

Collective responses to antipredator recruitment calls in the jackdaw (*Corvus monedula*)

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Abstract

Collective behaviour, whereby multiple individuals act together in a coherent, coordinated manner, occurs throughout nature. Self-organisation theory suggests that the maintenance of the collective behaviours shown by bird flocks and fish shoals, emerge as the result of simple rules of attraction among neighbours, with no need for leadership. Individuals in the models of self-organisation are assumed to be identical but in reality animals differ in aspects such as personality or motivation and in their social bonds with other conspecifics. Individual variation among group members means that certain individuals may exert disproportionate effects on the behaviour of groups and so in some cases, leadership is important for the initiation of collective behaviours. Moreover, cognitive processing of information about other individuals may play an important, but hitherto neglected role in the coordination of collective behaviours. This thesis examines the role of cognitive processes and of leadership in the formation of collective antipredator mobbing events in wild jackdaws (*Corvus monedula*). Mobbing presents a collective action problem as it entails substantial risks for individuals but, by driving away potential predators, provides collective benefits. Individuals may therefore benefit from processing information about the likely costs and benefits when deciding whether to join a mob. Recruitment to a mob is initiated through distinctive scolding calls, and information contained in these calls may be very valuable for individuals when deciding whether to join mobbing events. Chapter Two tested whether the number of callers influenced the number of individuals recruited to a mob. Individuals are expected to join a larger group because for an individual there is a reduced risk of predation. As predicted, I found that a greater number of callers does recruit a greater number of individuals. This work shows evidence that jackdaws discriminate between the calls of different individuals and is the first to show numerical assessment in an antipredator collective behaviour. Chapter Three tested whether the dominance rank of caller influenced the number of individuals recruited to a mob. A dominant individual may be expected to recruit more individuals as it is likely to be stronger and more able to drive away a predator. A dominant may also punish others for not responding. However, I found no influence of dominance rank of caller on the number of recruits. Punishment is unlikely to be important in jackdaw societies and any effect of rank may be obscured by other factors such as direct benefits from joining the mob, not contingent on dominance rank.

Social relationships between the recruits and the caller have not been considered in this study and individuals may be more likely to respond to a close affiliate than pay attention to an individual's dominance rank. Together, these results highlight the importance of investigating the cognitive processes involved in collective behaviours and also the characteristics of individuals who initiate collective behaviours.

Chapter one: General Introduction

The striking coordination and cohesion of multiple individuals acting together in a collective manner is seen right across the natural world from body cells (Misteli 2001) and bacteria (Cho *et al.* 2007), to fish shoals (Shaw 1978), bird flocks (King & Sumpter 2012) and human crowds (Helbing & Molnar 1995). These movements are puzzling as it is not evident how all members of the group act in concert to create such coordinated and seemingly complex behaviour. The naturalist Edmund Selous was so confused by the manoeuvres of bird flocks that he concluded that the individuals used telepathy to coordinate their flight (Selous 1931). In some cases of collective behaviour, leadership appears to be important (King *et al.* 2009) but in many cases there seems to be no leader. For the latter cases, theoretical models of self-organisation derived from mathematics and physics describing particle motion show that collective order can arise as an emergent property if all individuals in a group follow simple, local rules (Couzin *et al.* 2002).

Collective behaviour

The amazingly synchronous movements of coordinated animal groups such as flocks of birds, shoals of fish and swarms of insects have been described as having a ‘collective mind’ because they were thought to occur via transfer of thought or connectivity between all organisms involved (Selous 1931; Couzin 2007). Recent studies have shown that some collective animal movements can be influenced by a single individual leading the group (King *et al.* 2009). For example in chacma baboons (*Papio ursinus*) the highest-ranking individual dictates the movement of the group (King *et al.* 2008) and in paper wasps (*Polistes fuscatus*) the queen regulates worker foraging, acting as a central regulator of the colony (Reeve & Gamboa 1987). However, there are many cases in which leadership appears to play no role in collective behaviours (Conradt & Roper 2005; 2010), so an alternative explanation is necessary.

Theoretical and empirical research have demonstrated that collective behaviours can arise from local interactions between individuals in the absence of a leader or initiator. The

emergence of collective order through individuals each following simple, local rules is termed self-organisation and can create whole group behaviours greater than what any one individual could achieve on its own (Gueron *et al.* 1996; Sumpter 2006; Garnier *et al.* 2007). A well-known example of self-organisation is pheromone-laying in ants. On discovery of a food source, ants (*Lasius niger*) lay chemical pheromones on their trip back to the nest and by all individuals using the simple rule of following these trails, the colony appears to work collectively to exploit the food source (Beckers *et al.* 1992). Models of self-organisation describe how collective behaviours can arise from these simple rules.

A wealth of models, initially developed from mathematics and physics describing particle motion (Nicolis & Prigogine 1977), describe how collective behaviours can emerge from rules of self-organisation (Couzin *et al.* 2002; Garnier *et al.* 2007). Aoki (1982) and Reynolds (1987) were the first to relate the models to animal movements when they incorporated the behaviours of individuals in fish shoals and bird flocks respectively, into the models.

Theoretical models of self-organisation broadly agree on three general, simple rules; stay close to neighbours, maintain a minimum distance from others and travel in the same direction, and the patterns that arise reflect real collective animal motion such as fish shoals and insect swarms (Couzin *et al.* 2002). Only recently has there been the technology required to test the models against real field data. For instance, Ballerini *et al.* (2008) undertook the first large-scale study of collective behaviour in a biological system as the authors created 3D reconstructions of real starling flocks using high-speed stereophotography. While important advances have been made in our understanding of the simple rules governing collective behaviours, more work is needed to refine theoretical models for testing real data from field studies. The self-organisation models that describe these collective behaviours, although vital to understanding how a whole behaviour emerges from individual components, have certain downfalls; they do not describe the initial formation of collective behaviours and they assume that all individuals are identical.

Contrary to the assumptions of theoretical models, individuals in a collective group are not simply computerised points acting as identical independent agents; they show many differences, for example personalities, motivations and statuses, and they may prefer to affiliate with particular conspecifics. Because of these differences, individuals may benefit

from using information to adjust their interactions with different conspecifics so as to avoid conflict or enhance cooperation in a group. The mechanisms by which animals process, store and act on information from the environment are described as cognition (Shettleworth 2010).

Social cognition

Social cognition involves processing and acting on information about social companions, such as the relationships between individuals (Shettleworth 2010). The Social Intelligence Hypothesis, proposed by Humphrey (1976) (see also Jolly 1966), suggests that group-living animals face challenges not encountered by solitary species. For instance, in large social groups, individuals may benefit from identifying conspecifics, remembering previous interactions and keeping track of changing statuses (Kitchen *et al.* 2005; Clayton *et al.* 2007). These social demands are thought to select for sophisticated cognitive abilities in social species, in particular those that exhibit individualised social relationships (Dunbar 1998).

The majority of research on social intelligence has focused on behavioural and neuroanatomical studies of primates (Dunbar 1998; Reader & Laland 2002; Seyfarth *et al.* 2005; Lehmann *et al.* 2007). For example, there is substantial evidence that primates can recognise one another as individuals (Cheney & Seyfarth 1982; 1999), identify relationships among third parties (Cheney & Seyfarth 1980; 1986; Dasser 1988; Aureli *et al.* 1992) and track dominance hierarchies within their group (Bergman *et al.* 2003; Borgeaud *et al.* 2013). Further support for the Social Intelligence Hypothesis comes from comparative studies of brain anatomy. For instance, Dunbar (1998) reported correlations between group size and neocortex ratio (the ratio between the volume of the neocortex - thought to be the seat of higher cognitive function - and the rest of the brain) and attributed this relationship to the elevated cognitive demands of recognising and tracking individuals in larger groups. However, it is not just primates that experience many repeated interactions in their group and thus a substantial need to process social information; other social animals like dolphins (Connor 2007) and spotted hyenas (*Crocuta crocuta*) (Holekamp *et al.* 2007) demonstrate these features too and in order to determine if the Social Intelligence Hypothesis applies as a general evolutionary hypothesis, it is important to study multiple taxa.

Among birds, corvids are renowned for their remarkable cognitive abilities (Clayton & Emery 2005). Although corvids have a small absolute brain size in comparison with primates, very recently Olkowicz *et al.* (2016) have found that because their neurons are very densely packed, corvids actually have a similar number of neurons in the forebrain as primates. This may explain why corvids are capable of cognitive feats to rival the great apes (Emery 2004; Emery & Clayton 2004). The sophisticated cognitive abilities of corvids may arise in part due to the challenges of social life. For instance, scrub-jays engage in a behaviour called food-caching; the hiding of food to eat at a later date, which is cognitively demanding (Clayton *et al.* 2007). Observers can steal another's cache and to mitigate against this, cache protection strategies such as moving food to a new hiding place, are employed. For instance, Dally *et al.* (2006) showed that western scrub jays (*Aphelocoma californica*) engaged in more cache protection when being observed by another individual. Social relationships may also select for the sophisticated cognitive abilities of corvids. A common type of social relationship between individuals is dyadic relationships which are critical for inferring the dominance status of individuals. For instance, Bond *et al.* (2003) investigated dyadic relationships in two species of jay, the pinyon jay (*Gymnorhinus cyanocephalus*) which forms large social groups, and the western scrub-jay that is relatively non-social. Pinyon jays were faster than the scrub-jays to learn a set of dyadic relationships between objects, suggesting that the large social groups experienced by pinyon jays allows a high capability in recognising relationships (Bond *et al.* 2003), which is key for keeping track of changing dominance statuses. The typical corvid mating system of lifelong, monogamous pair bonds may also help to explain their remarkable cognitive abilities. It is advantageous for individuals to recognise and coordinate with their partner and anticipate their actions, in order to maximise their joint fitness. In support of this argument, birds with long-term monogamous pair bonds have particularly large brains (Emery *et al.* 2007; Shultz & Dunbar 2010).

The ability to identify partners and close associates may be highly advantageous for corvids as it permits the establishment of strong social bonds. There are a number of examples of individual vocal discrimination where the receiver identifies the caller as being in a particular class, for example, familiar or unfamiliar (Hopp *et al.* 2001; Kondo *et al.* 2010, Woods 2016). Another class type which may be useful to differentiate between is dominance rank. In order to enhance cooperation or avoid aggression with others, it may be

beneficial for individuals to identify that a conspecific is either of a higher or lower dominance. For instance, ravens (*Corvus corax*) became more stressed when playback experiments violated their expectancy of rank relations (Massen et al. 2014). This study by Massen *et al.* (2014) shows evidence for individual discrimination. Although individual discrimination between classes is a first step to recognition, it is not the same as recognising a conspecific as a particular individual. True individual recognition requires the receiver to learn an individual's distinctive characteristics and then apply this to individual-specific information about the signaller (Tibbetts & Dale 2007). Such true recognition has been demonstrated in large-billed crows (*Corvus macrorhynchos*), where audiovisual cues were used in expectancy violation paradigms (Kondo *et al.* 2012). Crows were found to look for longer in incongruent situations where expectations of an auditory stimulus after a visual stimulus were violated (Kondo *et al.* 2012). This study by Kondo *et al.* (2012) is the first to demonstrate cross-modal individual recognition in birds and raises the possibility that other corvids may also have the ability to show true recognition. Corvids may prefer to affiliate with certain individuals in their group to maintain social bonds so when they form flocks they are likely to identify these close associates and may change their behaviour accordingly.

Mobbing as a collective behaviour

Corvids engage in spectacular forms of collective behaviour such as winter flocking displays (Coombs 1961; Jolles *et al.* 2013) and antipredator mobbing behaviour. Mobbing is the joint assault of individuals on a predator to drive it from the area and is taxonomically widespread (Dugatkin & Godin 1992; Graw & Manser 2007; Kramps *et al.* 2002). Mobbing presents a collective action problem because approaching a predator may be a highly risky behaviour but its removal provides a substantial collective benefit. A greater number of individuals are likely to have more success when driving off a predator (Robinson 1985) and so recruits may weigh up the costs and benefits when deciding to join a mob. A mobbing event is often initiated by distinctive vocalisations from those who first identify the threat (Curio *et al.* 1978, Woods 2016) and an individual's decision to join a mob may be facilitated by the processing of information contained within these recruitment calls. Jackdaws employ recruitment calls termed scolding calls which, like other jackdaw vocalisations (Zandberg *et*

al. 2014), are known to be individually distinctive (Kings 2014). The identity of the caller may therefore provide useful information for jackdaws when deciding whether to join a mobbing event. For example, playback experiments by Woods (2016) showed that the recruitment calls of colony members elicited more responders than the calls of strangers. The mobbing behaviour of jackdaws provides unique opportunities to explore the role of caller identity and cognitive processes in initiating collective behaviours.

