Collective responses to acoustic threat information in jackdaws.

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Abstract

Navigating the physical world may present only a small fraction of the challenges faced by social animals. Sociality brings with it numerous benefits, including access to important information that may have otherwise been harder to come by. However, almost every aspect of these apparent benefits may also entail additional cognitive challenges, including how to interpret signals from conspecifics, who to attend to, and how to incorporate knowledge about signallers when deciding how to respond. One approach to understanding the cognitive abilities associated with social function is to investigate social species that take part in potentially costly group behaviours, where individual decisions must be made in a social context. In this thesis I explore how jackdaws (*Corvus monedula*), a highly sociable corvid species, use acoustic information to coordinate collective anti-predator responses. In Chapter Two I showed using playback experiments that the magnitude of collective responses to anti-predator recruitment calls known as "scolding" calls depends on the identity of the caller, with larger responses to familiar colony members than unfamiliar individuals. In Chapter Three I then used habituation-dishabituation experiments to show that this vocal discrimination operates at the level of the individual, with jackdaws discriminating between the calls of different conspecifics, regardless of their level of familiarity. In Chapter Four, I examined whether aspects of call structure conveyed information about threat levels. Here, I found that high rates of scolding calls were associated with elevated threats, and playback experiments suggested that this information might result in larger group responses. The finding that jackdaws are capable of mediating their response to alarm calls based on the identity of the individual caller, and on structural variation in call production, raised the question of whether jackdaws employed similar forms discrimination between acoustic cues made by predators in their environment. I investigated this in Chapter Five, using playback experiments to show that jackdaws responded not only to the vocalisations of resident predators, but that this ability extended to novel predators, and that responsiveness was mediated by the phase of the breeding season in which predators were heard. Together, these findings provide insights in to how discrimination among acoustic cues can mediate group behaviour in species that respond collectively to threats.

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(Photo: Richard Woods)

"THE JACKDAW sat on the Cardinal's chair!

Bishop and abbot and prior were there;

Many a monk, and many a friar,

Many a knight, and many a squire,

With a great many more of lesser degree,—

In sooth, a goodly company;

And they served the Lord Primate on bended knee."

- Thomas Ingoldsby, Esq. (The Rev. Richard Harris Barham), The Jackdaw of Rheims, 1840

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Jackdaws have proved a fascinating species to study. Many times they have proved frustrating and unpredictable, but at others they have impressed me hugely. I'm lucky to have had the opportunity to work with such characterful birds, and can testify that no place that I sat to write this PhD was free from the calls of jackdaws.

Declaration

No part of this dissertation has previously been submitted for any qualification. All work contained in this thesis was conducted under the supervision of Dr Alex Thornton and Dr Nick Royle. All of the work is my own, apart from what is specified below:

Chapter Two: Abigail Dearling and Thimothé Bertot assisted with data collection following protocols I developed.

Chapter Three: Charlotte Saville and Thomas Crouchet assisted with data collection and video analysis.

Chapter Four: Thomas Crouchet assisted with data collection and video analysis.

Chapter Five: Thimothé Bertot assisted with data collection.

Chapter One: General introduction

Background

Group living is challenging

The social environment has the potential to change relatively more quickly and unpredictably than the physical environment. The Social Intelligence Hypothesis (SIH) is the theory that the challenges arising from social living (Humphrey, 1976; Jolly, 1966) may drive the evolution of certain cognitive abilities.

Group living can be beneficial, but living together with other individuals also creates challenges. Early empirical studies revealed direct individual benefits including lowered predation risk, improved foraging efficiency, and easier access to potential mates, but highlighted significant costs associated with competition within social groups (Hamilton, 1971; Pulliam, 1973; Roberts, 1996). Costs may be incurred during intra-group competition for food or breeding opportunities. Further costs include higher rates of disease transmission and a higher parasite load than solitary species (Alexander, 1974). Minimising these costs can present variety of cognitive challenges. For example, recognising group members individually and tracking their relative rank could be beneficial in avoiding confrontation with superiors or taking advantage of subordinates (Cheney & Seyfarth, 1992). It may be important to know an individual's relationship to other group members when deciding whether to pick a fight with them or act in a way that is beneficial to them. In scenarios such as these, individuals may benefit from making use of social information in order to choose the most appropriate course of action. The SIH predicts that the cognitive challenges of making such social decisions may be more cognitively demanding than those present in the physical environment. To date, the cognitive demands of sociality have been researched in a somewhat haphazard way with inconsistencies in the way cognitive abilities are measured across studies. Furthermore, the majority of studies looking at the SIH have focussed on anthropoid primates (Bergman, Beehner, Cheney, & Seyfarth, 2003; Gillan, 1981; Jolly, 1966; Sallet et al., 2011). Of the limited work done outside primates, relatively little has addressed the cognitive challenges animals

face in their natural environments. In order to truly test the general validity of the SIH, social information use must be tested in a comparable way across a variety of social structures and different taxa. These cognitive abilities must be firmly linked to the social structures present. A useful method for exploring these ideas could be by looking at vocalisations. I will briefly review evidence supporting the SIH before moving on to discuss the study of vocal communication as a method of testing its validity.

Support for the Social Intelligence Hypothesis

The initial idea for the SIH was proposed by Alison Jolly during her work on lemurs before being explored further and formalised by psychologist Nicholas Humphrey, based on neuroanatomical and behavioural evidence (Humphrey, 1976; Jolly, 1966). Much support for the SIH comes from research on social mammals, with much of the most focussed and compelling neuroanatomical and behavioural evidence coming from studies of anthropoid primates (Dobson, 2012).

A number of studies have revealed that aspects of brain size, including absolute relative size, relative neocortex size and encephalisation quotient, correlate broadly with features of group living species such as group size or mating system (Pérez-Barbería, Shultz, & Dunbar, 2007; Shultz & Dunbar, 2010) . Species living in social groups tend to show increased encephalisation relative to solitary species, and this is commonly thought to reflect the need to remember an increased number of individuals and relationships (Finarelli & Flynn, 2009; Shultz & Dunbar, 2010). As brain tissue is highly energetically costly it is implicit that these more social species must have a demand for increased cognitive activity (Dobson, 2012). This "costly-tissue" theory has not been widely explored across taxa but has been shown in some species of freshwater fish where more social species had relatively large brains, but reduced digestive organs compared to non-social species (Kaufman, Marcel, & Pasquet, 2014). In a broader approach, increased brain size and increased group size have been shown to correlate in primates (Dunbar, 1992), but there is limited evidence for this in birds (Beauchamp & Fernández-Juricic, 2004; Healy & Rowe, 2007). One reason for this inconsistency may be the problem of

assuming that group size and social complexity are inherently linked. An increased group size only increases cognitive demands on the individual if the addition of members affects that individuals' optimal course of action. Many eusocial insects for example are able to operate in very large social groups, but the need for individual knowledge about fellow group members may be minimal. Furthermore some solitary species such as bears having relatively large brains for their size (Holekamp, 2007), hence the correlation between brain size and sociality is not universal.

Research into specific cognitive abilities provides a more diverse range of findings supporting the SIH. There is some evidence that social species have better performance than closely related non-social species in certain spatial and temporal memory tasks. In food-caching birds that live in large groups, pilfering by group members is a common problem for cachers. It would seem beneficial then, for the cacher not to return to a cache observed to have been pilfered. Less social caching species on the other hand, would rarely experience pilfering, particularly by conspecifics, and hence would be less likely to have learnt not to return to a pilfered cache. In an abstraction of this principle, highly social pinyon jays, *Gymnorhinus cyanocephalus,* and Mexican jays, *Aphelocoma ultramarina*, were tested against pair-living Clark's nutcrackers, *Nucifraga Columbiana,* and Florida scrub jays, *Aphelocoma coerulescens*, in a non-matching-to-sample test (Olson, Kamil, Balda, & Nims, 1995). This type of test is intended to abstract the ability to select *against* a particular option. This is related to sociality, where cachers in the more social species should be able to select against returning to a cache that they had observed being pilfered. Non-social species would be far less likely to experience conspecific pilfering and hence should be poor at this ability to select against a given option. In the test, subjects were shown a coloured dot on a screen. After a pause during which the screen was blank, two coloured dots were presented. In order to gain a food reward, the subjects had to peck at the dot that was a different colour to the original coloured dot. In this case the social species outperformed the non-social species. This experiment highlights the problem of teasing the socially driven cognitive ability from the ecologically driven cognitive ability. All the test species in this trial must remember where they cached (and most likely when), but only the social species have to deal with the problem of pilfering. Theory of mind, the ability to attribute mental states to ones self and others, has been

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suggested as an explanation for the ability to cache secretively and avoid returning to pilfered caches (Clayton, Dally, & Emery, 2007). The idea that a group-living bird like the pinyon jay may predict the behaviour of a pilfering thief is reported to explain why these birds are more likely to move a cache if they see a conspecific watching as they make the cache. This apparent theory of mind is offered (along with the performance in the coloured dot test) as superior cognitive ability resulting from a social lifestyle, thus supporting the SIH. However a more parsimonious view could be that the theory of mind is explained by associative learning, where birds follow the simple rule that if they see a conspecific during caching, they should move the cache. Similarly, the experimental result with the coloured dots could be explained by a cognitive bias, meaning that something in the ecology of the social pinyon jays and Mexican jays predisposes them to have better memory for colours than either Clarks nutcrackers or Florida scrub jays. This cognitive bias does not necessarily have to be related to sociality, and perhaps the abstraction linking the test results to the SIH is rather tenuous at best. Overall there is continued debate over the evidence for theory of mind in birds, with some studies producing results difficult explain through simple associative learning (Bugnyar, Reber, & Buckner, 2016), whilst others are critical of interpretations that suggest evidence of theory of mind (Heyes, 2015). A more robust test of the SIH might be to look at cognitive abilities with a more obviously social use.

In a structured society with a linear rank hierarchy where A outranks B, B outranks C, C outranks D and so on, it may be useful for any individual in the group to be able to infer that A outranks D or that C outranks F, and so on, without the need to directly observe the individuals in question interacting. Extrapolation of this kind is known as transitive inference. An ability to infer rank relationships is clearly irrelevant to solitary species, but may be advantageous in social species where a rank system is present. Several species demonstrate abilities consistent with transitive inference, for example chimpanzees, *Pan troglodytes*, were able to place a series of pictures in the correct order, even though they had only previously experience of the order of certain pairs of images from within the series (Gillan, 1981). Paz-y-Miño *et al* demonstrated transitive inference in pinyon jays in a series of experiments using three groups of male jays (Paz-y-Mino, Bond, Kamil, & Balda, 2004). In the first set of experiments, dominance hierarchies within each group was determined by

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observing interactions at a food source between each possible pair within a group. Ranks were then assigned to each group member based on dominant/submissive behaviour shown in each pair-wise encounter. Next birds were allowed to individually witness a dominance interaction between either two birds from a different group (control treatment), or one bird from a different group and one bird from their own group (experimental treatment). The observers were then allowed to interact at a food source with the birds from other groups that they had just observed. It was shown that when the focal bird interacted with an unfamiliar (from a different group) bird from the control treatment, they were slower to adopt a dominant or submissive demeanour than when they interacted with an unfamiliar bird from the experimental treatment. This suggests that pinyon jays that witness a familiar conspecific behave dominantly or submissively towards an unfamiliar conspecific, can infer information about their own dominance relationship to the unfamiliar conspecific, in an example of transitive inference. A similar but abstract experiment also successfully performed by pinyon jays was conducted where birds were trained to recognise the order of pairs of coloured lights before being tested with longer series where they had to use their knowledge of the pairwise relationships to place the whole series in order (Bond, Kamil, & Balda, 2003). This type of experiment still leaves the question of quite how far transitive inferences may extend somewhat unclear. Can pinyon jays infer the order of the entire series or can their success in the test be explained by a simple appreciation of the order of individual pairs of coloured lights?

Overall, support for the SIH is narrow in it scope, with most of the strong support being limited to a few focal species, mainly within the primates. It is clear that for the SIH to be valid, support must come from a range of taxa and be conducted in a comparable way, without ambiguity between the socially linked ability and the abstract experiments that are often used to test them.

Exploring social intelligence through vocalisations

Sound has been shown to convey social information in many species (Bergman et al., 2003; Charlton et al., 2011; McComb, Packer, & Pusey, 1994; Ramsier, Cunningham, Finneran, & Dominy, 2012). Acoustic signals have the benefit of

being a relatively instantaneous way for group members to share social information and the public nature of sound makes them a non-invasive route for researchers to gain insight into social information use. Darwin proposed that vocalisations in animals originated as involuntary consequences of muscular action brought about "when the sensorium is strongly excited" (Darwin, 1872). These, he claimed, developed in to basic expressions of an animal's emotions such as rage, pleasure, or pain. Since then, researchers have shown that animal calls can contain a level of information that is somewhat more impressive, with variation in call production to different stimuli and variation in listener response to differences in the perceived calls (Blumstein & Arnold, 1995; Macedonia & Evans, 1993; Seyfarth & Cheney, 2003).

How sociality affects call production and response has been an important focus of studies on animal communication (Bergman et al., 2003; Charlton et al., 2011; Freeberg & Krams, 2015; Ramsier et al., 2012). A basic requirement of calls for them to have any kind of social correlation is that they must be acoustically distinct, either at a categorical (male, female, young, old, kin, nonkin etc), or individual level. Overwhelmingly, studies that have looked at otherwise situationally specific calls have found repeatable acoustic differences that are indeed associated with animals that differ at a categorical or individual level (Blumstein & Munos, 2005; Janik, Sayigh, & Wells, 2006; Sharp & Hatchwell, 2013; Warrington, McDonald, & Griffith, 2015). However, just because different individuals, or different social categories of caller, can sound different, does not imply or necessitate a difference in response among listeners. In several studies, calls have been shown to be individually distinct, but this distinction has little or no bearing on listeners response (Bergman, 2010; McCulloch, Pomeroy, & Slater, 1999; Schibler & Manser, 2007). In other studies however, receivers in social species are shown to attend to caller identity at a categorical or individual level (Blumstein & Daniel, 2004; Cheney & Seyfarth, 1988; Proops, McComb, & Reby, 2009). Chacma baboons, *Papio ursinus*, provide a good example of a species that attends to a relatively high degree of social information present in vocalisations (Cheney & Seyfarth, 2007). Baboons discriminate between the grunts of individuals and respond differently to callers of differing rank and kinship to themselves. Cheney and Seyfarth's playback experiments (Cheney & Seyfarth, 2007) demonstrate that baboons even attend to changes in third-party relationships when listening in on vocal

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interactions between known conspecifics, an ability previously thought to be confined to humans. Most evidence that species attend to complex information in vocal cues such as third party rank or matrilineal relationships comes from primates (Digweed, Fedigan, & Rendall, 2007; Micheletta et al., 2012; Rendall, Rodman, & Emond, 1996). However a similar depth of attention to social information contained in vocalisations has been shown in other mammals such as spotted hyena, *Crocuta crocuta* (Holekamp, Sakai, & Lundrigan, 2007; Mathevon, Koralek, Weldele, Glickman, & Theunissen, 2010). The extent of such complex abilities has now been extended to birds, with playback experiments on ravens, *Corvus corax*, producing results consistent with them having an understanding of changes in third-party dominance relationships (Massen, Pašukonis, Schmidt, & Bugnyar, 2014). Studies that aim to test the SIH through vocalisations have tended to focus on calls that appear to have a predominantly social function, such as within-group contact calls, dominant/submissive calls, or calls associated with mating and courtship. The social information potentially contained in anti-predator alarm calls has received limited attention from researchers in comparative cognition, with most studies focussing on caller reliability (Blumstein, Verneyre, & Daniel, 2004; Cheney & Seyfarth, 1988; Hare & Atkins, 2001; Schibler & Manser, 2007; R. R. Swaisgood, Rowe, & Owings, 2003).

Anti-predator alarm calls

Many species have evolved anti-predator alarm calls, where distinct vocalisations are produced in response to predator cues (Caro, 2005; Hollén & Radford, 2009). While studies of primates have examined social knowledge in the context of calls produced in altercations among conspecifics (Cheney & Seyfarth, 1980) there has been relatively little work in the context of anti-predator alarm calls. In this thesis, I shall focus on alarm calls given only in an anti-predator context.

For an alarm call to function, it must have acoustic properties sufficiently specific to separate it from other call types, it must be produced only in certain contexts, and it must elicit a suitable response in receivers (Blumstein & Arnold, 1995; Hollén & Radford, 2009). Plenty of non-social information has been

demonstrated in alarm calls, with extensive research exploring the level to which alarm calls are functionally referential, and how much urgency is encoded in the call (Manser, 2001; Seyfarth & Cheney, 2003). Studies of this type have shown that whilst alarm calls can indicate the presence of a predator, they can also also contain highly specific information about the nature of the threat posed by the predator, such as whether it is terrestrial or aerial, whether it is moving, and how far away it is, to name but a few (Gyger, Marler, & Pickert, 1987; Seyfarth, Cheney, & Marler, 1980; Townsend & Manser, 2013). However, alarm calls may also contain information about the caller (Blumstein et al., 2004). Response to alarm calls may vary according to the identity of the caller, with receivers discriminating between categories of caller such as young versus old (Blumstein & Daniel, 2004), or between individual callers (Pollard, 2010). For individual discrimination to occur, there must be sufficient acoustic differences between the calls of different individual callers for receivers to tell them apart, but whilst many species produce alarm calls that are individually distinct (Pollard, 2010), not all of them differentiate their response as a result (Schibler & Manser, 2007). Where studies have found individual discrimination of alarm calls, they have tended to be specific in two ways. Firstly they have tended to focus on caller reliability as the underlying reason for responding selectively to different callers (Blumstein et al., 2004; Cheney & Seyfarth, 1988; Hare & Atkins, 2001). Secondly, they have focussed primarily on situations where alarm calls produce a fleeing response (Fallow & Magrath, 2010; Weary & Kramer, 1995). As a result, the effect of caller identity on alarm call responses that do not involve fleeing remains relatively unexplored. A good example of such a response is collective mobbing behaviour.

Mobbing

In a broad range of taxa, conspecifics group together in repelling a threat, usually in response to specific recruitment signals (Bowles, 2009; Curio, 1978; Graw & Manser, 2007; Scharf, Pamminger, & Foitzik, 2011). Mobbing usually refers to situations where conspecific group members collectively approach a predator and has been described in birds, fish, and mammals (Caro, 2005;

Dominey, 1983). A mobbing response often has the effect of driving away a predator, or at least causing it to give up on its hunting attempt, and there is evidence that mobbing can also provide a relatively safe way for naïve group members to learn about a predator (Curio, Ernst, & Vieth, 1978; Graw & Manser, 2007). Despite the apparent benefits of mobbing, recruits to a mobbing event may increase their personal risk because by taking part they move towards a potentially dangerous predator. Evidence suggests that the effectiveness of a mobbing response relies partly on sufficient numbers of conspecifics joining in (Curio, 1978; Flasskamp, 1994), but there are potentially severe costs associated with taking part. Thus, mobbing generates a collective action problem: the whole group would benefit if the predator is driven away, but individuals may benefit from acting selfishly and avoiding joining the mob. The amount of research testing how this problem is resolved is limited, but work on pied flycatchers, *Ficedula hypoleuca*, provides evidence suggesting that mechanisms of reciprocity, such as reciprocal altruism may help in minimising cheating in species that mob (Krama et al., 2012; Krams, Krama, Igaune, & Mänd, 2008). Such reciprocal cooperation may involve the ability to discriminate amongst different individuals, but in principle apparent reciprocity could arise through location based cues. For instance, rather than remembering specific individuals, flycatchers could remember the location (e.g. a nestbox) from which birds previously arrived to join in mobbing events and subsequently prefer to join mobs at those locations (Mcauliffe & Thornton, 2015; Russell & Wright, 2009). As yet, the extent to which animals employ individual discrimination in the coordination of mobbing events is unknown.

Many mobbing behaviours are initiated by recruitment signals produced by the individual that discovers the predator, with vocalisations being the predominant recruitment signal present in birds and mammals (Graw & Manser, 2007; Suzuki, 2012; Templeton, Greene, & Davis, 2005). These mobbing recruitment calls have been shown to be individually distinct in several species that mob, but the level to which this information affects overall recruitment remains unclear (McDonald, 2012; Micheletta et al., 2012; Yorzinski, Vehrencamp, McGowan, Clark, & McGowan, 2006). Indeed, mobbing provides interesting opportunities to integrate studies of collective behaviour and cognition.

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Traditionally, research on collective behaviour has been dominated by theoretical models in which group cohesion and coordination is explained through simple, local rules (e.g. alignment, short-range repulsion and long-range attraction between neighbours; Couzin, Krause, James, Ruxton, & Franks, 2002). However, there is evidence that cognitive processing of acoustic cues can influence collective group behaviour. For example in playback experiments simulating the presence of an opposing group, female lions, *Panthera leo*, adjusted their decision to collectively approach the opposing group depending on both the number of callers present in the playback and the size of their own group (McComb et al., 1994). Mobbing presents a similar form of collective action where individual responses to recruitment calls might be influenced by cognitive processing of information such as the identity of the caller and details of the threat present in the calls. Furthermore, although some species are known to recognize calls made by potential predators (reviewed in Blumstein, Cooley, Winternitz, & Daniel, 2007) little is known about whether acoustic cues contained within predator vocalisations may affect the mobbing responses of their prey.

