Organisation & Development of Anti-Predator Behaviour in a Cooperative Breeder

James R.S. Westrip

Supervised by: Dr. Matthew Bell (principal supervisor) and Dr. Per Smiseth

A thesis submitted in application for the degree of Doctor of Philosophy from The University of Edinburgh, School of Biological Sciences

2016

Author's Declaration

I, James R.S. Westrip, declare that;

a) this thesis has been composed by myself, and

b) either that the work is my own, or, where I have been a member of a research group, that I have made a substantial contribution to the work, such contribution being clearly indicated, and

c) that the work has not been submitted for any other degree or professional qualification except as specified, and

d) any included publications are my own work, except where indicated throughout the thesis, and summarised and clearly identified below*.

This work does not exceed 100,000 words.

SIGNED:

James Robert Samuel Westrip

---

* Part of Chapter 7 makes up part of a review article already published as: **Westrip, J.R.S. & Bell, M.B.V. (2015)** Breaking down the species boundaries: selective pressures behind interspecific communication in vertebrates. *Ethology*, **121**, 725-732.

Preface

This work was conducted as part of a collaborative research project; the Pied Babbler Research Project. The study individuals had already been habituated to human presence, and colour ringed. Thus my work has been aided by the effort put in previous to me joining the project, and the continued efforts of others to maintain habituation and colour ring the individuals. Dr. Matthew Bell and Assoc. Prof Amanda Ridley have provided input into experimental design, as well as reviewing and revising some of the chapters. Dr. Per Smiseth, Dr. Tom Flower, examiners and peer reviewers for journal submission also provided reviews of some of this work. Data collection in the field was assisted by Phoebe “Robbie” Hopper; genetic sexing data was provided by Dr. Martha Nelson-Flower; while reviewing of video data for chapter 4 was conducted by Laura Gordon as part of her Honours course. I outline below a rough estimate of my contributions to each of the chapters.

Chapter 1 – conception 100%, writing 95%

Chapter 2 – conception 100%, writing 95%

Chapter 3 – conception 90%, data collection 95%, analysis 100%, writing 75%

Chapter 4 – conception 95%, data collection 60%, analysis 100%, writing 80%

Chapter 5 – conception 60%, data collection 50%, analysis 100%, writing 95%

Chapter 6 – conception 95%, data collection 95%, analysis 100%, writing 80%

Chapter 7 – conception 100%, writing 95%

The "Possible Future Work" section of Chapter 7 has been incorporated into a review publication, and has already been published: **Westrip, J.R.S. & Bell, M.B.V. (2015)** Breaking down the species boundaries: selective pressures behind interspecific communication in vertebrates. *Ethology*, **121**, 725-732.

Abstract & Lay Summary

In order to reduce their predation risk, species have evolved a range of anti-predator behaviours. One co-ordinated anti-predator behaviour present in some group-living species is sentinel behaviour. In this behaviour individuals take up an elevated position and scan for threats, providing an alarm when one is spotted. However, this behaviour can lead to social conflict. Sentinel behaviour is a public good, i.e. the benefits are felt by all group members, but the costs only accrue to the actor. Thus it may be open to free loading, requiring individuals to monitor collaborators to prevent cheats. Additionally, individuals may vary in their alarm call reliability, which may select individuals to alter their behaviour based on caller ID. Monitoring others requires individuals to be closely associated, yet individuals may be spread out. For instance, foraging groups may be some distance from their nest, yet nestlings are particularly vulnerable. Adults should reduce their number of nest visits if a threat is nearby, so individuals returning from the nest may be selected to communicate about any perceived threats. Additionally, when perceiving threats, species need not use only conspecific information, because heterospecifics can also provide relevant information. In this thesis, I test these ideas in the Southern Pied Babbler (*Turdoides bicolor*), and I show that a) pied babblers monitor the quantity and quality of group-mates' anti-predator behaviour; b) babblers accompany naïve sentinels and I investigate whether this may be related to anti-predator teaching; c) babblers do not appear to actively communicate about perceived nest threats because they do not alter their provisioning rate based on heterospecific derived anti-predator information; while d) avian heterospecifics are more prevalent in the presence of pied babblers, and can be attracted to areas by playback of pied babbler calls. These

results show that species monitor both conspecifics and heterospecifics, and alter their behaviour based on the information they collect.

Acknowledgements

This research was funded by a Natural Environment Research Council DTG Studentship, and ethical permission was granted by the Edinburgh University Ethical Review Committee, ERC no: OS-02-12.

The first person I should thank is my supervisor Matt Bell. Not only has he supervised me through my scientific questions and queries, as well as my writing foibles, but has been a wonderful ear to listen to all of the troubles that have somehow decided to fall upon my family and friends over the past few years. I would like to thank him for putting his faith in me to be his student, and I hope I haven't been too much trouble.