Thesis aim

My thesis investigates whether the information provided in mobbing recruitment calls influences the formation of collective antipredator responses in the jackdaw (*Corvus monedula*). Jackdaws are a highly social species of corvid and groups show mobbing behaviour in response to aerial predators, making it an ideal species for the study of antipredator collective behaviours. Recruitment to a collective behaviour is initiated by distinctive alarm calls called scold calls. I investigate whether the magnitude of recruitment is affected by the number and dominance rank of individuals producing recruitment calls. Playback experiments by Woods (2016) showed that jackdaws discriminate between the calls of different individuals in collective antipredator responses, but it is not known whether jackdaws attend to the number of callers. Mobbing is a highly risky behaviour (Curio *et al.* 1978) and accurately assessing the number of calls in the mob is likely to be beneficial for a number of reasons. Firstly a larger group of individuals is likely to be more successful at driving away a predator (Robinson 1985) and secondly, the risk to a single individual decreases exponentially as the number of individuals in the group increases (Foster & Treherne 1981), thus joining a larger group may be more beneficial. Studies on the assessment of numerosity have been largely on captive animals, with individuals discriminating between different numbers of objects or sounds (Fernandes & Church 1982; Davis & Albert 1986; Beran 2007) or different-sized groups of food (Evans *et al.* 2009; Irie-Sugimoto *et al.* 2009). In contrast, the importance of numerosity has seldom been addressed in wild animals. A study by McComb *et al.* (1994) was one of the first to test for numerical assessment in the field. Using playback experiments of female lions (*Panthera leo*) roaring, the authors showed that females were less likely to approach simulated intruders when they were outnumbered. This study demonstrates the ability of a wild

animal to assess the number of opponents and change its behaviour in response (McComb *et al.* 1994). The study by McComb *et al.* (1994) and others (Wilson *et al.* 2001; Seddon & Tobias 2003) have investigated numerical assessment in inter-group conflicts but the importance of numerosity in an antipredator collective behaviour has yet to be examined. In Chapter Two, I use playback experiments of scold calls to test for the first time whether the number of callers initiating a mob influences the number of recruits.

In addition to the number of callers, aspects of caller identity may also be important to individuals when deciding whether to join a mob. An aspect of caller identity that has not been investigated is dominance status. Jackdaws exhibit a dominance hierarchy (Tamm 1977) and as dominant individuals are expected to be stronger and more able to drive away a predator, recruits may be more likely to respond to a mob initiated by a dominant than a subordinate. Moreover, it is possible that individuals may avoid future harassment or derive social prestige (Zahavi 1995) by joining dominants in risky activities. In Chapter Three I derived a dominance hierarchy from competitive interactions and using playbacks I tested whether the dominance rank of the caller influences recruitment to a mob. Together, this thesis aims to provide new insights into the role of caller identity in the initiation of, and the cognitive processes involved in, collective behaviours in the jackdaw.

Study populations

The Cornish Jackdaw Project was established at the University of Exeter, Penryn campus in 2012 and includes 100 nest boxes across three field sites in West Cornwall (Figure 1). The jackdaw colonies in the project are free-living populations and over 1,500 of individuals are colour ringed under British Trust for Ornithology licenses, to allow individual identification of the birds. The breeding season lasts from April to July each year and jackdaws have a single clutch per year with incubation lasting 17-18 days and nestlings fledging after approx. 35 days. Jackdaws are very social corvids and maintain lifelong, monogamous pair bonds (Röell 1978). Recordings of scold calls and playback experiments for this thesis were undertaken at two of the field sites across the nesting season from April to June 2016.

a)



b)



c)



Figure 1: Maps showing locations for the three field sites used in the Cornish Jackdaw Project. a) Penryn Campus, b) Pencoosse Farm, c) Stithians churchyard.

Summary of chapters

Chapter Two

Number of callers

This chapter investigates if the number of callers influences the recruitment of individuals to a mob. As mobbing is risky, individuals may benefit from weighing up the costs and benefits of joining. Numerical assessment is likely to occur as a greater number of individuals will be more successful and the risk to a single individual is lower in larger groups (Foster & Treherne 1981). Playback tracks were compiled for three treatment groups of one, three and five callers and I recorded the maximum number of recruits during playbacks conducted at eight locations at each of two field sites. As predicted, results showed that more callers recruited more individuals. This study shows evidence for individual discrimination of scold calls and is the first to show numerical assessment during an antipredator collective behaviour.

Chapter Three

Dominance rank

This chapter investigates if the dominance rank of the caller influences the recruitment of individuals to a mob. A dominant individual is likely to be more able to successfully drive away a predator so individuals may benefit from joining the mob if the initiator is dominant. In addition, social benefits such as prestige (Zahavi 1995) or avoidance of punishment (Clutton-Brock & Parker 1995) may be gained if individuals join a dominant. To calculate dominance ranks, observations of aggressive interactions between colour ringed individuals were recorded and a David's Score was calculated based on opponent interactions and the proportion of wins and losses (de Vries *et al.* 2006). The maximum number of recruits who responded to the playback tracks was recorded. My results showed no effect of rank of caller on the number of recruits. Punishment is unlikely to be common in jackdaw societies, which may explain the apparent lack of attention to the rank of the caller. I also consider whether unmeasured variables such as individual motivations or social relationships may over-ride any potential benefits of attending to caller dominance when deciding to join a mobbing event.

Chapter Two: Numerical Assessment in collective antipredator behaviour in jackdaws

Abstract

Collective behaviours are highly coordinated movements comprising many individuals. Theoretical models of self-organisation show that such coordination can emerge, without the need for a leader, if each individual follows simple rules of interaction with neighbours. However, models typically assume that all individuals are identical and interchangeable. Also, the models ignore the role of cognitive processes in guiding decisions about whether to join collective events. Antipredator mobbing presents a collective action problem as it may be highly risky to individuals, yet a greater number of individuals are likely to be more successful in driving away a predator. Individuals may therefore be expected to assess the costs and benefits to decide whether to join in with a mobbing event. Mobs are commonly initiated by recruitment calls produced by the individual who identifies the threat and individuals may therefore attend to information in these calls. The risk to a single individual is lower in larger groups, so animals may benefit from the ability to appraise the number of conspecifics involved in a mobbing event. Whether such numerical assessments play a role in mediating mobbing events in animals is unknown. I used wild jackdaws to test whether the number of callers influences the number of individuals recruited to a mobbing event and predicted that a greater number of callers would elicit more recruits. As predicted, playbacks simulating more callers were found to recruit more individuals. This study shows that jackdaws use individual discrimination of their recruitment calls to assess the number of conspecifics involved in initiating mobbing events, and use this information when deciding to join. This is the first evidence for the use of numerical assessment in a collective antipredator response and highlights the need for a greater understanding of the cognitive processes involved in collective behaviour.

Introduction

Animals from many different taxa form large groups of highly coordinated individuals which move together almost like a single ‘superorganism’, creating some of nature’s most amazing spectacles. Starling murmurations and fish shoal bait balls can number thousands of individuals and are among the most famous and striking examples of animal collective behaviours. Up until around the 1980s, it was not known how these seemingly complex movements were coordinated and telepathy between group members was suggested as an explanation (Selous 1931; Couzin 2007). Research has begun to reveal the processes through which collective behaviours in nature arise and are maintained. For instance, some studies have suggested a role for leadership by a high status individual in some collective behaviours. Collective movement decisions to a new foraging area were found to be consistently led by the dominant male in baboons (King *et al.* 2008) and Reeve and Gamboa (1987) demonstrated that the experimental removal of a paper wasp queen lead to a decrease in worker foraging effort, suggesting that she strongly influences foraging rate of the colony and acts as a central regulator. Despite this there are numerous cases in which coordinated, cohesive actions appear to emerge without such central regulation so an alternative explanation is needed.

Self-organisation theory has been used to explain how collective behaviours are coordinated without the need for a leader (Bonabeau *et al.* 1997; Garnier *et al.* 2007). Global behaviour can be achieved if each individual follows a set of simple rules based on local information (Garnier *et al.* 2007). Collective behaviours can allow animals to solve problems that no single individual could solve alone. A famous example of self-organisation is pheromone trails in ants. Ants produce pheromones to mark a foraging route and as others follow the chemical, the resulting line of individuals is formed on the basis of local information (Beckers *et al.* 1992; Sumpter 2006) and the ants appear to collectively exploit the food source. One of the first to relate self-organisation theory to animal behaviour was Reynolds (1987) who expanded the idea from models of physics and mathematics describing particle motion (Nicolis & Prigogine 1977), to simulate a bird flock, incorporating the behaviour of each individual independently (Reynolds 1987). Rules common to all models of self-organisation are described by Couzin *et al.* (2002). They are the rules of repulsion, alignment

and attraction; maintain a minimum distance from neighbours, travel in the same direction as others and do not become isolated. The resulting patterns from models incorporating these rules mimic natural collective actions like fish shoals and insects swarms (Couzin *et al.* 2002). Rules of self-organisation can be used to create human as well as animal patterns. For instance, Helbing and Molnar (1995) modelled human patterns of movement and found that individuals keeping a certain distance from obstacles resulted in the formation of distinct lanes of those moving in the same direction. However, all these theoretical models share a common limitation in treating individuals as identical; an unrealistic assumption in the natural world.

Each individual in these models of self-organisation is a computerised point and so all are treated as identical. In reality, animals exhibit great variation among individuals, including differences in personality, motivation or social status, all of which mean individuals are unlikely to act in exactly the same way. The differences between individuals are likely to affect their decisions when joining a collective behaviour or moving as part of a collective group, and there is growing evidence that individual characteristics and social relationships influence the initiation and maintenance of group movements (Petit & Bon 2010). The identity of conspecifics in the collective action may be important to individuals when deciding to join. For example, in a study on Tonkean macaques (*Macaca tonkeana*), certain individuals only joined a movement when a favoured partner had moved as well (Sueur *et al.* 2009). Similarly, when initiating a group movement, dominant green woodhoopoes (*Phoeniculus purpureus*) were more likely to be followed than subordinates and likewise with males over females (Radford 2004). These studies suggest that collective behaviour is influenced by information processing about the characteristics of other group members, but we still know little about the cognitive processes mediating collective behaviour. In particular, what information is used by individuals when making decisions to join collective activities that may entail substantial personal risk?

It may be particularly important for individuals to use cognitive processes to guide decisions when joining collective behaviours if those decisions can entail substantial personal cost. One such collective behaviour is mobbing; the joint attack of individuals on a predator to drive it from the area. Mobbing is a collective action problem because it provides a

collective benefit but entails substantial individual risk (Sordahl 1990). A mobbing event is usually initiated by recruitment calls from the individual who first spots a predator (Curio *et al.* 1978, Woods 2016) and an individual's decision to join a mob may depend on the information contained within the recruitment calls. It may be beneficial for individuals to assess the number of conspecifics in the mob prior to joining, because a larger group is likely to be more successful (Dominey 1981; Robinson 1985) and because of the dilution effect; the risk to a single individual decreases as the number of individuals in the mob increases (Foster & Treherne 1981). Many animals exhibit aspects of numerosity and studies have often compared quantities of 'many' versus 'few' (Davis & Prusse 1988; Reznikova & Ryabko 2011). For instance when rhesus monkeys (*Macaca mulatta*) were presented with a computerised quantity judgement task, they were found to select the larger of two sets of items (Beran 2007), and pigeons (*Columba livia*) have also been found to distinguish stimuli of different numbers (Emmerton *et al.* 1997). Most studies on numerical assessment have been undertaken in the lab but field studies are needed to investigate the adaptive value of numerosity in ecologically relevant contexts. For instance, McComb *et al.* (1994) used playbacks of roaring female lions to examine the role of numerical assessment during inter-group conflict and found that defending lions were less likely to approach their opponents when they were outnumbered. In potential contests where individuals pay a large cost if they lose, the ability to be able to assess the number of intruders may be very valuable when deciding whether to proceed with defence of the territory, or back down (Wilson *et al.* 2001; Benson-Amram *et al.* 2011). Whether numerical assessment is important in collective antipredator behaviour has never been investigated. I investigated whether numerical assessment of the number of individuals producing antipredator recruitment calls influences collective mobbing responses in wild jackdaws.

Jackdaws are a small, social corvid and are a suitable species to investigate the role of numerical assessment in collective antipredator responses as they use distinctive alarm calls (known as scold calls) to recruit conspecifics to mob predators (Woods 2016). Scold calls are known to be individually distinctive (Kings 2014) and jackdaws have been found to discriminate between the calls of different individuals, with calls of familiar colony members eliciting higher levels of recruitment than the calls of unfamiliar individuals (Woods 2016). Scold call discrimination may potentially allow listeners to determine the number of callers

attempting to recruit assistance for mobbing. I used playbacks simulating calling by one, three or five jackdaws to test whether the number of callers influenced the number of individuals recruited to a mob. I predicted that a larger number of callers would recruit more individuals.

Methods

Study site

All sound recordings and playbacks were conducted at two field sites in West Cornwall, UK. Colony Y at Stithians Churchyard, TR3 7AJ (N 50°11'25.98'', W 5°10'49.00'') and colony Z at Pencoos Farm, TR3 7DN (N 50°11'55.37'', W 5°10'7.48''). The jackdaws used in this experiment were all free-living adults, a large proportion of which had been colour ringed for individual identification under British Trust for Ornithology licenses. Recordings and playbacks took place from April to June, 2016.

