits by 44 individuals, Demonstrator_food*Stage, Est = 3.13 ± 1.27 $z = 2.46$, $P = 0.014$. Whiskers denote standard errors.

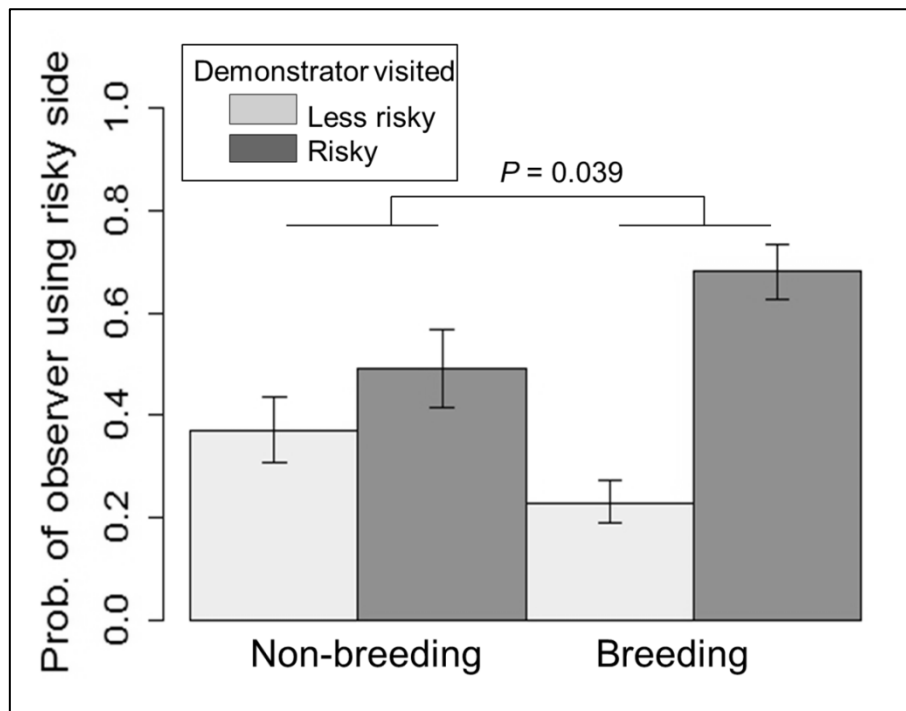


Figure 6.3 Table side. Predicted likelihood of observers using the risky side of the table based on where demonstrators landed and the season. GLMM, $n = 516$ visits by 85 birds, Demonstrator*Season, Est = 0.86 ± 0.42 , $z = 2.06$, $P = 0.039$. Whiskers denote standard errors.

6.3.2 Seasonal differences in motivation and risk perception

In both seasons, a greater proportion of individuals avoided consuming the novel test food than avoided foraging near the camera (non-breeding, 88% vs 22%; $\chi^2 = 14.57$, $df = 1$, $P < 0.001$; breeding, 77% vs 27%; $\chi^2 = 11.05$, $df = 1$, $P < 0.001$). Overall, the subset of individuals that participated in both seasons did not become significantly more or less fearful across the year for either type of stimuli (novel food, McNemar's $\chi^2 = 3.13$, $df = 1$, $P = 0.077$; camera, McNemar's $\chi^2 = 0$, $df = 1$, $P = 1$). The apparent trend towards significance in the case of novel foods can be explained by the fact that the majority of individuals did not differ in their fear of novel food between seasons (26 birds), but seven individuals were less fearful of novel food in breeding season, while one individual was more fearful during breeding season.

6.4 Discussion

I found that the type of risk and time of year are critical in determining jackdaws' use of social cues. Jackdaws were more likely to consume novel foods after witnessing a demonstrator do so throughout the year, but only copied risk-taking demonstrators in approaching a startling object during the breeding season. The greater stability of social cue usage around novel food may arise if birds perceived sampling novel food as riskier than approaching a startling object. Consistent with this suggestion, the total number of birds that consumed novel foods was lower than the number that approached the camera, regardless of season. The finding that jackdaws were only influenced by social cues in approaching a startling object during the breeding season suggests that, contrary to my expectations, breeding-related changes in motivation do not result in heightened individual risk-taking in this context. Instead seasonal changes in other factors such as the birds' social dynamics may generate differences in attention towards conspecifics that could have contributed to the patterns of social cue usage I found.

Jackdaw's consistently high levels of novel food avoidance provide empirical support for the suggestion that corvids are very neophobic (Chapter Five; Greenberg & Mettke-Hofmann, 2001). The jackdaw population had a comparatively larger percentage of food-wary individuals than what has been reported for populations of other passerine species when the data is compared over a similar number of trials (86-88% vs 26%; Marples, Roper, & Harper, 1998). Typically, low levels of neophobia are thought to facilitate innovation (Griffin & Guez, 2014; Reader & Laland, 2003), which aids behavioural adjustment to human-

induced environmental change (Anders Pape Møller, 2009). However, corvids counter this trend because they are among the most innovative of birds (Emery & Clayton, 2004; Nicolakakis & Lefebvre, 2000), and are often dependent on anthropogenic food sources (e.g. ravens, Baltensperger et al., 2013; O'Brien, Larcombe, Meyer, Forbes, & Dadour, 2010; jackdaws, Holyoak, 1968; Lockie, 1956), despite being highly neophobic (Chapter Five; Greenberg, 2003). These findings offer a potential route through which corvids may overcome their neophobia. If certain individuals approach novel foods or man-made objects, others can exploit the social information they generate, thereby overcoming their fear.

Despite the potential value of social information, these results demonstrate that the use of social cues to guide behaviour is not consistent, but rather depends critically on the nature of the stimulus and the time of year. Social cues only influenced behaviour around the startling object during breeding season, and it is unclear what aspect of seasonal change generated this pattern. Since more birds were willing to approach the camera than eat the novel foods in both seasons, approaching the camera may have been perceived as a less risky behaviour. With less risk or more motivation to approach risk, one would predict a reduced reliance on social cues. However, I did not find greater overall avoidance of the camera during the breeding versus the non-breeding season, so the seasonal increase in social cue use around objects is unlikely to stem from an increase in wariness of the camera alone. The seasonal effect can also not be attributed to a greater habituation to the camera over time because reduced fear of the camera would in theory have produced greater individual risk taking and lesser use of social cues; an opposite pattern of social cue usage to what I found. Instead, I suggest that the change in social cue usage may be influenced by seasonal changes in attention because jackdaws social interactions change across seasons (Röell, 1978). Since there are many seasonal behaviours that alter social interactions, such as winter roosting (Marzluff, Heinrich, & Marzluff, 1996), I suggest such seasonal differences in social cue usage may be common in other species, and could indicate that animals may be better able to adjust to man-made novelty at certain times of year.

In contrast, the wariness and use of social cues around novel food was stable across seasons, but the extent of reliance on social cues depended on the degree of the food's novelty. I found stronger social cue usage around food in the training versus the test trials. Birds had more experience with the habituation cheese in comparison to the training cheese, than they had with the training cheese in comparison to the test cheese. Therefore the contrast in experience between the two cheese types was much greater during training trials,

indicating that the perceived novelty of any stimulus may be a relative consequence of experience, not an absolute one that changes after a single exposure. If the perceived degree of novelty does not fade entirely after a single exposure to a stimulus, then social cues may still be relied upon during subsequent encounters, and could have guided choices during the test phase towards the training cheese.

Since jackdaws responded similarly to social cues around food in both seasons, social influences would likely shape how they exploit anthropogenic foods year round. Although dietary breadth is a predictor of success in urban areas (Charles & Linklater, 2013), dietary wariness and its reduction through social learning is not commonly studied in the context of anthropogenic disturbance. However, if individuals overcome their dietary wariness by observing others (e.g. McMahon, Conboy, O’Byrne-White, Thomas, & Marples, 2014) they may be better equipped to exploit human resources. As jackdaws are reliant on exploiting human-produced food in rural areas (Lockie, 1956) and corvids have been reported to consume human refuse (Rowley & Vestjens, 1973), social learning may be particularly important in allowing them to survive alongside humans.

When social influences increase the likelihood that animals interact with novel and threatening stimuli, social cues may also facilitate learning about such stimuli. Social learning can play a role in spreading human-dependent foraging through populations, thereby increasing human-wildlife conflict (e.g. Donaldson, Finn, Bejder, Lusseau, & Calver, 2012). However, as I found that not all social cues around novelty are equally influential, (i.e. whether observers copied demonstrators’ risk taking depended on the stimulus type and time of year) social learning may only occur in certain contexts. Determining where and how social cue usage leads to learning and to novel behaviours is likely to be critical in helping us reduce maladaptive responses to man-made novelty, and mitigate the effects of environmental change (see Chapter Seven).

6.5 Methods

6.5.1 Study site

Experiments were run in Cornwall, in the Southwest of the UK, on free-flying wild jackdaws that were colour ringed following capture in ladder traps or nest boxes as part of the Cornish Jackdaw Project. Two sites, each with two feeding tables were established in locations where humans visit and disturb the area several times an hour: one site in a busy

village churchyard (50°11'26"N, 5°10'51"W), the other in an active farmyard (50°11'56"N, 5°10'9"W). The sites were located within 1.5 km of each other. Only one individual was seen at both sites throughout the study and was excluded from the analysis. Sex was determined from a blood sample taken during ringing, and age determined by plumage characteristics or known hatch dates. The population is monitored throughout the year, so the stage of breeding attempts was known. Mild cheddar cheese was used as a reward in experiments at these sites and was familiar to all birds.

6.5.2 *Ethical Statement*

Experiments and bird ringing were carried out under approval of Home Office license (PIL 70/25311, PPL to AT 80/2371) and British Trust for Ornithology license (no. C6079, C5752, C5746), and conducted in accordance with the ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching ("Guidelines for the treatment of animals in behavioural research and teaching," 2012)

6.5.3 *Experimental set-up*

I conducted the same experiment twice within one year: during the non-breeding season in November to December 2014 ($n = 91$ trials; Table 6.S3), and breeding season from April to early May of 2015 ($n = 93$ trials; Table 6.S4) while the birds were building nests and laying eggs. All breeding season trials finished before the first chicks hatched so that birds were choosing food to feed themselves or their partners rather than their chicks.