Next I must give a big thank you to Mandy Ridley. I am so grateful to her for letting me join the Pied Babbler Research Project and conduct my research on the babblers. She has also provided excellent help with comments on my experimental set-ups and my manuscripts for which I shall be eternally thankful.

A massive thank you needs to go to Robbie Hopper, my field assistant out in South Africa. She had to put up with me constantly for 9 months, which is more than anyone deserves, and she threw herself fully into the pied babbler world. She was up before me every morning, and was always eager to get to the field. I owe her a huge debt of gratitude, because without her I would never have been able to collect as much data as I have, and her presence managed to save my sanity when things were

going slowly. Also, thank you to Laura Gordon who, as part of her honours project, went through all of my video data of foraging babblers.

Thanks also to all of the other members of team Babbler while I have been in the field. Lizzie Wiley, Sabrina Engesser, Alex Thompson, Rute Mendonça, Kate Beer and Margot Oorebeek all provided feedback whenever I asked, and were great company during my long stints in the desert. Another big thank you needs to go to Tom Flower and Martha Nelson-Flower. Tom showed such a great interest in my project and has helped so much with all of his comments, and I am indebted to Martha for her genetic data for sexing the babblers.

Thanks to Tim Clutton-Brock and Marta Manser for giving permission for me to use the Kuruman River Reserve as the basecamp for my study. Also thanks to Mr. & Mrs J. Kotze, Mr. & Mrs P. Kotze and Mr. & Mrs F. de Bruin for letting us babbler researchers have access to their farms to find the babbler groups when they went onto their land.

I also owe a lot of thanks to the in-field management of the reserve. Dave and Nanine Gaynor provided much logistical support, and I am indebted to Dave for teaching me how to become a car mechanic so that I could spend my weekends tinkering on my vehicular pride and joy “Sharon”. Thanks also to Michiel Jooste, Joseph Fenton, Heather McNabb-Jooste, Tim Vink, Sky Bischoff-Mattson, Lyndsey Marris and Lewis Howell for their running of the reserve and the running of the meerkat volunteers. A big thank you to all of the rest of the staff on the reserve for helping to make sure everything runs as smoothly as it can in the Kalahari; with a special thank you to Alta and he legendary “cheesy spaff”. And thank you to all of the volunteers who called in with babbler sightings – it really saved several hours of walking on some days – especially Dave Seager who was always on the radio every time he sighted them.

Thanks also to everyone who I have spent my time with in Africa. There are too many to mention everyone but particularly I would like to thank Simon Townsend and Markus Zöttl for their helpful comments; and thanks to Stuart, Nino, Dave, Pauline, Debbie, Philippe “Big P” Vullioud, Teja, Adam, Cini, Ruan, PJ, Keafon, and Sam for the Saturday night fun! I had the pleasure of all of their company for more than one field season and I could not have wished for a better bunch of people to spend my time with.

Back in Edinburgh there are several people I would like to thank. Per Smiseth and Emma Cunningham acted as the members of my postgraduate committee. They provided excellent feedback and comments throughout my time in Scotland and I would like to thank them very much for their input. I would also like to give thanks to the various members of the Wild Evolution Group who came along to my talks and gave me extra ideas to think about, as well as some really useful advice, in particular Josephine Pemberton, Craig Walling, Jarrod Hadfield and Ally Phillimore. Thanks also to my examiners Andrew Radford and Patrick Walsh for their comments.

I'd also like to thank all of the officemates, and other PhD students in the department who have been with me over my time in Edinburgh. Special thanks to Caroline Thompson, Charlotte Regan and Kara Dicks for their patience with my attempts to improve my R coding, and for "Bake Off" Wednesdays. Thanks also to Josh Moatt for letting me be an honorary member of Lismore RFC, and making tea breaks more exciting. Also I should thank Andrea Kemter, Becky Watson, Christine Tansey, Ele Silvester, Josianne Lachapelle, Liam Brierley, Lindsey McDonald, Maarit Mäenpää, Mizuho Fukushige, Nick Lowery, and Sinclair Cooper for being my "year-mates" and fellow Panto-ers in our first term in Ashworth.

Also I would like to give thanks to Rich Allen and Jack Shutt who have lived with me the past couple of years in Edinburgh. Not only have they been good company in the evenings, but they have been wonderful sounding boards for any ideas I have had, and have given great input. Their encouragement for me to go out birdwatching - as well as actively taking me out to the highlands - has helped me relax; especially as I have approached the end of my write up.