Playback Track creation

I recorded scold calls from known individuals using an Olympus LS-100 PCM recorder recording at 48.0Hz/16bit and a Sennheiser M67/K6 directional microphone with a Reinhardt windshield. To minimise the influence of potential confounding variables, I only used the calls of males in my experiments. The individuals targeted were known nest box users and therefore familiar to conspecifics within their breeding colony, and were identified by their unique colour ring combinations. In one case, the box of the target male was known but he was not ringed so, as jackdaws are sexually monomorphic, I determined which bird of the pair was the male using behavioural observations (females incubate the nest while males provision their partner with food). I approached the focal nestbox and in the majority of cases, being within 10m was sufficient to cause a scolding response. In five cases, climbing to the nestbox was necessary to elicit scolding. I recorded the calls of nine males at the Stithians colony and 11 males at the Pencoos colony.

I designed playback tracks to simulate calling by one (GS1 treatment), three (GS3 treatment) and five (GS5 treatment) individuals. These particular numbers reflect numbers of scolding birds that commonly initiate mobbing events, whilst also keeping the increase in the number of birds (two) constant between treatments. I used the open source audio software Audacity (audacityteam.org) to extract discrete scold calls from the field sound recordings, normalise the amplitude of calls and create playback tracks. All tracks followed the same structure which comprised 15 calls: three bouts of five separated by ten seconds with two seconds between calls in a bout to ensure the same rate of calling. The track began with ten seconds of silence so the total track length was one minute. Tracks comprising a single caller (GS1) used 15 different calls for that one individual (Figure 2a). Tracks comprising multiple callers used, in a random order, five different calls from three individuals (GS3) (Figure 2b) or three different calls from five individuals (GS5) (Figure 2c). While a natural scolding event may show some overlap between the calls of different callers, my design of playback tracks was used to ensure that calls by different individuals were salient to receivers. For seven of the individuals I recorded, the number of discrete scold calls available was limited, so calls had to be repeated within the playback track. Individual callers were randomly assigned to treatments, ensuring that all multiple-caller tracks had different combinations of individuals.

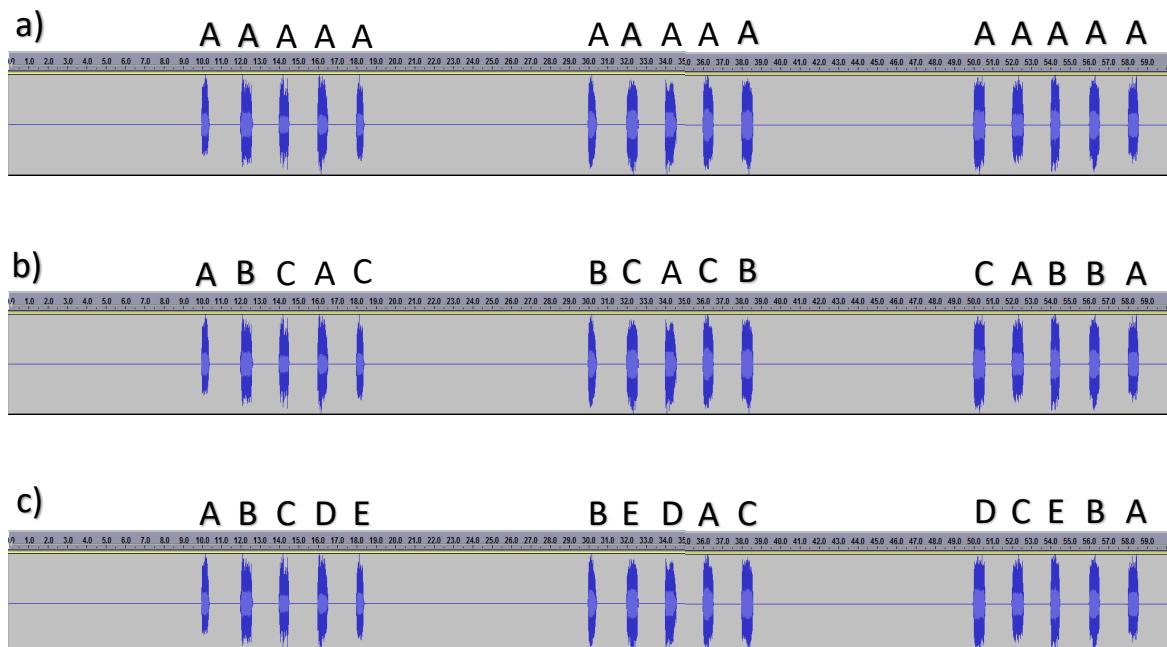


Figure 2: Playback tracks for a) a GS1 treatment b) a GS3 treatment and c) a GS5 treatment. All playback tracks follow the same structure: 15 calls separated into three sets of five, each separated by 10 seconds. Calls within a set are separated by two seconds meaning a single track lasts 60 seconds. The letters above the calls represent how the calls from the different individuals are spread throughout the track.

Playbacks

Experiments were performed using a remote controlled loudspeaker (FoxPro Fury 2) at eight locations within each of the two study sites. These locations were spread as far as possible from each other and less than 20m away from an occupied nest box (see Figures 3 and 4 for location of nest boxes). The average distance between locations at Stithians was 172.14m and between locations at Pencoosse was 155.71m. To minimise the potential influence of birds recognising their own calls, I conducted playbacks as far as possible from the nest-box(es) of the individual(s) whose calls were being broadcast. I conducted every playback treatment (GS1, GS3 and GS5) at each of the 16 locations, in random order between 7am and 6pm during the nesting period. All playback tracks used in the experiment were unique; no track was played more than once meaning a total of 16 playback tracks were used for each treatment (for a full list of the individuals used and their locations for playback experiments see Appendix 1). No more than three treatments were done per site per day and playbacks at the same site were separated by at least four hours. Within each location, the speaker was always placed in precisely the same orientation and position, on a field boundary wall, 1-2m off the ground. After setting up the speaker, I retreated 30-50m away to a concealed location with clear view of the sky and set up an HD Panasonic video camera (HC-X900) to record birds' responses. The volume on the FoxPro remote control was set to 20, replicating the volume of a scold response from a jackdaw at the same distance, as measured using a Voltcraft SL-100 sound level meter. I waited a minimum of five minutes after placing the speaker to allow nearby jackdaws to return to natural behaviour before broadcasting the playback treatment; GS1, GS3 or GS5.

I used the event logging software BORIS (Behavioural Observation Research Interactive Software: Friard & Gamba 2016) to transcribe the video records, noting the time the first bird responded, the time the last bird left, the number of recruits in total and if the recruits themselves scolded. A recruit was classified as any jackdaw that changed its behaviour in response to the playback either by flying around the speaker, landing in a nearby tree or changing direction towards the speaker. The experiment ended when the last bird had left the area.



Figure 3. Red stars indicate the eight locations for the number of caller playbacks at Stithians churchyard.



Figure 4. Red stars indicate the eight locations for the group size playbacks at Pencoos Farm.

Analysis

Data was analysed in R version 3.2.3 (R Core team, 2015). The package *glmer* was used to run a generalised linear mixed model with a Poisson error distribution with a log link function. The response variable used was the number of recruits. Treatment (GS1, GS3 or GS5), site (S or P), treatment order (1st, 2nd, 3rd playback at location) and time of day (continuous) were fitted as explanatory terms. As scolding by recruits could serve to amplify playback stimuli and wind could attenuate the broadcast sound, I fitted responsive scolding (yes/no) and windspeed (obtained from Carnkie Weather Station: carnkieweather.co.uk) as additional explanatory terms. Location (the eight locations at each of the two sites) was set as a random effect. I used Akaike's information criterion, AIC (Akaike 1973; Bozdogan 1987), to compare between alternative models. The model with the lowest AIC score best fits the data and was used to generate a minimum adequate model. Chisquared and P values for the terms in the minimal model were derived using the ANOVA function in R.

Ethical note

Birds used in this study had been ringed under BTO licenses (C5746; C5752; C5983). Experimental procedures adhered to the guidelines of the Association for the study of Animal Behaviour and were approved by the University of Exeter Biosciences Ethics committee.

Results

The average number of recruits for the whole experiment was 11.95. At both Stithians and Pencoose the minimum number of recruits who responded to the playbacks was zero. Stithians had a maximum of 53 and an average of 13.3 recruits. Pencoose had a maximum of 57 and an average of 10.6 recruits. Jackdaws typically responded 23.8 secs after the track was played at Stithians and after 31.1 secs at Pencoose. The average length of time that the response lasted was 3.7 mins at Stithians and 2.5 mins at Pencoose. The minimum adequate model with the lowest AIC score included treatment, responsive scolding, treatment order and time of day (Table 1, Table 2). The presence of responsive scolding by the recruits increased the number of individuals recruited to the playbacks (GLMM, $\chi^2_{48} = 130.75$, d.f. = 1, $P < 0.001$, Figure 5). Accounting for the influence of responsive scolding, I found an increase in the number of recruits as the number of callers in the playback track increased (GLMM: $\chi^2_{48} = 24.84$, d.f. = 2, $P < 0.001$, Figure 6). As confirmation, I also analysed the subset of the dataset in which no responsive scolding occurred ($N = 35$ out of 48 trials), and obtained the same result (GLMM: $\chi^2_{35} = 35.54$, d.f. = 2, $P < 0.001$). Post-hoc comparisons between treatment levels in the full model showed a statistically significant increase in recruits between one and three callers (GLMM; $\chi^2_{32} = 4.35$, d.f. = 1, $P = 0.037$) and between one and five callers (GLMM: $\chi^2_{32} = 17.27$, d.f. = 1, $P < 0.001$), but not between three and five callers (GLMM: $\chi^2_{32} = 2.36$, d.f. = 1, $P = 0.12$). Treatment order was negatively correlated with recruitment (GLMM: $\chi^2_{48} = 31.34$, d.f. = 1, $P < 0.001$). The later in the day the experiment was performed, the more recruits responded to the playback (GLMM: $\chi^2_{48} = 6.03$, d.f. = 1, $P = 0.014$). There was no difference in the number of recruits between the two sites (GLMM: $\chi^2_{48} = 0.035$, d.f. = 1, $P = 0.85$) and the wind speed at the time of playback did not influence the number of recruits (GLMM: $\chi^2_{48} = 2.67$, d.f. = 1, $P = 0.10$).

Table 1. Model summary for number of callers showing the full GLMM with all fixed effects and the Minimum Adequate Model (MAM) for only the significant fixed effects. Chisquared and p values are generated via the ANOVA function in R.

	Fixed effects	Estimate	St. Error	χ^2	DF	P value
Full Model	<i>Intercept</i>	2.05698	0.29837			
	Scold	1.64668	0.14562	127.8735	1	< 2.2e-16
	GS3	0.54270	0.16600	22.2095	2	1.504e-15
	GS5	0.72143	0.15340			
	Order	-0.53797	0.09249	33.8341	1	6.002e-09
	Time	0.11899	0.05986	3.9508	1	0.04685
	Wind	0.11960	0.07326	2.6657	1	0.10254
Minimum Adequate Model	<i>Intercept</i>	1.92422	0.25465			
	Scold	1.66480	0.14559	130.7528	1	< 2.2e-16
	Order	-0.49487	0.08839	31.3435	1	2.162e-08
	GS3	0.52793	0.16653	24.8384	2	4.040e-06
	GS5	0.74840	0.15217			
	Time	0.14375	0.05855	6.0286	1	0.01408

Table 2. AIC model summary for number of callers showing output for the full model with all fixed effects, the Minimum Adequate Model for only the significant fixed effects and the model for treatment and scolding only.