Mobbing in response to predator vocalisations

The olfactory, visual, or acoustic cues indicating the presence of a predator may be used by prey species to avoid a potentially costly encounter (Blumstein et al., 2002; Hettena, Munoz, & Blumstein, 2014; Lorenz, 1939). Prey responses to acoustic cues indicating the presence of a predator have been demonstrated in a broad range of species, with animals attending to predators' vocalisations, eavesdropping on alarm calls of other prey species, and even responding effectively to sounds produced by a predator moving through the environment (Emmering & Schmidt, 2011; Haff & Magrath, 2010; Hettena et al., 2014; Magrath, Pitcher, & Gardner, 2009; Templeton & Greene, 2007). Response to the vocalisations of predators has been shown in yellow-bellied marmots, *Marmota flaviventris*, a species that also demonstrates caller discrimination in their response to conspecific alarm calls (Blumstein et al., 2007; Blumstein & Daniel, 2004). Response to the calls of predators has also been shown in American crows, *Corvus brachyrhynchos*, a species that also produces individually distinct alarm calls, and is known to show sophisticated social

learning skills and heterospecific individual recognition abilities (Cornell, Marzluff, & Pecoraro, 2012; Hauser & Caffrey, 1994; Marzluff, Walls, Cornell, Withey, & Craig, 2010; Yorzinski et al., 2006). Clearly responses to the acoustic cues of predators are present in species that have relatively complex cognitive, and acoustic discrimination abilities. However, since most research in to prey's response to predator vocalisations has focused on a fleeing response, the extent to which mobbing might be influenced by predator vocalisations remains poorly understood.

Study species

Jackdaws, *Corvus monedula*, provide the ideal study system in which to explore the role of cognitive processes in mediating collective anti-predator responses. They live in structured societies in a broad range of habitats, are highly vocal, and collectively mob predators in response to specific recruitment signals.

What is a jackdaw?

Typically weighing 200-250g and with an overall length of 32-40cm, jackdaws are smaller members of the Corvidae family of passerine birds, which also contains crows, rooks, ravens, magpies, jays, and choughs. Corvids, along with parrots, have remarkably large brains compared to other birds, and have recently been shown to have twice the neural density of primates, packing a similar number of neurons into a much smaller volume (Olkowicz et al., 2016). In experiments, corvids demonstrated numerous complex cognitive abilities, including transitive inference, observational special memory, future planning, perspective taking, and causal reasoning, among others (Güntürkün & Bugnyar, 2016; A. Seed, Emery, & Clayton, 2009). This has lead researchers to draw comparisons between cognitive abilities found in corvids, and those present in primates (Emery & Clayton, 2004; A. Seed et al., 2009). Compared to most non-human primates however, corvids are relatively common in a range of habitats, and in many cases have adapted to live in urbanised areas where

many other native species have disappeared (Röell, 1978). Jackdaws are found throughout Eurasia, occupying many habitats, including forest, farmland, coastal areas, and they are particularly prevalent in areas of human habitation, where short cut grass found in parks and gardens provides safe foraging areas, and structures such as chimneys and church towers provide ideal nest sites. The attribute of being a cavity nester that will readily take to nestboxes makes studying them in the wild immensely practical. Jackdaws are visually distinguishable from other corvids by their small size, piercing light grey eyes and grey nape (both lighter in adults), as well as their somewhat quirky strutting style of walk.

Jackdaw society

That jackdaws were a key study species of Konrad Lorenz, who, along with Nikolaas Tinbergen and Karl von Frisch, won a 1973 Nobel Prize for work on animal behaviour, should give you a clue that this species has much to offer behavioural researchers. Lorenz was fascinated by jackdaws' social lives, so much so that he converted the attic of his house to allow for careful study of a flock of jackdaws that became resident there (Lorenz, 1952). In his book "King Solomon's Ring" he describes his observations of jackdaw behaviour in a remarkable narrative manner. Further work, in particular an expansive study on the jackdaws of Groningen in the Netherlands by August Röell (Röell, 1978), adds to that of Lorenz in providing a solid body of knowledge describing the social structure of jackdaw society.

Jackdaws live in colonies that may include many hundreds of birds. The majority of adults in a colony live in pairs. Jackdaws may remain unpaired for their first year of life, but after this they tend to remain in their pairs, with divorce being rare. Pairs may split if one partner dies, or occasionally very young pairs may split. Within each jackdaw colony, a linear dominance hierarchy exists (Verhulst & Salomons, 2004). Dominant birds are able to displace less dominant birds, for example when feeding, but may also use their dominance to acquire better nest sites. Members of a pair have the same rank, but this rank is determined by the fighting success of the male against other males from the colony (Röell, 1978). Whilst females may assist their mate in dominance fights,

fights between females are less common. Changes in rank position are relatively infrequent, but when rank changes do occur, anecdotal evidence suggests that knowledge of the change spreads through the colony rapidly. For example Lorenz described how an unpaired female, inherently at the bottom of the rank order, paired with a newly dominant unpaired male, and the female immediately began to exhibit dominant behaviour towards her formerly-higher-ranking colony members. In winter jackdaws travel around, often in groups, feeding largely on invertebrates found in open farmland. They regularly forage and fly in groups with other corvids such as rooks, *Corvus frugilegus* (Jolles, King, Manica, & Thornton, 2013)*.* Jackdaws in a local area come together in the evenings to form noisy pre-roost groups, which then fly together to roosting sites up to 15km away that may contain just a few hundred, or tens of thousands of individuals.
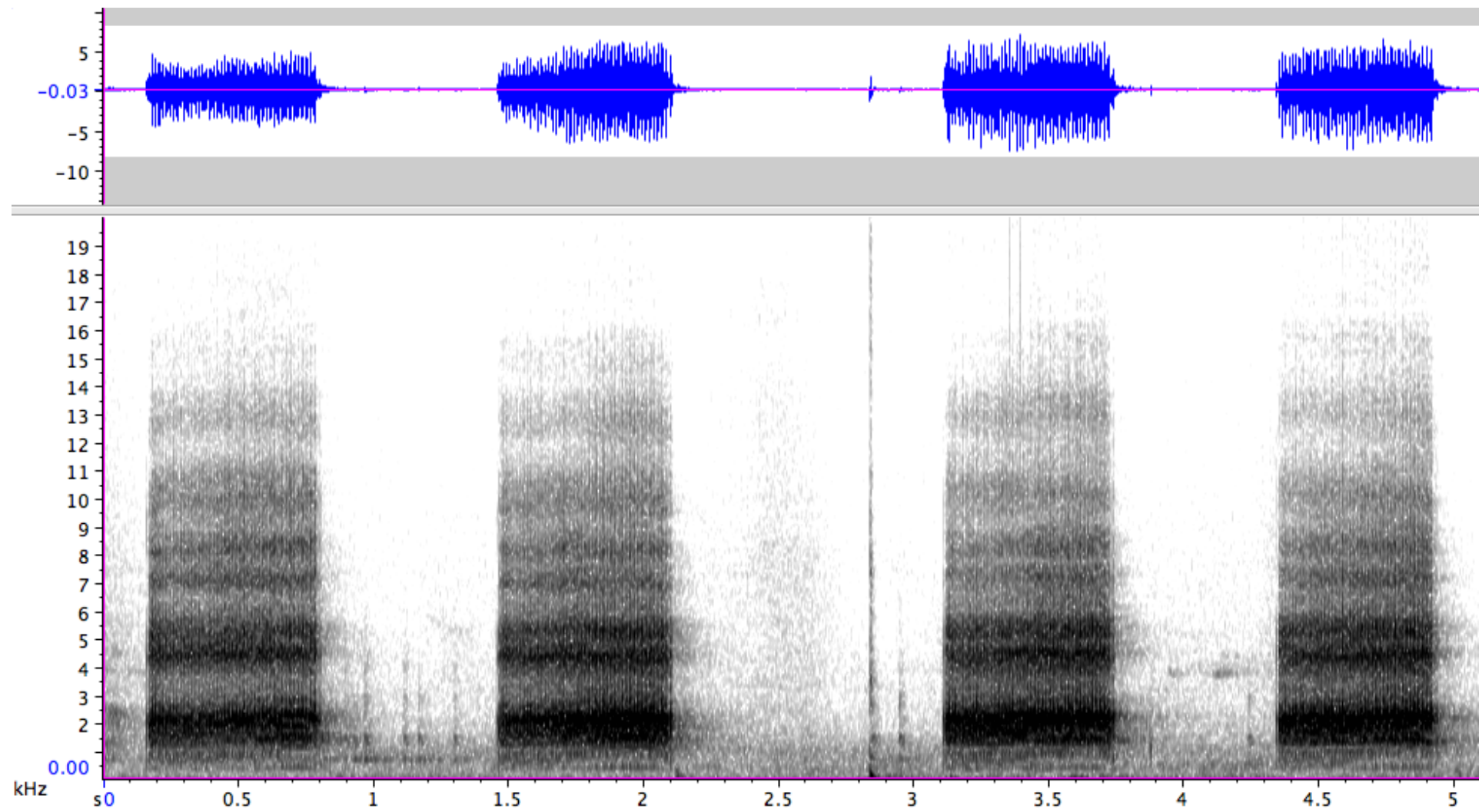
Breeding

In the breeding season (April-July), pairs select a cavity, typically in a tree, cliff, or building, in which they build a nest. Cavities are usually situated 5-10m from ground level and nests of adjacent pairs may be separated by as little as 1m but more typically, distances of 5-50m are common. Jackdaws often re-use cavities from previous years and may have several sites that they defend from other pairs, with occasional visits paid to favourite nest sites throughout the year, before settling on one in which they build their nest. Nest building may start in late March, but egg laying does not usually occur until mid April, with some nests being built completely in as little as one day. Nests consist of a heap of sticks sometimes with the addition of hair, moss, grass, or sadly even rubbish from the local area. One clutch is laid per year, and typically consists of 4-5 eggs, although this is variable (range at my study sites: 1-7). Eggs are incubated for 17-18 days, with the female performing the majority of incubation. She may leave the nest to forage occasionally, during which time the male may take over incubation, but often she will incubate exclusively with the male provisioning her with food. This difference in incubation effort between the male and female provides a useful way to identify the different sexes, particularly useful in the absence of colour rings. Once eggs hatch, incubation continues for a few days but then ceases. Since egg laying is sequential, and incubation

starts when the first egg is laid, hatching is also sequential, leading to differences in the size of chicks. This generally leaves older chicks larger and better able to compete for food from the parents. As a result of the limitations of provisioning, many chicks starve, with only one or two chicks usually surviving to fledge (Arnold & Griffiths, 2003). Both parents provision the nestlings until they fledge at 28-35 days. Fledglings remain dependent on parents for food provisioning for approximately a month post fledging.

Vocal communication

It is hardly surprising that jackdaws' vocal communication has become the topic of research, since they make their ubiquitous presence across Europe's centres of human population known by their seemingly constant chatter. Jackdaws' calls have formed the basis of the species naming in several languages, with their short contact calls sounding somewhat like "jack", giving rise to the English name jackdaw, whilst the French name for the species "choucas" is a similar interpretation, and the Dutch "kauw" is further evidence of quite how much this species is recognised by its calls. These short contact calls, that jackdaws make frequently when perched, when foraging on the ground, and particularly when flying, appear to serve as individual identifiers, allowing birds to keep track of each others location. Other similarly short calls have been identified as food calls made by parents to stimulate chick begging (Zandberg, Jolles, Boogert, & Thornton, 2014). However the jackdaw call most relevant to the subject of this thesis is the scolding call, which sounds less like "jack" and more like "Arrrrrgggggggg!". In contrast to the previously mentioned jackdaw calls, this call is a relatively long, harsh, monotonous, rattle (See Fig. 1.1). Scolding calls are an alarm call, in that they are often produced in response to threats, but they also serve to recruit conspecifics, who may then mob a predator if one is present, and make further scolding calls of their own. Acoustic analysis shows that these calls are individually distinctive (Kings, 2014).

Figure 1.1. Waveform (top) and spectrogram of a typical bout of jackdaw scolding calls.

General description of study system

The experiments presented in this thesis took place during the breeding seasons (April-July) of 2013, 2014, and 2015, at colonies of nesting jackdaws across west Cornwall, UK.

Main study sites

Recordings of jackdaws' vocalisations were made at three nestbox colonies near Penryn, Cornwall, UK. These three sites were selected and the first nestboxes installed during the summer of 2012. Each site had their own characteristics, whilst at the same time all offered suitable habitat for nesting jackdaws. The first site, referred to as colony X, consisted of 40 nestboxes attached to trees in an area of mature deciduous woodland adjacent to the university campus (50°10'22.9"N 5°07'04.1"W). 5km away, the second site, referred to as colony Y, was centred around the church at the village of Stithians (50°11'22.4"N 5°10'53.4"W) and consisted initially of 30 nestboxes attached to trees, both around the church and in hedgerows in fields backing on to the church. 1km from colony Y and 5km from colony X, the third study site, colony Z, was centred on the main buildings at Pencoose Farm (50°11'55.5"N 5°10'10.8"W) and consisted initially of 30 nestboxes attached both to buildings, and to trees in fields and hedgerows immediately adjacent to the farm buildings. At all sites, nestboxes were spaced at naturally realistic intervals of 5-30m, and 4-6m from ground level. Very occasionally nestboxes were damaged by wind or, sadly, by vandalism, necessitating replacement. Furthermore, the plywood used in the early nestboxes began to split after just a year, necessitating their replacement, performed outside of the breeding season, with nestboxes made from recycled plastic. These nestboxes proved more resilient to the elements although their weight made lifting them up ladders and securing them to trees of buildings somewhat more difficult. Each nestbox was equipped with a CMOS IR camera and microphone, both with cables running to ground level allowing sound and video to be recorded inside the nest without disturbing the nestbox itself.

Ringing and sexing

Coloured rings were attached to jackdaws under license (C5752 and C5746) from the British Trust for Ornithology (BTO). The task of catching jackdaws proved difficult, with a single individual ringed between September 2012, when the study began, and the start of the first breeding season in April 2013. Jackdaws were ringed in considerable numbers, in large part due to the success of ladder traps, typically baited with bread or grain. In the subsequent three years over 1500 jackdaws were fitted with individually distinct combinations of three coloured plastic rings, and one metal ring stamped with a unique BTO code. This ringing scheme provided a basis for identifying jackdaws occupying nestboxes, and later for identifying birds filmed during experiments and observations at feeding platforms, as part of research by my group. Concurrent with the ringing effort, blood and feather samples were taken from each bird during ringing, again under BTO license. This allowed molecular sexing of individuals (Griffiths & Double, 1998) which proved invaluable since male and female jackdaws are visually similar.

Life history monitoring

During the breeding season, nestboxes were checked daily through the use of nestbox cameras. Furthermore, a strategy of regular video and sound recording from inside nestboxes was used to collect data on nestbox ownership, and record behaviour and vocalisations of both parents and chicks. This allowed for the collection of life history data that was used to inform the implementation of experiments locally. For example, knowing which nests were occupied, and whether they contained eggs, chicks, or adult jackdaws, was used to inform the timing and location of playback experiments. Ladders were used to access active nests in order to fit or fix the nestbox cameras and microphones, measure chicks and eggs, put coloured rings on chicks, and check suspected failed nesting attempts. This use of ladders to access nests was kept to a minimum however, because it tended to alarm resident and local jackdaws. Indeed the focus on alarm calls in several of my experiments came about due to witnessing first hand the mobbing calls and subsequent flock of scolding jackdaws that would occasionally appear overhead as I attempted to access a nestbox.

Extra colonies used for playbacks

Whilst the three study sites at colonies X, Y, and Z allowed for recordings to be collected from known individuals, and playbacks to be presented in areas where potential recruits would be familiar with the individual used in the playback, the design of several of my experiments required that potential recruits should have not have prior experience of the individual featured in the playback. In order to obtain achieve this, and to minimize the number of playbacks performed at any one site overall, I performed playbacks at other colonies where individuals recorded at colonies X, Y, and Z would not have been heard. These colonies were found by exploring west Cornwall by car during jackdaws breeding season and looking for concentrations of nesting jackdaws. Old churches proved particularly fruitful in this respect, since jackdaws frequently nest in church towers where old slit windows often provide access to nesting cavities within. The abandoned wheelhouses of Cornish tin mines, long since closed for business, also attract concentrations of nesting jackdaws.

Thesis structure

Chapter Two

In Chapter Two I use playback experiments to test whether jackdaws collective mobbing response to scolding calls is affected by the identity of the caller. Playbacks are performed at locations both near to and away from active nests. Different categories of caller presented include nestbox residents, local colony members, strangers from a separate colony, and another sympatric corvid species as a control.

Chapter Three

In this chapter I delve further in to the findings from Chapter Two. I use playback experiments of scolding calls to determine whether jackdaws' collective responses to scolding calls are dependent on discrimination between individual callers, or whether they use broader-level discrimination between more or less familiar categories of caller.

Chapter Four

Here I examine whether jackdaws encode urgency in to the structure of their alarm calls using a two-part experiment. In the first part, I examine variation in jackdaws' scolding call rate in relation to different threat levels. In the second part I perform playback experiments to compare jackdaws' collective responses to fast vs slow rates.

Chapter Five

In this chapter I build on the findings of the first three data chapters and explore whether jackdaws respond to the calls of predators. The ability to generalise from known threats may allow animals to respond appropriately to new threats. Simultaneously, variation in response to predator cues may follow seasonal trends. Here I use playback experiments of predators and non-predatory species that are either resident or novel at the study sites, played at different

phases of the breeding season, in order to examine how jackdaws respond to acoustic cues of potential threats, whether they are able to respond effectively to novel predator cues, and how these responses vary across the breeding season.

Chapter Six

Here I discuss jackdaws' cognition of alarm calls and acoustic predator cues in light of my findings. I build on the ideas that stimulated the research and explore questions raised by my findings. I summarise key points and suggest directions for future work.

Note

Each data chapter is written as a stand-alone piece of work, thus some sections, such as descriptions of study species, study sites, and standard methods of recording and playback protocols may be repeated. I apologise for any inconvenience to the reader caused by this.

Chapter Two: Jackdaws care who calls in collective response decisions

Abstract

Recent advances show that simple, stereotyped interaction rules can enable animal groups to maintain strikingly coordinated collective movements. However, the mechanisms through which collective actions are initiated are poorly understood, particularly when joining collective responses entails considerable risk. In species where recruitment signals initiate collective responses to external threats, individuals may benefit from being selective in whom they join, but the role of signaller discrimination in coordinating group-level responses has yet to be tested. Here I show that in wild jackdaws, a colonial corvid species, collective responses to anti-predator calls are mediated by initiator identity. In playbacks at nestboxes, the calls of nestbox residents attracted most recruits, followed in turn by other colony members, non-colony members and rooks (a sympatric corvid). Playbacks in fields outside nest-box colonies, where the immediate threat to broods was lower, showed similar results, with highest recruitment to nearby colony members' calls. Responses were further influenced by caller sex: calls from non-colony member females were less likely to elicit responsive scolding by recruits than other calls, potentially reflecting social rank associated with sex and colony membership. These results show that vocal discrimination mediates jackdaws' collective responses and highlight the need for further research into the cognitive basis of collective behaviour.

Key words: Alarm calls, cognition, collective behaviour, individual recognition, recruitment, vocal communication

Introduction

From army ants to human armies, groups of conspecifics across many taxa exhibit collective responses towards external threats, often in response to specific recruitment signals (Bowles, 2009; Curio, 1978; Graw & Manser, 2007; Scharf et al., 2011). Such collective behaviours have become a major focus of research (Couzin, 2009; Petit & Bon, 2010) but their underlying mechanisms remain poorly understood. Joining a collective threat response can be highly risky, so individuals are expected to be selective when deciding whether to take part. Alarm calls can signal not only the presence and nature of threats (for reviews see (Seyfarth et al., 2010; Vehrencamp & Bradbury, 2011)) but may also provide listeners with information on the identity of the caller (Blumstein & Munos, 2005; Cheney & Seyfarth, 1988; Micheletta et al., 2012). In group-living species where there is a range of potential callers and receivers, the ability to discriminate between the alarm calls of different group members may provide important benefits in deciding whether or not to respond.

In the majority of cases, alarm calls function to promote evasive responses in receivers. Where calls signal threats that are imminent and severe, individuals may benefit from responding with evasive action regardless of who produced the call. Meerkats, *Suricata suricatta*, for example, produce individually distinctive alarm calls, but habituation-dishabituation experiments show that responses are unaffected by the identity of the caller (Schibler & Manser, 2007). This lack of discrimination is likely to reflect the severity of the threat: meerkats live under high predation pressure, and failure to respond to an alarm call may prove fatal. The severity of the costs of not responding is thus likely to outweigh any potential benefits of responding selectively.

Caller characteristics may be more likely to influence alarm responses in scenarios where the risk implied by the alarm is relatively low, or when particular categories of individuals are especially vulnerable. In yellow-bellied marmots, *Marmota flaviventris,* for example, group members increase vigilance behaviour and reducing foraging significantly more in response to the alarm calls of vulnerable juveniles than those of adult females. They do not, however, appear to discriminate between the calls of different individuals within the same age/sex category, despite the fact that individual calls are acoustically distinct (Blumstein & Daniel, 2004).

Selective responses on the basis of individual caller identity may also be advantageous if some callers are unreliable. For instance in a now classic study with vervet monkeys, *Chlorocebus pygerythrus*, Cheney and Seyfarth (1988) made particular individuals appear unreliable by repeatedly broadcasting their intergroup "wrr" calls (a low-threat response to the presence of another vervet group) when no other group was present. As a result, group members ceased responding both to these calls and to other acoustically distinct intergroup calls by the same individual. If, however, the habituation phase was followed by the intergroup call of a different individual, then group members responded normally, indicating that responses depend on the perceived reliability of the caller. In contrast, such selective responses were not apparent if the threat level was raised from the apparent presence of another group to the presence of a predator. Here, group members habituated to the repeated leopard-specific alarm calls of a particular individual nevertheless showed strong responses if they then heard the same individual's eagle-specific call. These results suggest that threat level plays an important role in determining the impact of individual caller identity on receivers' responses to alarms.