Each trial consisted of a 90 minute presentation of food alongside a motion-activated camera with flashing lights (see Figure 6.4). Twenty pieces (1cm^3) of cheese were placed on a feeding table, split evenly into the 4 corners of the table. The camera was placed approximately 10cm away from one side of the table, such that two of the food choices were considerably closer to the camera. The camera housing had small red, blue and green lights that flashed repeatedly within 1-2 seconds of a bird's landing (camera housing dimensions 90x80x120mm; Concept Shed, Falmouth, UK). A separate camcorder (Panasonic HC-V130) was set up 20m away to verify that the motion camera detected all visitors. Each time a bird landed on the table it counted as a visit.

Cheese was replenished once during the trial if all pieces had been eaten. In trials where cheese of different colours was presented (see stages below), their location was switched at the rebait. One trial was run at each table every day.

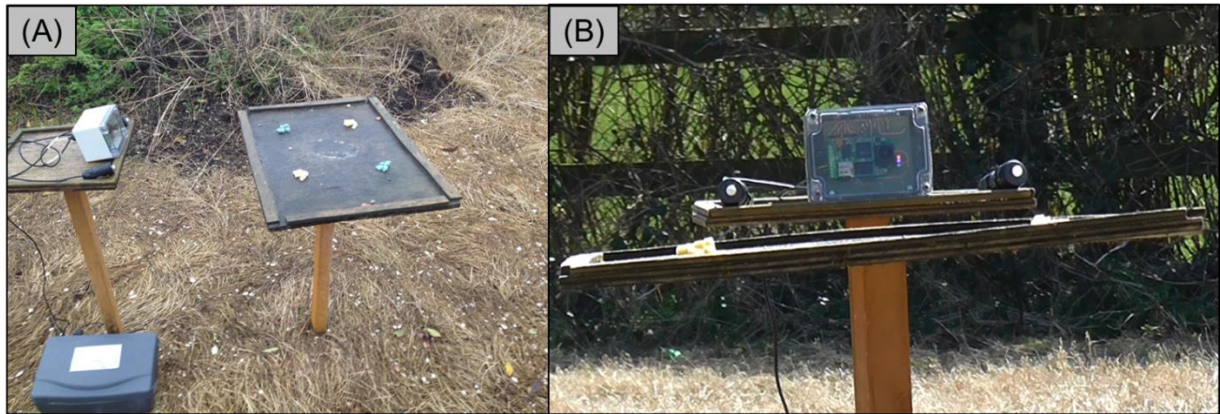


Figure 6.4 Table setup with flashing motion camera. (A) Aerial view of a training stage trial with blue cheese. (B) View from the table with camera lights flashing. There were two tables set up at each of the two study sites.

6.5.4 Experimental stages

The experiment had several stages (adapted from Marples et al., 1998), all which had the motion camera present: *habituation*, *training*, *verification*, and *testing*. In the *habituation* phase I presented plain, undyed yellow cheese, to determine which individuals would eat a familiar food at the table. *Training* trials offered a novel colour alongside undyed cheese, allowing for the separation of neophobia (fear of approaching the food) from dietary conservatism (reluctance to incorporate novel foods into the diet, *sensu* Marples & Kelly, 1999), as birds feeding on familiar cheese next to the training colour were not deterred by the sight of the novel colour. In the non-breeding season, both tables at one site received red as their training colour, while the other site received blue. In breeding season one site received green and the other black. All four colours have previously been shown to elicit avoidance in captive birds (e.g. Marples, Quinlan, Thomas, & Kelly, 2007). Moreover, the hesitancy jackdaws demonstrated towards them during initial training trials confirmed they were also aversive to wild birds. The experiment moved on to the *verification* stage if all cheese reliably disappeared from the table for at least three trials in a row. *Verification* trials contained only the training colour to ensure that individuals were attracted to this colour without regular cheese present. Finally, in *test* trials, birds were given a choice test containing two piles of their training cheese, and two of a novel cheese colour. The population that received blue for training received red as their novel colour, and vice versa. The same reversal of training and novel cheeses occurred for the breeding season colours. Thus trained colour preferences were group-specific, yet arbitrary (see Figure 6.1).

Cheese was coloured by melting and adding food-safe dyes (Sainsbury's brand). The same number of drops of dye was used for each colour over the course of the experiment. Measurements of each cheese were taken using a spectrometer to verify that birds could discriminate between them. Spectral readings were separated by at least 3.6 just noticeable differences (JNDs; values less than one JND are indistinguishable (Vorobyev & Osorio, 1998) and were plotted in the avian visual space using the pavo package in R (Maia et al., 2013) (see Figure 6.S1).

6.5.5 Data analysis

Both motion and camcorder videos were analysed for each trial. For each visit of each trial the following information was recorded: the configuration of cheese on the table when the bird arrived, the visiting bird's identity, and the colour, amount and location of cheese eaten (either camera side of table or not). Food was never knocked off the table by foraging birds, nor did I observe birds stealing food gathered by others, so only individuals visiting the table had the opportunity to feed during the experiment (i.e. there was no scrounging or theft). All bird identities were verified by an additional coder, blind to the stage of the experiment. In the few ($n=16$) instances where there was a discrepancy between colour-ring combinations recorded by coders, original videos were consulted and a decision on bird identity was made.

6.5.6 Statistical Analysis

All data were analysed in R (R Core Team, 2015). Birds were deemed to have access to a demonstrator if a conspecific landed to forage at the table less than 30 seconds before their arrival, since foraging groups that I observed tended to gather for longer than this time around the table. As the mere presence of conspecifics has been shown to influence corvids' levels of object exploration (Miller et al., 2014; Stöwe, Bugnyar, Heinrich, & Kotrschal, 2006), observations without demonstrators were removed (401 observations in food analysis, 770 observations in location analysis). This criterion allowed for a comparison of food and location choices based on social information use, not social facilitation. Unringed birds could act as demonstrators, but only individually recognisable, ringed birds were included as observers. Observers' food choice (novel/familiar) and table side choice (near to/far from the camera) were analysed as separate GLMMs (R package, lme4; Bates, Maechler, Bolker, & Walker, 2013) with a binomial error structure and logit link function. The food choice analysis only included *training* and *testing* observations when birds had a choice between

familiar and novel cheese (169 observations had no food choice). Any birds that had not eaten the familiar cheese prior to that stage were removed (88 observations). The side choice analysis included all experimental stages, but only visits where cheese was available on both sides (262 observations removed). Models investigated the main effects of the observer's sex and age, the season of the trial, the demonstrator's choice, the observer's choice in the other response variable (i.e. their food during side analysis; their side during food analysis) and two-way interactions between all main effects on whether observers chose the riskier option ($Y = 1$, $N = 0$). Models also included the potential effects of trial number and experimental stage. Since one table took two more trials than any other to progress past the *training* stage, trial number was capped at the highest number that all tables shared. Bird identity and trial were fitted as random effects. Final models were determined following backwards stepwise elimination of variables based on model AIC values (Zuur et al., 2009). Effects were retained if their exclusion increased AIC values by at least 2. Once final models had been established, P-values and effect sizes of contributing variables were calculated for reporting in text, but all tables refer to changes in AIC (see Tables 6.S1-2).

Differences in social information use between stimuli type or season could arise if approaching the novel food and the camera was differentially risky. To test differences in risk aversion between stimulus types, I conducted chi-squared tests on the proportion of birds that never consumed a piece of novel food in test trials, versus the proportion that never foraged on the risky side of the table (near the camera). I also determined whether the population was stable in these traits over the seasons by conducting a McNemar's chi squared test on the subset of birds ($n = 39$) that participated at both time points. McNemar's test is for paired data and can be used with binary responses.

6.6 Supplementary materials

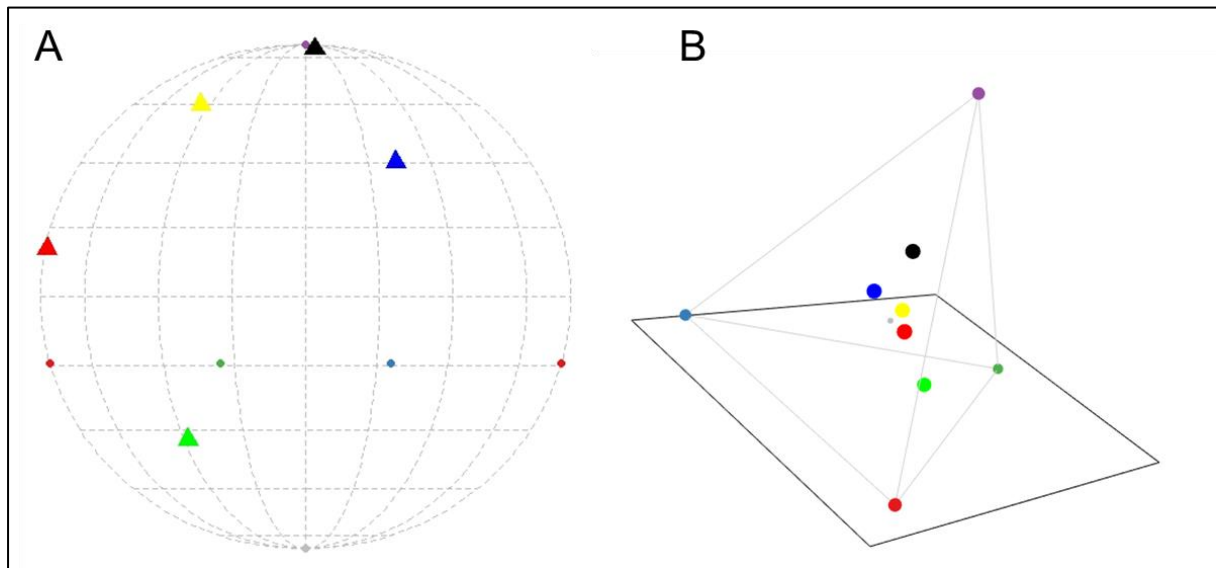


Figure 6.S1 Colour plots. Two dimensional (A) and three dimensional (B) projection plot of cheese types in the avian tetrahedral visual space. Both plots show that cheese colors are visually distinct. Cheese colors are represented by triangles in (A), by central points in (B). Circles in (A) and triangle vertices in (B) provide reference points to the limit of visible wavelength for each receptor type.