Fixed Effects	Residual Df	Residual Deviance	dAIC	Weight
Full: Treatment+ Scold+Order+Site+ Time+Wind	39	155.3799	1.3	0.34
Treatment+Scold+ Order+Time (MAM)	41	156.5303	0.0	0.66
Treatment+Scold	43	190.2287	28.4	0.00

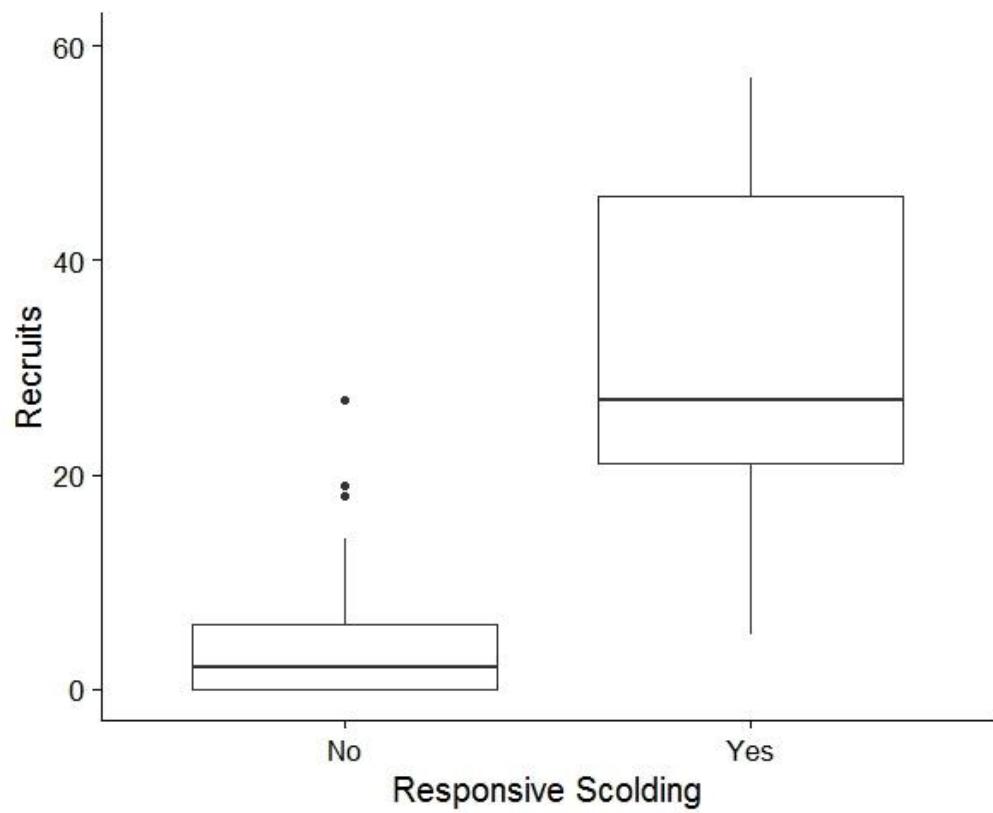


Figure 5: Number of recruits in the presence or absence of responsive scolding. Median, upper and lower quartiles shown.

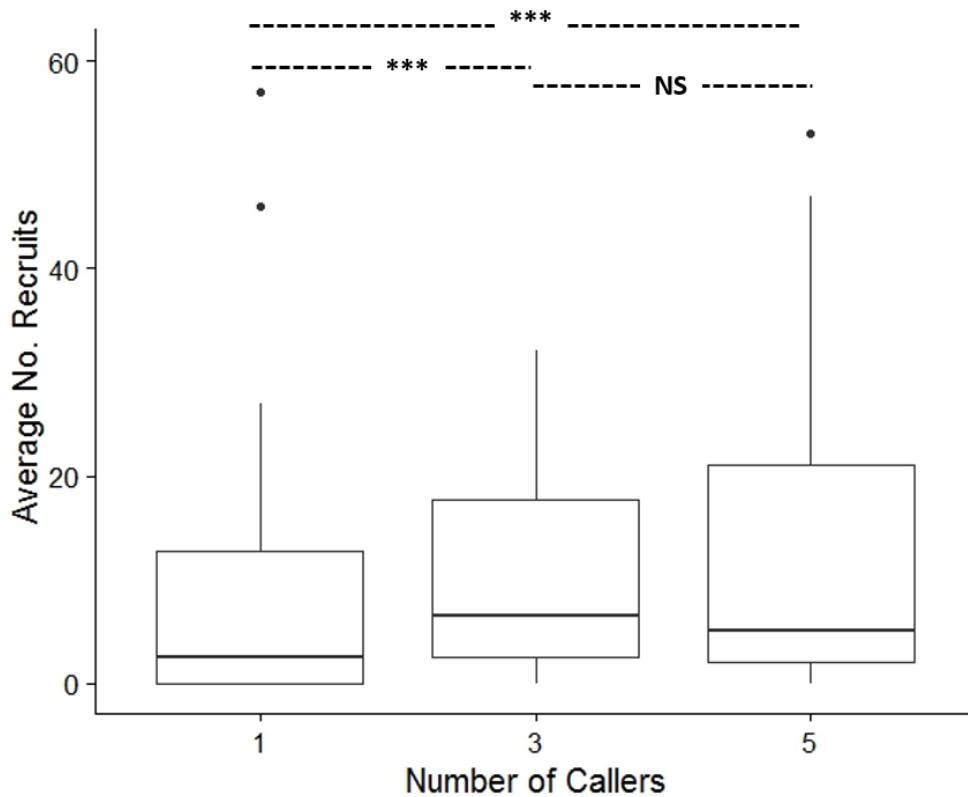


Figure 6: Average number of recruits in response to playbacks for one, three and five callers. Median, upper and lower quartiles shown.

Discussion

Little is known about the cognitive processes involved in collective behaviours and what information is used by individuals when deciding to join collective actions. Here I investigated whether the number of callers influenced the number of recruits to a mob. As predicted, I found that more callers recruited more individuals to a mobbing event. These results show that jackdaws use vocal discrimination to assess the number of individuals producing recruitment calls. This is the first time numerical assessment has been shown to influence collective antipredator responses.

Jackdaws may derive a number of benefits from preferentially joining larger mobbing groups. Firstly, as the number of individuals involved in a mobbing event increases, the risk to a single individual decreases exponentially (Foster & Treherne 1981; Cresswell & Quinn 2011). Secondly, a greater number of individuals is better able to drive away a predator (Dominey 1981; Robinson 1985) so individuals are expected to join an already large mob as success is more likely. Lastly, larger numbers of mobbing individuals are likely to force a predator to leave the area more quickly so individuals need invest less time and energy in mobbing than if defending in a smaller group (Krama & Krams 2005).

The decision to join a larger mob must be underpinned by cognitive processes that enable individuals to appraise group sizes. If decisions are based on information contained in recruitment calls, individual call discrimination may be necessary to determine the number of different individuals calling. In my experiments, the total number of calls and the rate of calling was the same across all playbacks, with the only difference being the number of individuals whose calls were represented. By demonstrating differential responses based only on the number of individuals calling, my study confirms and extends previous findings that jackdaws discriminate between the scold calls of different individuals (Woods 2016). This individual call discrimination provides the basis for potential recruits to determine the number of callers through numerical assessment. While previous studies on captive corvids have shown evidence for numerical assessment (Ujfalussy *et al.* 2014), with individuals discriminating between different numbers up to 30 (Ditz & Nieder 2016), my work provides evidence that such abilities play an important function in guiding behaviour in the wild.

Although my findings show that jackdaws employ numerical assessment under natural conditions, they also suggest there may be limitations to this ability. While there was an overall effect of experimental treatment on the number of recruits, post-hoc comparisons revealed that there was no difference in the number of recruits between three and five callers. There may be a number of possible reasons for this. Firstly, there may be no further benefit to the jackdaws in assessing the number of callers above three. For example, Robinson (1985) found that beyond a certain size, an increase in the number of individuals in colonies of yellow-rumped caciques (*Cacicus cela*) provided no further antipredator benefits. Secondly, there may be cognitive limitations that limit the ability to assess the number of callers above a certain threshold (McComb *et al.* 1994). In meerkats (*Suricata suricatta*), for example, Bousquet *et al.* (2011) investigated group decisions during foraging and found that a threshold of two or three group members could initiate departure to a new location. While there is evidence from laboratory studies that some corvids can discriminate considerably larger numbers (Ditz & Nieder 2016), the magnitude of differences in callers may have limited discrimination between treatments in my experiment. Discrimination between pairs of numbers typically follows Weber's law whereby the ratio of the difference between the two numbers resolves the discrimination, rather than the absolute difference between them (Bogale *et al.* 2011). In my study, the absolute difference between the number of callers was equal across treatments (ie. an addition of two callers from one to three to five), but the ratio between one and three is larger, and thus may be easier to discriminate, than that between three and five. Lastly, the occurrence of responsive scolding, which stimulated additional recruitment, may have further masked apparent differences between experimental treatments. To determine the cognitive limits of jackdaw numerosity one could manipulate the ratios between the number of callers in the playback tracks and test if there is a maximal limit of number of callers that the jackdaws can identify. Furthermore, numerical assessment may integrate social information and this could be tested by asking; are jackdaws more likely to respond to two familiar individuals or five unfamiliar ones?

Certain conditions of my experimental design and a lack of suitable equipment available to me may have influenced the results of my experiment. The order the playbacks were done

at each location was negatively correlated with the number of recruits; the first playback recruited more individuals than the third. Despite attempts being made to increase the time between playbacks at the same location, a tight time frame meant that in some instances, playbacks occurred on consecutive days. The jackdaws in that location may have become habituated to playbacks and ceased to respond. Due to the proximity of locations at both sites (average of 172.14m at Stithians and 155.71m at Pencoose), it is very likely that the same individuals would have responded to multiple playbacks. With the equipment available, it was very difficult to measure and control for these repeat responses in the field and thus in my analysis. Future work should consider ways to identify the individual jackdaws that respond to playbacks, for example using GPS tags (c.f. Nagy *et al.* 2013).

In conclusion, I present the first evidence that numerical assessment is important to a wild animal when deciding to join a collective antipredator behaviour. I have shown that in wild jackdaws, individual call discrimination allows assessment of the number of callers recruiting to a mobbing event, and thus affects the magnitude of the group response. While research on collective behaviour has tended to emphasise simple, mindless rules (Couzin *et al.* 2002; Garnier *et al.* 2007), these findings emphasise the potential importance of cognitive processes in the formation of collective responses in nature.

Appendix 1: Tables to illustrate how the individuals were used and the date carried out, for all playback tracks for Chapter Two

Appendix Table i: The box number of the different individuals used for each treatment at each location at the Stithians site and the date of which each playback was carried out.

Site	Location	Treatment	Individuals used	Date
Stithians	S1	GS1	Y29	04/05/2016
Stithians	S1	GS3	Y11,04,07	15/04/2016
Stithians	S1	GS5	Y07,19,29,01,11	02/05/2016
Stithians	S2	GS1	Y10	14/04/2016
Stithians	S2	GS3	Y06,04U,29	08/05/2016
Stithians	S2	GS5	Y04U,11,19,06,10	03/05/2016
Stithians	S3	GS1	Y07	15/04/2016
Stithians	S3	GS3	Y07,11,01	12/04/2016
Stithians	S3	GS5	Y29,06,11,04U,01	09/05/2016
Stithians	S4	GS1	Y06	25/04/2016
Stithians	S4	GS3	Y01,07,10	13/04/2016
Stithians	S4	GS5	Y01,04,07,10,11	11/04/2016
Stithians	S5	GS1	Y04U	06/05/2016
Stithians	S5	GS3	Y04,10,11	12/04/2016
Stithians	S5	GS5	Y11,07,01,10,04U	08/05/2016
Stithians	S6	GS1	Y01	15/04/2016
Stithians	S6	GS3	Y10,01,04	13/04/2016
Stithians	S6	GS5	Y04,07,10,11,01	11/04/2016
Stithians	S7	GS1	Y11	14/04/2016
Stithians	S7	GS3	Y04U,29,10	06/05/2016
Stithians	S7	GS5	Y19,04U,06,29,07	03/05/2016
Stithians	S8	GS1	Y19	27/05/2016
Stithians	S8	GS3	Y29,19,04U	26/05/2016
Stithians	S8	GS5	Y01,29,04U,19,10	01/06/2016

Appendix Table ii: The box number of the different individuals used for each treatment at each location at the Pencoosse site and the date of which each playback was carried out.

Site	Location	Treatment	Individuals used	Date
Pencoosse	P1	GS1	Z30	14/04/2016
Pencoosse	P1	GS3	Z15,26,20	26/04/2016
Pencoosse	P1	GS5	Z14,22,18,20,19	24/04/2016
Pencoosse	P2	GS1	Z14	15/04/2016
Pencoosse	P2	GS3	Z19,30,26	24/04/2016
Pencoosse	P2	GS5	Z18,28,20,26,22	30/05/2016
Pencoosse	P3	GS1	Z26	18/04/2016
Pencoosse	P3	GS3	Z18,28,22	25/04/2016
Pencoosse	P3	GS5	Z22,14,28,02,30	21/04/2016
Pencoosse	P4	GS1	Z20	18/04/2016
Pencoosse	P4	GS3	Z02,22,18	24/04/2016
Pencoosse	P4	GS5	Z30,19,14,18,15	25/04/2016
Pencoosse	P5	GS1	Z22	21/04/2016
Pencoosse	P5	GS3	Z30,19,15	12/04/2016
Pencoosse	P5	GS5	Z02,20,15,19,18	28/04/2016
Pencoosse	P6	GS1	Z02	18/04/2016
Pencoosse	P6	GS3	Z14,22,19	26/04/2016
Pencoosse	P6	GS5	Z20,02,26,30,28	19/04/2016
Pencoosse	P7	GS1	Z43	23/05/2016
Pencoosse	P7	GS3	Z15,24,02	07/05/2016
Pencoosse	P7	GS5	Z15,26,24,22,20	08/05/2016
Pencoosse	P8	GS1	Z28	27/04/2016
Pencoosse	P8	GS3	Z24,02,28	10/05/2016
Pencoosse	P8	GS5	Z24,30,22,28,26	03/05/2016

Chapter Three: Initiator's dominance rank does not influence recruitment to collective antipredator responses in jackdaws

Abstract

Leadership may be important in the initiation of collective animal behaviours. Dominance rank may influence leadership and some studies on dominance influencing group movements appear to be controversial. Dominance might be particularly influential in behaviours that incur substantial personal risk such as antipredator behaviours. Mobbing is one such behaviour and is the assault of individuals on a predator to drive it from the area. Mobbing is a collective action problem because it creates a benefit to all but may entail considerable individual risk. A larger number of individuals to drive away a predator will be more successful, therefore individuals must make a decision when to join. Mobs are usually initiated by recruitment signals produced by the individual who identifies the threat. Signals from high-ranking individuals may be particularly effective in recruiting others to a mob as dominants are likely to be stronger and more able to drive off a predator, and subordinates may be punished for not responding to a dominant. I used wild jackdaws to test for the first time whether dominance rank of a signaller influences recruitment to a mob. I used competition at feeding tables to determine dominance and playback experiments to broadcast recruitment calls. Contrary to predictions, I found no relationship between rank of caller and number of recruits. Jackdaws may have no need to avoid punishment by dominants, may be motivated instead by direct benefits of mobbing or by their social relationships with the caller rather than the caller's rank. Further work is necessary to determine how individual characteristics and social network structure influence the formation of costly collective behaviours.