I would also like to thank the people who have been through so much with me over the past three and a half years; my parents. Not only have they had to go through serious personal illness, they have also had the strain of me rambling on at them about my thesis when they have had far more important things to think about. Without their calming influence over the course of my PhD I would not have reached the end of it, and I am indebted to them for installing in me my love of nature. Lastly, thanks to one person who will never know that I have completed this thesis; one of my oldest friends, Ben St. Joseph, with whom I ran around the East Anglian countryside and really discovered the world outside my door. Ben sadly died during my first field season, and the biggest regret of my entire PhD is that I was unable to get back from the Kalahari for his funeral. This thesis is for him, and my parents.

Postscript to Acknowledgements: After initially submitting my thesis, my father sadly passed away. He never saw me get through my viva, and will never know that I have handed in the corrected version of my thesis. I owe so much to him, and my mother, for instilling the love of natural history into me which has led me to conducting this degree. No words can express how much I miss him, but I hope that he would have been at least a little bit proud of what I have achieved.

Table of Contents

Chapter 1: Introduction

“Nature, red in tooth and claw” (In Memoriam A.H.H., Alfred, Lord Tennyson, 1850)

Individuals are not lone entities within their environment. Throughout their lives they come into contact with a variety of other individuals, including their predators and prey; heterospecific competitors; and, if they are a social species, their group mates. While social living does bring benefits, it can also create an array of social dilemmas, and conflicts between group members. In this introduction, and throughout this thesis I identify, investigate, and discuss such social dilemmas; and how a group-living, cooperative breeder has evolved mechanisms to solve them.

1.1 Predator-Prey Arms Race

Predators and their prey evolve adaptations and counter-adaptations in co-evolutionary cycles as part of a constant arms race, termed the Red Queen Effect (Van Valen, 1973), after *Through the Looking Glass* where the Red Queen says to Alice "here…it takes all the running…to keep in the same place" (Carroll, 1871). The anti-predator adaptations that have evolved in prey species are diverse, including morphological features such as protective shells, spines, mimicry and camouflage (e.g. Seeley, 1986; Lüning, 1992; Skelhorn et al., 2010; Nelson, 2014); life-history traits (e.g. Lüning, 1992); chemical defences (e.g. Reichstein et al., 1968; Dumbacher et al., 2009); and behavioural adaptations. In the first section of this introduction, I examine some of the key anti-predator behaviours relevant to this thesis.

1.1.1 Group Living

Individuals may join groups for selfish reasons to avoid predation (Hamilton, 1971), for instance because the probability of attack is inversely proportional to group size (the ‘dilution effect’; Williams, 1966a; Hamilton, 1971; e.g. in water skaters, Foster & Treherne, 1981); or because grouping reduces an individual’s ‘domain of danger’ (the ‘selfish herd’; Hamilton, 1971). This has recently been shown to be a possible driver for Cape fur seal (*Arctocephalus pusillus pusillus*) grouping because their predator, the great white shark (*Carcharodon carcharias*), selectively targets individuals with a greater ‘domain of danger’ (De Vos & O’Riain, 2010). By joining groups, individuals can also reduce their predation risk due to confusion of predators. With many prey individuals, predators may find it difficult to target a single individual. Thus an individual may more likely to avoid predation than if they were alone or in a smaller group (Neill & Cullen, 1974).

The presence of more individuals may also assist in reducing total predation levels. More individuals means a greater defensive barrier to predators. Groups can provide a coordinated active defence against predators, which may be more successful at driving away predators than only a small number of individuals (e.g. Kruuk, 1964; Andersson & Wicklund, 1978). Grouping does not need to be permanent either; species may congregate only when they are particularly vulnerable. This is especially prevalent in breeding colonies (e.g. seabirds) and insect emergences (e.g. see Gochfeld, 1980; Sweeney & Vannote, 1982). These congregations attract predators but, by coming together in one place, they swamp predators so that they are satiated. Therefore, despite many individuals being killed, proportionally fewer individuals die than if they bred sparsely (e.g. Sweeney & Vannote, 1982).

1.1.2 Vigilance & Sentinel Behaviour

Grouping can also aid in predator detection. Individuals are selected to spend at least some of their time vigilant, scanning for predators; the amount of which may be influenced by perceived threats levels (e.g. perceived predator presence or habitat type; Caraco et al., 1980; Li et al., 2009; Morrison, 2011; Huang et al., 2012; Teichroeb & Sicotte, 2012). When individuals come together in a group, the total amount of time with at least one vigilant individual may be greater than when an individual is alone (e.g. Bertram, 1980). For instance, larger ostrich (*Struthio camelus*) groups have at least one individual vigilant for greater percentage of the time (Bertram, 1980). However, not only does grouping increase total levels of vigilance, but additionally each individual is able to be less vigilant and devote more time to other activities than individuals in smaller groups (e.g. Bertram, 1980; Caraco et al., 1980; Fischer & Linsenmair, 2007; Li et al., 2009). Therefore there may be a double vigilance benefit from group living – greater protection with less personal effort expended – as long as individuals can coordinate their vigilance.