Tables 6.S1-S2. Detailed binomial GLMM statistical analysis. Final models are marked in bold, and were reached when no remaining factors could be dropped without AIC values increasing by at least 2. Random effects of bird identity and trial were included in all models. Obs = Observer, Dem = Demonstrator

<u>n = 212 visits, 44 individuals</u>	<u>ΔAIC</u>
Obs_food~ Dem_food + Trial_num+ Stage+ Obs_side + Dem_food*Stage + Age + Dem_side + Season + Dem_food*Season + Dem_food*Trial_num + Sex + Dem_food*Age	0.0
Obs_food~ Dem_food + Trial_num+ Stage+ Obs_side + Dem_food*Stage + Age + Dem_side + Season + Dem_food*Season + Dem_food*Trial_num + Sex	-2.0
Obs_food~ Dem_food + Trial_num+ Stage+ Obs_side + Dem_food*Stage + Age + Dem_side + Season + Dem_food*Season + Dem_food*Trial_num	-1.9
Obs_food~ Dem_food + Trial_num+ Stage+ Obs_side + Dem_food*Stage + Age + Dem_side + Season + Dem_food*Season	-1.7
Obs_food~ Dem_food + Trial_num+ Stage+ Obs_side + Dem_food*Stage + Age + Dem_side + Season	+0.5
Obs_food~ Dem_food + Trial_num+ Stage+ Obs_side + Dem_food*Stage + Age + Dem_side	-1.6
Obs_food~ Dem_food + Trial_num+ Stage+ Obs_side + Dem_food*Stage + Age	0.0
Obs_food~ Dem_food + Trial_num+ Stage+ Obs_side + Dem_food*Stage	+1.8

Table 6.S1 Dem_food = Influence of demonstrator's food choice on observer food choice (Novel = 1, Familiar = 0). Dem_side = Influence of demonstrator's table side choice on observer food choice (Scary side = 1, Less scary side = 0). Since no females observed a demonstrator eating a novel cheese, Demonstrator_food:Sex interaction was not included. Age could only just be dropped. When included, younger birds were borderline more likely to eat novel food colors (Est = 1.83±0.93 z = 2.0, P = 0.05).

<u>n = 506 visits, 81 individuals</u>	<u>ΔAIC</u>
Obs_Side ~ Dem_side + Season + Dem_side*Season + Obs_Food + Stage + Dem_food + Age + Dem_side*Age + Trial_num + Dem_side*Trial_num + Sex+ Dem_side*Sex + Dem_side*Stage	0.0
Obs_Side ~ Dem_side + Season + Dem_side*Season + Obs_Food + Stage + Dem_food + Age + Dem_side*Age + Trial_num + Dem_side*Trial_num + Sex+ Dem_side*Sex	-1.7
Obs_Side ~ Dem_side + Season + Dem_side*Season + Obs_Food + Stage + Dem_food + Age + Dem_side*Age + Trial_num + Dem_side*Trial_num + Sex+ Dem_side*Sex	-1.5
Obs_Side ~ Dem_side + Season + Dem_side*Season + Obs_Food + Stage + Dem_food + Age + Dem_side*Age + Trial_num + Dem_side*Trial_num	-1.1
Obs_Side ~ Dem_side + Season + Dem_side*Season + Obs_Food + Stage + Dem_food + Age + Dem_side*Age + Trial_num	+0.1
Obs_Side ~ Dem_side + Season + Dem_side*Season + Obs_Food + Stage + Dem_food + Age + Dem_side*Age	-0.9
Obs_Side ~ Dem_side + Season + Dem_side*Season + Obs_Food + Stage + Dem_food + Age	-0.1
Obs_Side ~ Dem_side + Season + Dem_side*Season + Obs_Food + Stage + Dem_food	-2.0
Obs_Side ~ Dem_side + Season + Dem_side*Season + Obs_Food + Stage	+1.0

Table 6.S2. Dem_side = Influence of demonstrator's table side on observer table side. (Scary side = 1, Less scary side = 0). Dem_food = Influence of demonstrator's food choice on observer table side (Novel = 1, Familiar = 0)

Table 6.S3 Number of trials run per experimental stage per table in the non-breeding season.

	Habituation	Training	Verification	Test
Church Wall	4	10	1	7
Church Field	4	7	4	6
Farm Coop	5	9	2	9
Farm Silo	4	9	1	9

Table 6.S4 Number of trials run per experimental stage per table in the breeding season.

	Habituation	Training	Verification	Test
Church Wall	5	5	3	7
Church Field	6	6	3	7
Farm Coop	5	10	2	7
Farm Silo	6	12	2	7

Chapter Seven

Discussion

Corvid neophobia in a human dominated world^{8,9}



⁸ Parts of the section of this chapter entitled “Determining the ecological consequences of neophobia” have been published in: Greggor, A. L., Thornton, A., & Clayton, N. S. (2015). Neophobia is not only avoidance; improving neophobia tests by combining cognition and ecology. *Current Opinion in Behavioral Sciences*, 6, 82–89.

⁹ Parts of the section “Using cognition for conservation” have been adapted from: Greggor, A. L., Clayton, N. S., Phalan, B., & Thornton, A. (2014). Comparative cognition for conservationists. *Trends in Ecology & Evolution*, 29(9), 489–495

Neophobia is often suggested to function as a species-level trait that shapes animals' foraging and space-use decisions to reinforce their ecological niche (Greenberg & Mettke-Hofmann, 2001; Mettke-Hofmann, 2014). Accordingly, neophobia is expected to be elevated in species that occupy particularly dangerous niches (Brown, Chivers, Elvidge, Jackson, & Ferrari, 2013; Greenberg, 2003), and to be reduced in generalist species that benefit from exploiting novelty (i.e. the Neophobia Threshold Hypothesis; Greenberg & Mettke-Hofmann, 2001), sometimes with innovative behaviour (Greenberg, 2003). Many species follow these trends. For example: parrot species that feed on insects, and therefore are more likely to encounter poisonous food, are more neophobic than leaf-eating species (Mettke-Hofmann et al., 2002); invading cane toads that are expanding their niche have lower neophobia than native populations (Candler & Bernal, 2015); and specialist kangaroo rats show higher neophobia than generalist species (Daly, Rauschenberger, & Behrends, 1982). However, what about species that occupy a dangerous niche, but are also ecological generalists? The case of corvids highlights how the two hypotheses surrounding neophobia can produce conflicting predictions about a species' optimal level of neophobia, since corvids are neophobic and yet are mainly generalist species that inhabit a diverse range of environments. Is the high neophobia of the corvid family the result of occupying a dangerous niche, and if so, how do they overcome their fear to be such a generalist set of species?

This dissertation has examined the causes and ecological consequences of neophobia in corvid species. I have shown that individuals are consistent in their neophobia during, but not between seasons (Chapter Three); that the links between neophobia and fitness are not straightforward (Chapter Four); that urban and rural populations do not differ in neophobia, but may differ instead in how they categorize types of stimuli (Chapter Five); and that individuals often use social information when approaching novelty, but these effects depend on the type of stimulus (Chapter Six, see Table 7.1 for full summary of results). When considered together, the chapters highlight several aspects of neophobia that deserve future research if the causes and ecological consequences of neophobia are to be understood. Namely, the stability of neophobia amid changing environmental conditions, the influence of the social environment, and what happens when neophobia subsides need to be explored further. Each of these topics will be crucial to explaining the relationship between corvid neophobia and their generalist niche. I will propose that learning, not just neophilia or curiosity, is a crucial yet understudied link in determining how neophobia influences a species' ecological niche breadth, and may be important to understanding corvid success.

Finally, I will develop ideas about how insight into neophobia, alongside learning processes, is necessary for predicting and mitigating animals' responses to novelty in the context of human induced environmental change.

Table 7.1 Summary of Results

Chapter	Main research questions	Main findings	Conclusions
<u>Three</u> Consistency in neophobia	Do neophobia levels and/or reactions to novel people change seasonally? Does dominance influence neophobia levels? Are individuals consistent in their novelty responses across time, and between novelty types?	It depends. Object neophobia levels did not change, but fear of novel people is lower in breeding season. No. Dominants were more likely to approach in control and tests. It depends. Individuals were consistent within seasons for both measures, but not consistent between seasons in object neophobia. Responses towards both novelty types correlated only in breeding season.	When tested over a short time period, individuals can be consistent, but may not be over longer periods. Reactions to novel people and objects involve different mechanisms.
<u>Four</u> Fitness, CORT, and neophobia	Do neophobia levels predict reproductive success, the ability to forage, and the developmental quality of offspring? Does the rearing environment influence offspring CORT levels?	No. Neophobia does not correlate with fitness, provisioning rates, or offspring's body condition and hormone levels. Yes. Larger broods had higher baseline CORT and later hatching nests had higher stress-induced CORT.	Neophobia may not incur obvious costs or benefits while breeding. Rearing conditions influence stress physiology, which might explain variation in adult neophobia levels.
<u>Five</u> Neophobia across urban gradients	Are corvids more neophobic than other species? Do urban populations have lower neophobia?	Yes. Corvids were more fearful of all object types than non-corvid species. No. Neophobia levels were similar across urban gradients, but urban birds were less wary of litter.	Despite increased neophobia in comparison to other species, corvids respond similarly to urban gradients as other birds do. Urban birds have

	Do corvids respond differently to the objects after conspecifics forage near them?	Yes. Corvids were less wary of natural and litter objects after a conspecific had foraged, but still avoided novel objects	different novelty categories than rural ones. Social cues may help corvids make these distinctions.
<u>Six</u> Social information and response to novelty	Do social cues influence novelty approach in different seasons? Do social cues encourage risk taking equally around different stimuli types?	Yes. Social cues encourage the consumption of novel food all year. No. Social cues only encourage approach towards risky objects in breeding season, while they were equally influential for food all year.	Social cues may allow more neophobic individuals to overcome their fear and exploit anthropogenic novelty.

7.1 Revisiting the corvid neophobia paradox

In Chapter Five I found evidence that several members of the corvid family are highly neophobic in direct comparison to other bird species, even when presented with natural-type objects that they encounter every day. Moreover, the jackdaw population I studied had a larger percentage of food wary individuals than percentages reported for other wild passerine species (Chapter Six; Marples, Roper, & Harper, 1998). This evidence confirms the common, but largely unquantified suggestion that corvids are a highly neophobic family (Greenberg & Mettke-Hofmann, 2001; Heinrich et al., 1995; Heinrich, 1988). In the case of UK corvids, their high levels of neophobia cannot be explained by several of the factors that often are suggested to contribute to a dangerous niche. For instance, corvids do not face high predation pressure from natural predators in contexts where neophobia would help them because their only, albeit rare, predators are large raptor species that come from above (Coombs, 1978), not from ground-based novel objects or food. What corvids do face is conflict with humans. It has been argued, for instance, that ravens' high neophobia around food could be a product of human persecution at bait sites (Heinrich, 1988). Meanwhile evidence suggests that corvids have responded to persecution stemming from human conflict with increased wariness (Clucas & Marzluff, 2012). However, such wariness does not explain how corvids can be so successful across a variety of habitats, because neophobia alone should restrict learning (Seferta, Guay, Marzinotto, & Lefebvre, 2001) and niche breadth (Mettke-Hofmann, 2014).