Selective responses may be particularly likely if responding to a call increases rather than reduces individual's exposure to threats. This is the case in collective anti-predator responses, where individuals that respond to recruitment calls move *towards* the threat, placing themselves in more danger than if they did not respond (Berziņš et al., 2010). Consequently, receivers may respond preferentially to callers with whom they are familiar or have strong social relationships. For instance, playback experiments on crested macaques, *Macaca nigra*, show that individuals are more likely to respond to the recruitment calls of group members with whom they have strong social bonds (Micheletta et al., 2012). Such selective responses could, in principle, have substantial effects in determining the magnitude of collective anti-predator responses involving the coordinated action of numerous individuals, but this possibility has yet to be tested.

Jackdaws, *Corvus monedula*, provide an ideal opportunity in which to investigate whether collective responses to threats depend on caller identity under natural conditions. They breed colonially and live in structured groups with a defined linear rank hierarchy and form long-term monogamous pair

bonds (Lorenz, 1931; Röell, 1978). In response to threats, jackdaws produce a harsh, rattling, "scolding" call, which typically serves to recruit other group members to the location of the caller. Recruits may further respond with their own scolding calls, and if a predator is present the group may aggressively mob it (Lorenz, 1952). Responding to a scolding call is likely to entail time and energy costs, as well as risks associated with exposure to the threat (Curio & Regelmann, 1985, 1986). Given these costs, it may be beneficial for jackdaws to respond preferentially to scolding calls from their mate or a fellow colony member, rather than to those of unfamiliar jackdaws. Recruitment to a mate's scolding call could have direct fitness benefits by increasing survival for both the mate and their young, and preferentially joining more familiar individuals may generate more cohesive and effective collective response (Barber & Ruxton, 2000). Some authors have also suggested that collective responses may be maintained through reciprocity, with individuals assisting those that have assisted them in the past (Krama et al., 2012; Krams et al., 2008; but see Russell & Wright, 2009). Given the high costs of joining in collective responses and the potential benefits of selective responses, I predicted that jackdaws would base their decision on whether or not to respond to a scolding call on the identity of the caller.

I performed playbacks of scolding calls from known individuals near the nests of wild jackdaws to test whether individuals discriminate between the calls of one of the *resident* pair at a nestbox, a *local* bird nesting in the same colony as resident pair and a *stranger* from a different colony. The calls of local rooks, *Corvus frugilegus*, were used as a sympatric heterospecific controls. To test whether high levels of threat over-ride the advantages of selective responses (Schibler & Manser, 2007), I repeated the experiment both near focal nestboxes, where the perceived predation threat is expected to be relatively high, and in fields away from the nestbox colonies, where the imminent threat to nesting birds is lower. I recorded the maximum number of recruits to each playback and whether recruits made scolding calls of their own. I predicted that during playbacks away from nests there would be highest responsive scolding and recruitment to playbacks of colony-members' alarm calls, less to those of unfamiliar jackdaws from different groups, and least of all for rook calls. Given the greater threat levels, I predicted less discriminating responses to playbacks within nestbox colonies.

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Methods

Study sites and species

All recordings and playbacks were conducted at three jackdaw colonies near Penryn in West Cornwall, UK. Colony X (50°10'22.9"N 5°07'04.1"W), is ~5km from the other two colonies, Y (50°11'22.4"N 5°10'53.4"W) and Z (50°11'55.5"N 5°10'10.8"W) which are themselves ~1.5km apart. The jackdaws used in the study were all free-living adults, a large proportion of which had been colour-ringed under license from the British Trust for Ornithology. One hundred nest boxes were spread across the three sites at naturally realistic distances from each other (5-30m). Recording and playback took place during the breeding seasons of April-June 2013 and 2014. All recordings used for playbacks were from jackdaws that were individually identifiable either from their colour-ring combinations or focused behavioural monitoring to confirm ownership of a particular nestbox. The sex of each individual was determined through behavioural observations from outside the nest box and CMOS IR nest-box cameras (females are responsible for the vast majority of the incubation (Röell, 1978)) and later confirmed through molecular sexing (Griffiths & Double, 1998).

Collecting scolding recordings

To record the scolding calls of known individuals, I approached focal nestboxes, keeping the identified bird(s) in view. In many cases, walking towards the nestbox within 0-10m was sufficient to cause a scolding response. If residents did not scold spontaneously, I elicited scolding by placing a ladder against the tree/building in question and climbing to within 1m of the nestbox. I recorded a minimum of ten discrete calls from each of 25 jackdaws from 23 different nest-boxes across the three sites. To obtain recordings of rooks for use as controls in playbacks, I approached a rookery adjacent to jackdaw colony Y where adult rooks were nesting. All recordings were made using an Olympus LS-100 portable digital recorder, recording at 48.0Hz/16bit, and a Sennheiser M67/K6 directional microphone and saved as uncompressed WAV files.

Creating playback tracks

I created playback tracks using the software package Audacity (www.audacity.sourceforge.net). Each playback consisted of three sets of eight scolding calls spread over 15 seconds, separated by 30 second periods of silence, mimicking a natural bout of scolding calls. Tracks started and ended with 30 seconds of silence. A small proportion of the calls recorded contained audible background noise from wind or traffic, which I removed from raw recordings using the high pass filter in Audacity, filtering out only frequencies below 800Hz which includes wind and traffic noise but does not overlap with the calls themselves. The amplitude of all playback tracks was normalised. Discriminant function analysis of call features confirm that, similar to jackdaw food calls(Zandberg et al., 2014) and contact calls (Wascher, Szipl, Boeckle, & Wilkinson, 2012), and the scolding calls of other corvids (Yorzinski et al., 2006), jackdaw scolding calls are individually distinctive .

Playback procedure

I performed playbacks using Foxpro GX7 Fury remote controlled loudspeakers. Playback volume was determined using a Voltcraft SL-100 sound level meter to calibrate the output of the speaker to the sound level recorded from a scolding jackdaw at the same distance. At each colony, playback experiments were conducted in one of two distinct locations types, labelled *Near* and *Away*, that differed in the level of threat posed by predators to nesting jackdaws and their broods.

During *near* playbacks the speaker was placed directly below a focal nestbox, to simulate a high threat to the resident nesting birds and their chicks. I used four experimental treatments. *Resident* treatments consisted of calls from one member of the pair occupying the focal nestbox, whose partner was likely to be in the vicinity, *local* from a jackdaw of the same colony (nesting 100-300 meters of the *resident* nestbox), *stranger* from a jackdaw at a different colony, and *rook* calls as a control.

The procedure for *away* playbacks simulated a lower threat intensity, with the speaker placed in an open area 50m from the nearest nestbox, equidistant from the focal *resident* nest and the nest of the *local* bird used in the

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near playbacks. As the speaker was placed away from any nestbox, the distinction between *resident* and *local* treatments was no longer meaningful, so these treatments were combined into a single *colony-member* treatment. After placing the speaker in position, an observer then took up a position concealed either in a car or beneath camouflaged netting with a clear view of the playback area and waited 15 minutes to allow any nearby jackdaws to return to normal behaviour. During this time the observer set up a Panasonic HC-X900 high-definition camcorder with a view encompassing the speaker at the bottom of shot and the sky for at least 50 meters in all directions above the playback location. The playback treatment (*colony-member*, *stranger,* or *rook*) was then broadcast from the speaker via remote control. Treatments were conducted in random order over the period that nests contained chicks, with no more than two playbacks per day per nest-box (separated by at least four hours) to avoid habituation.

From each video, I noted details of two main responses. First, whether or not any jackdaws made scolding calls in response to the playback. Second, the total number of jackdaws recruited to the playback. Recruits were classified as any jackdaw that moved to within 30m of the speaker (this could include circling flight, landing in a tree, or changing direction towards the source of the playback). Jackdaws that were already within 30m of the playback area when playback commenced were only included if their behaviour changed during the playback, by scolding in response to the playback, moving towards the speaker and either landing or circling close to it. Data recording ceased when the playback track had finished and recruited jackdaws began to disperse.

Statistical Analysis

Data were analysed using R version 3.1.1 (R Core Team, 2014). The g*lmer* function was used to run generalised linear mixed models (GLMMs) with year, batch (each three- or four-treatment set of jackdaw treatments and one rook treatment) and colony (X, Y, or Z) fitted as random terms in all models to account for repeated measures. For all models, I performed preliminary analyses that included all treatments in order to examine the difference in response to rook and jackdaw playbacks. Following this I analysed only

jackdaw treatments so that I could include data such as caller sex and caller identity that were unavailable for rook playbacks. *Near* and *away* data were analysed separately as they contained different treatment groups. Model simplification was carried out by stepwise deletion of non-significant terms. ANOVAs were used to compare models at each simplification step (Crawley, 2012) and to compare between the responses to specific pairs of treatments within each final, minimal GLMM.

To test whether caller identity significantly affected the probability that jackdaws would produce scolding calls in response to playbacks, I fitted the presence or absence of responsive scolding (1,0) as a binomial response term in two GLMMs, one for *near* data and another for *away* data. Treatment (*resident*, *local, stranger*, and *rook* for *near* playbacks and *colony-member, stranger,* or *rook* for *away* playbacks) was fitted as an explanatory variable. Current wind speed (measured at Carnkie Weather Station, 3km west of site Y; www.carnkieweather.co.uk) was fitted as an additional explanatory term as it could influence the attenuation of playback stimuli. When comparing jackdaw treatments, caller identity was fitted as a random term, and sex as an additional explanatory term.

The magnitude of group responses to playbacks may be influenced both by the initial playback stimulus and any subsequent responsive scolds. I therefore conducted separate analyses to examine first the effects of playback treatments on recruitment in cases where responsive scolding occurred, and second where the only scolds were produced by the loudspeaker. I conducted four GLMMs (with and without responsive scolding, both *near* and *away*) with the number of recruits fitted as a Poisson-distributed response. In each case, treatment and wind speed were fitted as explanatory terms, with sex fitted as an additional term for comparisons between jackdaw treatments.

Results

1) Does caller identity affect the probability of responsive calling?

a) Near to nests:

Treatment had a significant influence on the probability of responsive scolding for playbacks performed *near* to nests (GLMM; χ^2 = 12.64, d.f. = 3, P = 0.005). Recruits were significantly less likely to scold in response to *rook*s than to *locals* (χ^2 = 23.87, d.f. = 1, P < 0.001), or *strangers* (χ^2 =17.89, d.f. = 1, P < 0.001) and less likely to scold to *rooks* than *residents* although this trend was marginally non-significant (χ^2 =3.61, d.f. = 1, P = 0.057).

When restricting the analysis to jackdaw treatments only, there was no effect of treatment (GLMM; χ^2 = 0.989, d.f. = 2, P = 0.610; Fig.2.1a; Table 2.S2) or caller sex (χ^2 = 0.686, d.f. = 1, P = 0.408) and there was no interaction between treatment and caller sex (χ^2 =0.338, d.f. = 2, P = 0.845).
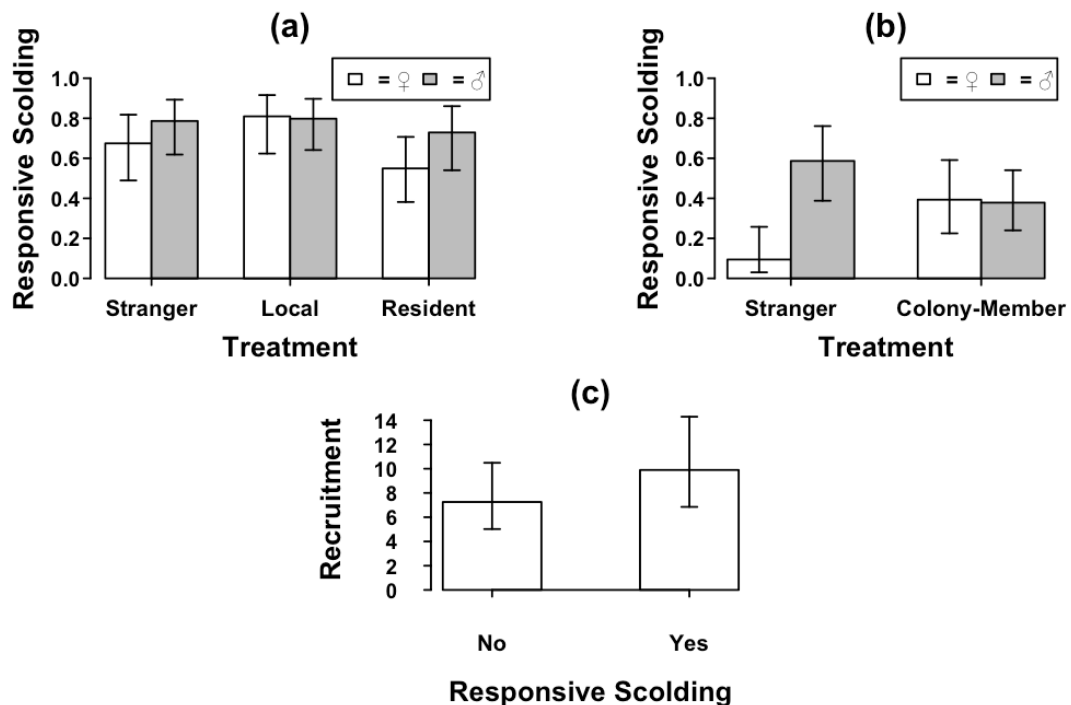
b) Away from nests:

Treatment had a significant influence on the probability of responsive scolding for playbacks performed *away* from nests (GLMM; χ^2 = 8.766, d.f. = 2, P = 0.013). Recruits were significantly less likely to scold in response to *rooks* than jackdaw *colony-members* (χ^2 =7.823, d.f. = 1, P = 0.005), or *strangers* (χ^2 =5.108, d.f. = 1, P = 0.024).

Restricting the analysis to jackdaw treatments, there was a significant interaction between treatment and sex (GLMM; χ^2 =4.366, d.f. = 1, P = 0.037; Fig.2.1b; Table 2.S3). Recruits were less than half as likely to scold in response to playbacks of female *strangers* than to male *strangers* (χ^2 =6.214, d.f. = 1, P = 0.013), and both male (χ^2 =7.823, d.f. = 1, P = 0.005) and female *colony-members* (χ^2 =5.052, d.f. = 1, P = 0.025).

2) Does responsive scolding affect recruitment?

Across all playback experiments, the number of recruits was significantly higher when jackdaws scolded in response to playbacks than when there was no responsive scolding (GLMM; χ^2 =17.386, d.f. = 1, P < 0.001; Fig.2.1c). For ease

of interpretation, I therefore analysed levels of recruitment in playbacks where responsive scolding occurred separately to cases where it did not.

Figure 2.1. (a) Probability of responsive scolding to playbacks near to nests, depending on caller sex and experimental treatment. White bars: female; grey bars: male. (b) Probability of responsive scolding to playbacks away from nests, depending on caller sex and experimental treatment. White bars: female; grey bars: male. (c) Number of jackdaws recruited to playbacks where responsive scolding occurred or did not occur. All bars show means ± SE derived from minimal models.

3) How does treatment affect the number of recruits?

a) Near to nests with responsive scolding

In cases where responsive scolding occurred following playbacks *near* to nests, there was a significant effect of treatment on recruitment (GLMM; χ^2 =20.10, d.f. = 3, P < 0.001). Recruitment to *rooks* was significantly higher than to *strangers* (χ^2 =6.447, d.f. = 1, P = 0.011), but not significantly different to *local* (χ^2 =2.758, d.f. = 1, P = 0.097), or *resident* (χ^2 = 0.010, d.f. = 1, P = 0.920) playbacks.

Restricting the analysis to jackdaw treatments only, there was a significant effect of treatment (GLMM; χ^2 =11.63, d.f. = 2, P = 0.003; Fig.2.2a; Table 2.S4). Recruitment during *resident* playbacks was significantly higher than playbacks of *local* (GLMM; χ^2 =10.21, d.f. = 1, P = 0.001), and *stranger* (χ^2 =4.446, d.f. = 1, P = 0.035). Recruitment to *local* and *stranger* playbacks was not significantly different (χ^2 =1.031, d.f. = 1, P = 0.310). There was no significant effect of sex (χ^2 = 0.679, d.f. = 1, P = 0.410), and no interaction between caller sex and treatment (χ^2 = 1.437, d.f. = 2, P = 0. 488).

b) Near to nests without responsive scolding

Treatment had a significant effect on recruitment for playbacks performed *near* to nests when no responsive scolding occurred (GLMM; χ^2 =66.62, d.f. = 3, P < 0.001). Recruitment was significantly lower for *rook* playbacks than for any of the jackdaw treatments (*rooks* vs. *resident* (χ^2 =57.91, d.f. = 1, P < 0.001), *local* (χ^2 =12.65, d.f. = 1, P < 0.001), or *stranger* (χ^2 = 7.987, d.f. = 1, P = 0.005).

Restricting the analysis to jackdaw treatments, there was a significant overall effect of treatment on recruitment, with the highest mean levels of recruitment in response to *resident* calls followed by *colony-members* and finally *strangers* (GLMM; χ^2 = 11.33, d.f. = 3, P = 0. 003; Fig.2.2b; Table 2.S5). Post-hoc comparisons between treatments showed marginally non-significant trends for lower responses to *strangers* than both *residents* (GLMM; χ^2 = 3.275, d.f. = 1, P = 0.070) and *locals* (GLMM; χ^2 = 3.388, d.f. = 1, P = 0.066), with no significant difference between *residents* and *locals* (GLMM; χ^2 = 0.768, d.f. = 1, P = 0.380). There was no effect of sex (χ^2 = 0.306, d.f. = 1, P = 0.580), and no interaction between caller sex and treatment (χ^2 = 1.794, d.f. = 2, P = 0. 408).

c) Away from nests with responsive scolding

Treatment had a significant effect on recruitment for playbacks performed *away* from nests when responsive scolding occurred (GLMM; χ^2 = 23.13, d.f. = 2, P < 0.001). Recruitment to *rook* playbacks was significantly higher than to *strangers* (χ^2 =5.314, d.f. = 1, P =0.021), and marginally higher than to *colony-members* (χ^2 =3.666, d.f. = 1, P = 0.056).

Restricting the analysis to jackdaw treatments, there was a significant effect of treatment (GLMM; χ^2 = 9.872, d.f. = 1, P = 0.002; Fig.2.2c; Table 2.S6) recruitment during *colony-member* playbacks was significantly higher than during *stranger* playbacks (GLMM; χ^2 = 12.48, d.f. = 1, P < 0.001). There was no effect of sex (χ^2 = 0.522, d.f. = 1, P = 0.470) and no interaction between sex and treatment (χ^2 = 2.774, d.f. = 1, P = 0. 096).

d) Away from nests without responsive scolding

Treatment had a significant effect on recruitment for playbacks performed away from nests when no responsive scolding occurred (GLMM; χ^2 = 122.4, d.f. = 2, P < 0.001). Recruitment was significantly lower for rook playbacks than either colony-members (GLMM; χ^2 = 116.9, d.f. = 1, P < 0.001) or strangers (GLMM; $\chi2$ = 5.314, d.f. = 1, P = 0.021).

Restricting the analysis to jackdaw treatments, there was no effect of treatment (GLMM; χ^2 = 0. 690, d.f. = 1, P = 0. 406; Fig.2.2d; 2.S7). There was no difference in recruitment to colony-member compared to stranger playbacks (LMM; χ^2 = 0.961, d.f. = 1, P = 0. 327). There was no effect of sex (χ^2 = 0.481, d.f. = 1, P = 0.488), and no interaction between sex and treatment (GLMM; χ^2 = 2.259, d.f. = 1, P = 0.133).
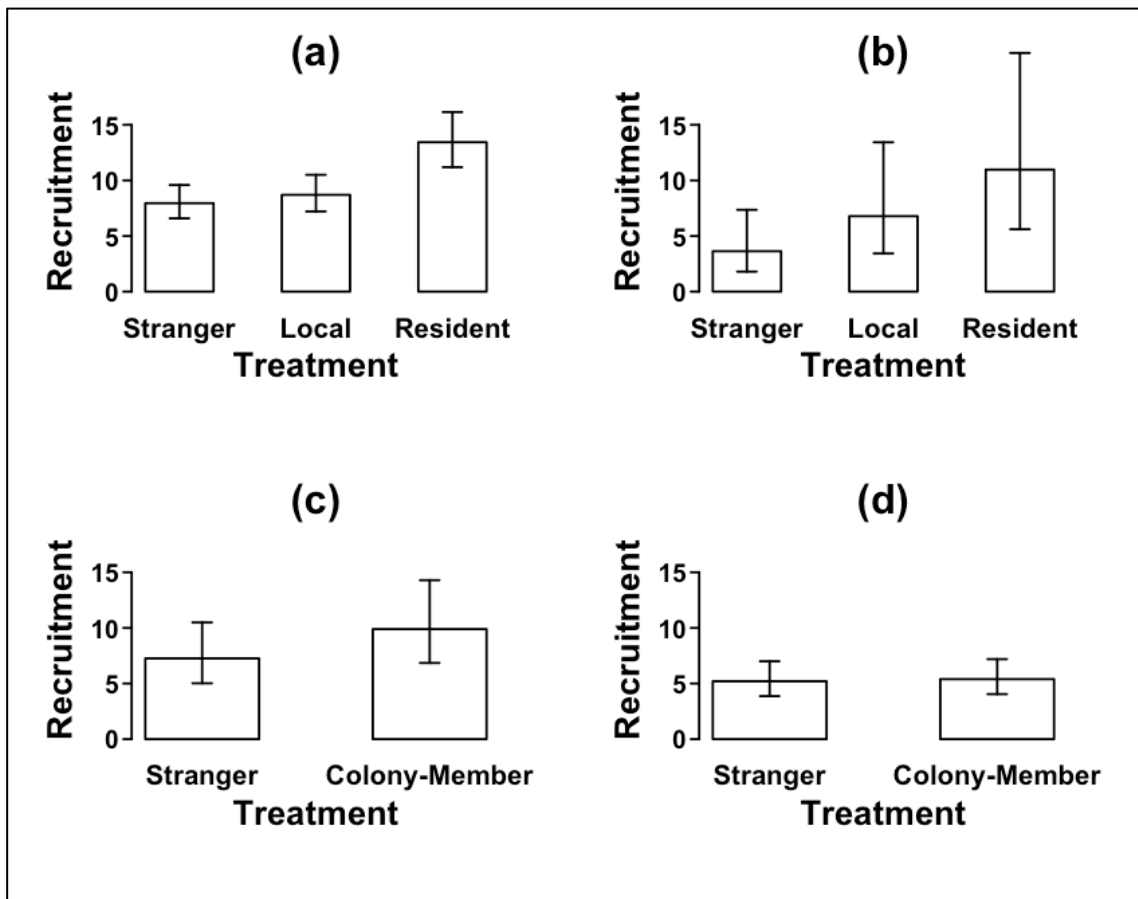
Figure 2.2. (a) Number of jackdaws recruited to playbacks near to nests when responsive scolding occurred. (b) Number of jackdaws recruited to playbacks near to nests when responsive scolding did not occur. (c) Number of jackdaws recruited to playbacks away from nests when responsive scolding occurred. (d) Number of jackdaws recruited to playbacks away from nests when responsive scolding did not occur.