Introduction

The highly coordinated movements of large numbers of animals can form remarkable structures and individuals in some cases, are so synchronised that they appear to move like a single ‘superorganism’. Collective behaviours such as starling murmurations and fish shoal bait balls can number thousands of individuals and the mechanisms behind their coordination puzzled biologists for a long time. Theoretical models of self-organisation were developed to explain how collective behaviours are maintained (Couzin *et al.* 2002; Garnier *et al.* 2007) but they tend to assume that all group members are identical and follow the same simple rules of interaction with their neighbours. In reality, individual variation means that certain individuals may exert disproportionate effects on the behaviour of groups (Couzin *et al.* 2005; Conrardt *et al.* 2009; King *et al.* 2009). Leadership by certain individuals may result from instances where it is advantageous for the group to be coordinated (King *et al.* 2009).

Leadership may be especially important in initiating group movements where there are advantages to the group remaining cohesive (Sugiyama 1976; Leca *et al.* 2003). For instance, if a group splits into subgroups, individuals may be more vulnerable to predation (Landeau & Terborgh 1986; Cresswell & Quinn 2011) and may experience reduced foraging success, due to increased vigilance (Hunter & Skinner 1998). Leadership can reduce the chance of splitting if group members are motivated to follow the leader (Reebs 2000; Petit & Bon 2010). Certain individuals may be more influential than others in leading group movements. For instance, particular Tonkean macaques only joined a group movement if a favoured partner had moved as well (Sueur *et al.* 2009). The characteristics of leaders may vary across space and contexts. For example leaders may be more knowledgeable or more highly motivated towards a certain resource. A minority of informed individuals can lead the whole group as shown in an experiment by Reebs (2000) where a small number of experienced golder shiner fish (*Notemigonus crysoleucas*) were able to lead a greater number of untrained individuals out of the shade to be fed at the right time of day. Leadership may also be influenced by personality traits. For example, bold sticklebacks (*Gasterosteus aculeatus*) were found to show greater initiative towards leaving cover to look for food than shyer individuals (Harcourt *et al.* 2009). Leadership may also be influenced by dominance

rank as shown in several taxa (Feist & McCullough 1976; Peterson *et al.* 2002; Radford 2004; King *et al.* 2008).

Dominant individuals are often likely to be particularly influential in initiating group movements. In some cases, this may be because they possess superior knowledge. In cooperatively breeding green woodhoopoes (*Phoeniculus purpureus*), for example, dominants have typically been on the territory for longer than other group members and so have greater local knowledge (Radford 2004). Dominants are particularly likely to be followed when initiating group movements (Radford 2004). Dominant individuals may also be influential in initiating group movements because of their resource holding potential. In a study on chacma baboons, King *et al.* (2008) presented a food source which the dominant male could monopolise and prevent subordinates from gaining access to. Here, the dominant male consistently acted as leader in initiating movements towards the experimental food site, presumably because he acquired the greatest benefit from influencing the group's movement (King *et al.* 2008). However, contrary to the study by King *et al.* (2008), where the dominant male appeared to lead the group, Strandburg-Peshkin *et al.* (2015) suggested that group movements of baboons are democratic, meaning that the decision-making process is shared between individuals. Indeed, the role of leadership in group movements remains controversial, and contradictory findings are common in the literature (Leca *et al.* 2003; King *et al.* 2008; King *et al.* 2011; Strandburg-Peshkin *et al.* 2015). One, as yet unexplored context in which dominant individuals might be expected to be particularly influential, is in cases where joining a collective event involves substantial personal risk, such as during collective antipredator behaviour.

Mobbing is the collective assault of individuals on a predator to drive it from an area and may be a highly risky for the mobbers involved. Mobbing is a collective action problem as driving away a predator provides a great benefit to all but joining a mob entails considerable individual risk. A greater number of individuals are likely to be more successful (Robinson 1985) so individuals must make a decision about when to join a mob. Recruitment signals, such as distinctive vocalisations, are usually produced by the individual who first has contact with the predator, to draw others in to the area (Curio *et al.* 1978, Woods 2016). An individual's decision to join a mob may be based on information contained within these

calls, as shown in Chapter Two where the number of callers influenced the number of individuals joining the mob. Individuals might be expected to preferentially respond to the recruitment calls of dominant individuals as dominants are likely to be stronger and more able to drive off a predator, thus joining a dominant may reduce individual risk compared to joining a low-ranking group member. There may also be reputational benefits to joining a dominant who is recruiting. ‘Image scoring’ generates a reputation for an individual so in return for helping a dominant, an individual may receive social benefits like access to food or mates (Nowak & Sigmund 1998; Wedekind & Milinski 2000). Dominants may punish subordinates who do not join either by physical attack or refusal to join mobbing events initiated by a cheater (Clutton-Brock & Parker 1995). For instance, Feh (1999) studied Carmargue horse (*Equus caballus*) alliances and found that the subordinate male of a pair received repeated aggression from the more dominant individual when it tried to monopolise a mare on its own without helping in defence against other stallions. I investigated whether dominance rank influences recruitment to a mobbing event in the jackdaw.

Jackdaws are a small, social corvid species that lives in groups with a clear dominance hierarchy (Wechsler 1988; Tamm 1977), individualised social relationships such as lifelong, monogamous pair bonds (Röell 1978; Henderson *et al.* 2000) and strong parent offspring bonds (Röell 1978; Henderson *et al.* 2000). They show mobbing behaviour in response to predators which makes them an ideal species for the study of collective behaviour. Jackdaws produce scold calls which function in recruitment (Woods 2016) as demonstrated in Chapter Two. Scold calls are known to be individually distinctive (Chapter Two, Kings 2014) and collective responses are likely to be influenced by discrimination between different callers. For example Woods (2016) showed that individuals were more likely to respond to familiar than unfamiliar individuals. Scold call discrimination may potentially allow listeners to determine the dominance rank of the individual attempting to recruit assistance for mobbing, but it remains unknown whether the caller’s dominance rank influences levels of recruitment. I used interactions between individuals on feeding tables to determine dominance hierarchies and then used playback experiments to test whether the dominance rank of the caller influenced the number of individuals recruited to a mob. I predicted that a more dominant individual would gather more recruits.

Methods

Study site

All sound recordings and playbacks were conducted as in Chapter Two at two field sites in West Cornwall, UK. Colony Y at Stithians Churchyard, TR3 7AJ (N 50°11'25.98'', W 5°10'49.00'') and colony Z at Pencoose Farm, TR3 7DN (N 50°11'55.37'', W 5°10'7.48''). All jackdaws used in this study were free-living adults, colour-ringed under British Trust for Ornithology licenses. Recordings and playbacks took place from April to June, 2016.

Dominance hierarchy

Video cameras were set up at two baited feeding tables at each of the two field sites for 2.5 hours in the morning, 4 times a week across the breeding season in 2016. Tables 50cm² were suspended in trees or attached to barn walls, about 3m off the ground and had a pile of grated cheese placed in the middle of the table. Multiple individuals could feed from the table at a time. Using the individual colour rings, interactions between marked jackdaws were recorded. Behaviours comprised displacement (bird A supplants bird B within 2secs), aggression (physical violence eg. kick or peck), submission (bowing head to another) or tolerance (birds on table simultaneously). David's scores (DS) (David 1987) were created from these interactions based on the proportions of wins and losses of individuals (Gammell *et al.* 2003; de Vries *et al.* 2006) and from this dominance ranks were obtained. When studying wild populations it is common for uncertainty to occur due to variation in sample sizes (de Vries *et al.* 2006) and an advantage of DS is that it takes this into account. The DS for each individual, i , is calculated as follows:

$$DS = w_1 + w_2 - l_1 - l_2$$

w_1 denotes the sum of the number of times individual i defeats individual j divided by the total interactions between these two. It is unrealistic to treat the importance of these interactions for determining rank as equal, so the calculation weights the value of a win based on the quality of the opponent: w_2 is the sum of w_1 weighted by the w_1 value of its

opponents. I_1 denotes the sum of the number of times individual j defeats i divided by the total interactions between them and again I_2 is weighted according to the I_1 values of opponents.

The cause of a low number of interactions between two individuals might be due to chance. The dyadic dominance index D_{ij} of i over j corrected for chance assumes the interactions between different individuals are equally likely to occur. It is defined as:

$$D_{ij} = \text{observed proportion wins} - \{(\text{observed proportion wins} - \text{expected proportion wins}) * \text{Prob}[\text{observed proportion win}]\}$$

The expected proportion of wins is 0.5 and the Prob[observed proportion] is the probability that the observed proportion will occur by chance. DS are calculated from this dyadic dominance index. So the fewer the number of interactions between a pair, the greater the adjustment of the proportion of wins value toward the proportion expected by chance. David's score takes into account the relative strengths of opponents so defeating another individual which has had more wins gives a larger score than defeating an individual which has not had many (Gammell *et al.* 2003; de Vries *et al.* 2006). As well as this, an individual's rank is independent from the interactions it is not involved in (Gammell *et al.* 2003; de Vries *et al.* 2006). I assigned ranks separately to the two sites, Stithians and Pencoose, according to position in the hierarchy after the DS had been completed.

Playback Track creation

I recorded scold calls from known individuals, identified by their unique colour rings, using an Olympus LS-100 multi-track linear PCM recorder recording at 48.0Hz/16bit and a Sennheiser M67/K6 directional microphone with a Reinhardt windshield. As using both sexes creates confounding effects, the only individuals I used in my experiments were male. The targeted males occupied nest boxes and were also known to frequent feeding tables at the field sites (see 'Dominance hierarchy' section above). To record scold calls I approached the focal nestbox and in the majority of cases being within 10m was sufficient to elicit scolding. Climbing to the nestbox was required in five cases to prompt scolding. For seven

males at Sithians and for 10 at Pencoosie I had both the dominance rank and scold call recordings so these individuals were used to make playback tracks.

I used the open source audio software Audacity (audacityteam.org) to extract discrete scold calls from the field sound recordings and create playback tracks after first normalising the amplitude of all calls. Tracks all followed the same structure which comprised 15 calls: three bouts of five scold calls separated by ten seconds with two seconds between calls in a bout to ensure the same rate of calling (Figure 7). For seven individuals, the number of calls was limited so calls were repeated within the playback track. 10 seconds of silence began each track making total track length one minute. Two tracks were created for each focal male with the 15 calls placed in a two different, random orders.



Figure 7. Dominance playback track comprising 15 calls from a single individual of known dominance, separated into three bouts of five calls, each separated by ten seconds. Calls within a bout are separated by two seconds.

Playbacks

Experiments were performed using a remote controlled loudspeaker (FoxPro Fury 2) placed in precisely the same orientation and position, on a field boundary wall one to two metres off the ground and less than 20m away from the individual's current nest box (see Figure 8 and 9 for location of boxes). I selected to play the calls from individuals with a range of dominance ranks. Two trials were run at each focal nest box on different days at different times, with the speaker placed on one side of the box for track one and on the other side for track two. Playbacks were broadcast from the location of the caller's box because playing tracks from a caller in an unfamiliar location may have recruited individuals purely because the calls were not expected from that area. Playbacks were conducted in a random order between 7am and 6pm, no more than three treatments were done per site per day and playbacks at the same site were separated by at least four hours. Playbacks for both Chapter Two and Chapter Three were undertaken alongside one another during the nesting period in

a randomised order (for a full list of dates of playbacks see Appendix 1 and 2). After setting up the speaker, I moved to a concealed area with a clear view of the sky, 30-50m away and recorded the jackdaws' responses with an HD Panasonic video camera (HC-X900). The volume on the FoxPro remote control was set to 20, replicating the volume of a scold response for a jackdaw at the same distance as measured on a Voltcraft SL-100 sound level meter. After placing the speaker I waited a minimum of five minutes before broadcasting the playback track, to allow nearby jackdaws to relax as my entering the field site may have disrupted their behaviour.