Thus, neophobia is only one part of the process. While neophobia may allow corvids to initially avoid dangerous stimuli that humans create, the evidence I outline below suggests that learning to classify novel stimuli is equally important, and is crucial to explaining how corvids can be so neophobic, yet also such generalists. First, however, I will explain what evidence I have found that neophobia is under selection at all.

7.1.1 Selection on neophobia: individual variation, stability and fitness consequences

The ability of natural selection to influence any cognitive trait depends on there being individual variation that is heritable and influences fitness outcomes (Thornton, Isden, & Madden, 2014). Since fear-related traits such as startle responses (van Oers, Drent, de Goede, & van Noordwijk, 2004), exploration tendencies (Dingemanse, 2002), and stress hormone levels (Jenkins et al., 2014) have been shown to be heritable, the heritability of neophobia is not a topic I am going to explore further here (however, see Dingemanse, 2002). Although such explorations are warranted, especially in wild populations, they will not be helpful for explaining selection on neophobia unless individuals vary, are consistent in their behaviour, and experience differential fitness outcomes based on neophobia levels (Thornton & Wilson, 2015).

Although corvid species in my experiments expressed elevated neophobia in comparison to other species, individual corvids differed substantially in their responses. I found evidence for individual variation in every data chapter. In captive rooks, individuals differed in their fear of objects and of people (Chapter Three). Similarly, individual wild jackdaws differed in their object neophobia (Chapter Four), wariness of new foods, and their approach of a consistently presented, yet startling object (Chapter Six). When I assessed several species of corvids in Chapter Five, I found differences between the first arriving individuals and how long it took conspecifics to forage, thereby implying that the first arriving birds had lesser neophobia than late arriving birds. Individuals in natural foraging groups usually differ in their neophobia levels (Aplin, Farine, Mann, & Sheldon, 2014; Benson-Amram & Holekamp, 2012), and the corvid species studied in this dissertation appear to be no exception.

For there to be selection on the expression of neophobia as a trait, individual variation must be consistent over time, or at least be consistent within similar life stages or environmental conditions that could provide predictable selection pressures, such as seasons. Jackdaws were consistent in their neophobia within breeding season (Chapter Four), and

rooks were consistent within seasons in their object neophobia and fear of novel people (Chapter Three). Since studies rarely address changes in ecology and behaviour over the full annual cycle (Marra et al., 2015), despite such changes being vital to survival and reproduction amid fluctuating environmental conditions, I also assessed neophobia across seasons. I found that even though individuals may not be consistent throughout the year, the mean levels of neophobia in a group or population are surprisingly robust to seasonal change. In rooks, the expression of object neophobia within a social group did not change across seasons, even though hunger or motivation for food increased. Meanwhile a similar number of wild jackdaws avoided novel foods and approaching a startling object across seasons. Conversely, responses to novel people—a stimulus that may also trigger an anti-predator reaction (Frid & Dill, 2002)—were reduced during breeding season (Chapter Three).

What could explain the difference in group stability between different types of neophobia and stimuli that are more predator-relevant? Behavioural fear reactions are linked to increases in stress hormones (Romero, 2004), and these hormones are known to vary seasonally in a variety of species (Romero, 2002). Theoretically, any stimulus that evokes an anti-predatory response would be more directly linked to hormone levels than those that depend first on a novelty assessment before fear circuits are triggered (as is the case for neophobia; Chapter One). Therefore responses towards novel people may be influenced more heavily by seasonal changes in hormone levels than would responses to novel foods or objects. This theory is supported by the fact that even the sight of a predator can trigger stress hormone release (Cockrem & Silverin, 2002a; Vitousek, Jenkins, & Safran, 2014), while evidence is mixed as to whether the presence of novel objects elicit the same reaction (Mettke-Hofmann et al., 2006; Richard et al., 2008). The environmental conditions under which seasonal fluctuations in hormones and food availability influence variation in cognitive mechanisms is a growing topic (Maille & Schradin, 2016), and is particularly relevant to understanding why seasonally changing resources do not seem to influence group or population neophobia levels.

With evidence for individual variation and for stability in neophobia, at least within-seasons (Chapters Three and Four), selection could act on neophobia as a trait. One would expect that if corvids had high neophobia because they fill a niche made dangerous through conflict with humans, then (1) higher neophobia may have fitness benefits; and (2) levels of neophobia should be elevated around humans. However, I found no evidence linking neophobia and short-term reproductive success (Chapter Four), or evidence that neophobia

differs across population that might be experience contrasting costs and benefits for neophobic behaviour (Chapter Five). There are several potential explanations for these null results. Firstly, although I found no impact of neophobia on the quality of offspring or the rearing environment they experience, variation in neophobia could impact survival under different environmental conditions. For example, the influence of exploratory behaviour on reproductive success has been shown to depend on food availability in great tits, such that it only predicted success in certain years (Dingemanse, Both, Drent, & Tinbergen, 2004). Therefore the lack of connection between neophobia and fitness could be due to the conditions of the particular year I tested. Meanwhile, the fact that I found no population level difference in neophobia between urban and rural areas suggests that neophobia may not be differentially favoured in either of these environments. However, the density of human population may not be an accurate indicator of environmental conditions that create conflict with corvids. Alternatively, I might have found differences had I compared habitats that were denser than the urban areas I tested (which were closer to the suburban range of habitat disturbance).

Neophobia levels could be important for determining survival at a different life stage or time of year than the one I measured. For example, artificially increasing levels of neophobia in juvenile whitetail damselfish (*Pomacentrus chrysurus*) by exposing them to predatory alarm cues, has been shown to increase survival upon reintroduction to the wild at a time when they would be naïve to predators (Ferrari et al., 2015). Later in life, such as during breeding, this same behaviour may not influence the number of offspring they produce, but would have influenced their chances of reaching breeding age. Meanwhile, there could be habitat-specific changes to human activity during the summer months—as opposed to the winter when I tested urban/rural dynamics—that could trigger population differences between habitats. However, the stability of group neophobia that I found between seasons (Chapter Three, Six) makes it less likely that temporal differences in human activity would influence population neophobia levels in this way.

Long-term studies of the survival rates and lifetime reproductive success of individuals of varying neophobia levels could reveal whether neophobia influences fitness under different yearly conditions and life stages. That being said, the studies I conducted indicate that neophobia may not be associated with fitness outcomes despite the individual variation and high levels of neophobia that corvids express. Perhaps instead the individual variation in neophobia I measured is merely an artefact of the different developmental

conditions that individuals encountered (Chapter Four). Overall, the question of why corvids are so neophobic still remains.

7.1.2 Social setting

Regardless of the origin of corvid neophobia, it should still in theory impact individuals' foraging patterns and habitat use, thereby helping to shape species' niche breadth. Determining whether neophobia levels have ecological consequences requires that neophobia be tested in an ecologically valid context. The social setting is an often neglected part of ecological validity in laboratory studies of behaviours like neophobia (Dall & Griffith, 2014), because individuals are often tested in isolation (e.g. Bebus, Small, Jones, Elderbrock, & Schoech, 2016). The influence of the social environment on neophobia should not be ignored because the behaviour of conspecifics can increase novelty approach (Chapter Six), can enhance neophobia (at least towards novel odors, e.g. Crane, Mathiron, & Ferrari, 2015), and promote group conformity in responses to novelty (Miller, Laskowski, Schiestl, Bugnyar, & Schwab, 2016; van de Waal, Borgeaud, & Whiten, 2013). Rules of interactions between conspecifics, via a dominance hierarchy, for instance, can also mediate the costs and benefits of neophobic behaviours (Chapter Three). The influence of conspecifics on group level behaviour can have important ecological consequences, as the addition of individuals that recover faster from a novel, acute stressor can influence group foraging success (Pruitt & Keiser, 2014). The mechanisms by which conspecifics influence neophobic reactions in the wild are still uncertain, because social cues can emanate from the direct presence of conspecifics, or from the consequences of their actions (Galef & Giraldeau, 2001). More importantly, it is not yet clear which of these mechanisms most impacts the later learning about novel stimuli, as novel behaviours can spread socially throughout populations (e.g. Aplin et al., 2015).

7.1.3 After neophobia subsides

Neophobia is expected to have ecological consequences (Greenberg & Mettke-Hofmann, 2001), such as hindering innovation (Greenberg, 2003) and learning (Seferta et al., 2001), and restricting dietary breadth (Greenberg, 1983). However, neophobia and dietary wariness do not always correlate with traits such as higher dietary specialisation as expected (Camin, Martin-Alberracin, Jefferies, & Marone, 2015). Such discrepancies indicate that the mechanisms by which neophobia would influence such species-level traits are unclear. The lack of mechanistic understanding points to a potential issue with the connection between

neophobia and ecological consequences. By definition, neophobia only impacts responses when stimuli are novel, but objects, foods, and spaces are unlikely to only be encountered once per lifetime. Therefore, perhaps neophobia does not reduce corvids' ecological breadth, restrict behavioural plasticity or influence fitness outcomes because corvids overcome their neophobia over time.

Even though corvids demonstrate high neophobia in comparison to other species across urban and rural areas (Chapter Five), I found evidence that urban populations adjusted to their environment in exhibiting lesser wariness around litter-type items. Therefore, instead of demonstrating a general reduction in wariness, corvid species only showed reduced fear of objects that would be regularly associated with food. This specificity in wariness is not unique to corvids, as the other species I tested also differed in their latencies around litter between the urban and rural areas. Moreover, such patterns are not unique to my experiment because there is evidence that species along the edge of their range, such as sparrows, only show reduced wariness towards the types of novelty that would be of use to them, e.g. food instead of objects (Liebl & Martin, 2014). Therefore although demonstrating a specificity of wariness could help explain how corvids are able to be successful; it certainly is not a unique trait.

The existence of specific “safe” categories is not enough to explain corvids' generalist niche without an understanding of the mechanism that allows novelty to be placed into “safe” or “dangerous” categories. One way that corvids might be able to speed up their categorization of novelty is through social learning. In other species, for example, social learning can circumvent inherently high or low neophobia because it can enhance neophobic avoidance of unknown predators (Crane et al., 2015), and in jackdaws I found that social cues can encourage foraging on novel food items (Chapter Six). While social learning of novel predators is a well-researched topic (see Griffin, 2004 for a review), and social learning about novel food is well documented in the laboratory (e.g. Visalberghi, Valente, & Frigaszy, 1998), how wild animals learn about non-predatory objects is an area still open for study. Additionally, it is not clear if certain species, such as corvids, are more likely to use social information in the wild than other species that might not be so wary of novelty.