Discussion

A number of recent studies have shown that individual characteristics and social relationships can have substantial effects on group structure and cohesion during collective movements (Jolles et al., 2013; Nagy, Akos, Biro, & Vicsek, 2010; Petit & Bon, 2010). It has also long been known that, in certain species, the identity of alarm callers can affect individual receivers' responses (Blumstein & Daniel, 2004; Cheney & Seyfarth, 1988; Micheletta et al., 2012). Here I show for the first time that alarm caller identity mediates the magnitude of collective responses to threats. Our analyses show that jackdaws discriminate between

different callers when responding to recruitment calls, and that responsive scolding can further magnify the magnitude of the group response.

In the absence of responsive scolding, I found greater levels of recruitment in response to the calls of jackdaws than those of rooks. However, this pattern was reversed when responsive scolding by jackdaws occurred, potentially because the additive effects of calls by the two species, which associate frequently and share common predation risks (Bossema, Baeyens, Zeevalking, & Leever, 1976), magnified the intensity of the recruitment stimulus. When restricting the analyses to responses to jackdaw calls only, it is clear that it not only the species of the caller, but also its individual characteristics have important effects on group responses. When playbacks were performed *away* from nestboxes, recruits flew away from the colony towards the source of the playback. Here, the calls of *colony-members* elicited more recruits than those of *strangers*, but this difference occurred only when playbacks combined with the additive influence of responsive scolding by recruits. This is consistent with vocal discrimination on a categorical level of unfamiliar vs familiar callers (Hare, 1998). However, a number of my findings suggest that jackdaws also employ more fine-scale vocal discrimination when responding to alarm calls.

Firstly, receiver responses were affected not only by their familiarity with the caller, but also by the caller's sex. Notably, the effects of caller sex depended on the spatial location of the playbacks, with patterns of responsive scolding to playbacks away from nests also suggesting that responses may be mediated by the caller's perceived rank. Here, the responses to *stranger* females were significantly lower than to any other treatment. This finding is consistent with reduced responses to lower ranking callers since a female's rank in jackdaw colonies is determined by that of her partner (Lorenz, 1931; Röell, 1978). An unknown female is therefore by default outranked by all members of a colony. If caller rank can affect decisions to join collective responses, this raises the possibility that responding may play a role in signalling social prestige (Doutrelant & Covas, 2007; Wright, 2007; Zahavi, 1995), but further work is needed to test this possibility.

Secondly, playbacks revealed important differences in responses to different individuals within a colony. When playbacks were performed *near* to nestboxes I found that recruitment increased progressively from *stranger* to

local to *resident* playbacks. This pattern was apparent when responsive scolding did not occur, but was stronger when it did. One possibility is that one member of the resident pair recognised its own call, stimulating a heightened response. However, this scenario seems unlikely because all known examples of vocal self-recognition in birds are based on syllable order rather than recognition of individual syllables (Hauber & Sherman, 2001; McArthur, 1986). Jackdaw scolding calls are monosyllabic so the opportunity for self-recognition of a pattern of syllables does not exist. Furthermore, as anyone who hears a recording of their own voice will appreciate, the attenuation of sound through air and the bones of the cranium means that individuals' perception of their own voice is likely to sound different to a recording (Porschmann, 2000).

A more plausible explanation is that the pattern of recruitment near to nests is based on discrimination between known individuals within the colony. This could be a spatial association whereby calls elicit a higher response in the location where they are most frequently heard; hence *resident* calls played back at their own nestbox produce a stronger response. However, since birds move around and join in scolding events throughout the colony this it is unlikely that a strict spatial association can account for the findings. Instead I suggest that, as suggested in studies of primates (Micheletta et al., 2012), social relations between caller and receiver mediate the pattern of recruitment. In my study, the rapid and dynamic movements of birds responding to playbacks made it impossible to determine the identity of individual recruits, so my conclusions must remain speculative. Nevertheless, patterns of response are consistent with a role for social relationships between callers and recruits. The nearest birds to a *resident* playback performed at the nest are likely to be the caller's partner and other closely associated individuals. The strength of social bond between the caller and nearby birds is likely to decrease across playbacks from *resident* to *local* to *stranger* and this could determine the strength of behavioural and vocal response by nearby birds which will in turn stimulate further recruitment.

In summary I show that collective anti-predator behaviour in jackdaws is strongly affected by caller identity, with both recruitment and responsive scolding varying between different callers. Most research on collective behaviour emphasises simple, reflexive mechanisms (Couzin, 2009; Sumpter, 2006), but my work demonstrates that more complex cognitive processes can

play an important role in mediating collective responses. In jackdaws, the ability to discriminate between the vocalisations of different callers provides crucial information to conspecifics deciding whether to take part in costly collective events.

Supplementary material

Table 2.S2. GLMM of factors affecting responsive scolding near to nests.

	Wald statistic (x^2)	df	P
Wind	0.973	1	0.324
Sex	0.686	1	0.408
Treatment	0.989	2	0.610
Sex*Treatment	0.338	2	0.845

Data from 66 playbacks were fitted to a binomial distribution with binary response terms (Yes or No) indicating whether or not any scolding by recruits occurred during each playback. Playbacks were performed near to 23 nestboxes with random terms including batch (estimated variance component = 0.067, SE = 0.258), caller identity (estimated variance component = 0.603, SE = 0.777), colony (estimated variance component = 0.000, SE = 0.010), and year (estimated variance component = 0.000, SE = 0.000).

Table 2.S3. GLMM of factors affecting responsive scolding away from nests.

	Wald statistic (χ^2)	*df*	*P*
Full model			
Wind	7.634	1	0.006
Sex*Treatment	4.366	1	0.037
Sex	0.320	1	0.572
Treatment	0.042	1	0.836
Minimal Model	**Effect size**	**SE**	
Constant	-5.030	1.760	
Wind	0.192	0.069	
Sex*Treatment	See Fig 1b		

Data from 66 playbacks were fitted to a binomial distribution with binary response terms (Yes or No) indicating whether or not any scolding by recruits occurred during each playback. Playbacks were performed at 23 locations away from nestboxes with random terms including batch (estimated variance component = 0.142, SE = 0.377), caller identity (estimated variance component = 0.000, SE = 0.000), colony (estimated variance component < 0.000, SE < 0.000), and year (estimated variance component = 0.000, SE = 0.000).

Table 2.S4. GLMM of factors affecting recruitment near to nests when responsive scolding occurred.

	Wald statistic (χ^2)	df	P
Full Model			
Treatment	11.63	2	0.003
Sex	0.679	1	0.410
Sex*Treatment	1.437	2	0.488
Wind	0.015	1	0.901
Minimal Model	**Effect size**	**SE**	
Constant	2.068	0.194	
Treatment			
Stranger	0	0	
Local	0.107	0.136	
Resident	0.523	0.160	

Data from 46 playbacks were fitted to a poisson distribution with recruitment fitted as the response term indicating the number of jackdaws recruited to each playback. Playbacks were performed near to 23 nestboxes with random terms including batch (estimated variance component = 0.249, SE = 0.499), caller identity (estimated variance component = 0.084, SE = 0.289), colony (estimated variance component = 0.018, SE = 0.133), and year (estimated variance component = 0.000, SE = 0.000).

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Table 2.S5. GLMM of factors affecting recruitment near to nests when responsive scolding did not occur.

	Wald statistic (χ^2)	df	P
Full Model			
Treatment	11.33	2	0.003
Wind	6.401	1	0.011
Sex*Treatment	1.794	2	0.408
Sex	0.306	1	0.580
Minimal Model	**Effect size**	**SE**	
Constant	2.613	1.052	
Treatment			
Stranger	0	0	
Local	0.943	0.365	
Resident	1.099	0.308	
Wind	-0.110	0.032	

Data from 20 playbacks were fitted to a poisson distribution with recruitment fitted as the response term indicating the number of jackdaws recruited to each playback. Playbacks were performed near to 14 nestboxes with random terms including batch (estimated variance component = 0.649, SE = 0.806), caller identity (estimated variance component = 0.000, SE = 0.000), colony (estimated variance component = 0.000, SE = 0.000), and year (estimated variance component = 1.757, SE = 1.326).

Table 2.S6. GLMM of factors affecting recruitment away from nests when responsive scolding occurred.

	Wald statistic (χ^2)	df	P
Full Model			
Treatment	9.872	1	0.002
Sex*Treatment	2.774	1	0.096
Sex	0.522	1	0.470
Wind	0.039	1	0.843
Minimal Model	**Effect size**	**SE**	
Constant	2.205	0.318	
Treatment			
Stranger	0	0	
Colony-member	0.584	0.169	

Data from 24 playbacks were fitted to a Poisson distribution with recruitment fitted as the response term indicating the number of jackdaws recruited to each playback. Playbacks were performed at 24 locations away from nestboxes with random terms including batch (estimated variance component = 1.051, SE = 1.025), caller identity (estimated variance component = 0.089, SE = 0.299), colony (estimated variance component = 0.000, SE = 0.000), and year (estimated variance component = 0.000, SE = 0.000).

Table 2.S7. GLMM of factors affecting recruitment away from nests when responsive scolding did not occur.

	Wald statistic (χ^2)	*df*	*P*
Sex*Treatment	2.259	1	0.133
Wind	1.165	1	0.280
Treatment	0.690	1	0.406
Sex	0.481	1	0.488

Data from 42 playbacks were fitted to a Poisson distribution with recruitment fitted as the response term indicating the number of jackdaws recruited to each playback. Playbacks were performed at 20 locations away from away from nestboxes with random terms including caller identity (estimated variance component = 2.309, SE = 1.519), colony (estimated variance component = 0.171, SE = 0.413 and year (estimated variance component = 0.000, SE = 0.000). Batch was not included as it caused the model to fail to converge.

Chapter Three: Individual vocal discrimination during collective alarm response in wild Jackdaws.

Abstract

The social strategies of individuals across many species rely on the ability to discriminate between signals produced by different conspecifics. Where signals serve to recruit others, such discrimination may also influence collective behaviour, but this has yet to be investigated. Here I show that in wild jackdaws, a social corvid species, individual vocal discrimination affects the magnitude of group-level anti-predator mobbing responses, regardless of whether receivers are familiar with the individual producing the recruitment call. Jackdaws breed colonially but exhibit dynamic fission-fusion dynamics and may encounter both familiar and unfamiliar individuals during social foraging, roosting and predator defences. I tested the functional consequences of individual discrimination for group behaviour using a habituation-dishabituation-rehabituation playback paradigm in which callers were either equally familiar or entirely unknown to receivers. In both contexts, levels of recruitment declined when calls of the same individual were played repeatedly, increased again in response to a different caller and then fell again during subsequent rehabituation playbacks of the initial caller. Our results highlight the crucial but often overlooked role of individual signal discrimination in mediating the magnitude and potential efficacy of costly group activities.

Keywords Alarm calls, cognition, collective behaviour, individual discrimination, recruitment, vocal communication

Introduction

The ability to discriminate between individuals is a pre-requisite for the formation of social relationships and a fundamental building block for many socio-cognitive strategies, allowing animals to adjust their behaviour depending on who they are interacting with (Seyfarth & Cheney, 2015). Theory suggests that individual discrimination can play a major role in the evolution of cooperative and collective activities (Trivers, 1971). For instance, such discrimination may underpin decisions to engage in potentially costly group activities, for example by allowing animals to avoid investing in activities with unreliable partners (Hammond & Axelrod, 2006). However, evidence that individual discrimination guides group behaviour in wild animals in functionally relevant contexts is limited.

A common form of group behaviour vertebrates is mobbing, whereby members of a group move towards a threat together, often in response to an alarm signal from a group member (Dugatkin & Godin, 1992). Since moving towards a threat places individual group members closer to potential danger, the ability to discriminate between alarm signallers may allow receivers to respond selectively to more reliable individuals or those with which they have a stronger social connection. In birds and mammals, vocal signals commonly function to instigate mobbing, and in some species these mobbing calls are known to be individually distinctive (McDonald, 2012; Micheletta et al., 2012; Yorzinski et al., 2006). However, evidence that receivers can perceive and act on these acoustic differences is rare and limited only to subtle individual-level responses, such as orientation towards loudspeakers during playback experiments (McDonald, 2012; Micheletta et al., 2012). Thus, the role of individual vocal discrimination in determining the magnitude of ecologically relevant, group-level responses is unknown. Given that the size of mobbing groups affects their efficacy in deterring predators (Robinson, 1985), such effects are likely to have crucial fitness consequences. Moreover, to my knowledge only one study has tested whether receivers can differentiate between the mobbing calls of unknown signallers (McDonald, 2012), yet in large, fluid fission-fusion societies there may be strong benefits to rapidly learning to discriminate between unknown individuals. Here I use jackdaws

(*Corvus monedula*) to address the functional role of individual vocal discrimination in guiding responses to both known and unknown individuals in a mobbing context in the wild.

Jackdaws, a highly social corvid species, live in dynamic fission-fusion colonies where new individuals join and others may leave (Röell, 1978), and different colonies may come together to form large foraging or roosting flocks (Jolles et al., 2013). Mobbing in response to individually distinctive scolding alarm calls involves recruits flying towards and circling the source of the initial scolding whilst often making scolds of their own (Chapter Two). This carries energetic and time costs, whilst placing recruits nearer to any potential predator. Given this apparently high cost of responding, the ability to quickly learn to ignore unreliable callers, whether previously known or unknown, could provide significant personal benefits to receivers. In a previous study (Chapter Two) I found that jackdaws differentiate their mobbing response to the scolding alarm calls of different callers. Recruitment was higher to scolds of colony-members than to unknown individuals, and highest of all when the scolds of a resident bird were played near its nestbox. However, it is not known whether these differences in response result from individual vocal discrimination or whether jackdaws simply respond more readily to alarm calls they experience more often. I therefore performed a habituation-dishabituation-rehabituation experiment at colonies of nesting wild jackdaws to test whether jackdaws can discriminate between the mobbing recruitment calls of familiar and unfamiliar individuals.

Methods

Scolding call recording and playback preparation

Scolding calls were recorded during March-May 2015 from wild jackdaws living in three colonies, X, Y, and Z, near Penryn in Cornwall, UK. Approximately 5km separates colony X (50°10'22.9"N 5°07'04.1"W), from colonies Y (50°11'22.4"N 5°10'53.4"W) and Z (50°11'55.5"N 5°10'10.8"W), themselves ~1.5km apart. The jackdaws recorded were breeding birds utilising nestboxes, 100 of which were installed in August 2012, distributed across the

three sites at intervals (5-30m) realistically simulating natural nest densities. Birds were identifiable visually from coloured rings fitted under British Trust for Ornithology licences (C5752 and C5746). Sex was determined through molecular sexing (Griffiths & Double, 1998) of blood samples collected during ringing. Where a bird did not have rings, observations using binoculars and CMOS IR cameras fitted inside nestboxes were used to confirm nestbox ownership and sex (females undertake the majority of incubation; Röell, 1978) of a focal bird immediately prior to sound recording.

Individual adult jackdaws were visually identified at their nestboxes. Approaching at ground level to within 10m was usually sufficient to elicit scolds from the focal individual. If birds did not scold on initial approach, I elicited scolding by climbing to within 1m of the nestbox was using a ladder. I recorded 789 discreet scolding calls from 12 male and 12 female jackdaws during the breeding season from March to May 2015. A Sennheiser M67/K6 directional microphone connected to an Olympus LS-100 portable digital recorder was used to record 16bit uncompressed WAV files at a sample rate of 48.0Hz.

Playback tracks were created using the software package Audacity (www.audacity.sourceforge.net). Three sets of five unique scolds from a particular individual were arranged on each track with each set lasting 10s and 15s of silence separating sets (Fig. 3.S3). Tracks started and finished with 10s of silence. In rare instances where recorded scolds contained audible low-frequency background noise from wind or traffic, a high pass filter in Audacity removed noise below 800Hz, which does not overlap with the frequency of the scolding calls themselves. I created 7-10 playback tracks for each recorded jackdaw using unique scolds in each track whenever possible. In the small number of cases where I did not obtain a sufficient number of scolds, the order of individual scolds was randomised. Amplitude was normalised across playback tracks.

All playback tracks were assigned unique file names and loaded on to remote-controlled Foxpro GX7 Fury loudspeakers. A Voltcraft SL-100 sound level meter placed a known distance from the loudspeaker was used to calibrate playback volume of the speaker to the natural sound level measured at the same distance from a scolding jackdaw. This loudspeaker volume setting was then used during all playbacks.

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Playback procedure and responses measured

All experiments took place during the jackdaws' breeding season in May 2015. Playbacks were performed in two types of location: *familiar* playbacks took place within one of my three study sites (X, Y, and Z) using calls of birds from the same site, while *unfamiliar* playbacks took place at nesting colonies of jackdaws at least 5km from my study sites. Colonies for *unfamiliar* playbacks were located by searching in West Cornwall with suitable nesting habitat, such as churches and old derelict mining buildings, for groups of congregating jackdaws and confirming that these congregations were centred on active nesting colonies. Playback tracks were loaded on to a Foxpro GX7 Fury remote control loudspeaker that was placed within a colony of nesting jackdaws. For *unfamiliar* playbacks, the loudspeaker was placed 20-50m from the nearest visibly active nest. Similarly, for *familiar* playbacks the loudspeaker was placed 20-50m from the nearest active nestbox. In both types of location, the speaker was placed in a hedge, bush, or low tree and pointed towards the centre of the nesting colony.

Playback sessions were filmed by an observer from a concealed position with a clear view of the area 30 m around the loudspeaker. Playback commenced following 10 minutes that allowed for any disturbance caused by placing the loudspeaker to subside. A habituation-dishabituation-rehabituation protocol (Rendall et al., 1996) was used whereby unique playback tracks of individual A's calls were played every 7 minutes until habituation occurred, followed by a dishabituation track of individual B's calls, and finally a rehabituation track of individual A. The criteria set for habituation was defined as three consecutive playback tracks where recruitment was less than half of the maximum observed in that session. The rehabituation track functioned to test whether any increase in response to jackdaw B was simply a spontaneous return to pre-habituation response levels. For each playback, including a 30 second period immediately afterwards, I recorded, in real time, the maximum number of recruits, defined as any jackdaw that moved to within 30m of the speaker. Jackdaws within 30m of the speaker before the playback were only counted as recruits if they altered their behaviour during playback by either changing direction if flying, or taking off if previously perched. Scolding by

recruits in response to playbacks is known to have an amplifying effect on recruitment (Chapter Two), so for each playback I noted from video records whether recruits to each playback made scolds of their own.

Statistical analysis

Generalised linear mixed models (GLMMs) were run using R version 3.2.3 (R Core Team, 2014). In all models, experiment identity (assigned to each set of playbacks), playback location, signaller identity, and signaller track number (assigned to each playback track created for each individual) were included as random terms to account for repeated measures. To determine the effects of caller identity and familiarity on recruitment, I ran a model with the total recruitment fitted as a Poisson-distributed response term, with playback *type* (H1 = first habituation, HF = final habituation, DH = dishabituation, and RH = rehabituation), and familiarity (whether the signallers used in playbacks were familiar or unfamiliar to receivers) as explanatory terms. Responsive scolding (Yes/No, whether recruits made scolds of their own), sex of playback individuals and wind speed were fitted as additional explanatory terms. To test whether the occurrence of responsive scolding was itself influenced by playback type and familiarity, I also ran a second model, with responsive scolding fitted as a binary response term using a binomial error structure. Model simplification was carried out through stepwise deletion of non-significant terms, including all biologically meaningful two-way interactions. ANOVAs were used to compare models at each simplification step (Crawley, 2012) and for post-hoc planned comparisons between the responses to specific playback types within each final, minimal GLMM.