I used the event logging software BORIS (Behavioural Observation Research Interactive Software: Friard & Gamba 2016) to transcribe the video records, noting the time the first bird responded, the number of recruits in total, the time the last bird left and any scolding produced by the recruits themselves in response to the playback. Any jackdaw that changed its behaviour in response to the playback either by flying around the speaker, landing in a nearby tree or changing direction towards the speaker was classified as a recruit. The experiment ended when the last bird had left the area.



Figure 8. Red stars indicate locations for the dominance playbacks at Stithians churchyard.



Figure 9. Red stars indicate locations for the dominance playbacks at Pencoosse farm.

Analysis

Data was analysed in R version 3.2.3 (R Core team, 2015). The package *glmer* was used to run a generalised linear mixed model with a Poisson error distribution with a log link function. The response variable used was the number of recruits. Dominance rank, site (S or P) and time of day (continuous) were fitted as explanatory terms. Responsive scolding (yes/no) and windspeed (obtained from Carnkie Weather Station: carnkieweather.co.uk) were fitted as additional explanatory terms as scolding by recruits could serve to amplify playback stimuli and wind could attenuate the broadcast sound. An interaction effect between rank and site was the last explanatory term to be included because any potential effects of relative dominance rank may differ between sites. Caller ID was set as a random effect to account for repeated measures of the same caller. I used Akaike's information criterion, AIC (Akaike 1973; Bozdogan 1987), to choose the statistical model that best fits the data: the model with the lowest AIC score was used to generate a minimum adequate model. Chisquared and P values for the terms in the minimal model were derived using the ANOVA function in R.

Ethical note

Birds used in this study had been ringed under BTO licenses (C5746; C5752; C5983). Experimental procedures adhered to the guidelines of the Association for the study of Animal Behaviour and were approved by the University of Exeter Biosciences Ethics committee.

Results

The average number of recruits for the whole experiment was 10.95, only one recruit lower than for Chapter Two. The minimum number of recruits who responded to the playbacks at both Stithians and Pencoosse was zero. Playbacks at Stithians recruited a maximum of 42 and an average of 13.6 individuals. Playbacks at Pencoosse recruited a maximum of 58 and an average of 9.57. Individuals responded on average 30.6 secs after the track was played at Stithians and after 24.2 secs at Pencoosse. Responses lasted 2.52 mins at Stithians and 3.96 mins at Pencoosse on average. The minimum adequate model with the lowest AIC score included responsive scolding and time of day (Table 3, Table 4). The presence of responsive scolding by the recruits increased the number of individuals recruited to the playbacks (GLMM, $\chi^2_{34} = 8.65$, d.f. = 1, $P = 0.0033$, Figure 10) and more recruits responded to the playbacks conducted later in the day (GLMM: $\chi^2_{34} = 13.50$, d.f. = 1, $P < 0.001$, Figure 11). The effect of time of day may be strongly influenced by one playback that elicited 58 recruits. If this datapoint is removed the trend for increasing numbers of recruits throughout the day remains, but becomes marginally non-significant (GLMM: $\chi^2_{33} = 3.12$, d.f. = 1, $P = 0.077$). The rank of the caller did not influence the number of individuals who were recruited in response to the playback (GLMM: $\chi^2_{34} = 0.066$, d.f. = 1, $P = 0.80$, Figure 12). This result held if trials in which responsive scolding occurred were removed ($N = 28$ trials where scolding did not occur) (GLMM: $\chi^2_{28} = 0.015$, d.f. = 1, $P = 0.90$). There were no differences in recruitment number between the sites (GLMM: $\chi^2_{34} = 0.60$, d.f. = 1, $P = 0.44$) and no interaction between rank and site (GLMM: $\chi^2_{34} = 0.012$, d.f. = 1, $P = 0.91$). Wind speed did not influence the number of recruits (GLMM: $\chi^2_{34} = 3.21$, d.f. = 1, $P = 0.073$).

Table 3. Model summary for dominance showing the full GLMM with all fixed effects and the Minimum Adequate Model (MAM) for only the significant fixed effects. Chisquared and p values are generated via the ANOVA function in R.

	Fixed Effects	Estimate	St. Error	χ^2	DFs	P value
Full Model	<i>Intercept</i>	2.05571	0.72986			
	Time	0.25072	0.06361	15.5382	1	8.086e-05
	Scold	0.32006	0.15181	4.4448	1	0.03501
	Wind	-0.14145	0.07892	3.2125	1	0.07308
	Site	-0.53671	1.17149	0.6023	1	0.43770
	Rank	0.01984	0.11605	0.0662	1	0.79688
	Rank*Site	0.02539	0.23634	0.0115	1	0.91443
Minimum Adequate Model	<i>Intercept</i>	1.95643	0.27545			
	Time	0.226720	0.06171	13.4982	1	0.0002388
	Scold	0.42143	0.14327	8.6531	1	0.0032651

Table 4. AIC model summary for dominance showing output for the full model with all fixed effects including the interaction between rank and site, the full model without the interaction and the Minimum Adequate Model (MAM) for scolding and time only.

Fixed Effects	Residual Df	Residual Deviance	dAIC	Weight
Full model with Rank*Site interaction	26	93.87	4.3	0.08
Rank+Site+Scold+Time+Wind	27	93.82	2.3	0.22
Scold+Time (MAM)	30	95.79	0.0	0.70

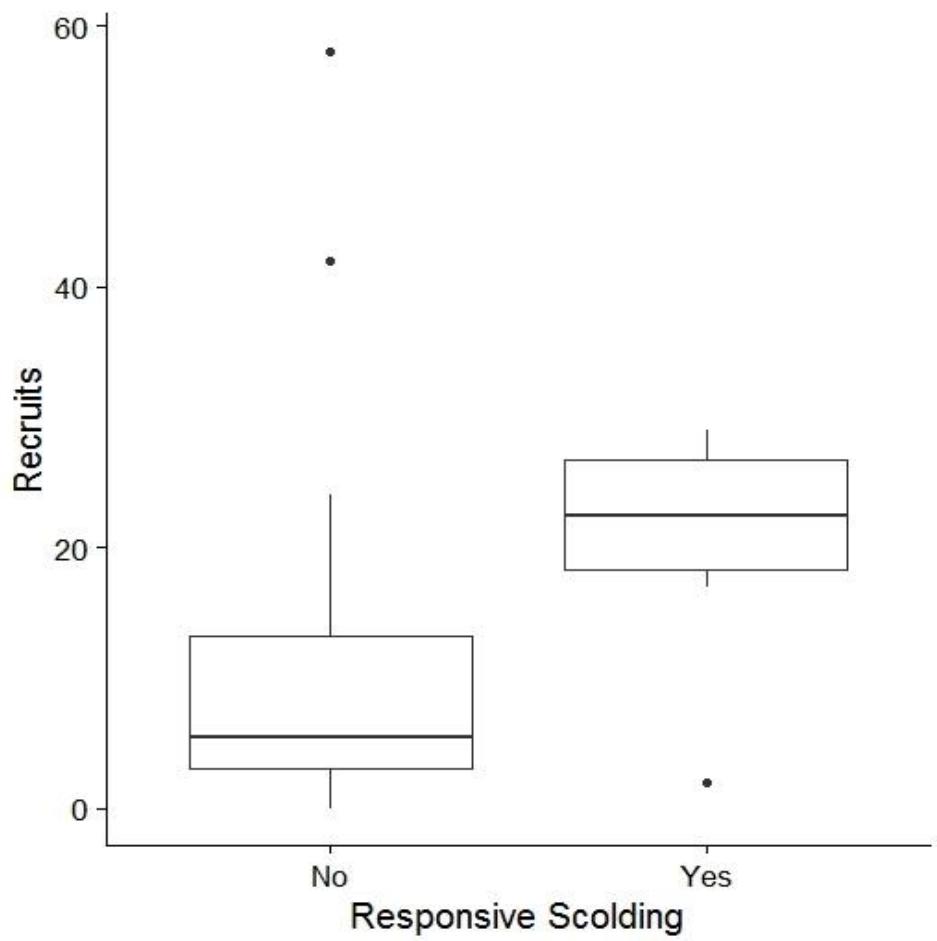


Figure 10: Number of recruits in response to playbacks where responsive scolding did or did not occur. Medians, upper quartile and lower quartile shown.

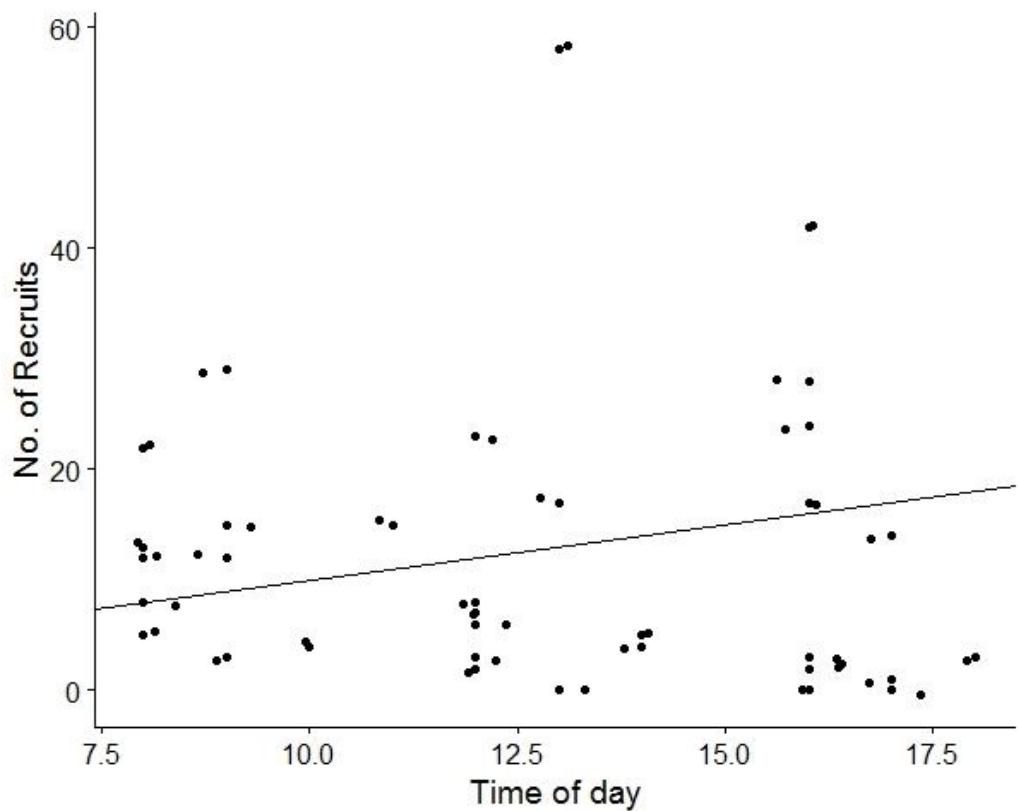


Figure 11: Number of recruits in response to playbacks undertaken at different times of day. To allow visual inspection of all datapoints in the figure, overlapping datapoints were separated using the ‘Jitter’ ggplot function in R. Removing the playback at the top centre of the graph maintains the trend but renders the result marginally non-significant.

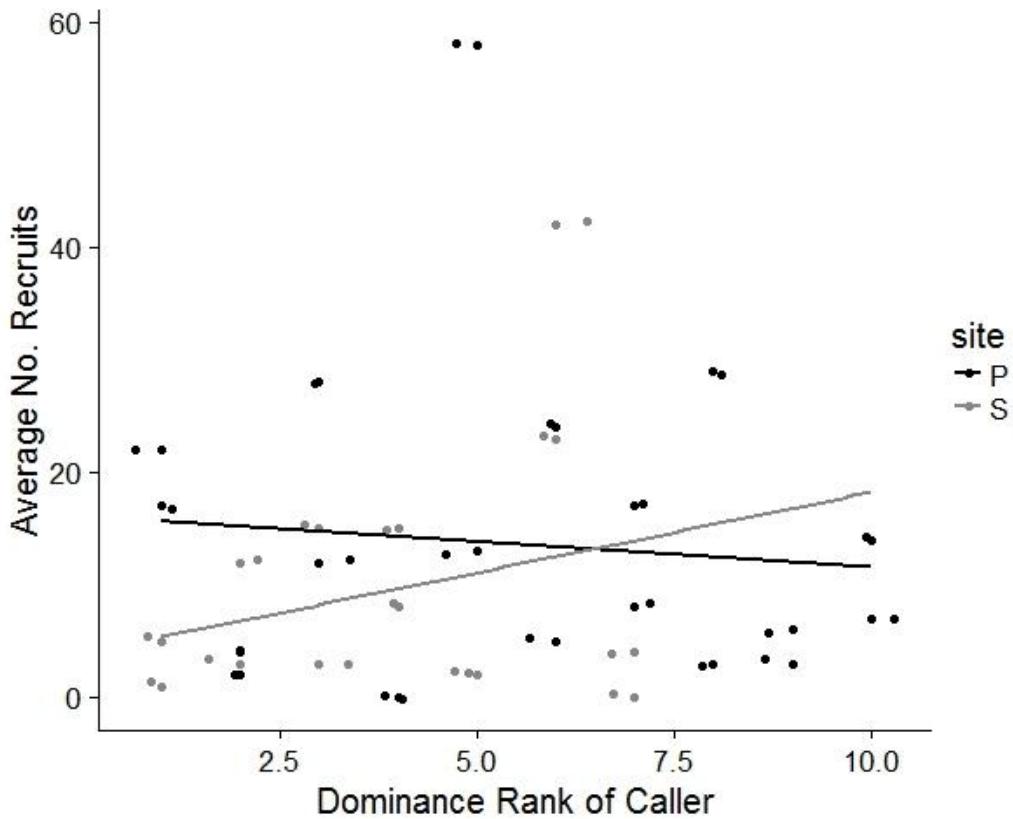


Figure 12: Average number of recruits in relation to the dominance rank of the caller. Most dominant individuals were assigned a rank of one and least dominant individuals assigned a rank of ten. Sites are shown separately as hierarchies were calculated separately. To allow visual inspection of all datapoints in the figure, overlapping datapoints were separated using the 'Jitter' ggplot function in R.