In order for information about the relative safety or danger of a novel stimulus to spread through a population, it must contain some individuals that are willing to approach and produce initial information. Since corvid populations contain a diversity of individuals

(some with high neophobia, some with low neophobia), similarly to all other species that have been tested (e.g. Aplin et al., 2014; Benson-Amram & Holekamp, 2012), it seems likely that the individuals with higher neophobia could readily learn from others about beneficial and dangerous types of novel stimuli. If social learning occurs with regularity, then this might explain why I found no difference in fitness between individuals of high and low neophobia (Chapter Four); highly neophobic birds could still benefit from others' novelty approach. Overall, although I found potential explanations for how corvids may overcome their neophobia, it is still not clear why they are so wary in the first place, and whether this wariness is related to conflict around humans.

7.2 Determining the ecological consequences of neophobia

The issues raised in the case of corvid neophobia highlight how little we understand about the mechanisms by which neophobic behaviours should predict ecological traits in the wild. Without an understanding of the duration of neophobic responses, or the processes that occur after neophobia subsides to produce continued avoidance or to encourage approach, it is difficult to predict how a neophobic response would influence species-level traits, unless animals were often encountering entirely novel stimuli. In the case of corvids, that are suggested to also be highly neophilic or curious once they have overcome their neophobia (Greenberg & Mettke-Hofmann, 2001; Heinrich, 1995), perhaps it is their curiosity, not their initial fear that most influences their success across a diversity of habitats, since high exploration is often associated with generalist species (Mettke-Hofmann, 2014). However, this hypothesis deserves a separate set of investigations to verify wild birds' curiosity, especially since none of the objects I presented in the wild were ever investigated by birds that had overcome their neophobia enough to approach the food or their nest box.

Ultimately, understanding what drives seemingly neophobic behaviour is crucial to predicting what consequences it may have. For example although species or individuals may appear to differ in their neophobia, they could actually differ in fear reactivity, information processing, or past experience; each of which would generate a different ecological consequence. Pairing neophobia tests with measures of behaviour towards known fearful stimuli, or with other tests of general fearfulness, such as startle tests that measure how long animals take to resume normal behaviour after being surprised (Martins et al., 2007), could determine whether differences stem from variation in fear reactivity. Accordingly, sometimes other fear-related behaviours correlate with neophobia (Turro-Vincent, Launey, Mills, Picard,

& Faure, 1995), and other times they do not (Carter, Marshall, Heinsohn, & Cowlshaw, 2012; Seferta, Guay, Marzinotto, & Lefebvre, 2001), potentially indicating situations where neophobic responses are influenced by information processing, not fear. Pairing neophobia tests with cognitive measures, such as habituation, categorization, or memory tests is rarely done, but could help determine how long neophobic responses would be expected to last. Just as general cognitive ability may best be determined through batteries of tests targeting specific cognitive processes (Thornton et al., 2014), neophobia tests will be more accurate if tested with multiple measures to determine an individual's or species' propensity for fear across contexts. Such batteries may also help us understand the longer term impact of neophobia in the environment, such as how animals learn about the novelty they encounter.

Whether or not neophobia inhibits learning is an important component of these secondary processes, yet is still up for debate. Neophobia is often suggested to prevent learning (Seferta et al., 2001), and would therefore be a trait of individuals that are poor learners. For example, the persistence of neophobia around stimuli that are safe could indicate a failure to learn that risk is absent, i.e. a failure to inhibit their avoidance response (e.g. Chivers, McCormick, Mitchell, Ramasamy, & Ferrari, 2014). However, it is not clear that neophobia always inhibits learning or the creation of novel behaviours, or that the most neophobic individuals lack in learning ability (see review in Griffin & Guez, 2014). The evolution of aposematic signals in prey species, for instance, relies on the fact that individual predators have an initial wariness of novel and bright colours, and that they will rapidly learn to continue to avoid them (Alatalo & Mappes, 1996). If the initial wariness that animals experience around brightly coloured prey inhibited learning, it would be counterintuitive to expect animals to evolve such easily detected coloration. One could argue that perhaps neophobia around novel foods and dietary conservatism function differently than other types of neophobia in inhibiting learning because they may involve different processes, such as taste sensitivity, and they do not often correlate with other types of neophobia within individuals (Coleman & Wilson, 1998). However, there are also reasons to suspect that not all neophobia around objects will equally inhibit learning.

In theory there could be two ways to learn a novel behaviour, or innovation, when presented with a novel object, and neophobia may not be expected to inhibit both types of learning. The first, more common form of innovation would involve trial and error learning, where persistence might aid in finding a solution (Cole & Quinn, 2012). In these types of innovations, neophobia would likely inhibit or slow down the likelihood of an animal

acquiring a novel behaviour (Benson-Amram & Holekamp, 2012; Griffin & Guez, 2014). Conversely, innovation that involves, for example, causal reasoning or abstraction of general rules, might benefit from hesitations to approach if it allows animals time to inhibit their initial responses and think about the problem. Tests have yet to be done on whether neophobic individuals do better with problems involving rule learning, but there is evidence that individuals with high neophobia are not worse at learning about novelty in general, but instead exhibit a slower “cognitive style” (Sih & Del Giudice, 2012). Supporting this claim, neophobic individuals seem to be proficient with different types of learning than low neophobia individuals, such as better reversal learning instead of faster initial associative abilities (Amy, van Oers, & Naguib, 2012; Bebus et al., 2016; Guillette, Hahn, Hoeschele, Przyslupski, & Sturdy, 2014). Reversal learning abilities are widely used as a measure of behavioural flexibility (e.g. Tebbich, Stankewitz, & Teschke, 2012), which could imply that for certain species, neophobia may in fact promote adaptability. If this theory is supported by tests in the future, then corvids’ high neophobia could actually help explain their renowned intellectual abilities, at least in certain contexts.

Investigating neophobic behaviours and their ecological consequences is exceedingly important given that species increasingly need to deal with human-induced changes in the environment. This dissertation has highlighted areas that desperately need more research if the causes and consequences of neophobia are to be understood for corvids and more generally for other species (see Table 7.2). Neophobia is only one of the several processes that contribute to responses toward novelty, because, as I have shown and argued, social cues and learning are likely to influence responses over time. The explicit use of these wider areas of cognition to guide conservation research and management efforts is a relatively new theme. Therefore I will discuss neophobia in the context of the range of cognitive processes pertinent to conservation efforts that deserve future research.

7.3 Using cognition for conservation

Animal behaviour is an important component of conservation (Candolin & Wong, 2012). Behaviour drives ecological patterns, such as dispersal and predator-prey interactions, thereby impacting the distribution of species and influencing ecosystem functioning. Many urgent animal conservation issues (e.g. eradicating invasive species, Sutherland et al., 2014) depend upon successfully manipulating behaviour. But what ultimately shapes behavioural patterns? Behaviour is an interaction with the environment stemming from what animals

perceive, learn, remember, and decide to do; all of which make up cognition in its widest sense (Shettleworth, 2010). Cognitive mechanisms therefore underlie behavioural responses, and are central to understanding behaviour that is relevant to conservation contexts (Figure 7.1).

Table 7.2 Summary of future research directions generated from this thesis.

Topic	Outstanding questions
Developmental causes	-Does variation in juvenile stress hormone expression translate to individual differences in adult neophobia?
Cognitive and hormonal mechanisms	-Does within-individual stress hormone expression differ depending on the type of novel stimulus being presented? At what level does stress facilitate attention towards novelty as opposed to flight? -How do animals learn about non-predatory objects? -Do social cues equally reduce neophobia in less fearful species? -Do social cues facilitate learning about novelty by encouraging approach, or are observers attending to and learning from the actions of others around novelty? -Are wild corvids more neophilic than other species and could this explain their success?
Consequences	-Does neophobia influence fitness in urban areas or when resources are less abundant? -Does neophobia influence survival outside of breeding season? -Are more neophobic individuals better rule learners? -Do different types of neophobia (such as food wariness vs object neophobia) impact learning in different ways? -Do more neophobic individuals interact with their environment differently, such as having a restricted dietary breadth?

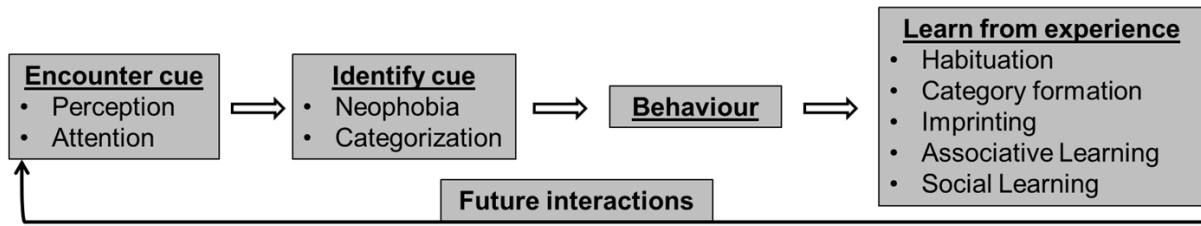


Figure 7.1 Cognition and the stages of conservation-relevant behaviour: The stages of interaction that an animal goes through to produce behaviour are written in bold. Learning does not necessarily occur, but when it does it influences future interactions. Effective behavioural manipulations for conservation can involve intervention at various stages. The internal state of the individual will influence their response at each stage.

Animal conservation incorporates diverse policies and wildlife management methods, and some, including re-introductions (Urbanek, Duff, Swengel, & Fondow, 2005), trapping (Phillips & Winchell, 2011), invasive species mitigation (O'Donnell, Webb, & Shine, 2010), and deterrents (Schakner & Blumstein, 2013) rely on manipulating animals' behavioural responses. These interventions could be improved with insights from comparative cognition. For example, avian collisions with man-made structures kill millions of birds every year—including threatened and endangered species (Drewitt & Langston, 2008)—and are linked to population decline (Phipps, Wolter, Michael, MacTavish, & Yarnell, 2013). Existing solutions, like strategically placing (Drewitt & Langston, 2008), or altering structures (Alonso, Alonso, & Munoz-Pulido, 1994), have had only limited success (G. R. Martin, 2011). Crucially, wind farm deterrents will only be effective if they are reliably perceived, and rapidly learned; both of which are facets of cognition. Cognitive theory can thus help predict how best to manipulate and exploit attentional biases, innate responses, and learning tendencies to enhance conservation efforts. Because basic cognitive principles can be applied throughout the animal kingdom, these tactics can be employed to address diverse problems.