Results

Playback type significantly affected recruitment (χ^2 = 23.359, d.f. = 3, P < 0.001; Fig.3.1; Table 3.S1). The overall level of recruitment was lower to *familiar* than *unfamiliar* playbacks (χ^2 = 3.91, d.f. = 1, P = 0.048), but the pattern of responses to experimental treatments was similar, with no significant interaction

between type and familiarity (χ^2 = 7.302, d.f. = 3, *P* = 0.063). The sex of caller did not affect recruitment (χ^2 = 0.093, d.f. = 1, *P* = 0.761). Recruitment in response to playbacks was significantly higher in cases when responsive scolding occurred (GLMM; χ^2 = 79.568, d.f. = 1, *P* < 0.001; note that occurrence of responsive scolding itself was unaffected by playback type; Table 3.S2).

Comparing between playback types, recruitment to H1 was significantly higher than to HF (χ^2 = 0.05, d.f. = 1, *P* < 0.001), showing that habituation had occurred. Recruitment subsequently increased during the dishabituation trials (HF vs DH: χ^2 = 9.57, d.f. = 1, *P* = 0.002) and then significantly fell again during rehabituation trials (DH vs RH: χ^2 = 5.77, d.f. = 1, *P* = 0.016). The results for each individual experiment are illustrated in Fig. 3.S1 and Fig 3.S2.
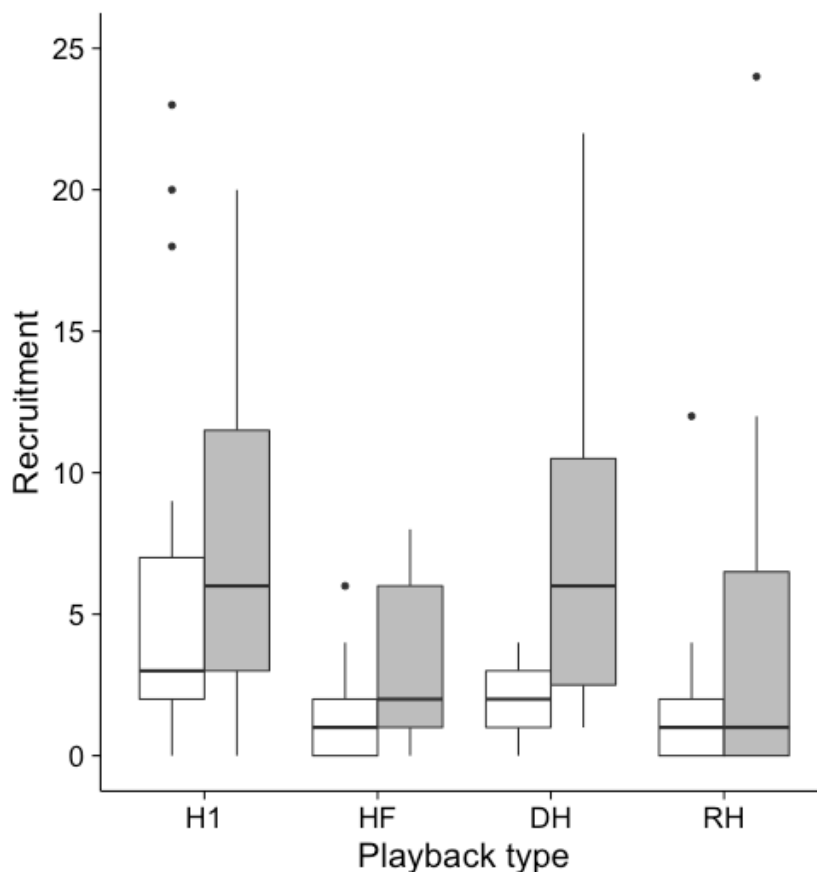
Figure 3.1. Number of jackdaws recruited to different playback types, split by whether receivers were *familiar* (white) or *unfamiliar* (grey) with the caller. Boxes show inter-quartile range (IQR) above and below median line. Whiskers indicate range of data lying within 1.5 x IQR of the upper and lower IQRs.

Discussion

Our results show that collective responses to alarm calls can be influenced by vocal discrimination between different callers, even when receivers and callers are unfamiliar to each other. Repeatedly playing back calls of the same individual led to a steep reduction in numbers of recruits, presumably as a result of habituation. However, subsequently playing back the call of a new individual caused recruitment to increase again relative to the final habituation playback. Recruitment levels then declined again during the final rehabituation phase, suggesting that listeners recalled the identity of the caller from the habituation phase and lowered their responsiveness accordingly on hearing its calls again. These patterns were similar irrespective of recruits' familiarity or unfamiliarity to the caller, indicating that jackdaws can spontaneously discriminate between different callers without prior experience of either caller.

Our study shows that, in common with many primates and some other bird species (McDonald, 2012; Micheletta et al., 2012; Seyfarth & Cheney, 2015), jackdaws discriminate between conspecific alarm calls at the level of the individual caller, and not just based on broad categories such as age,sex or familiarity (Blumstein & Munos, 2005). Critically, I show for the first time that such discrimination can influence the magnitude of group level responses. Large mobs may be more effective at deterring predators (Hoogland & Sherman, 1976; Krams, Berziņš, & Krama, 2009; Robinson, 1985), but joining mobbing events can be very risky (Krama & Krams, 2005; Poianai & Yorke, 1989), so mechanisms underpinning decisions to join may have important fitness consequences. In my experiments, individual discrimination appeared to generate particularly strong effects among birds that were unfamiliar with the callers. The ability to learn to discriminate rapidly between callers may have strong advantages for animals such as jackdaws that live in fission-fusion societies and may need to make rapid decisions on the reliability of unknown individuals. Playbacks of familiar birds produced similar results, but apparent differences between experimental treatments may have been diluted by social relationships between callers and receivers. Furthermore, the individuals featured in the familiar playbacks could have been present during the playbacks themselves, with the possibility that bird B made responsive scolds during

playbacks of bird A, and vice versa. This could have also had a diluting effect on any change in response at the dishabituation.

Our findings raise the possibility that jackdaws may use individual vocal discrimination to coordinate cooperative coalitions or implement reciprocal responses. Studies of predator mobbing at nests by pied flycatchers, *Ficedula hypoleuca*, suggest that breeding pairs will assist distant neighbours that have assisted them in the recent past (Krama et al., 2012). However, as nest locations are stable, such reciprocity may not require individual vocal discrimination (Russell & Wright, 2009). Determining the role of individual discrimination in implementing cooperative exchanges and collective action in spatially variable contexts is an important goal for future research (Mcauliffe & Thornton, 2015).

Supplementary material

**Table 3.S1.** GLMM of factors affecting recruitment.

	Wald statistic (χ^2)	df	P
Full model			
Familiarity	4.508	1	0.034
Playback type	23.359	3	<0.001
Responsive scolding	79.568	1	<0.001
Sex	0.093	1	0.761
Wind	0.122	1	0.726
Familiarity*Sex	2.474	1	0.116
Playback type*Familiarity	7.302	3	0.063
Minimal Model	**Effect size**	**SE**	
Constant	0.754	0.221	
Familiarity			
Familiar	0	0	
Unfamiliar	0.424	0.205	
Responsive scolding			
No	0	0	
Yes	1.375	0.146	
Playback type			
H1	0	0	
HF	-0.891	0.189	
DH	-0.233	0.156	
RH	-0.670	0.202	

Data from 120 playbacks were fitted to a Poisson distribution with recruitment fitted as the response term indicating the number of jackdaws recruited to each playback. 30 separate experiments were performed at 16 locations with random terms including caller identity (estimated variance component = 0.163, SE = 0.404), experiment identity (estimated variance component = 0.199, SE = 0.446), playback location (estimated variance component = 0.000, SE = 0.000), and signaller track number (estimated variance component = 0.160, SE = 0.400).

Table 3.S2. GLMM of factors affecting responsive scolding.

|	Wald statistic (χ^2)	df	P
Familiarity	0. 270	1	0.603
Playback type	6.993	3	0.072
Sex	0.000	1	0.994
Wind	0.778	1	0.378
Familiarity*Sex	0. 085	1	0.771
Playback type*Familiarity	1.445	3	0. 695

Data from 120 playbacks were fitted to a binomial distribution with binary response terms (Yes or No) indicating whether or not any scolding by recruits occurred during each playback. 30 separate experiments were performed at 16 locations with random terms including caller identity (estimated variance component = 0.000, SE = 0.000), experiment identity (estimated variance component = 0.000, SE = 0.000), playback location (estimated variance component = 2.198, SE = 1.483), and signaller track number (estimated variance component = 0.000, SE = 0.000).
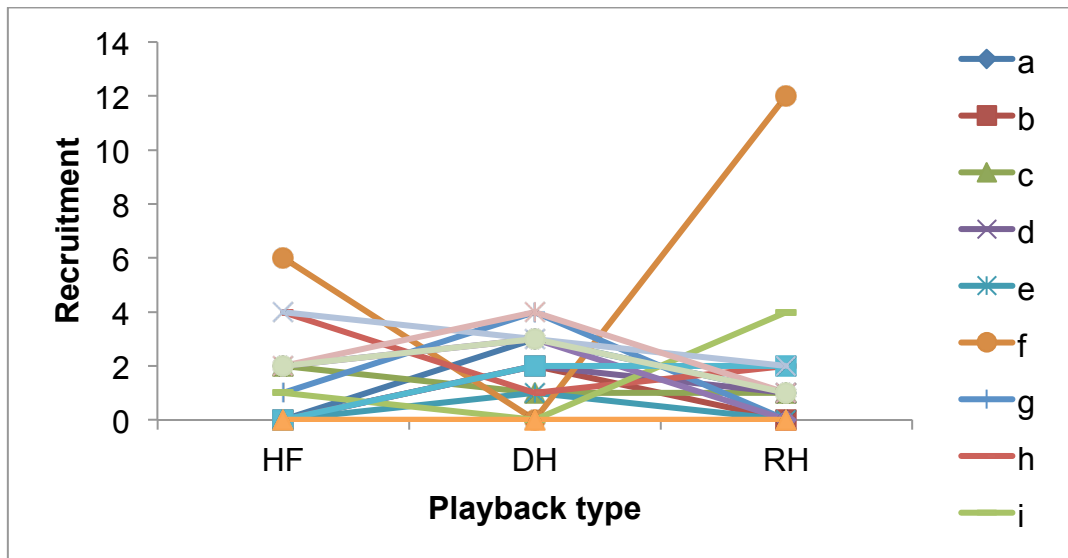
Figure 3.S1 Raw data showing the number of jackdaws recruited to different playback types when receivers were *familiar* to callers, plotted from raw data. Each colour indicates a separate experiment identity.
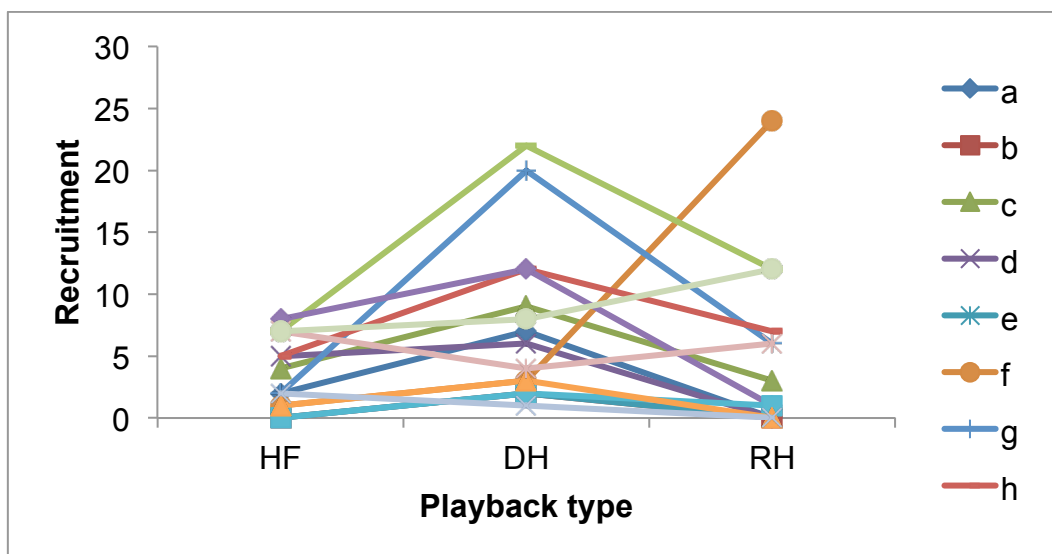
Figure 3.S2 Raw data showing the number of jackdaws recruited to different playback types when receivers were *unfamiliar* to callers, plotted from raw data. Each colour indicates a separate experiment identity.
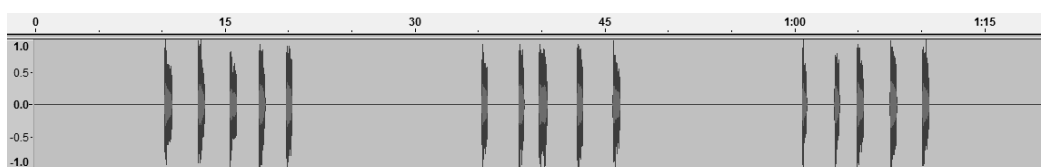
Figure 3.S3. Waveform of a standard playback track showing arrangement of individual calls within the track. y-axis = amplitude (dB), x-axis = time (s).

Chapter Four: Jackdaws' alarm calling rate depends on threat level and mediates collective response

Abstract

Alarm calls have been shown to contain information about not just the presence, but also the nature of a threat. Whether alarm calls are functionally referential, or one call type is produced generically to a range of non-similar threats, information encoded in the structure of alarm vocalisations can provide animals with useful information about threats. Calls may vary in the number of repetitions, or the rate at which they are produced, and such variation has been shown to correlate with the level of urgency associated with the threat. Most work on alarm call variation has dealt with prey species that respond by fleeing. However some evidence indicates that features such as call rate may also influence collective responses in species that respond by approaching and mobbing the threat. Here I present evidence that variation in the rate of production of anti-predator recruitment calls is linked to different levels of threat in wild jackdaws, *Corvus monedula*, with more urgent threats eliciting faster calling rates. Using playback experiments, I then go on to show that call rate influences group responses. These results demonstrate that information contained in patterns of alarm calling may allow social species to respond adaptively during anti-predator collective mobbing.

Key words: Alarm calls, call rate, cognition, collective behaviour, recruitment, vocal communication

Introduction

Acoustic alarm signals serve an important role in many animal communities, serving to inform receivers about the presence and nature of potential threats. Alarm calls may vary in the type of threat to which they refer, or indicate a particular level of urgency, or indeed both. Functionally referential alarm calls have been demonstrated in a range of vertebrates, typically in cases where the optimal response strategy differs for different threat-categories such as aerial versus terrestrial predators (Gyger et al., 1987; Manser, Seyfarth, & Cheney, 2002; Seyfarth et al., 1980; Zuberbühler, 2000). However functionally referential alarm calls are by no means universal, their occurrence being mainly associated with species that occupy complex habitats and forage as a coordinated group (Furrer & Manser, 2009). More commonly, alarm calls have been shown to encode a level of urgency. Urgency-dependent alarm call variation is common both in species that demonstrate functionally referential alarm calls such as meerkats, *Suricata suricatta*, and in species such as marmots, *Marmota spp.*, which do not (Blumstein, 2007; Manser, 2001).

The level of urgency encoded in an alarm call may relate to how far away a threat is, how fast a threat is moving or approaching, or a physical attribute of a threat that affects the risk it poses (Townsend & Manser, 2013). Different species have been shown to encode urgency into their alarm calls by modifying different call attributes, including acoustic parameters such as fundamental frequency and duration, or by varying call structure such as the amount of repeated call elements. For example, black-capped chickadees, *Poecile atricapilla*, produce alarm calls with a higher number of a particular element in response to avian predators of a smaller size, which pose a higher threat to chickadees than larger birds of prey (Templeton, 2007). Using an alternative strategy, Cape ground squirrels, *Xerus inauris*, encode urgency by shortening the duration and raising the pitch of their calls when threats are closer to the signaler (Furrer & Manser, 2009). Another element of alarm calls that may encode urgency is the rate at which the alarm call is issued. Higher alarm calling rates have been positively correlated with increased risk, by studies exploring both the rate of alarm calls produced to differing levels of risk, and by focusing instead on receivers response to alarm calls of differing rate. The

former "production specificity" has been demonstrated in yellow-bellied marmots, *Marmota flaviventris,* where the rate of alarm calling has been shown to increase as a function of risk experienced by the caller in (Blumstein & Armitage, 1997). Meanwhile the later "perception specificity" has been shown in eastern chipmunks, *Tamias striatus*, where receivers were more likely to flee in response to higher rate alarm calls (Weary & Kramer, 1995). Similar patterns have been found in American robins, *Turdus migratorius,* showing that alarm call rate as a signal of threat urgency is not unique to mammals (Vanderhoff & Eason, 2009). However, whilst this mechanism of conveying urgency has been explored somewhat in species that demonstrate a fleeing response to alarm calls, little is known about the influence of alarm call rate in situations such as mobbing, where alarm calls serve to recruit conspecifics towards the location of a threat. In American crows, *Corvus brachyrhynchos*, experimental presentations of model predators showed that more dangerous threats induce high mobbing call rates and elevated recruitment, but it is not known if call rate directly influences levels of recruitment (Yorzinski & Vehrencamp, 2009). Joining an anti-predator collective mobbing event can help drive away dangerous predators, but entails substantial risk (Curio & Regelmann, 1985, 1986) , so information about threat urgency, encoded in the rate of a conspecific's alarm call, may be particularly useful in deciding whether to respond.

Jackdaws, *Corvus monedula,* provide an opportunity to explicitly test the influence of call rate on a collective alarm response. In this species, recruits converge on the signaler in response to harsh 'scolding' alarm calls produced in response to threats (Röell, 1978). The number of recruits has been shown to vary in response to details such as the identity of the signaler, with higher recruitment to the calls of familiar colony members than to those of previously unheard conspecifics (Chapter Two). Scolding calls are known to be individually distinct (Kings, 2014), and receivers have been shown to differentiate between callers based on individual identity, rather than simpler categories such as familiar versus unfamiliar (Chapter Three). Functionally referential mobbing alarm calls have been shown to occur in some birds (Suzuki, 2012), but there is no evidence that jackdaws produce them. Given that jackdaws attend to details of an alarm call such as caller identity, further details such as calling rate may affect the response of receivers. Scold call characteristics may vary according

to the threat perceived by the signaler, but may also vary amongst signalers. For instance, individual differences in threat sensitivity could lead to variation in scolding, with certain jackdaws being more likely to call, or scolding consistently faster or slower than others to similar threat stimuli.

To examine the effect of alarm call rate on collective response in wild jackdaws I conducted two linked studies. In the first, I investigated whether the alarm call rates of individual jackdaws varied in response to simulated lower and higher risk situations, and whether patterns of individual alarm call rate were repeatable within and between each simulated threat level. In the second study, I investigated the effect of high and low rates of scolding call playback on the magnitude of jackdaws' collective responses.

Methods

Recording and playback locations

Recordings were made at nestbox colonies of free-living jackdaws near Penryn in West Cornwall, UK. One hundred nestboxes were located at naturally-realistic intervals of 5-30m across three colonies X (50°10'22.9"N 5°07'04.1"W), Y (50°11'22.4"N 5°10'53.4"W) and Z (50°11'55.5"N 5°10'10.8"W) with the distance between colonies ranging from 1.5km to 5km. Adult jackdaws from the three colonies, the majority identifiable from coloured rings fitted under license from the British Trust for Ornithology, were used as the subjects for collecting observations and recordings. Recording and playback took place during the breeding season of April-June and 2015. The sex of ringed individuals was known through molecular sexing (Griffiths & Double, 1998), whilst un-ringed individuals were sexed on the basis that females perform the majority of the incubation (Röell, 1978), utilising observations recorded on both CMOS IR nestbox cameras and from outside the nestbox.

Previous work has shown that social bonds between caller and receiver can influence patterns of recruitment (Chapter Two, Chapter Three). To avoid the any confounding effects resulting from potential previous experience of callers by receivers, I performed playbacks at colonies a minimum of 5km from

the colony in which the caller was resident. Experimental playbacks were performed at 23 locations within active jackdaw nesting colonies across West Cornwall.

A) Measuring individual scolding sensitivity to threats

To determine whether alarm call rate in jackdaws varies in relation to the perceived severity of a threat, I stimulated jackdaws to produce scolding calls using two methods, designed to represent lower and higher level threats. Repeatability within individuals was then compared both within and between stimulation methods. The two threat simulation methods used for stimulating a scolding response were as follows:

Lower level threat simulation

A focal nestbox was observed from a concealed position until a known individual from the nesting pair was identified to be in, or near (less than 10m) of the nestbox. Once the individual had been positively identified, I approached at a walking pace to a position at the base of the tree or wall on which the nestbox was mounted, stopping 2m horizontal distance from the front of the nestbox where I stopped and remained motionless. An Olympus LS-100 portable digital recorder, recording at 48.0Hz/16bit, and a Sennheiser M67/K6 directional microphone and was used to record any vocalisations by the focal jackdaw, with recordings saved as uncompressed WAV files. Recording started at the time that I finished walking in to position and continued for 120s after which point I retreated, again at a walking pace. I wore the same dark clothing for every recording.

Higher level threat simulation

In this protocol the threat was heightened to simulate the practice of nest-checking that is commonly undertaken at my study sites. Preliminary observations indicated that this practice was highly likely to elicit a scolding response from resident adult jackdaws. An individual was identified at their nestbox as in method 1 above. Again I approached walking but carried a ladder

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and instead of stopping at ground level, I placed the ladder adjacent to the nestbox and climbed to within 1m of the nestbox. I remained motionless and recorded the focal individual for 120s from the time I arrived in position. Following this I retreated, taking the ladder with me, at walking pace.