Discussion

The role of leadership in initiating group movements remains a topic of debate (King *et al.* 2009; Petit & Bon 2010). One potential characteristic of leaders that has been shown to be important in some studies, is high dominance rank (King *et al.* 2008). However, previous research has not examined whether dominance rank of initiators is important to group members when deciding to join antipredator mobbing events. Here, I found that, contrary to my prediction, the dominance rank of caller does not influence the number of jackdaws recruited to a mob.

High ranking individuals are known to have disproportionate influence on group movements in a number of species (King *et al.* 2008; Sueur & Petit 2008; Radford 2004; King *et al.* 2009; Petit & Bon 2010). In my study however, the rank of individuals producing antipredator scolding calls was unrelated to the number of jackdaws recruited. There are a number of potential reasons why rank may not have had an effect. The potential effects of rank on group behaviour may depend on the extent to which low-ranking individuals face a threat of punishment from dominants. Snowdon and Cleveland (1980) found that cooperatively breeding pygmy marmosets (*Cebuella pygmaea*) responded most strongly to the contact calls of the dominant male than to other group members. This may be explained by the fact that marmosets have a despotic social structure in which only the dominant pair breed (Digby *et al.* 2006), and subordinates may receive aggression for failing to respond to the dominant. Similarly, in chimpanzees (*Pan troglodytes*) the pant-hoot calls (used to establish and maintain groups) of the alpha male were attended to more than those of other individuals (Mitani & Nishida 1993) and as punishment is a common occurrence in chimp societies (Rohwer 2007), individuals may avoid being punished by responding to the dominant's calls. In contrast, jackdaw colonies exhibit low levels of reproductive skew and overt physical aggression is relatively rare, especially after pairs have secured nest-sites (pers. obs.). Thus jackdaws may have no need to avoid punishment by joining dominant individuals in risky mobbing events.

It is also possible that any benefits of attending to dominance rank may be overridden by other factors. In my study, responsive scolding by recruits during some playbacks served to

stimulate further recruitment and may have masked the signal from dominants. Moreover, any influence of the rank of the caller may have been further obscured by the importance of social relationships between group members. In playback experiments by Micheletta *et al.* (2012), crested macaques (*Macaca nigra*) responded more strongly to the alarm calls of close affiliates than distant affiliates. Similarly, chacma baboons have been found to follow those with whom they have social ties, during collective departures, rather than pay attention to the dominance rank of the initiator (King *et al.* 2011). Jackdaws, like primates, exhibit stable social relationships (Röell 1978; Henderson *et al.* 2000). There is evidence that these bonds affect the structure of flocks, with birds tending to stick close to one particular individual within large winter flocks (Jolles *et al.* 2013), and playback experiments show that jackdaws preferentially respond to the calls of their own colony members rather than strangers (Woods 2016). Thus, it is possible that upon hearing scolding calls, jackdaws' decisions to join mobbing events or not are driven more by their social relationship with the caller, than by the caller's dominance rank. Alternatively, patterns of recruitment may be driven by variation in the direct benefits of joining the mob that are not dependent on social relationships or dominance ranks.

Jackdaws may derive a number of direct benefits from responding to recruitment calls, irrespective of the rank of the bird that produced them. A predator in proximity of the nest may be dangerous regardless of who is advertising it, so it may be in an individual's interest to attempt to drive it away. If the risk of ignoring a potential predatory event is greater than the costs of responding if it is false, then individuals would be expected to respond to recruitment calls. Individual motivations including daily activities may influence whether individuals respond to recruitment calls. For instance, I found that more individuals were recruited to playbacks conducted later in the day (Figure 11), perhaps because during the morning time budgets are concentrated on foraging (Coombs 1961, pers. obs.). Moreover, individuals may gain opportunities to assess and learn about predators during mobbing events (Curio *et al.* 1978b; Graw & Manser 2007) in which case it is only important that a threat has been identified, not the rank of the bird who has done so. Because of these potential direct benefits of responding to recruitment calls, jackdaws may not need to recognise the caller in terms of their rank. It is also possible that jackdaws lack the ability to relate the calls they hear to the dominance rank of the individual that produced them. While

jackdaws are known to discriminate between the calls of different individuals (Zandberg *et al.* 2014, Woods 2016, Chapter Two), it is not yet known whether, like other corvids (Kondo *et al.* 2012) they show “true individual recognition”, integrating information from different sensory modalities to form a representation of specific individuals (Tibbetts & Dale 2007). Further work is needed to establish whether jackdaws’ responses to calls are driven by social knowledge of caller characteristics.

The lack of any effect of dominance in this study may also have been influenced by constraints to my experimental design. In particular, the sample size of callers with known dominance ranks was relatively low, limiting the statistical power of my analyses. In addition, the dominance hierarchies were obtained through foraging competitions and this might not reflect dominance in other contexts. Nagy *et al.* (2013), for example found that dominance hierarchies in foraging contexts were entirely independent from those observed in aerial flocks. Finally, the rank of listener may be important. My experiment did not take into account the dominance rank of potential recruits, so any effect of rank of caller would be obscured if individuals of both higher and lower rank than the caller responded to the playback. In future research, it would be useful to obtain the identity of the responding individuals, either through direct observation of colour rings (though rings are difficult to see when birds are in flight) or using GPS tags (c.f. Nagy *et al.* 2013), to determine if recruitment is influenced by the relative differences in rank between callers and receivers.

Knowing the identity of responding individuals would also be useful for two further reasons. Firstly to investigate how the nest box occupant responded to his calls being played at his own nestbox. If a certain male consistently reacted to his own calls with responsive scolding, recruitment is likely to be higher due to him being a visual as well as an auditory stimulus. Secondly, identifying the recruits could avoid a potential issue of pseudoreplication. The locations for the playbacks were very close together in some instances (< 10m) and it is likely that the same jackdaws were responding to multiple playbacks.

There is controversy regarding the importance of dominance in leadership of collective behaviours. My work suggests that dominance may not be important in jackdaw recruitment to an antipredator collective behaviour. Punishment is unlikely to be common

in jackdaw societies and factors such as social relationships, direct benefits and individual motivations may be likely to play a role in the recruitment of individuals to antipredator collective behaviours. Investigating the characteristics shown by initiators and followers is important to understand the formation of risky collective behaviours.

Appendix 2: Tables showing the date all playback tracks for Chapter Three were carried out

Appendix Table iii: The date of which each playback for Chapter Three was carried out at the Stithians site.

Site	Box	Bird ID	Playback no.	Date
Stithians	Y01	WMYV	Dom 1	11/04/2016
Stithians	Y01	WMYV	Dom 2	04/05/2016
Stithians	Y06	XMSX	Dom 1	24/04/2016
Stithians	Y06	XMSX	Dom 2	05/05/2016
Stithians	Y07	WMGW	Dom 1	14/04/2016
Stithians	Y07	WMGW	Dom 2	07/05/2016
Stithians	Y10	OWGM	Dom 1	12/04/2016
Stithians	Y10	OWGM	Dom 2	06/05/2016
Stithians	Y11	YMBZBZ	Dom 1	13/04/2016
Stithians	Y11	YMBZBZ	Dom 2	04/05/2016
Stithians	Y29	WMBZX	Dom 1	03/05/2016
Stithians	Y29	WMBZX	Dom 2	05/05/2016
Stithians	Y19	OMSX	Dom 1	10/05/2016
Stithians	Y19	OMSX	Dom 2	16/05/2016
Stithians	Y35	WMWY	Dom 1	02/06/2016
Stithians	Y35	WMWY	Dom 2	04/06/2016

Appendix Table iv: The date of which each playback was carried out for Chapter Three at the Pencoosse site.

Site	Box	Bird ID	Playback no.	Date
Pencoosse	Z15	RMBZP	Dom 1	11/04/2016
Pencoosse	Z15	RMBZP	Dom 2	03/05/2016
Pencoosse	Z18	WBBM	Dom 1	12/04/2016
Pencoosse	Z18	WBBM	Dom 2	05/05/2016
Pencoosse	Z19	GMWG	Dom 1	20/04/2016
Pencoosse	Z19	GMWG	Dom 2	07/05/2016
Pencoosse	Z28	GMGY	Dom 1	11/04/2016
Pencoosse	Z28	GMGY	Dom 2	02/05/2016
Pencoosse	Z30	BZMOW	Dom 1	15/04/2016
Pencoosse	Z30	BZMOW	Dom 2	04/05/2016
Pencoosse	Z26	YMBZW	Dom 1	14/04/2016
Pencoosse	Z26	YMBZW	Dom 2	05/05/2016
Pencoosse	Z20	GMRZY	Dom 1	20/04/2016
Pencoosse	Z20	GMRZY	Dom 2	06/05/2016
Pencoosse	Z14	YMGB	Dom 1	14/04/2016
Pencoosse	Z14	YMGB	Dom 2	04/05/2016
Pencoosse	Z02	OMGY	Dom 1	11/04/2016
Pencoosse	Z02	OMGY	Dom 2	06/05/2016
Pencoosse	Z22	RMGZW	Dom 1	25/04/2016
Pencoosse	Z22	RMGZW	Dom 2	04/05/2016
Pencoosse	Z05	GMOG	Dom 1	16/05/2016
Pencoosse	Z05	GMOG	Dom 2	20/05/2016
Pencoosse	Z43	GBRM	Dom 1	18/05/2016
Pencoosse	Z43	GBRM	Dom 2	21/05/2016
Pencoosse	Z38	RMBW	Dom 1	03/06/2016
Pencoosse	Z38	RMBW	Dom 2	01/06/2016

Chapter 4: General Discussion

The emergence of collective behaviours can be explained by self-organisation theory which suggests that simple, local rules are all that is necessary to create such synchronised, coordinated and cohesive group movements. However, these models make unrealistic assumptions about the real world: in particular they typically assume individuals are identical, independent agents. In reality, animals show great variation and in some cases, individuals can exert disproportionate effects on the behaviour of groups (Couzin *et al.* 2005; King *et al.* 2009). Leadership may be important in initiating group behaviours and dominance may be expected to be an important characteristic of leaders (King *et al.* 2009). My thesis used the jackdaw to investigate the cognitive processes involved in, and the influence of dominance on, the initiation of a collective action which carries considerable risk. I focused on mobbing behaviour which is a common but risky form of collective antipredator behaviour (Curio *et al.* 1978; Frankenberg 1981). Jackdaw mobbing events are typically initiated by distinctive alarm calls known as scolding calls. These calls are produced by the individual that discovers a potential predator and serve to recruit conspecifics to drive away the threat (Curio *et al.* 1978, Woods 2016). Individuals may be expected to use information contained within these scold calls to decide when to join the mob.

The literature on collective behaviour emphasises the importance of simple, mindless rules which are followed by all group members, and does not usually consider the importance of cognitive processes (Bonabeau *et al.* 1997; Couzin *et al.* 2002; Detrain & Deneubourg 2006). Chapter Two focused on the cognitive processes animals employ when deciding to join a mobbing event, specifically acoustic discrimination of individual calls and numerical assessment. Most studies of numerosity in animals have been undertaken in the lab (Emmerton *et al.* 1997; Uller *et al.* 2003; Beran 2007), so the ecological function of numerosity has received little attention. My study in the field allows the potential adaptive benefits of numerical assessment to be examined in an ecologically relevant context. This is the first study to investigate numerical assessment in the context of an antipredator collective behaviour. I performed playback experiments using scold calls to investigate whether the number of callers influenced the number of recruits to a mob. The ability to

assess the number of callers may be important as a greater number of individuals are likely to be more successful at driving away a predator (Dominey 1981; Robinson 1985) and the risk to a single individual from a predator decreases exponentially as group size increases (Foster & Treherne 1981). As predicted, my results showed that as the number of callers increased, a greater number of individuals were recruited. Jackdaws can discriminate between individual calls and thus determine the number of callers.