While elements of cognition have been explored in conservation contexts (Brown, 2012; Sih, Ferrari, & Harris, 2011; Sih, 2013), discussions that integrate the breadth of cognitive theory in applied conservation are lacking. Below I outline the range of cognitive principles that can be used by conservationists, at each stage of problematic behaviour (Figure 7.1). Specifically I will discuss the perceptual principles that influence behaviour towards novel cues, and emphasize the role of learning in determining repeated responses. Different mitigation tactics may be required for maladaptive behaviours that originate from attraction or aversion to novel cues.

7.4 Cognition as adaptation

Animals possess perceptual biases and specializations in learning and memory that have evolved in response to the specific challenges of their ancestral environments (Shettleworth, 2010). Human-induced environmental change generates evolutionarily novel cues and potentially imposes strong selection pressures on these biases and specializations. Cognitive adaptations can therefore be as powerful as morphological adaptations in helping or hindering animals when environments change. For example, a cognitive mechanism that causes avoidance of novel food is as encumbering as a specialized feeding apparatus that prevents an animal from eating that food. Identifying the cognitive biases of target species requires stepping outside our own sensory experience and evaluating the saliency of novelty from the animal's perspective (Van Dyck, 2012). Even though not all species' cognitive biases are perfectly catalogued, fundamental perceptual and learning theories are highly relevant across species.

7.4.1 Perception of novelty

How animals perceive novel cues critically influences their response. Novel cues that resemble evolutionarily relevant cues are more likely to evoke common responses (i.e. the cue similarity hypothesis; Sih et al., 2011) that can be adaptive (e.g. fleeing novel predators that resemble existing ones; Blumstein, 2006). This helps explain why introduced species are more successful in novel environments that are similar to their ancestral ones (Blackburn & Duncan, 2001). However, when novel cues match relevant cues, but fail to produce beneficial outcomes, animals are at risk of perceptual errors and evolutionary traps (see Robertson, Rehage, & Sih, 2013 for a review). For example, the colour, shape and motion of plastic waste often resembles that of natural prey, provoking fishes, turtles, seabirds, and marine mammals to ingest them, with fatal consequences (Derraik, 2002).

7.4.1.1 Categorization

Both adaptive and maladaptive responses to cue similarity can be explained through categorization. Categorization involves classifying or differentiating cues based upon perceptual or conceptual similarity (Shettleworth, 2010), and allows novel cues to be processed and learned more quickly and efficiently (Wasserman, 1995). Although some animals can categorize disparate cues, generally novel cues that perceptually overlap with known cues are more easily classified. For example, prey more easily categorize novel

predators that resemble native ones (Ferrari et al., 2007). However this same process can lead to damaging miscategorization. For example, buprestid beetles (*Julodimorpha bakewelli*) are attracted to beer bottles whose colour and contours mimic those of their mates (Gwynne & Rentz, 1983). Miscategorization could be prevented by designing bottles of different colours and textures (i.e. “cue disarming”; Robertson et al., 2013).

Humans have long exploited perceptual and categorization errors to shape behaviour. We take advantage of them in household pest control with bug zappers and poisonous baits, but we can also use them for conservation purposes. Insight into the aspects of cues that evoke inappropriate behaviour allows us to reduce perceptual errors (Robertson et al., 2013). For example, using lamps with larger wavelengths could help reduce the impact of man-made lights on moths (van Langevelde, Ettema, Donners, WallisDeVries, & Groenendijk, 2011), and simple alterations to lighthouses, and oil rigs can prevent birds from succumbing to artificial light cues (Jones & Francis, 2003; Poot et al., 2008). Nevertheless, conservationists need to explore solutions beyond reducing perceptual errors because they represent but a small fraction of possible cognitive manipulations. Fundamentally much behaviour is not driven by automatic responses to cue similarity, but by experiences with cue novelty.

7.4.1.2 Neophobia

Fearing, or failing to fear man-made cues can generate problematic behaviour. Negative emotional responses to novel cues, termed neophobia, are adaptive in helping animals avoid unknown dangers (Greenberg & Mettke-Hofmann, 2001). However, when humans produce novelty, high levels of neophobia can prevent adaptive responses, such as inhibiting animals from incorporating new foods into their diet (Chapter Six, Marples et al., 1998), whereas low neophobia levels can aid in invading novel habitats (Sol et al., 2011). The extent to which neophobia produces avoidance behaviour depends upon the species (Greenberg & Mettke-Hofmann, 2001), the individual’s temperament (Réale et al., 2007), developmental stage, and experience (Greenberg & Mettke-Hofmann, 2001; Marples et al., 2007). Since neophobia can be quantified in laboratory and field avoidance tests (e.g. Chapter Three-Six, Seferta et al., 2001), measuring variation in neophobic behaviour within a population could predict how animals will respond to novel cues. With this information, the principles of neophobia can be applied to modify novel cues and increase or decrease fear responses.

Increasing fear responses can reduce human-animal conflict in farming and fishing contexts. Animals raid farms and steal catches, creating conflict with humans that results in needless culling and negative attitudes towards wildlife, often reducing support for local conservation programs (Hill, Osborn, & Plumpton, 2002). Capitalizing on animals' adaptive fear responses by amplifying biologically relevant surprise and danger signals can reliably deter animals from feeding (Schakner & Blumstein, 2013), and tapping into neophobia could further enhance avoidance behaviour. For example, animals' fear responses to naturally aversive startle displays (Olofsson, Eriksson, Jakobsson, & Wiklund, 2012) and alarm calls (Shettleworth, 2010) would be amplified if combined with cues that elicit neophobia, such as moving and changing objects (Corey, 1978). Additionally, incorporating other naturally aversive stimuli into deterrents, such as noxious chemicals like chili powder (Sitati & Walpole, 2006) or quinine (e.g. Caller & Brown, 2013; Rowland, Ruxton, & Skelhorn, 2013), could increase avoidance (see Schakner & Blumstein, 2013). Conversely, decreasing fear or indifference and increasing attraction to novelty can be useful in other conservation contexts such as attracting specific species to make culling more targeted and decrease the impact on other wildlife (Travaini et al., 2013).

While lessons from perception can manipulate initial reactions towards stimuli, shaping subsequent interactions requires an understanding of learning.

7.4.2 Learning

Learning is a change in cognitive state that results from experience (Shettleworth, 2010). Learning is crucial to conservation because it can allow animals to acquire appropriate behavioural responses to novel cues (Garcia, Thurman, Rowe, & Selego, 2012). Basic learning abilities are ubiquitous, but what, when, and how animals learn depends upon several factors. Evolved learning biases can direct attention towards adaptive cues, but only if evolutionarily relevant cues are preserved (Brown, 2012). Learning biases can favour certain sensory modalities. For example, animals more easily associate nausea with a taste than a shock or a light (the Garcia effect; Garcia et al., 1974). Natural selection has directed attention towards taste cues around food because taste more reliably predicts the presence and quantity of toxins. Generally, experiences that are more biologically relevant and perceptually salient are learned faster than less relevant ones (Shettleworth, 2010).

7.4.2.1 Habituation

Habituation, measured as a decrease in response to a repeated cue, is considered the simplest form of learning, and allows animals to filter irrelevant information (Rankin et al., 2009). Habituation as a term is often used to describe the process of behaviourally adapting to anthropomorphic disturbance across contexts ranging from chronic noise (Anderson, Berzins, Fogarty, Hamlin, & Guillette, 2011) to human visitors (Ellenberg, Mattern, & Seddon, 2009), even though such examples may not fit the strict psychological definition the term implies. Therefore, different underlying processes can contribute to what is labelled “habituation” between contexts, so animals might not tolerate shipping noise as readily as disruptions from tourists. However, whether animals generalize their habituation to new disturbances in the wild is currently unknown. The degree to which animals habituate has serious consequences for conservation programs depending on the context. For example, crop deterrents will be less effective on animals that easily habituate, (e.g. corvids; Baxter & Robinson, 2007), and animals that habituate poorly might be less tolerant to disturbances caused by habitat fragmentation. Too much habituation around new dangers such as roads will result in unnecessary fatalities, and declining local populations. Lacking habituation, i.e. avoiding non-threatening stimuli, will be equally problematic in limiting species’ abilities to adapt in otherwise suitable habitats.

Habituation relies on experiencing predictable cues (Shettleworth, 2010) and can be prevented by amplifying differences in cues between presentations and timing presentations unpredictably. For example, randomly rotating crop deterrents between objects of different colours, sizes, and shapes, and by pairing them with different sounds will help prevent habituation (however, deterrents must also produce aversive experiences or cue variation will still fail to deter, e.g. Muirhead, Blache, Wykes, & Bencini, 2006). In promoting habituation to minimize the effects of human disturbance, predictability should be maximized. For example, ecotourists in areas with disturbance-sensitive animals could be encouraged to wear similar clothes, follow similar paths, and only visit at specific times of day. Assessing the flexibility of such habituation responses is critical in predicting whether animals will adaptively distinguish new threats from novel, non-threatening stimuli.

7.4.2.2 Imprinting

Imprinting is a specialised form of learning that occurs during a short sensitive period in development to create strong preferences for one’s own species (Immelmann, 1975),

specific foods, habitats (Davis, 2008) or sites (Immelmann, 1975). Imprinting can propagate parental behavioural patterns in future generations. For example, habitat imprinting can spread preferences for urban habitats, thereby facilitating animals' urbanization (Evans, Hatchwell, Parnell, & Gaston, 2010). Imprinting on evolutionarily novel cues can cause maladaptive behaviours. For instance, zebra finches (*Taeniopygia guttata*) solicit an incorrect mate after imprinting upon a different species (Bischof & Clayton, 1991).

Imprinting manipulations can aid conservation efforts—like translocation programs that depend upon animals preferring suitable environments (Binder, Priddel, Carlile, & Kingsford, 2013)—and are often used in salmonid (Salmonidae) release programs (Brown & Day, 2002). Exposing animals to a particular stimulus during their sensitive phase, like the post-larval period for many insects (Davis, 2008), can create life-long preferences. Additionally, imprinting can be used as tool to guide other desired behaviours. For example, the Whooping Crane Eastern Partnership successfully exploited filial imprinting to lead reintroduced whooping cranes (*Grus americana*) through their first migration. After being exposed to costumed people during early development, the birds imprinted on the costumes so faithfully that they followed an ultralight aircraft flown by their “foster mothers” (Urbanek, Fondow, Zimorski, Wellington, & Nipper, 2010).