B) Experimental test of the effect of scolding rate

i) Creating playback tracks

Playback tracks were created using scolding calls of 18 jackdaws from the recordings made in method 1 above. These were supplemented with additional calls of five different known individuals, recorded opportunistically using methods similar to method 1, with the distance between the caller and the microphone ranging from 2m to 50m. In total, I used high quality scolds from 23 individual jackdaws, made up of 11 males and 12 females to explore any effect of caller sex in playbacks.

I used the software package Audacity (www.audacity.sourceforge.net) to create a fast and slow playback track for each of the 23 individuals recorded. Every track consisted of three sets of eight scolding calls, with 30s of silence between sets and 10s silence at the start and finish of each track. Sets of eight scolds were chosen to mimic a realistic number of scolds made by a wild jackdaw during a natural scolding bout. Fast tracks were created to mimic the fastest rates I observed jackdaws naturally scolding at, with one scold played every 1.2s. Slow rate tracks featured one call every 2.4s, chosen to be clearly slower than the fast rate, whilst keeping overall track length comparable and remaining within the range of rates observed naturally. The order of scolds in every track was randomised and, wherever possible, no single scold was used more than once. In rare instances where limited numbers of scolds were recorded for a particular individual, some scolds were used more than once. In a minority of cases where a recording contained a small amount of background noise, I removed this using a high pass filter in Audacity whilst creating each track. This attenuated the amplitude of low frequency recording artefacts such as traffic or wind noise below 800Hz but did not interfere with the frequencies

present in the scolding calls themselves. Scold amplitude within and between tracks was normalised to remove any effect of volume on playback responses.

ii) Playback procedure

A Foxpro GX7 Fury remote controlled loudspeaker was used during playbacks performed at each of the 23 locations within jackdaw colonies in West Cornwall. Playback volume was calibrated by comparing the volume of the loudspeaker to that of a real jackdaw at the same distance using a Voltcraft SL-100 sound level meter. Playbacks were performed on two days with one playback per site per day. One day separated the two playback dates. To balance any potential effect of playback *order* on jackdaws' responses, on the first day fast playbacks were played at 11 locations and slow playbacks were played first at the other 12 locations. Scolds from the same individual were used for both fast and slow playbacks at a given location.

On arrival at each jackdaw colony, I placed the loudspeaker and an Olympus LS-100 portable digital recorder in a hedge or densely branched low tree that was within 50m of visibly active jackdaw nest sites. I then retreated to a position of concealment with a good view of the area at least 50m in all directions from the loudspeaker. After waiting 5-10 minutes for any apparent disturbance amongst local jackdaws caused by placing the loudspeaker to subside, I began filming the area around the loudspeaker with a Panasonic HC-X900 high-definition camcorder. The playback track was then triggered via remote control. For each playback I noted the sex and identity of the caller featured on the playback track. Using observations recorded at the time, and later confirmed by analysis of the HD video, I recorded the total number of recruits to the playback. I also recorded whether or not recruits made scolding calls of their own, as previous work has shown this "responsive scolding" to increase recruitment (Chapter Two, Chapter Three). Jackdaws were counted as recruits if they moved to within 30m of the loudspeaker during the playback. Jackdaws already within this area were only counted as recruits if they changed their behaviour during the playback, by making scolding calls, circling the loudspeaker, or flying towards the loudspeaker and landing within 30m. Data collection stopped when the track came to an end.

Statistical Analysis

Analysis of data was performed using R version 3.2.4 (R Core Team, 2016). Repeatability of natural rates of scolding in wild jackdaws was calculated using the 'rptR' package that utilised generalised linear mixed effects models (GLMMs) with a log link. For analysis of threat simulation results, a GLMM was performed using the *glmer* function with identity (the individual identity of the focal bird in the simulation) fitted as a random term to account for repeated measures. For analysis of experimental playback results, GLMMs were again performed with location (each of the 23 colonies where playbacks were conducted) fitted as a random term in all models to account for repeated measures. Initially I analysed all data in order to explore any meaningful interactions between terms. For analysis of experimental playback results I then separately analysed two subsets of differing *orders* (fast-slow and slow-fast) to explore the interactions identified.

Stepwise deletion of non-significant terms was used to simplify models. During each simplification step, models were compared using ANOVAs (Crawley, 2012). The *Anova* function was used to extract test statistics, degrees of freedom, and *P* values for maximal and minimal models.

Results

A) Does threat level influence scolding rate?

Jackdaws' scolding rate was significantly higher (GLMM; χ^2 = 13.74, d.f. = 1, *P* < 0.001; Fig.4.1, Table 4.S1) during the high threat protocol (mean of 10.82 ± 2.96 scolds/minute) than during the low threat protocol (mean of 7.90 ± 1.68 scolds/minute). Jackdaws' scolding rate was not affected by the sex of the focal individual (χ^2 = 0.043, d.f. = 1, *P* 0.836), but scolding rate varied significantly between simulations performed on different dates (χ^2 = 25.52, d.f. = 1, *P* <0.001). Individual jackdaws' rate of scolding was not repeatable across different trials within the low threat protocol (R = 0, SE = 0.149, CI = 0, 0.459, P = 0.772), or between the high and low threat protocols (R = 0, SE = 0.217, CI = 0, 0.615, P = 0.954). Sample size limitations meant it was not possible to

calculate the repeatability of individuals' scolding rate within the high threat protocol.
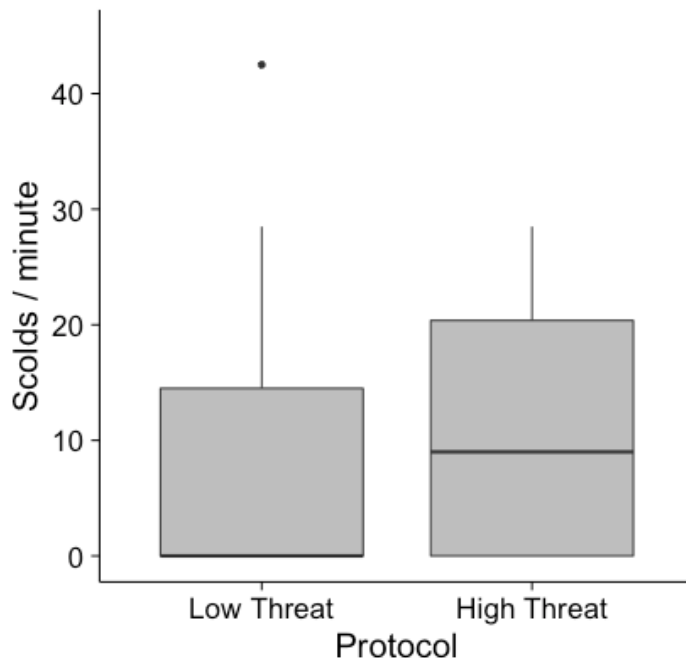
Figure 4.1. Boxplot of observed scolding rate to high and low threat protocols Boxes show inter-quartile range (IQR) above and below median line. Whiskers indicate range of data lying within 1.5 x IQR of the upper and lower IQRs.

B) Does scolding rate influence recruitment?

When all data was analysed together, three two-way interactions were present in the minimal model (Table 4.S2). Firstly, there was a significant interaction between the *order* of presentation and the *rate* of scolding (χ^2 =12.461, d.f. = 1, $P < 0.001$). Secondly, there was also a significant interaction between *rate* and the presence (yes/no) of *responsive scolding* (χ^2 =5.800, d.f. = 1, $P = 0.016$). Finally, there was an interaction between *order* and the presence of *responsive scolding* (χ^2 =4.983, d.f. = 1, $P = 0.026$). However, the rarity of cases in which no responsive scolding occurred (only 15 out of 46 playbacks) made it difficult to interpret these interactions if responsive scolding was treated as a binary (present/absent) term. I therefore repeated the analysis, replacing the presence/absence of *responsive scolding* with the total number of responsive scolds made during each playback. Modelled now as a numerical

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variable, the number of responsive scolds had a significant effect only as a single term, correlating positively with higher recruitment (χ^2 =10.56, d.f. = 1, P = 0.001; Fig.4.2). I once again found a significant interaction between *rate* and *order* (GLMM; χ^2 =5.546, d.f. = 1, P = 0.018; Fig.4.3). To explore the interaction between rate and order, I analysed different orders separately.
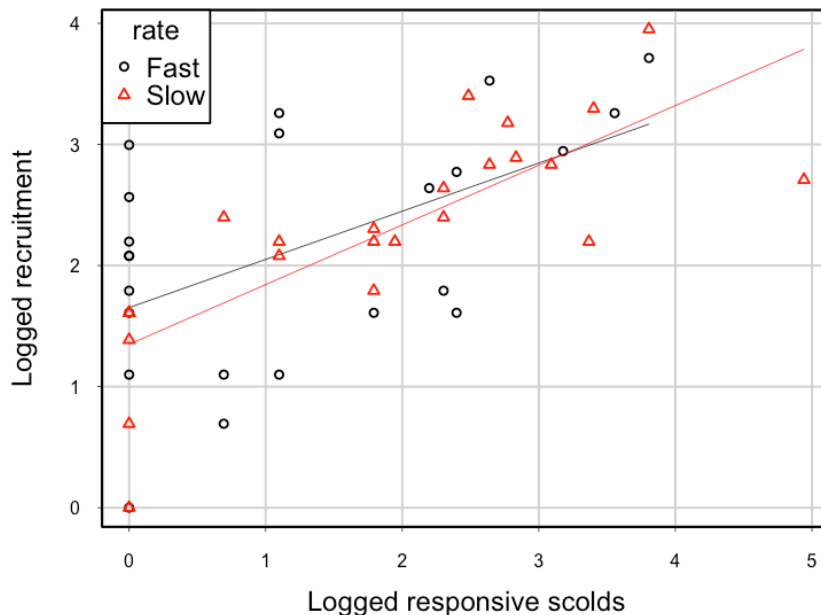
Figure 4.2. Scatterplot of logged raw data showing recruitment plotted against the number of responsive scolds for each playback experiment.

When playback *order* was fast followed by slow, there was a non-significant trend for fewer recruits in response to the slow playback (χ^2 =3.441, d.f. = 1, P = 0.064; Fig.4.3). There was a significant positive correlation between the number of *responsive scolds* and recruitment (χ^2 =7.228, d.f. = 1, P = 0.007). When playback *order* was instead slow followed by fast, there was no effect of *rate* (χ^2 =1.251, d.f. = 1, P = 0.263). Once again recruitment correlated positively with the number of responsive scolds (χ^2 =11.878, d.f. = 1 , P < 0.001).
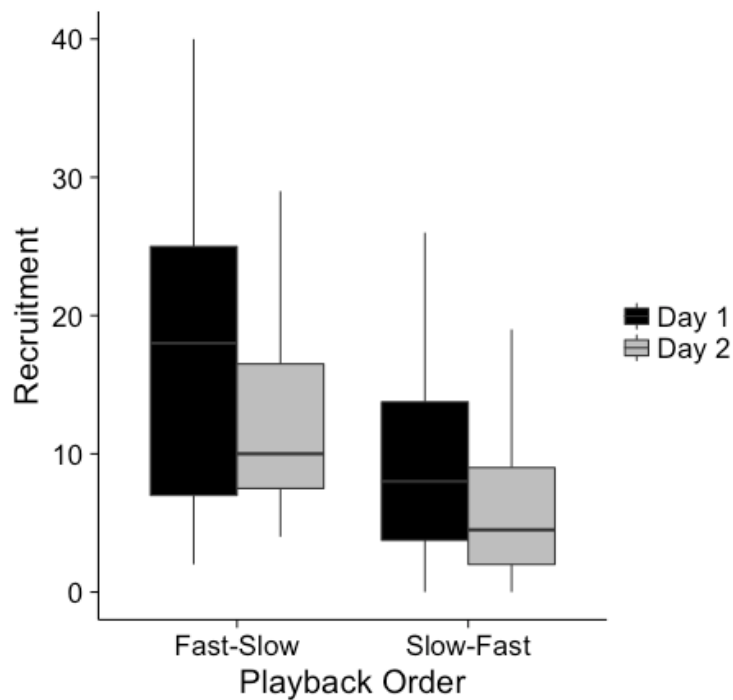
Figure 4.3. Box and whisker plot of raw data for playback order vs recruitment. Boxes show inter-quartile range (IQR) above and below median line. Whiskers indicate range of data lying within 1.5 x IQR of the upper and lower IQRs.

Discussion

Research has shown that the structure of animal alarm calls may vary according to perceived differences in detected threats, both in species that use functionally referential alarm calls, and in those that do not (Blumstein, 2007; Manser, 2001). Furthermore, variation in attributes of an alarm call's structure has been shown to affect the response of receivers in a range of species (Templeton, 2007; Townsend & Manser, 2013). One attribute of an alarm call that has been shown to vary according perceived properties of a threat and to have a direct bearing on conspecifics' alarm response is the rate at which the alarm call is repeated (Blumstein & Armitage, 1997; Vanderhoff & Eason, 2009; Weary & Kramer, 1995). Whilst most previous studies on alarm calling rate have focussed on species that demonstrate a fleeing response (but see Yorzinski & Vehrencamp, 2009), this study suggests for the first time that the rate of an alarm call may have a direct influence a collective mobbing response. In the first part of the study, jackdaws produced different rates of alarm calls in

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response to different simulated threat levels. Analysis of the second, experimental phase of the study provides some evidence that recruitment to jackdaw alarm calls varies according to the rate of alarm calling and receivers' previous experience of a particular caller.

Jackdaws scolded at a higher rate when they were presented with a relatively higher simulated threat. This "production specificity" mirrors observations in studies of escape-inducing alarm calls in species such as yellow-bellied marmots (Blumstein & Armitage, 1997) and approach-inducing mobbing calls in American crows (Yorzinski & Vehrencamp, 2009). I did not find any evidence of consistent individual differences in alarm call rate either within repeats of the same simulated threat level or between the two threat levels. This suggests that call rate may not serve as a reliable indicator of an individuals' threat sensitivity. However, it must be noted that the sample size used for this analysis was limited by logistical and time constraints on collecting observations.

Analysis of the full experimental dataset revealed a significant interaction between scolding call rate and the order of playback presentations. Conducting separate analyses for each order showed that when fast rate playbacks were presented before slow rate playbacks, there was a trend towards higher recruitment to the fast playback and lower recruitment to the slow playback. In contrast there was no difference in recruitment to fast and slow rate playbacks at locations where the slow rate was presented before the fast rate. This pattern of lower responses to slow than fast rates only if fast rates are heard first is highly similar to that found in experiments on the fleeing responses of eastern chipmunks (Weary & Kramer, 1995). It is difficult to draw firm conclusions on the effect of playback order in my study because the different orders (fast first or slow first) were presented at different jackdaw colonies. Local conditions at each playback location such as number or density of potential recruits may have varied between colonies, thus it seems prudent not to compare the fast-slow and slow-fast playback order groups directly. Nevertheless, one might speculate that the apparent difference between the effect of rate depending on which rate was played first could be explained by jackdaws becoming habituated to the alarm calls of the individual used in the playback. My previous work has shown that jackdaws attend to the identity of the alarm caller

(Chapters 2 & 3). Since there was no threat present during any of the alarm playbacks, local jackdaws may have become less responsive to the apparently unreliable caller following the first day of playbacks, and hence been less inclined to respond on the second day of playbacks.

Responsive scolding during playbacks correlated positively with total recruitment. This supports my findings in previous jackdaw studies (Chapter Two, Chapter Three). Since responsive scolding was absent in only 15 of 46 playbacks, fitting it as a binary term in models rendered interpretation of interactions difficult, so I instead fitted the total number of responsive scolds during each playback as a numerical term. Although there was no interaction between rate and the number of responsive scolds, I cannot rule out the possibility that responsive scolds may have increased recruitment sufficiently to dampen or mask and difference in recruitment that may have existed if the only scolds produced during the playback were from the loudspeaker.

In Chapter Three, I showed that individual caller identity has an effect on recruitment to alarm calls. In the current study, there was minimal opportunity for receivers to gain information about the caller's identity, as playbacks were deliberately designed to feature jackdaws that were unfamiliar at the colony where the playback took place. When responding to the scolding calls of familiar individuals, it is possible that jackdaws may modulate their responses according their relationships with, or their prior experience of the behaviour of the caller. For instance, although I found no evidence for repeatability in individual scold rates, my analyses were limited by small sample sizes and the range of contexts in which calls were recorded, so I cannot rule out the possibility that jackdaws do indeed call at consistent rates in response to particular threat levels. If this were the case, then receivers' responses to a given individual's scold calls might depend on them having previous experience of the caller's calling rate in response to different threats. Understanding how knowledge of others' reactions to threats influences responses to alarm calls would be an intriguing direction for future research.

Overall, this study supports findings from previous research on the effects of alarm call rate. Since callers increased their rate in response to increased threat in the first part of the study, and playbacks of different alarm rates affected receivers' response, variation in jackdaws' alarm calling rate

demonstrates both "production specificity" and "perception specificity" (Macedonia & Evans, 1993; Marler, Evans, & Hauser, 1992). In demonstrating an effect of alarm calling rate in a species that has a collective mobbing response rather than a fleeing response, I hope to open the possibility that variation in alarm calling rate may have more widespread application than is currently thought. Further work could further explore individual sensitivity to threats, and start to ask whether social species may benefit from individualised knowledge of the range of variation present in group members' alarm signal production.

Supplementary material

Table 4.S1. GLMM of factors affecting scolding rate.

	Wald statistic (χ^2)	df	P
Full Model			
Threat	13.74	1	<0.001
Sex	0.043	1	0.836
Date	25.52	2	<0.001
Minimal Model	**Effect size**	**SE**	
Constant	1.1828	0.544	
Threat			
low	0.000	0.000	
high	0.514	0.140	
Date			
12/05/2015	0.000	0.000	
13/05/2015	-0.390	0.184	
27/05/2015	0.621	0.123	

Data from 51 threat simulations were fitted to a poisson distribution with scolding rate fitted as the response term indicating the number of scolds produced during 120s of simulated threat. Simulations were presented to 25 focal individuals at their nestboxes with the random term of focal bird identity included (estimated variance component = 6.444, SE = 2.539).

Table 4.S2 GLMM of factors affecting recruitment, with responsive scolding modelled as a binary term.

	Wald statistic (χ^2)	*df*	*P*
Full model			
Rate	0.348	1	0.555
Order	4.060	1	0.044
RS	2.149	1	0.142
Sex	0.768	1	0.381
Rate*Order	12.20	1	<0.001
Rate*RS	5.329	1	0.021
RS*Order	4.698	1	0.030
Rate*Order*RS	1.863	1	0.172
Minimal model			
(n/a see Table 4.S3)			

Data from 46 playback experiments were fitted to a Poisson distribution with recruitment fitted as the response term indicating the number of jackdaws recruited to each playback. RS = Responsive Scolding (Yes or No). Simulations were presented to 23 locations with the random term of playback location included (estimated variance component = 0.390, SE = 0.625).

Table 4.S3 GLMM of factors affecting recruitment, with responsive scolding modelled as a numerical term.

	Wald statistic (χ^2)	*df*	*P*
Full model			
Rate	1.283	1	0.257
Order	3.248	1	0.071
RSn	9.976	1	0.002
Sex	1.157	1	0.282
Rate*Order	5.546	1	0.018
Rate*RSn	3.053	1	0.081
RSn*Order	1.333	1	0.248
Rate*Order*RS	2.079	1	0.149
Minimal model (See Fig. 4.2)			

Data from 46 playback experiments were fitted to a Poisson distribution with recruitment fitted as the response term indicating the number of jackdaws recruited to each playback. RSn = Responsive Scolding (Total number during each playback). Simulations were presented to 23 locations with the random term of playback location included (estimated variance component = 0.527, SE = 0.726).

Chapter Five: Jackdaws respond to the vocalisations of predators whether resident or novel, and response varies seasonally.

Abstract

An ability to detect and respond to cues in the environment that indicate a potential threat has clear adaptive value. However, given that predators often behave stealthily, there are limited opportunities for prey species to acquire knowledge about such threats first-hand. Failure to respond appropriately to a novel threat poses serious problems when dealing with a changing environment. One way that animals may be able to respond adaptively to novel threats is by generalising responses from known threats to novel threats that produce similar cues. However, when responding to threats is costly, and vulnerability to different predators follows seasonal variation, it may be beneficial for species to vary their response accordingly. Mobbing is a potentially risky anti-predator response, so species that mob may be highly selective in varying their response to cues, such as vocalisations, that a predator may produce. To test this I performed playback experiments where I played the calls of different predators to nesting colonies of wild jackdaws, *Corvus monedula*, during different phases of their breeding season. I found that jackdaws showed group responses to the calls of both resident and novel predators, but not to non-predators, and that their responsiveness to predator playbacks increased across the breeding season. These findings provide novel insights into the role of acoustic predator cues and levels of reproductive investment in driving collective threat responses, and have important implications for understanding the potential adaptability of group-living corvids to changing environments.

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Introduction

Adaptability in the face of a changing environment can be fundamental to survival. For instance, the arrival of a novel predator that fails to elicit a defensive response can devastate naïve prey species (Duncan & Blackburn, 2004; Gompper, 2002; Roemer, Donlan, & Courchamp, 2002). This is clearly demonstrated in situations where novel predators have arrived at an evolutionarily isolated population of potential prey, such as those found on islands (Johnson & Stattersfield, 1990). New Zealand is a prime example where many endemic species were driven to extinction by the arrival of humans and rats (Duncan & Blackburn, 2004). Continental species may also encounter novel predators, for example when a change in climate alters the geographical ranges of predator or prey populations (Roemer et al., 2002). Consequently, mechanisms allowing animals to identify and respond to novel predators may be highly adaptive.