In some cases, leadership may be important in initiating collective actions but studies differ on whether initiation is shared between group members (Strandburg-Peshkin *et al.* 2015) or is undertaken by one individual (King *et al.* 2008). Dominance may be one important characteristic of leaders in coordinating group movements (Peterson *et al.* 2002; King *et al.* 2008), but it is not known if high-ranking individuals are particularly influential in recruiting conspecifics to collective antipredator responses. A dominant individual may be expected to gather more recruits because it is likely to be stronger and more able to drive off a predator and it also may conceivably punish others for not helping (Clutton-Brock & Parker 1995; Feh 1999). In Chapter Three I calculated a dominance hierarchy from competitive foraging interactions and performed playback experiments to investigate whether the dominance rank of the caller influences recruitment to a mob. My results showed that rank of caller did not influence the number of recruits. I concluded that social relationships, direct benefits and individual motivations may play a part in whether and when jackdaws decide to join a mob. In summary, my thesis found that jackdaws show numerical assessment and individual discrimination of calls but more work needs to be done to establish the importance of dominance in the initiation of mobs. Below I discuss some of the key themes emerging from my research.

Alarm calling

Alarm calling is widespread in many taxa (Hollén & Radford 2009). Some animals are known to produce specific alarm calls in response to different predator types (functionally referential alarm calling; Seyfarth *et al.* 1980; Manser *et al.* 2002) and calls may also signal the degree of the threat (Blumstein & Armitage 1997; Manser 2001; Leavesley & Magrath 2005; Templeton *et al.* 2005). Almost all studies on alarm calling however, have focused on

calls that induce a fleeing or avoidance response. In contrast, some alarm calls are known to recruit conspecifics to collectively mob predators, but these recruitment alarm calls have received relatively little research attention (Graw & Manser 2007; Yorzinski & Vehrencamp 2009; Micheletta *et al.* 2012). Of the few experimental studies that have examined responses to recruitment alarm calls, most have focused on individual-level responses (Graw & Manser 2007; McDonald 2012; Micheletta *et al.* 2012) rather than group-level collective responses. My thesis addressed this gap in our knowledge by focusing on alarm calls that serve to recruit others to a collective antipredator response and is the first to do so. Investigating group-level responses to recruitment alarm calls allows us to examine the cognitive processes involved in deciding whether to join a risky collective behaviour, and how these processes influence the magnitude of the collective response.

In Chapter Two I showed that a larger number of callers recruited more jackdaws to a mob. The experiment for this chapter was designed such that playback treatments were identical apart from the number of different individuals whose calls were incorporated into the playback track. Therefore, my result from Chapter Two demonstrates that jackdaws must discriminate between the calls of different individuals. This confirms and extends the results of Woods (2016) who showed that jackdaws responded preferentially to colony members than to unfamiliar individuals. However it is not yet known whether jackdaws exhibit true individual vocal recognition; integrating a call with knowledge of the individual that made the call (Tibbetts & Dale 2007). If jackdaws do not associate calls with the characteristics of the individuals that produced them, this could explain my results from Chapter Three. Here, I showed that the dominance rank of the caller did not influence the number of recruits. Jackdaws may be able to distinguish the calls of individuals in the playback tracks but do not associate them with that individual's dominance status. The fact that other corvids are known to exhibit true, multi-modal recognition (Kondo *et al.* 2012) casts some doubt on the likelihood of this explanation, but further work is needed to determine whether jackdaws integrate information from vocalisations with social knowledge about the caller.

Collective action problems

Mobbing poses a collective action problem as joining is very risky to individuals but driving away a predator provides a great collective benefit (Curio *et al.* 1978; Frankenberg 1981). A greater number of individuals are likely to be more successful at driving away a predator (Robinson 1985). Bildstein (1982) investigated passerine birds mobbing Northern Harriers (*Circus cyaneus*) and noted that cheating may occur by individuals who do not engage in the mob but still benefit from elimination of the predator. Several studies have presented ways of resolving the collective action problem. One method may be through reciprocal altruism; an individual assists another only if that assistance will be reciprocated in the future (Nowak 2006; Raihani & Bshary 2011). For instance, Krams *et al.* (2008) suggested that reciprocity could be used to explain patterns of mobbing behaviour in pied flycatchers. Pairs who had ‘defected’ by not assisting in the mobbing of a stuffed predator, never received assistance from their neighbours in later mobbing events (Krams *et al.* 2008). This study has proven controversial, and Russell and Wright (2009) have suggested that the apparent reciprocal altruism was suggested to result from a byproduct mutualism (an individual performs a selfish behaviour which is non-intentionally beneficial to another undertaking the same act). Additionally, the study by Krams *et al.* (2008) did not take into account any potential social relationships between individuals. It is possible that in some systems individuals may be more likely to pay attention to the affiliations they have with the initiators of a mob (Micheletta *et al.* 2012) than whether they helped previously or not. Further work is necessary to determine whether reciprocity plays a role in resolving collective action problems in mobbing animals. Another explanation that may help to resolve the apparent collective action problem is that individuals invest in cooperation conditionally, so as to maximise the direct benefits of cooperating (Clutton-Brock 2002). For instance an individual might join a mob only when in good condition, when mobbing with familiar others or when the costs of investing are low. In Chapter Two I showed support for the idea that jackdaws might join a mob when the costs of cooperating are low, as more individuals joined a larger mobbing group, presumably because they experience a lower risk from a potential predator than in a smaller group (Foster & Treherne 1981). Further support for the idea of conditional investment comes from my findings in Chapter Three. Here I showed that more individuals were recruited to mobs later in the day, presumably because they had spent the morning

foraging (Coombs 1961, pers. obs.) Jackdaws may not invest time in joining a mob if they have other priorities.

Numerical assessment

Numerosity in animals has been widely investigated in laboratory studies of a range of animals including the African grey parrot (*Psittacus erithacus*) (Pepperberg 1987), homing pigeons (*Columba livias*) (Emmerton *et al.* 1997), red-backed salamanders (*Plethodon cinereus*) (Uller *et al.* 2003) and rhesus monkeys (*Macaca mulatta*) (Beran 2007). However, to understand the evolution of numerosity, studies in the field are required so the adaptive benefits for wild animals can be considered. Existing work on wild populations has largely focused on inter-group conflict (McComb *et al.* 1994; Wilson *et al.* 2001; Seddon & Tobias 2003; Kitchen 2006) (but see Lyon (2003) for a suggestion that birds may count their eggs to avoid falling victim to brood parasites). My study shows that a collective antipredator behaviour is another context in which numerical assessments are important. One potential mechanism that may be behind the jackdaw's ability to assess number is subitising (Davis & Prusse 1988).

Subitising is a form of pattern recognition that is used to rapidly assess small quantities of items up to a maximal limit, typically no more than six (Kaufman *et al.* 1949; Davis & Prusse 1988; Reznikova & Ryabko 2011). The term subitising was coined by Kaufman *et al.* (1949) in a review of several studies in which human subjects were presented with a set of dots for less than one second and asked to report the number they saw. When the number of dots presented exceeded six, the speed and accuracy with which the subjects could identify the number of dots decreased (Kaufman *et al.* 1949). If the jackdaws in my study are relying on subitising as the mechanism for numerical assessment then we might expect them to have a maximum limit in their ability to assess the number of callers. Indeed, my results from Chapter Two support this by showing that there was no difference in the number of recruits between three and five callers. There is evidence that other species may also have an upper limit in their ability for numerosity. A study by Bousquet *et al.* (2011) investigated decision making for group movements in meerkats and found that a maximum of two or three callers initiated movement of the group to a new location. Similarly, studies on horses (*Equus ferus*

przewalskii) (Bourjade *et al.* 2009) and fish (*Gasterosteus aculeatus*) (Sumpter *et al.* 2008) have also found the upper limit of distinction to be around three. Contrary to these studies, the literature suggests that jackdaws, and other corvids, may be capable of discriminating larger numbers than three (Koehler 1950; Bogale *et al.* 2014; Ditz & Nieder 2016). An alternative interpretation of my result that jackdaws had apparent difficulty in distinguishing between treatments may be explained by Weber's law. Weber's law states that the ratio of the difference between a pair of numbers is how they are differentiated, not the absolute difference between them (Bogale *et al.* 2011; Ujfalussy *et al.* 2014). For instance, in Chapter Two, my treatments all had an equal absolute difference between them (ie. an addition of two callers from one to three to five), but the ratio between three and five is smaller and may be more difficult to discriminate, than between one and three. Further work is needed to examine the limits of numerical assessment in jackdaw mobbing events. To test whether jackdaw responses to a mob follow Weber's law, pairs of different numbers of caller could be presented in playback experiments and the number of recruits recorded. Another idea to test could be whether numerical assessment integrates social information; would jackdaws be more likely to respond to a smaller number of known colony members or a greater number of strangers?

Dominance and Leadership

Dominance has been suggested as important in the initiation of group movements (King *et al.* 2009) but this is controversial (King *et al.* 2008; Strandburg-Peshkin *et al.* 2015). Dominance has not been investigated in the initiation of an antipredator collective behaviour. In Chapter Three I investigated whether the dominance rank of a caller influenced the number of individuals recruited to a mob. My prediction was that dominant individuals would receive more recruits. One suggested reason for this is that jackdaws may join a mob to avoid punishment.

Punishment may explain the maintenance of cooperation despite incentives for individuals to cheat and reap the benefits of others' cooperation without contributing themselves (Clutton-Brock & Parker 1995; Raihani *et al.* 2012). Mobbing is a cooperative dilemma because individuals may be tempted to cheat, yet the more individuals that contribute, the

more likely that a predator will be deterred, providing a collective benefit (Robinson 1985). Contrary to my prediction, the results from Chapter Three showed no effect of dominance rank on recruitment. Jackdaws may have no need to avoid punishment by dominants because they have low reproductive skew and a limited amount of aggression between individuals. Nevertheless, punishment inflicted by dominant individuals may be important in cooperation and collective behaviours in other animal species. For instance, pygmy marmosets (Snowdon & Cleveland 1980) and chimpanzees (Mitani & Nishida 1993) have both been shown to respond preferentially to the contact calls of the most dominant animal in the group. In theory, it is possible that in both these species the threat of punishment can help to explain why the dominant animals appear to be so influential. In practise, it is often difficult to explain how punishment can promote future cooperation. Punishment could deter cheating if punished individuals learn to cooperate (Clutton-Brock & Parker 1995). However, as over a century of research on animal learning demonstrates, it is extremely difficult for a recipient of punishment to learn to associate a failure to perform an action (e.g. join a mob) with punishment (Raihani *et al.* 2012). Further work needs to be done on the role of dominance mediated by punishment in collective behaviours.

During recruitment to a collective behaviour such as a mob, individuals may base their decision to join on the reliability of the caller and certain callers may be more reliable than others. There is striking individual variation in the propensity for jackdaws to scold in the populations used in my study (pers. obs.). Consequently, individuals may not pay attention to those that have a strong tendency to scold often and in situations where there is no visible threat. For instance Hare & Atkins (2001) investigated the reliability of alarm calling in Richardson's ground squirrels (*Spermophilus richardsonii*) and found selective diminishment of vigilance to unreliable callers. In a case of 'the boy that cried wolf', the neighbours of a 'super-scolder' jackdaw may habituate and cease to pay attention to its scold calls. It may be the case that variation in reliability of scolding is more important than variation in dominance rank, hence I found no effect of rank on number of recruits.

Individuals involved in collective actions may attend to the social relationships they have with the initiator of the behaviour (King *et al.* 2011; Micheletta *et al.* 2012), instead of attending to their dominance. The social relationships within a group can be identified and

displayed using social networks, and these can be used to test hypotheses (Croft *et al.* 2011). For instance, at my study sites within the Cornish Jackdaw Project, we have extensive information on social network structure through patterns of association at pit-tag detecting feeders. These social networks could, in theory, allow us to test whether patterns of foraging associations predict responses to scolding recruitment calls. For example, are individuals that associate together often more likely to respond to the scold calls of one another? Social network analysis would allow greater understanding of social relationships in jackdaws and aid understanding of the composition of collective behaviours.

Conclusion

My thesis used wild jackdaws to investigate the role of numerical assessment and dominance in the initiation of a collective antipredator behaviour. I have shown evidence for individual discrimination of scold calls and for numerical assessment. I have found that dominance rank does not influence recruitment. Social relationships, individual motivations and direct benefits should all be considered in the importance of dominance in collective behaviour initiation. We need to understand more about the cognitive processes underpinning the formation and maintenance of collective behaviours in nature. Understanding the initiation of collective behaviours in the jackdaw ultimately allows investigation into the evolution of collective behaviours.

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