7.4.2.3 Associative learning

Animals from nematodes to humans (Heyes, 2012) can learn associations between cues, or between cues and a behaviour, to better predict and respond to events in their environment. Whether associations form depends on the timing between the behaviour and its consequence (contiguity), the reliability (contingency) and salience of the stimulus, and the biological appropriateness of the association (Shettleworth, 2010). The breadth and scope of associatively learned behaviour allows the following principles to be employed in many contexts.

Associative learning occurs through classical or operant conditioning. In classical conditioning, an animal's natural reflex (Unconditioned Response, UR) toward a behavioural trigger (Unconditioned Stimulus, US) is associated with a novel cue (Conditioned Stimulus, CS), so that the novel cue elicits the response (i.e. creating a Conditioned Response, CR). Famously, Pavlov demonstrated that a dog will salivate (CR) at the sound of a bell (CS) if it reliably precedes food (US) (Shettleworth, 2010), thereby learning to predict the occurrence of food.

Instead of creating associations between stimuli, operant conditioning creates associations between behaviour and its rewarding or unpleasant consequences. These associations increase or decrease the preceding behaviour, and can create novel behaviour as small variants in responses are positively or negatively reinforced. In conservation contexts, possible rewards and punishments inherent to the situation need be assessed, and unwanted rewards or punishments removed. Failing to evaluate cues can reinforce unwanted behaviour unintentionally. For instance, if predators gain access to fishing catches while a mildly irritating deterrent is broadcast, the deterrent will be associated with positive outcomes, making it a “dinner bell” (Carretta & Barlow, 2011). However, with careful planning, operant conditioning can be a highly effective conservation tool. For example, wildlife managers successfully reduced trappings of native species while managing feral cat populations through aversive conditioning by fostering associations between a negative cue (nausea-inducing chemicals in trapping baits) and the experience of feeding in the trap (Phillips & Winchell, 2011).

7.4.2.4 Category learning

Categories based upon perceptual similarity can form by learning simple associations between common aspects of cues (cue generalization) (Soto & Wasserman, 2010). Miscategorization of novel cues through cue generalization can result in perceptual errors, which is why altering cues can directly change behaviour. If novel cues cannot be altered, miscategorization can be prevented by changing the animal’s categories through training using associative learning principles. For example, greater bilbies (*Macrotis lagotis*) were trained to categorize cats, an invasive species, as predators by associating a multimodal cat stimulus with an unpleasant handling experience and repeated predation attempts (Moseby, Cameron, & Crisp, 2012) .

Some animals are capable of categorization that does not hinge on perceptual similarity, but instead stems from associations between concepts, such as higher-order categorization (perceptually dissimilar, e.g. grouping garbage bins and children in one broad “things that drop food” category), and abstract categorization (neither functionally nor perceptually similar, e.g. sameness versus differentness). Being able to classify novelty into biologically relevant categories might help some animals cope with the large number of unfamiliar cues in novel environments. For instance, learning “safe” versus “unsafe” categories could allow animals to minimize costly avoidance behaviours and use effective

flight responses (e.g. selectively responding to specific “unsafe” humans as predators; Levey et al., 2009, or selectively categorizing litter-type objects as “safe”; Chapter Five). These complex forms of categorization might facilitate efficient responses across diverse environments, but they require more presentations to learn than perceptually similar categories (Katz, Wright, & Bodily, 2007). Therefore, limiting the amount of perceptual overlap between items prevents cue generalization and forces animals to rely on conceptual categorization; making learning about novelty more time consuming for some species and impossible for others. Preventing easy categorization in this way can be desirable, for example, when designing traps for species monitoring. Altering the appearance, scent, and location of the trap will hinder animals from categorizing them as dangerous, and allow more of them to be re-trapped.

7.4.2.5 Social learning

Social learning, the ability to learn from others, can spread novel behaviour faster than genetic change, and with fewer costs than individual learning (Boyd & Richerson, 1985). Social learning can simply involve drawing attention towards a location or cue (i.e. local or stimulus enhancement), with subsequent positive reinforcement perpetuating future attention and behaviour towards that cue (Shettleworth, 2010). Therefore, attention toward small social cues can facilitate population-level behavioural changes (Thornton & Clutton-Brock, 2011), including the approach of novelty (Chapter Six).

As with all learning, social learning is constrained by animals’ cognitive biases. For example, monkeys will learn to fear snakes but not flowers when simultaneously presented with conspecific fear responses (Cook & Mineka, 1989). Social learning would be favoured over individual learning in situations where the latter might be dangerous or difficult (Thornton & Clutton-Brock, 2011). Interacting with novel foods, predators, and environments is inherently risky; therefore animals are liable to use social information when novelty arises. In conservation contexts, social learning can, for example, spread information about novel predators in reintroduction programs (Griffin, 2004), and increase the viability of reintroduced hatchery-reared fish (Brown & Laland, 2001). Therefore, whenever possible, programs should allow animals to see conspecifics or trainers performing behaviours they wish to encourage.

7.5 Conclusions

The unadulterated places left for wildlife are shrinking, imposing novel selection pressures on animals' morphological and cognitive adaptations. Animals' flexibility in behaviour relies on them being able to distinguish dangerous from benign novelty. The success of species, such as corvids, that have been able to utilize a combination of wariness and rapid learning to thrive amid such environmental change offer clues into why other species have been unable to adjust. By focusing on cognitive mechanisms, such as neophobia, cues and experiences can be manipulated to improve the efficacy of behaviourally-focused conservation efforts. Many cognitive mechanisms are well-researched in the field of comparative cognition, yet rarely utilized tested in the field or used in animal conservation.

Initiating dialogue between comparative cognition and conservation will allow for applications of cognitive theory to be further developed and tested. With shared conservation goals, comparative psychologists can direct their research towards species of conservation concern, and conservationists can benefit by applying new cognitive insights to difficult problems. Moreover, such research also offers new opportunities to examine flexibility in the realm of cognition and behaviour too (Hockings et al., 2015).

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Appendix Table 1. Sample of conflicting neophobia tests. W= Wild, C=Captive, WC=Wild-caught. Ob= latency to approach a novel object; Sp= amount of movement in a novel space; DC = amount of time before incorporating a novel food into the diet (dietary conservatism); Cort= magnitude of corticosterone response; Startle= latency to resume normal behavior after a sudden, frightening event; TI= time spent immobile after being restrained; (+), (-), (/) refer to positive, negative, and no relationship between the two variables; ?= unknown. NE=Novel environment. *Experimental outdoor ponds open to predation pressure.

Species	Wild or captive	Correlations	Novel stimuli (# trials)	Forced entry to NE	Reward near novelty	Compared to familiar stimuli
Jackdaw (<i>Corvus monedula</i>) (Schuett et al., 2012)	W	Ob (+) Sp	stuffed toy (1) NE (1)	Y	Y	N
zebra finch (<i>Taeniopygia guttata</i>) (Schuett, Godin, & Dall, 2011)	C	Males: Ob (+) Sp Females: Ob (/) Sp	green woolly ball (1) NE (2)	N	N	N
mountain chickadee (<i>Poecile gambeli</i>) (Fox et al., 2009)	WC	Ob (/) Sp	plastic pink panther key chain (1) NE(1)	N	N	Y (Ob) N (Sp)
Starlings (<i>Sturnus vulgaris</i>) (Boogert et al., 2006)	WC	Ob (/) SP	coloured clothes pins, styrofoam mounted on cardboard, yellow reflective material, white opaque tube cap ,white spool of purple wire, green pen cap (variable) NE (variable)	Y	Y	Y (Ob) N (Sp)

zebra finch (<i>Taeniopygia guttata</i>) (Martins et al., 2007)	C	Ob (/) SP Cort (+) Startle	AA battery, green purse (2) NE (2)	Y	N (Ob) Y (SP) Y (Startle)	N (Ob) N (SP) Y (Startle)
Great tit (<i>Parus major</i>) (Verbeek, 1994)	C	Ob (-) Sp	penlight battery, pink panther toy (variable) NE (1)	?	N(Ob) Y (Sp)	Y (Ob) N (Sp)
Great tit (<i>Parus major</i>) (Cole & Quinn, 2014)	WC, W	Ob (-) Sp	Rigid black and white flag (1,2) NE (1)	?	Y (Ob) N (Sp)	Y (Ob) N (Sp)
Japanese Quail (<i>Coturnix japonica</i>)(Turro-Vincent et al., 1995)	C	Food neo (/) TI DC (+) TI	colored jackbean and field beans (variable)	NA	N	N
Japanese Quail (<i>Coturnix japonica</i>)(Marples & Brakefield, 1995)	C	Sp (/) DC	Seven spot ladybirds (<i>Adalia bipunctata</i>) (5) NE (1,2)	Y	Y	Y (DC) Y (Sp)
Pumpkinseed fish (<i>Lepomis gibbosus</i>) (Coleman & Wilson, 1998)	W*	Ob (/) Food neo	Metre stick (variable) Aquatic vegetation (variable)	NA	N	N
pied-flycatchers (<i>Ficedula hypoleuca</i>) (Ruuskanen &	WC	Ob (+) predator disturbance Ob (/)Sp	pink and yellow plastic duck (2) Sparrow hawk mount(1) NE (2)	Y	N (Ob) N (Sp) Y (predator disturbance)	N

Laaksonen, 2010)						
Chacma baboons (<i>Papio ursinus</i>) (Carter, Marshall, et al., 2012)	W	Ob (/) Predator wariness	Food pieces	NA	N	N

Appendix Two

Flight Initiation Distance

A common way of measuring how tolerant animals are of humans is to determine how close they will allow people to approach (McCleery, 2009; Anders Pape Møller, 2009). Flight initiation distance (FID) is a measure of the distance at which an animal flees an approaching predator, or in this case, a person (Frid & Dill, 2002; Ydenberg & Dill, 1986). By collecting FID measures of corvids along urban-rural gradients near both of the study sites, I was able to determine to what extent humans are viewed as a threat in both places, and whether this differs depending on the type of habitat. During the winter months between December 2012 and early March 2014, I collected a total of 219 FID approaches.