One way that species are able to deal with novelty is through stimulus generalisation (Watson & Rayner, 1920) whereby a reflexive or learned response to a specific stimulus is extended to similar stimuli. Prey animals often show sensitivity to a variety of cues indicating the presence of a predator, acquired through natural selection, learning from experience, or a combination of the two. These cues are commonly visual or olfactory (Blumstein et al., 2002; Land & Nilsson, 2002), but can also be acoustic. A number of birds and mammals have been shown to be sensitive to the sounds produced by potential predators, including noises associated with movement and social vocalisations (Blumstein et al., 2007; Haff & Magrath, 2010; Hauser & Caffrey, 1994; Petrželková & Zukal, 2001; Searcy & Caine, 2003; R. Swaisgood, Rowe, & Owings, 1999). Stimulus generalisation of predator sounds helps explain several examples where prey responded appropriately to the acoustic cues of predators found outside the prey's geographical range, where the cues were similar to the sounds of predators found within the prey's range. For example Blumstein et al. (Blumstein et al., 2007) suggest that yellow-bellied marmots, *Marmota flaviventris*, responded to wolf calls, with which they had no prior experience, in a similar way to coyote calls, a common predator, as a result of acoustically similarities between the two canid species' vocalisations. Likewise

another study showed that ring-tailed lemurs, *Lemur catta*, responded to the acoustic cues of novel predators that sounded similar to the red-tailed hawks heard commonly at the study site (Macedonia & Yount, 1991).

Although stimulus generalisation can provide major advantages by enabling animals to respond appropriately to novel threats, incorrectly attributing a cue to the wrong threat can be costly. For example, reed warblers, *Acrocephalus scirpaceus* can fail to make the distinction between the cues of predatory sparrowhawks, *Accipiter nisus,* and brood-parasitic common cuckoos, *Cuculus canorus*, Batesian mimics of the sparrowhawk (Welbergen & Davies, 2011). Thus by providing a stimulus that falls within the range that warblers categorise as sparrowhawk cues, the cuckoo elicits a fleeing response from its host, providing it with an opportunity to lay eggs in the warbler's nest. Given that generalising stimuli can be costly, it is perhaps unsurprising that the degree to which stimulus generalisation occurs can depend on the cost of an incorrect response. For example naïve predators were shown to discriminate less between poison frogs and their harmless mimics when the toxicity of the model was higher (Darst & Cummings, 2006). It is clear that responses to cues indicating potential threats can vary.

Some variation in parental response to threats has been linked temporally to the stage of the breeding cycle. Two main, non-mutually exclusive hypotheses seek to explain the variation in defensive effort that many species demonstrate over the course of their breeding attempts. The *offspring vulnerability hypothesis* (Harvey & Greenwood, 1978) suggests that parents should vary their effort in offspring defense temporally, depending on how vulnerable their offspring are to predation at a given time. This hypothesis receives limited support from studies in both birds and mammals (R. Swaisgood et al., 1999). For example Zenaida doves, *Zenaida aurita*, were shown to increase their level of nest defense at the point chicks hatched, but then maintained a consistent defensive effort as chicks aged (Burger et al., 1989). An alternative framework, the *offspring value hypothesis* (Andersson, Wiklund, & Rundgren, 1980), suggests that parents should increase their investment in brood defense according to the likelihood their young will survive to reproductive age. This strategy has been demonstrated in several bird species where parents increase the intensity of nest defence across the breeding cycle

(Fasanella & Fernández, 2009; Halupka, 1999; Onnebrink & Curio, 1991) and may be particularly common in animals with relatively slow reproductive rates, and altricial young that require considerable parental investment. The support given to both theories highlights the range of strategies parents take in responding to threats throughout a breeding attempt. However, no study has yet tested whether temporal patterns of threat sensitivity differ between cues associated with familiar and novel threats. Furthermore most of the studies looking at temporal changes in parents' threat response have utilised visual stimuli such as predator models, with little attention given to acoustic cues.

Jackdaws, *Corvus monedula*, provide an ideal species in which to examine these issues. Jackdaws are a highly cosmopolitan, colonial corvid whose range extends from central Asia to Western Europe (Röell, 1978). The species of predators present vary across this broad range, and predator assemblages are likely to have shifted over evolutionary time. Like many other corvid species, jackdaws are known for their flexible behaviour and adaptability to changing environments (Emery & Clayton, 2004; Greggor, Clayton, Fulford, & Thornton, 2016b; Nicolakakis & Lefebvre, 2000). Consequently, one might expect they would be capable of responding appropriately to novel predators, potentially by generalising from experience with similar predators. As cavity-breeders, jackdaw eggs and nestlings are vulnerable to small raptors such as kestrels and arboreal mammalian predators such as pine martens *Martes martes* (Johnsson, 1994) and grey squirrels, *Sciurus carolinensism* (an invasive species from North America that has been implicated in a number of egg and nestling disappearances at my study sites; Thornton & McIvor, unpublished data). Fledglings are initially poor fliers, with foxes, *Vulpes vulpes,* and other terrestrial predators posing a risk alongside a range of raptors that regularly prey on young jackdaws. Given that jackdaws produce a single brood a year and must invest heavily in parental care (Röell, 1978), the offspring value hypothesis would predict that they should increase their anti-predator responses as the breeding season (and consequently the parental investment into the current brood) progresses. Consequently, their responsiveness to novel stimuli that are classified as threatening may show similar patterns.

I performed playback experiments near colonies of nesting jackdaws to examine jackdaws' attendance to the calls of predators. Firstly, I examined

whether jackdaws responded to the calls of resident species, including examples of those that pose either terrestrial or aerial threats. Aerial threats were represented by two raptors; the common buzzard, *Buteo buteo*, and peregrine falcon, *Falco peregrinus*, whilst terrestrial threats were represented by the grey squirrel and fox. Secondly, focusing on aerial predators alone, I compared jackdaws' responses to the calls of novel versus resident species. Novel predators were represented by the South American aplomado falcon, *Falco femoralis,* and North American red-tailed hawk, *Buteo jamaicensis*. I performed acoustic analysis of all avian species used in playbacks to help explain any patterns of response. Thirdly, In order to examine how jackdaws' response to threats may change over the course of their breeding attempt, I repeated all predator playbacks during three distinct phases of the breeding cycle. Two passerine birds; the resident collared dove, *Streptopelia decaocto*, and novel North American Baltimore oriole, *Icterus galbula*, were included as non-predatory controls throughout.

Methods

Study sites and species

Playbacks were conducted at three jackdaw colonies near Penryn in West Cornwall, UK. Colony X (50°10'22.9"N 5°07'04.1"W), is ~5km from the other two colonies, Y (50°11'22.4"N 5°10'53.4"W) and Z (50°11'55.5"N 5°10'10.8"W) which are themselves ~1.5km apart. The jackdaws used in the study were all free-living adults. One hundred nest boxes were spread across the three sites at naturally realistic distances from each other (5-30m). Playbacks took place during the breeding season of April-June 2014 at a total of ten locations spread across the three study sites, selected to be at least 50m from the nearest jackdaw nest, and at least 200m from other playback locations.

Creating playback tracks

All sounds used in playbacks were obtained from the Xeno Canto database (http://www.xeno-canto.org). Recordings for each species were selected for

high signal-noise ratios, and for the context in which calls were produced. I chose common contact calls used for within-species communication, rather than more unusual vocalisations, those produced in aggressive contexts, or as part of complex songs.

Recordings were processed using the software package Audacity (www.audacity.sourceforge.net) to create playback tracks. Playback tracks began with 10s of silence followed by 30s of calls at the natural rate of the species in question, ending with 10s of silence. In rare instances where audible background noise was present on the available recordings, this was reduced using the high pass filter on audacity, cutting the amplitude of frequencies below 150Hz. This filtering reduced low frequency environmental noise such as wind or traffic, but did not encroach on the frequency range used by any of the species featured. Amplitude of calls within each playback was normalised. For each species, seven unique playback tracks were produced, each featuring the same number of calls, of the same type, randomly ordered, and sourced from different recordings.

Playback procedure

Playbacks were performed at three distinct phases of the breeding season, during *nest-building*, during *incubation* when nests contained eggs but no chicks, and finally during the time that nests contained *nestlings*. I did not extend the experiment into the post-fledging phase because pilot trials indicated that playbacks conducted at this time were not comparable with the previous three phases. Fledglings form noisy crèches with 50-200 young jackdaws congregating while parents continued to feed them. These crèches concentrated the spatial distribution of fledglings and parents that were previously spread out across suitable nest sites within each colony and so responses to playback varied dependent on crèche location rather than between treatments. Moreover, within the mêlée of rapidly moving birds it was impossible to differentiate between adults and fledglings, making it impossible to compare adults' responses to those from earlier stages.

During each of the three phases used, 12 playbacks of each species were undertaken. During *nest-building* phase however, numbers were limited to

three aplomado falcon playbacks, six buzzard playbacks, ten collared dove playbacks, seven fox playbacks, five Peregrine playbacks, and one red-tailed hawk playback. Playback numbers in this first phase were restricted by the short window between nest site selection and egg laying, with jackdaws frequently building a nest and laying their first eggs within a very short time, as low as 24 hours, leaving little time to perform *nest-building* phase playbacks.

To avoid habituation, the temporal order of playback locations, along with the species being played back, was pseudo-randomised such that no one species was presented more than once per day at a particular colony, and consecutive playbacks were performed at non-adjacent playback locations. Playback tracks were played using a remote controlled Foxpro GX7 Fury loudspeaker. Volume was adjusted to match the natural level of each species that could be commonly heard locally (dove, buzzard, squirrel) measured on a Voltcraft SL-100 sound level meter. For other species, volume was matched to similar species heard locally.

Prior to each playback, the loudspeaker, along with an Olympus LS-100 portable digital recorder recording at 48.0Hz/16bit used to record jackdaws' vocal responses to playback, was placed by an observer who then retreated to a point of concealment commanding a clear view of the playback area. 10 minutes was allowed for any disturbance caused by placing the speaker to dissipate. A Panasonic HC-X900 high-definition camcorder was set up to record the area 50m around the loudspeaker. Playback was then started via remote control. Responses recorded included the number of jackdaws recruited to the playback was recorded and any vocalisations made by recruits. Jackdaws were only counted as recruits if they moved closer than 30m to the speaker whether by circling flight, landing near the speaker, or clearly altering direction towards the loudspeaker. Jackdaws closer than 30m at the start of playback were only counted as recruits if their behaviour changed during playback by making vocalisations, moving towards the speaker, and either landing or circling close to it. Data recording ceased when the playback track had finished and recruited jackdaws began to disperse. Videos were subsequently transcribed to confirm or correct observations made in the field.

Acoustic Analysis

To provide a descriptive overview of similarities between avian calls to help explain patterns of results, Raven Pro 1.5 (Bioacoustics Research Program, 2014) was used to perform a spectrographic cross correlation (SPCC). SPCC functions by sampling all the measurable parameters of a pair of calls across their duration, then sliding one call past the other and producing a peak correlation value between 0 (no correlation) and 1 (maximum correlation) at the position of highest correlation (Charif, Waack, & Strickman, 2010; Clark, Marler, & Beeman, 1987). Ten exemplar calls for each avian species used in playbacks were randomly selected and edited into 60 unique tracks. All tracks were then compared to each other utilising Raven's batch correlation function to produce a 60 by 60 correlation table. From this, mean values for each species pair were used to create a final correlation table.

Statistical Analysis

R version 3.2.4 (R Core Team, 2016) was used to analyse data. Generalised linear mixed models (GLMMs) were performed using the g*lmer* function from the lme4 package (Bates, Maechler, Bolker, & Walker, 2015). Repeated measures were accounted for by fitting Location (each of the ten different points that playbacks were performed at) and track (the particular track used in a playback) as random terms in each model. The *anova* function was used to test the significance of removing variables during model simplification (Crawley, 2013), while the *Anova* function was used to determine the effects of individual terms within maximal and minimal models. Because data for recruitment was highly non-normal, I performed GLMMs with a binary response term indicating whether or not (1,0) any jackdaws were recruited to each playback. To compare between levels of factors of interest I performed GLMMs on subsets of the data in post hoc pairwise comparisons.)

Results

1) Do jackdaws respond to playbacks of resident predators?

The probability that jackdaws were recruited to playbacks was significantly higher to playbacks of resident predators than to the non-predatory collared dove control (GLMM; χ^2 =6.215, d.f. = 1, P = 0.013, Figure 5.1, Table 5.S1). Since the data was highly non-normal, comparisons between predator species were not possible.
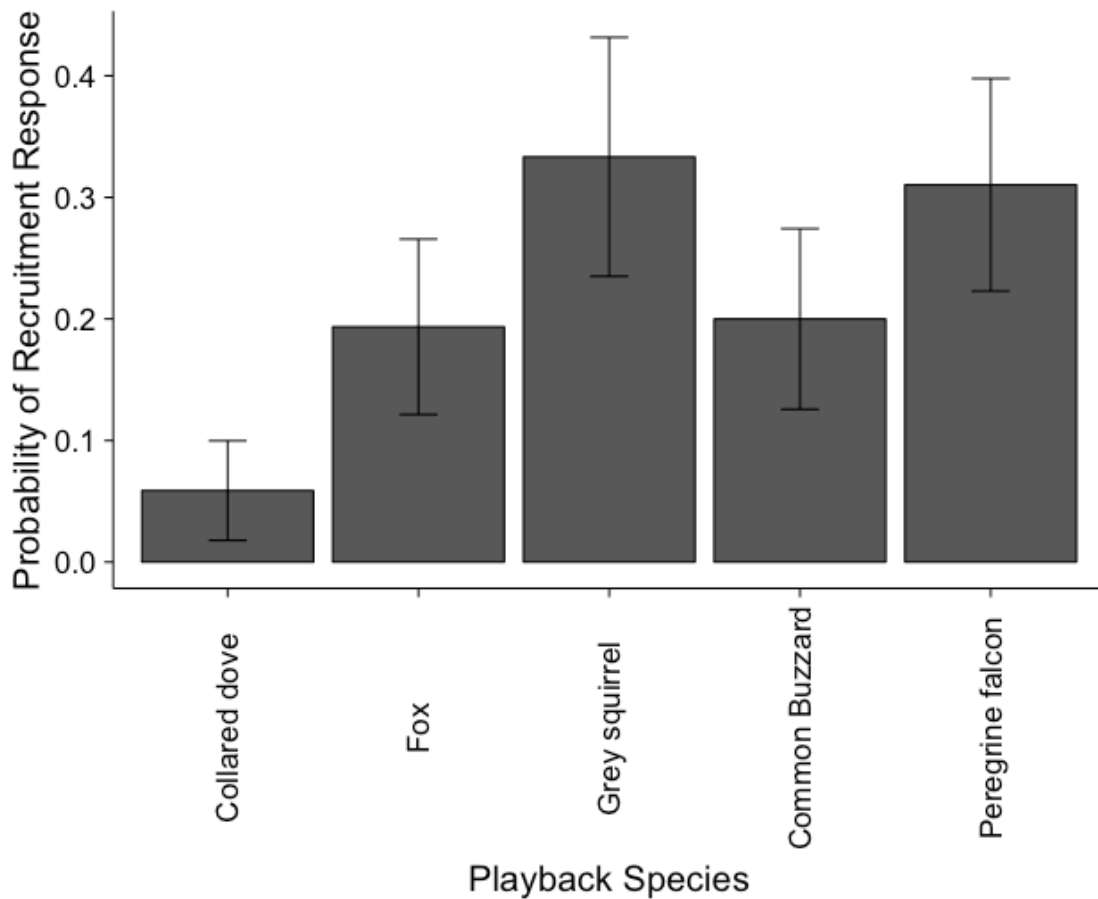
Figure 5.1. Probability of any jackdaws being recruited to playbacks of different resident species. Bars show means ± SE.

2) Does jackdaws' response vary between resident and novel avian predators?

The likelihood of recruitment occurring across all avian playbacks was higher to calls of predators than to non-predatory controls (χ^2 = 7.833, d.f. = 1, *P* 0.005, Figure 5.2) and this was not significantly affected by whether playback species were resident or novel (χ^2 = 0.041, d.f. = 1, *P* 0.839).
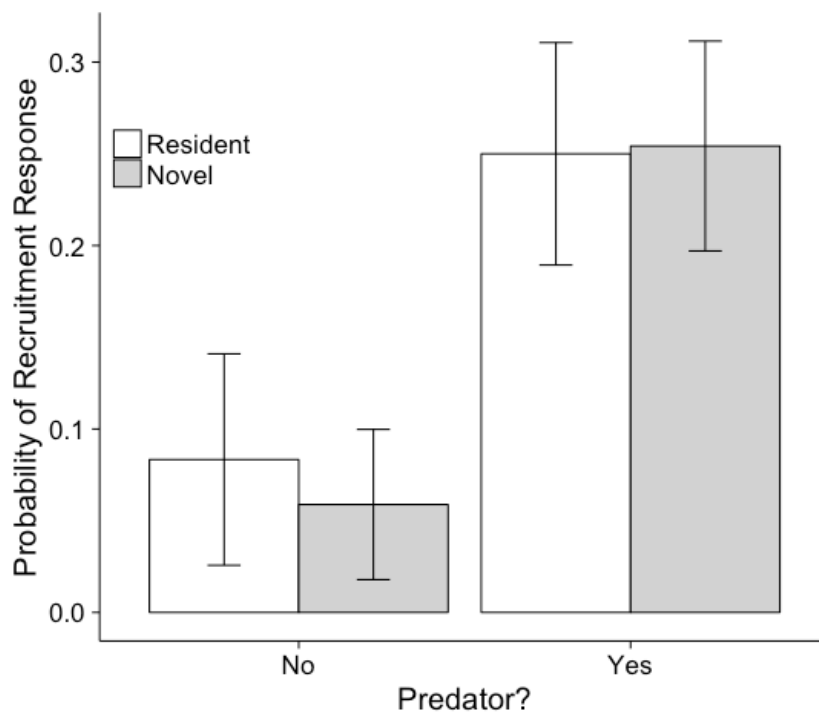
Figure 5.2. Probability of any jackdaws being recruited to playbacks of predatory or non-predatory avian species split by whether playback species is resident or novel. Bars show means ± SE.

Results of acoustic batch correlation of exemplar calls from avian species used in playbacks are shown in Figure 5.3. Within species, the mean correlation was 0.595. Mean correlation between avian predator species was 0.207 but between avian predators and non-predatory controls the mean correlation was comparatively lower at 0.063.

	Collared Dove	Baltimore Oriole	Peregrine Falcon	Aplomado Falcon	Common Buzzard	Red-Tailed Hawk
Collared Dove	**0.813355556**	0.00005	0	0.00015	0.00063	0.0019
Baltimore Oriole		**0.766311111**	0.10458	0.04127	0.24951	0.10818
Peregrine Falcon			**0.7708**	0.26398	0.10672	0.33754
Aplomado Falcon				**0.2514**	0.08426	0.25583
Common Buzzard					**0.483422222**	0.19397
Red-Tailed Hawk						**0.487311111**

Figure 5.3. Batch correlation results for all avian species used in playbacks. Darker colours indicate a higher correlation value.

3) Does jackdaws' response to playbacks vary at different phases of the breeding season?

Probability of jackdaws being recruited to playbacks increased significantly across the breeding season (χ^2 =17.01, d.f. = 1, P < 0.001, Figure 5.4, Table 5.S3). Comparing between consecutive phases, instances of recruitment were not significantly different between the *nest-building* and *incubation* phases (χ^2 =0.038, d.f. = 1, P = 0.846), and recruitment to playbacks during the *nestling* phase was significantly more likely than during *nest-building* and *incubation* (χ^2 =14.29, d.f. = 1, P < 0.001).
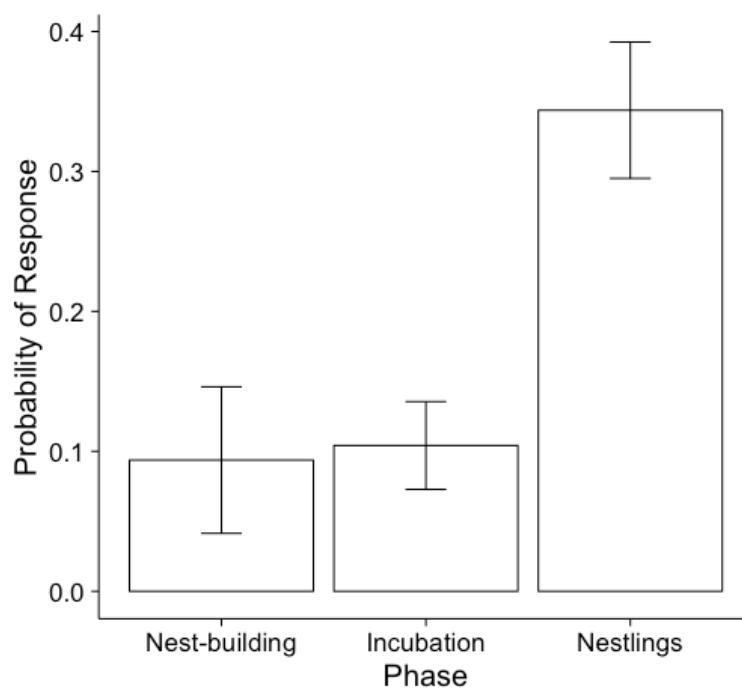
Figure 5.4. Probability of any jackdaws being recruited to playbacks during different phases of the breeding season. Bars show means ± SE.