Methods

All FID measures were collected during daylight hours. Each day before beginning data collection, I verified that my walking approach speed was consistent (0.5m per second) by laying down a precut 5m string, and timing several approaches. I then walked at a normal pace around the study sites or around nearby urban or rural areas. Since several species of corvid (e.g. rooks and jackdaws) are rarely found alone in the winter (Lockie, 1956), approaches were directed at single individuals and groups of corvids. Upon identifying a corvid (or corvid group), I dropped a small weight to mark my start location (since starting location influences approach distance; Blumstein, 2003) and begin my approach. I then approached at the 0.5m per second pace, keeping my eyes focused on the bird(s). If I was approaching a lone individual, I would drop a second weight when it either flew or hopped away, and would continue approaching the place where the bird was initially located. If approaching a group of birds I would drop one weight when the first bird flew and a second weight when the last bird flew. Once I reached the initial location of the bird(s), I used a measuring wheel to walk back and determine the distance to each of my weights. Since a birds' height above the ground can influence their FID (Blumstein et al., 2004), if the bird(s) had initially been located in a tree, or on a man-made structure, I used a protractor with a viewfinder and a hanging weight to determine their angle of height from the starting location. Using the distance between my measurement location and the birds' original location, I calculated their height above the ground with the angle I measured between myself and their height (taking into account the height of my own eyesight from which the angle was

measured). For each measure I noted the type of habitat: rural (open farmland, or covered forest), urban area (covered by buildings, streets, many houses), or urban park (manicured lawns, frequented by many people). Since my aim was to measure the response of a typical corvid in either location, for groups, I used the mean value of the first and last bird as the FID of that observation.

Analysis

I determined whether corvids were more fearful of humans in either of the study sites or across urban/rural areas by running a Linear Mixed Model with a Gaussian distribution. FID was log transformed to make it normally distributed and the model took into account the study area (East or Southwest of the UK), habitat type, start distance, the size of the bird group being approached (lone birds = 1), and their height off of the ground. Species was added as a random effect to mop up variation between species of different body sizes since it is known that larger birds flush at greater distances (Blumstein, 2006a).

Results

There was an interaction between habitat type and region, such that corvids in rural parts of the East were more fearful of people than birds in urban areas or in the Southwest (see Figure A2.1). Also, as has been previously shown (Blumstein, 2003; Blumstein et al., 2004), birds flushed at longer distances the farther away the approach started (LMM, $n = 219$, $\text{Est} = 0.01 \pm 0.00$, $z = 2.05$, $P = 0.040$), and birds sitting at higher heights flushed at shorter distances ($\text{Est} = -0.07 \pm 0.01$, $z = -8.03$, $P < 0.001$).

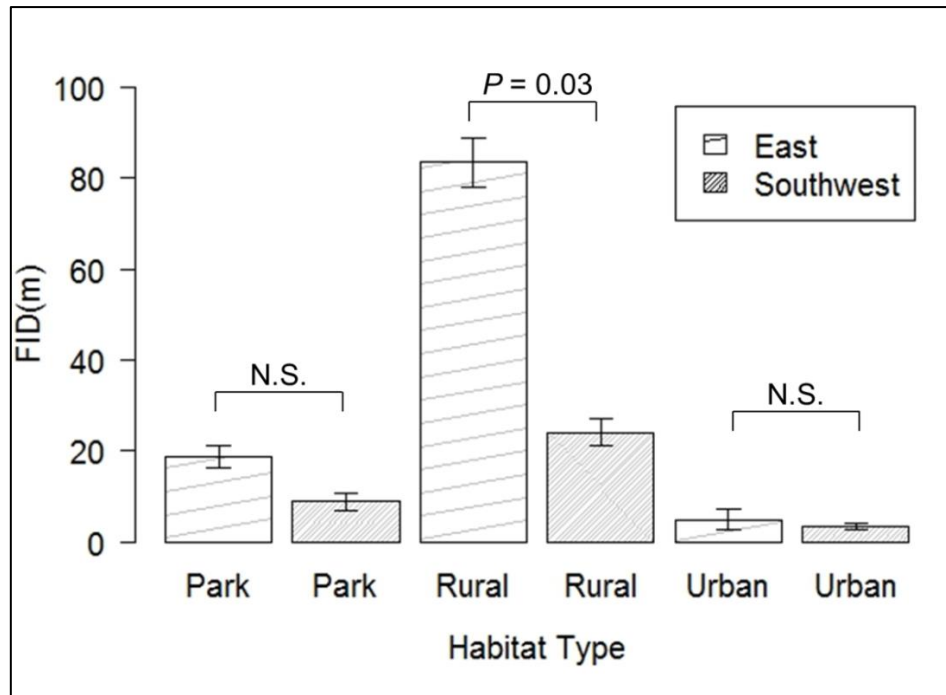


Figure A2.1 Plot of raw FID data by study area and habitat type. The interaction term between area and habitat type was significant when comparing rural habitats between areas; LMM, $n = 219$, $\text{Est} = -0.79 \pm 0.37$, $z = -2.13$, $p = 0.0334$. Whiskers represent standard errors.

Conclusions

The birds had similar FID measures in comparison to what has been collected on other corvids, apart from rural areas in the East, where FID was exceptionally high (see Table A1.1). Since the Madingley field site was composed entirely of rural areas in the East, corvids there were more fearful than corvids tested in the Southwestern Cornish sites that were made up of a more heterogeneous landscape.

Species	N	FID (meters)	paper
Western scrub jay	130*/71**	15.8*	(Blumstein et al., 2004)
<i>Aphelocoma californica</i>		13.8**	
Australian raven	48*/21**	23.8*	(Blumstein et al., 2004)
<i>Corvus coronoides</i>		29.6**	
Australian raven	70	25.6 ± 22.6	(Blumstein, 2003)
<i>Corvus coronoides</i>			
American crow	15 per gradient	26-30 ⁺	(Clucas & Marzluff, 2012)
<i>Corvus brachyrhynchos</i>		6-10 ⁺⁺⁺	
Hooded crow	15 per gradient	18-23 ⁺	(Clucas & Marzluff, 2012)
<i>Corvus cornix</i>		12-16 ⁺⁺	
		<10 ⁺⁺⁺	

Table A2.1 FID measures of corvids reported in the literature. *Measure taken at heights < 3m. **Measure taken at heights > 3m. ⁺ Measure taken in rural areas. ⁺⁺ Measure taken in suburban areas. ⁺⁺⁺ Measure taken in urban areas.

Appendix Three

Nest Success Data

See Chapter Two for an explanation of methods used for collecting nest success data

Analysis

Although data was collected at the Madingley site from 2010-2014 and at the Cornish sites from 2013-2015, I only compared seasons when data was collected at both sites (i.e. 2013, 2014). I looked at the relative rates of success, the number of chicks fledged and the quality of chicks within and between nest sites. Nest success rates were compared within and between sites with separate chi-square goodness fit tests (No. nests fledging young versus No. nests with hatching young). The number of chicks that fledged per nest was compared to national level UK statistics on jackdaw fledging rates. Measures of chick quality (in this case, chick mass in grams) were normally distributed, and were compared within and between sites with a Linear Mixed Model, and a Gaussian distribution. I assessed the influence of the year, site, and the interaction between the two on chick mass. I included nest box ID as a random effect because jackdaws are known to return to the same box in subsequent years (Röell, 1978), and therefore measures are not likely to be fully independent.

Results

Nest success rates did not differ across or within sites between the two seasons measured (see Table A3.1). The mean number of fledglings per nest in each season in Madingley (2013, 1.90 ± 0.63 ; 2014, 1.73 ± 0.58) was slightly lower than nationally compiled data on UK jackdaw nest success from 1967 to 2013 (2.27, $n = 64$ nests per year) (Robinson, Marchant, et al., 2015). Meanwhile the mean number of fledglings per nest in Cornwall (2013, 2.0 ± 0.69 ; 2014, 2.26 ± 0.85), was much closer to the national averages. The quality of chicks also varied depending on the site and the year (LMM, $n = 320$, Site*Year interaction, Est. = -37.71 ± 8.70 , $z = -4.34$, $P < 0.001$; see Figure A3.1).

	Madingley	Cornwall	Between site comparison
2013	44/60	19/31	$\chi^2 = 0.11$, df = 1, $P = 0.738$
2014	54/75	39/47	$\chi^2 = 0.13$, df = 1, $P = 0.715$
Within site comparison	$\chi^2 = 0.13$, df = 1, $P = 0.715$	$\chi^2 = 0.43$, df = 1, $P = 0.512$	

Table A3.1 Nest failures across two years in both sites. Number of nests that fledged chicks/Number of nests that hatched chicks.

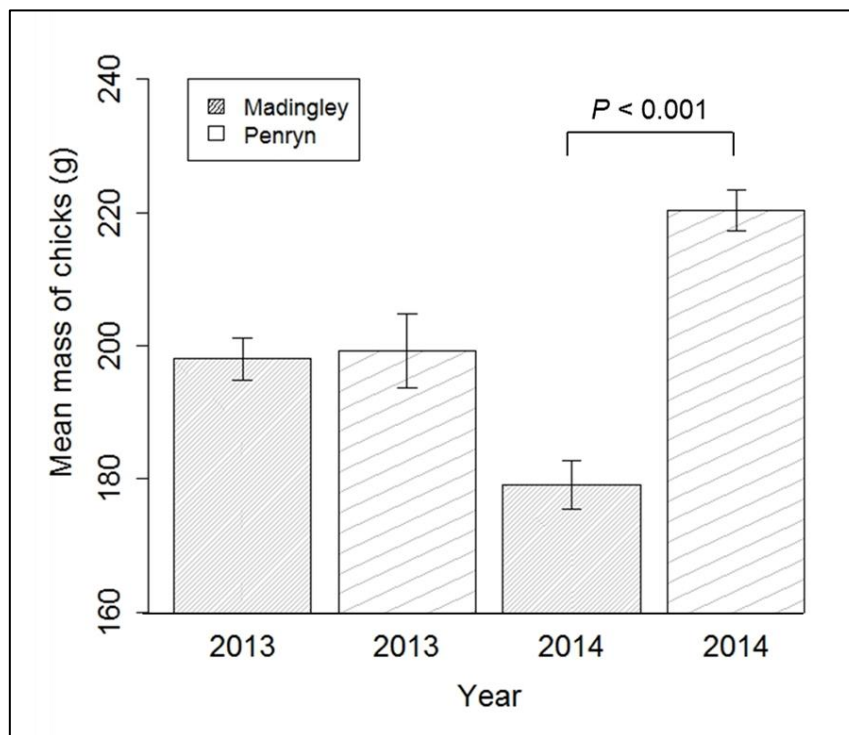


Figure A3.1 Mean mass of chicks across sites and seasons.

Conclusions

The overall proportion of breeding nests that were able to fledge young at both sites was very similar. However, since fewer young were fledged per nest in Madingley and nestlings were of poorer quality there, the data indicate that Madingley was a more challenging environment than the Cornish sites in 2014. Therefore, both sites seemed to vary independently of each other. If each site offered different foraging obstacles, then different levels of neophobia or other behaviours that could influence dietary breadth or foraging success might be favoured in each location (although see Chapter Four).