Discussion

My results show that jackdaws are able to respond adaptively to acoustic cues indicative of the presence of both resident and novel predators, adjusting their levels of anti-predator response as the breeding season progresses. Overall, playbacks of predators elicited higher recruitment than non-predators, and, when focussing on avian playbacks, there was no difference in recruitment between playbacks of resident and novel species. Recruitment to playbacks was higher during the nestling phase of playbacks when jackdaw nests contained chicks, compared to playbacks performed during either nest-building or incubation.

In my experiments, responsiveness to playbacks of predator vocalisations was higher than to non-predators. This result supports previous work showing that prey species attend to the sounds of their predators (Blumstein et al., 2007). Given that vocal communication is highly important in corvid societies (Clayton & Emery, 2007; Marzluff, 1988; Zandberg et al., 2014), it is perhaps unsurprising that jackdaws are also able to respond appropriately to acoustic cues associated with potential threats, effectively "eavesdropping" on potential predators.

Whilst much research have focussed on temporal changes in responsiveness to visual predator stimuli across breeding attempts (Burger et al., 1989; Fasanella & Fernández, 2009; Halupka, 1999; Onnebrink & Curio, 1991), this study shows that acoustic predator cues can produce similar patterns of response. My finding that jackdaws were more responsive to predator playbacks when nestlings were present, having been relatively unresponsive to the same acoustic cues during the nest-building and incubation phases could be interpreted as support for either the offspring vulnerability (Harvey & Greenwood, 1978) or the offspring value hypothesis (Andersson et al., 1980). On the one hand, nestlings may be considered more conspicuous and vulnerable to predators than eggs due to their size and noisy begging calls. On the other hand, increased parental responsiveness when nestlings are present could also be linked to higher levels of sunken investment. My results thus illustrate the difficulties in disentangling the two hypotheses. In theory it may be possible to discriminate between the hypotheses by focusing on

changes in parental defences within phases where offspring vulnerability remains constant; for instance if egg vulnerability is stable throughout the incubation period, any increase in parental defences could be attributed to increasing parental investment over time. Additional playbacks conducted repeatedly throughout the course of each phase, coupled with detailed information on temporal changes in predation risk may help to address these issues.

Evidence suggests that stimulus generalisation is broadened when threats are higher (Darst & Cummings, 2006). Consequently, one may expect that adult jackdaws would be less likely to generalise to novel predators during the first two experimental phases when they were less responsive to resident threats. However, I found that the pattern of responsiveness to playbacks of resident and novel species was similar across all three phases of the breeding season. Whilst it could be argued that the strong responses towards novel predators were just reactions to their novelty *per se*, rather than jackdaws accurately identifying them as a threat, the consistently low response to both resident dove and novel oriole suggests instead that jackdaws generalised the novel stimuli as belonging to predators or non-predators rather than simply familiar or novel. This generalised response could be due to acoustic similarities between the predators used in the experiment. This idea is supported by my acoustic correlation analysis that indicates generally higher correlation between the calls of different raptor species than between or within the mammal and passerine calls used in the experiment.

Our results suggest an important contributing factor to jackdaws' adaptability (Greggor, Clayton, et al., 2016b) and broad geographical distribution (Röell, 1978). Jackdaws are found throughout Eurasia, occupy a range of habitats from busy cities to forests and sea cliffs and exploit a diverse variety of resources, so an ability to respond appropriately to novel threats is likely to be highly adaptive. Moreover, as they are limited to one nesting attempt per year, and with most pairs producing a maximum of two fledglings (Röell, 1978), defensive strategies may be more stringent than in species that can undertake multiple nesting attempts annually. The need for diligent defense of young is heightened by chicks' dependency on adults for food and social information critical to their survival (Federspiel, 2010).

Further work is clearly needed to better understand the role acoustic cues play in patterns of predator responsiveness. My findings indicate that generalised responses to known predator calls may be extended to novel acoustic cues, but the detailed patterns of responsiveness across a breeding season remain to be tested.

Supplementary Material

Table 5.S1. GLMM of factors affecting the probability of any recruits to playbacks of resident species.

	Wald statistic (χ^2)	df	P
Full Model			
Predator	6.215	1	0.013
Phase	11.01	2	0.004
Minimal Model	**Effect size**	**SE**	
Intercept	-4.857	1.205	
Predator			
No	0.000	0.000	
Yes	2.051	0.823	
Phase			
Nest-Building	0.000	0.000	
Incubation	0.773	0.886	
Nestlings	2.241	0.868	

Data from 148 playback experiments were fitted to a binomial distribution with probability of any recruits fitted as the response term indicating whether or not any jackdaws were recruited to each playback. 25 different playbacks tracks were used and playbacks were performed at 10 different locations, with playback track (estimated variance component < 0.001, SE <0.001) and location (estimated variance component = 1.242, SE = 1.115) fitted as random terms.

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Table 5.S2. GLMM of factors affecting the probability of any recruits to playbacks of avian species.

	Wald statistic (χ^2)	df	P
Full Model			
Predator	7.833	1	0.005
Phase	12.58	2	0.002
Resident	0.041	1	0.839
Minimal Model	**Effect size**	**SE**	
Intercept	-3.766	0.937	
Predator			
No	0.000	0.000	
Yes	1.649	0.590	
Phase			
Nest-Building	0.000	0.000	
Incubation	0.127	0.855	
Nestlings	1.714	0.802	

Data from 169 playback experiments were fitted to a binomial distribution with probability of any recruits fitted as the response term indicating whether or not any jackdaws were recruited to each playback. 33 different playbacks tracks were used and playbacks were performed at 10 different locations, with playback track (estimated variance component < 0.001, SE <0.001) and location (estimated variance component = 0.197, SE = 0.443) fitted as random terms.

Table 5.S3. GLMM of factors affecting the probability of any recruits to playbacks of different species.

	Wald statistic (χ^2)	df	P
Full Model			
Predator	8.387	1	0.004
Phase	17.01	2	<0.001
Resident	0.357	2	0.550
Minimal Model	**Effect size**	**SE**	
Intercept	-3.955	0.870	
Predator			
No	0.000	0.000	
Yes	1.718	0.575	
Phase			
Nest-Building	0.000	0.000	
Incubation	0.045	0.717	
Nestlings	1.657	0.676	

Data from 224 playback experiments were fitted to a binomial distribution with probability of any recruits fitted as the response term indicating whether or not any jackdaws were recruited to each playback. 43 different playbacks tracks were used and playbacks were performed at 10 different locations, with playback track (estimated variance component < 0.001, SE <0.001) and location (estimated variance component = 0.743, SE = 0.862) fitted as random terms.

Chapter Six: General Discussion

In this thesis I have explored ecological and social challenges faced by group-living corvids in the wild. While corvids have become the focus of extensive research in animal cognition in recent years, studies of corvids in the wild remain rare. I found that jackdaws, *Corvus monedula,* demonstrate discrimination of subtle differences in acoustic cues produced by conspecifics, sympatric species, and even novel, non-native species. Several of the differential responses identified here appear to present adaptive advantages for individual jackdaws' successful navigation of their social environment. Moreover, while research has tended to treat ecological and social drivers of cognition as separate (Dunbar, 2003; Humphrey, 1976) (Humphrey 1976; Dunbar Social Brain paper), my work highlights their inter-twined nature: the ecological problem (avoiding predation) occurs within a social context.. Here I will lay out the key findings from each data chapter and explore the combined implications of their findings, as well as discussing questions raised by the study as a whole, and what directions this might suggest for future research in this fascinating area.

Main findings

In Chapter Two I found that jackdaws discriminate between the anti-predator recruitment "scolding" vocalisations of different callers. In playbacks conducted in fields adjacent to nest-box colonies, the scolding calls of colony members elicited greater recruitment than those of birds from other colonies. Similarly, when playbacks were conducted near to nestboxes, where the perceived level of threat would be higher, I found that recruitment was highest to calls from a bird resident at that nestbox, with lower recruitment to calls from a local colony member, and lowest recruitment to the calls of birds from other colonies. Responsive scolding by recruits had the general effect of increasing recruitment, and thus magnifying the patterns described above. Interestingly, I also found an interaction between playback treatment and sex, whereby female strangers from outside the colony elicited the fewest recruits during playbacks performed in fields adjacent to nestbox colonies, but only when responsive

scolding was present. Whilst this sex interaction could have implications for an effect of social dominance in jackdaws collective alarm response, the dominance hierarchy of birds involved in the study was not yet known in sufficient detail to make a detailed analysis of this. However overall, the results of this study provide the first evidence that collective responses to recruitment alarm calls in wild animals are mediated by the identity of the caller. Although variation in response between my treatment groups could be explained by callers discriminating between categories of caller, such as familiar versus unfamiliar, there are hints that discrimination based such broad rules might not be sufficient to explain the results. For example it would be hard to explain the difference between recruitment to scolds of resident and local colony members during playbacks performed near to nestboxes in terms of familiarity since recruits should be familiar with both callers.

In Chapter Three I designed a habituation-dishabituation-rehabituation playback experiment to test whether jackdaws discriminated between individual callers, or whether patterns found in Chapter Two were better explained by a selective response based on broader criteria such as familiarity between caller and receiver. The results of these playbacks showed that recruitment decreased during habituation to scolding calls of a particular individual caller, but then rose during dishabituation to a different individual's calls, and decreased once more during the following rehabituation playback of the first caller. This pattern was similar whether receivers were familiar with both birds featured in the playback, or unfamiliar with them. These results show that jackdaws can discriminate between alarm calls of individual conspecifics, irrespective of their familiarity with either caller. This confirms that information about a caller's individual identity, contained within scolding calls, mediates the magnitude of jackdaws collective alarm response. In several other species where caller identity affects response to an alarm call, other cues contained in the alarm call are often found to contain details about the nature of the threat (Blumstein & Armitage, 1997; Graw & Manser, 2007), but this remains relatively unexplored in the responses of species that mob (Yorzinski & Vehrencamp, 2009). My work suggests that individual vocal discrimination may play an important, but as yet unexplored role in coordinating collective responses in

many social species. Jackdaws also provide a good opportunity to explore variation in alarm call production that may contain information about the urgency associated with a threat, and how this affects a collective mobbing response.

In Chapter Four I first conducted simulations of two different levels of threat to active nestboxes. Resident jackdaws produced scolding calls at a higher rate when the perceived threat was higher (a human experimenter climbing up to, rather than merely walking near, the nestbox), but the call rates of individuals did not show evidence of repeatability, either within or across contexts. In order to explore whether these threat-related differences in call rate were matched with specific variation in jackdaws' collective responses, I conducted a playback experiment where higher and lower rates of scolding alarm calls were presented at colonies, making sure that receivers had no prior experience of the individuals whose calls were used in the playbacks, and randomizing playback order. I found a significant interaction between the rate of alarm calls in the playback, and the order of playback presentation (fast first or slow first). Exploring subsets of each order, I found a trend for fewer recruits in response to slow rates of scolding playback, but only when the fast rate was presented before the slow rate. By showing that alarm call rate affects recruitment to jackdaws scolding alarm calls, I present the first evidence that the level of urgency, encoded in a recruitment alarm call, can affect the magnitude of a collective mobbing response. In a previous study, call characteristics conferring urgency has been shown in the recruitment alarm calls of another corvid, the American crow, *Corvus brachyrhynchos*, where signalers produced mobbing recruitment calls at a higher rate to more dangerous stimuli (Yorzinski & Vehrencamp, 2009). However, this study did not examine whether variation in patterns of calling had direct effects on recruitment. My findings in Chapter Four support and build upon this earlier work, linking changes in rate of alarm calling associated with higher urgency to changes in response to the call.

Taken together, Chapters Two, Three, and Four demonstrate a previously unknown level of complexity apparent in jackdaws' production of and response to alarm calls. In Chapter Five I examined whether this attention to acoustic cues from conspecifics extends to the acoustic cues of other species.

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In playback experiments I showed that jackdaws are able to respond adaptively to the acoustic cues of both native and non-native predators. This finding matches evidence from similar studies in other species (Hettena et al., 2014). Furthermore, I showed that jackdaws' responses to predator calls increased over the course of their breeding attempt. In contrast to previous studies that have used visual stimuli to examine how prey species' responses to predator cues change across a breeding cycle (Burger et al., 1989; Fasanella & Fernández, 2009; Halupka, 1999; Onnebrink & Curio, 1991), my findings show that acoustic cues alone can produce similar patterns. Rather than offer particular support to either the offspring value hypothesis (Andersson et al., 1980) or offspring vulnerability hypothesis (Harvey & Greenwood, 1978), my results could be interpreted in both ways, thus highlighting the difficulty in teasing apart the two hypotheses.

Jackdaws, socially intelligent?

Many studies have explored cognitive abilities in birds, with corvids forming a major part of this research (Emery & Clayton, 2004; Güntürkün & Bugnyar, 2016; A. Seed et al., 2009). Specifically, studies on jackdaws have explored spatial memory, transitive inference, inhibitory control, post-conflict affiliation, gaze following (to both conspecifics and humans), neophobia and social learning, flock structure, individual discrimination of heterospecifics, and vocal discrimination of conspecifics (Davidson, Clayton, & Thornton, 2015; de Kort, Emery, & Clayton, 2006; Greggor, Clayton, Fulford, & Thornton, 2016a; Greggor, McIvor, Clayton, & Thornton, 2016; Jolles et al., 2013; Kabadayi, Taylor, Bayern, & Osvath, 2016; Logan, Emery, & Clayton, 2013; Mikolasch, Kotrschal, & Schloegl, 2013; Scheid & Bugnyar, 2008; Scheid, Range, & Bugnyar, 2007; Von Bayern & Emery, 2009; Wechsler, 2012; Zandberg et al., 2014). Whilst this list is not exhaustive, the cognitive abilities, in particular relating to social behaviours, are impressive. The experiments in this thesis stem from questions about collective behaviour, sociality, and cognition. Several skills relevant to the social intelligence hypothesis are highlighted.

The ability to discriminate between individual callers when responding to

scolding alarm calls. Why might this ability have arisen? In considering what benefits may exist to a jackdaw joining a mobbing event there are several aspects to consider. Mobbing may cause the predator to give up its hunt and move on (Curio, 1978). Since my experiments involved acoustic cues only, I cannot comment on the effectiveness of jackdaws' mobbing behaviour in causing a predator to cease its hunting attempt, although anecdotal evidence from other studies providing limited evidence (Lorenz, 1952; Röell, 1978). Recruits to a mobbing event may gain information about a predator, or indeed learn about novel predators (Curio et al., 1978; Graw & Manser, 2007). This could well be the case in jackdaws, where evidence suggests that jackdaws remember individuals of other species (e.g. humans), and will repeatedly mob individuals once they have been identified as a threat (Davidson et al., 2015; Lorenz, 1952). The reliability of a caller is often proposed as a major cause of variation in response to alarm calls (Blumstein et al., 2004). This would appear plausible in explaining why jackdaws discriminate between callers, except that the patterns of discrimination shown in my experiment do not obviously reflect caller reliability. The habituation to the first caller in Chapter Three could be explained by reliability, since no predator is present during the playbacks, and recruits may stop responding in a similar "crying wolf" pattern to that found in vervets (Cheney & Seyfarth, 1988). However, the pattern of recruitment in Chapter Two is harder to explain, since there were the same number of calls for each treatment, and treatments were presented in a random order, thus although no predator was present, the apparent reliability, resulting from the experimental design, of each treatment was consistent throughout. The lower response to the *stranger* treatment in particular does not fit in with an explanation based on reliability, since potential recruits would have no previous experience of these callers, and hence no basis for ranking them relative to the familiar resident and local treatments. An explanation of my findings in terms of byproduct mutualism (Russell & Wright, 2009), may seem more parsimonious than other mechanisms suggested to mediate variation in avian mobbing such as reciprocal altruism (Krams et al., 2008; Trivers, 1971), but it struggles to explain the clear individual caller discrimination ability I demonstrate in Chapter Three. Instead, simple associative learning mechanisms may explain patterns of mobbing in response to different callers. For example nesting jackdaws will more likely experience the scolding calls of conspecifics that scold nearby.

These are likely to be jackdaws nesting in the local area, hence through attending to repeated local mobbing events, jackdaws could learn to associate a mobbing response with specific calls and locations. Hence if a call is novel, as in the stranger treatment from Chapter Two, or familiar, but in a novel location, as in the local treatment, this may provide a weaker recruitment stimulus than a call, such as the resident treatment, that is both familiar and presented at a location where that call has have previously been heard. The pattern of recruitment found in Chapter Two, particularly in playbacks performed near to nests, could hence be explained in terms of associative learning. However, this mechanism is less useful in explaining the clear discrimination of individual callers presented subsequently in Chapter Three. Thus a better explanation could be that jackdaws integrate information about a call's location and familiarity with information about a specific caller's reliability when responding to mobbing alarm calls. Jackdaws may prefer to nest to near close associates, hence larger responses to calls of resident birds near their nestboxes (where the partner of the scolding individual is likely to be nearby) than to other colony members, and larger responses to colony members (who potential recruits could be familiar with) than strangers (who thy could not). Thus findings in Chapter Two may also reflect patterns of social relationships.

Social responses to ecological problems?

One of the problems of the Social Intelligence Hypothesis highlighted in the introduction is separating the ecological and social drivers of cognitive abilities (Emery, Seed, Von Bayern, & Clayton, 2007). Rather than solving this dichotomy, the results presented in this thesis underline just how difficult it is to separate the ecological and social value of particular cognitive abilities. For example, predation is an ecological problem experienced by all prey species whether social or solitary. However, social species have little choice but to deal with predation in a social context. Food caching provides an example of behaviour with a clear ecological driver: the need for species to sustain themselves when food is less plentiful (Vander Wall & Balda, 1981). However, food caching species that live in social groups also face an additional challenge: the need to keep the cache location secret from conspecifics who might pilfer it (Clayton et al., 2007). Thus the drivers behind anti-pilfering strategies such as

re-caching previously hidden foods are both social and ecological. A similar mixture of social and ecological drivers best explains the patterns seen in my studies. Chapter Five shows that jackdaws respond to acoustic cues indicating the presence of a predator. The drivers of this behaviour could be assumed to be entirely ecological were it not for evidence suggesting that jackdaws can learn to identify threats through social learning (Davidson et al., 2015; Lorenz, 1952; Röell, 1978). On one hand, the patterns of response to jackdaws' scolding calls described in Chapters Two, Three, and Four are inherently social, since the responses recorded are informed by second-hand (i.e. social) information about a threat, rather than direct detection of cues indicating the presence of a predator. On the other hand, as mentioned above, predation is an ecological problem. Thus rather than try to explain the cognitive abilities involved in terms of social versus ecological drivers, I would argue that this dichotomy is invalid and support for the SIH must be drawn from interpreting the relative impact of the social and ecological drivers on behaviour, rather than trying to find instances where they act in isolation.

Future directions

Research on cognition and the adaptive significance of social behaviours that may drive the development and evolution of cognitive abilities is a busy area within studies on animal behaviour (Freeberg & Krams, 2015; Greggor, Clayton, et al., 2016b; Olkowicz et al., 2016; A. M. Seed & Boogert, 2013; Seyfarth & Cheney, 2015). However, with a few notable exceptions, research remains largely confined to laboratory settings. The expansion of cognitive studies in the wild is a clear priority for future research if I are to understand how cognition evolves (Morand-Ferron, Cole, & Quinn, 2016). The experiments contained in this thesis have sought build on previous research and in doing so, has highlighted areas where cognition and social behaviours still need to be addressed. Whilst I have explored patterns of behaviour resulting from acoustic cues, I am constantly reminded of the other sensory cues that may be causative, or result from a particular behaviour. The visual impact of a large jackdaw mobbing display has rarely failed to impress those who see it for the first time. Jackdaws have been shown to respond to visual cues in several studies (Davidson, Clayton, & Thornton, 2014; Davidson et al., 2015; Scheid &

Bugnyar, 2008; Scheid et al., 2007; Von Bayern & Emery, 2009). Whilst these studies identify certain visual abilities such as individual recognition, the extent to which such abilities are used in the wild, particularly in a social context, and how they integrate cues across sensory modalities, remains unknown.

Conclusions

Perhaps a certain irony is due when considering that jackdaws are one of the few animal species that has appeared to thrive despite humans' alteration and destruction of the natural world. This in itself should provide impetus for future study of this species, as jackdaws have survived the challenges of an environment that has likely changed at one of the fastest rates experienced across evolutionary time. I hope this thesis encourages the idea that behavioural flexibility is possible in part through the use of social information. Dealing with environmental change is a challenge for every species, and whilst social living may benefit group members, providing novel responses to ecological challenges not possible among solitary species, the mechanisms by which these responses occur can be cognitively demanding. The continued exploration of how social information is used in the context of collective behaviours is an important direction for future research. Whilst this thesis and many other studies have focused on a particular signal modality, I hope that future research is able to use a more holistic approach, allowing insight into how integration of cues of multiple modalities may influence the behaviour of social species.

Although the word "primate" referred to a religious figure when used by the Reverend Richard Harris Barham in his epic 1840 poem "The Jackdaw of Rheims", he unwittingly links the humble jackdaw with the fascinating discoveries of modern day primatologists (Barham, 1840). If he had the chance to review current cognitive and social research on both primates and corvids, he may have been pleasantly surprised at his accidental forethought. Darwin, on the other hand, might have raised an eyebrow at the range and depth of information currently being discovered in the vocalisations produced by animals "when the sensorium is strongly excited" (Darwin, 1872).

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