A specialised form of coordinated vigilance seen in group living species is sentinel behaviour (Bednekoff, 2015). Frequently this involves an individual taking up an exposed position in order to scan for possible threats. This is usually an elevated position so that the individual has the best view possible. The selective pressures for sentinel behaviour have been suggested to be both altruistic (Hamilton, 1964; Griesser, 2003) as well as selfish (Bednekoff, 1997; Clutton-Brock et al., 1999). However, whatever the original selective pressure for sentineling, there are some ecological and social settings that are frequently associated with sentinel behaviour. Most terrestrial species that conduct sentinel behaviour are found in dry, tropical regions (Bednekoff, 2015), and frequently these species can be found in large groups where individuals repeatedly interact (Trivers, 1971). This might aid the evolution of sentinel systems because it increases the likelihood of reciprocation from group members. These groups may also be kin-biased (e.g. Sherman, 1977), thus there may be inclusive fitness benefits from conducting the behaviour too.

Sentinels can provide benefits to groups in multiple ways. The presence of a sentinel can allow individuals to increase food uptake (e.g. Hollén et al., 2008; Bell et al., 2009). Sentinels may provide a sentinel call while there is no threat present, and this can allow foraging individuals to decrease personal vigilance and increase foraging efficiency (e.g. Hollén et al., 2008; Bell et al., 2009). Sentinels also warn the group with an alarm call when a threat is spotted. This allows group members to become alert and, if necessary, make a coordinated flee to cover (see Bradbury & Vehrencamp, 2011).

1.1.3 Alarm Calling

Alarm calls can have several different functions. They may inform predators that they have been spotted (e.g. Murphy, 2006), or alert others to possible threats. Alerting calls are public sources of information that can enable receivers to determine the type and degree of threat (Cheney & Seyfarth, 1990; Leavesley & Magrath, 2005; Furrer & Manser, 2009a & b; Fallow & Magrath, 2010; Gill & Bierema, 2013), and make the appropriate response (e.g. Manser et al., 2001; 2002). This is usually increased personal vigilance or a coordinated movement to cover (see Bradbury & Vehrencamp, 2011). The direction of a threat may also be encoded within alarms, but this may be restricted to higher urgency calls, with low urgency calls requiring visual confirmation of direction (Manser & Fletcher, 2004).

Rather than inducing vigilance or flight, some alarm calls act to recruit others (both con- and heterospecific) to mob predators, in an attempt to force them away from the area (e.g. Gehlback & Leverett, 1995; Pavey & Smyth, 1998; Templeton & Greene, 2007). These mobbing calls contain a similar array of information as in alerting calls, with information about the degree and type of threat being conveyed (Hennessy et al., 1981; Welbergen & Davies 2008; Griesser, 2009). A key aspect of mobbing calls is that the information being signalled is being made publicly available by the signaller, in order to attract as many others to join the mob as possible (e.g. Gehlback & Leverett, 1995; see Bradbury & Vehrencamp, 2011).

1.2 The Social Problems of Anti-Predator Behaviour

While grouping, sentinel behaviour and alarm calling can provide obvious benefits to individuals, co-ordinated anti-predator behaviours do create a number of social dilemmas. In this thesis I seek to understand how these dilemmas may be resolved. I now review some of the social dilemmas that may exist in co-ordinated anti-predator systems, and highlight possible mechanisms that may overcome them.

1.2.1 The Public Good

A public good is a communal resource or behaviour from which multiple individuals benefit, but the costs of collecting the resource or conducting the behaviour are only felt by the contributing individual(s). Anti-predator behaviour has, so far, received little explicit research interest as a public good. Instead, it has been predominantly characterised as either a purely selfish behaviour (Bednekoff, 1997; Clutton-Brock et al., 1999) or kin selected altruism (Hamilton, 1964; Griesser, 2003). However, anti-predator behaviour does fit the criteria for a public good. The benefits of grouping, vigilance, alarm calls, and protected foraging are felt by all individuals (Williams, 1966a; Hamilton, 1971; Bertram, 1980; Hollén et al., 2008; Bell et al., 2009; see also Bradbury & Vehrencamp, 2011); and there have been documented costs for carrying out anti-predator behaviour (e.g. Rasa, 1987; Ridley et al., 2013). For instance, sentinels suffer increased likelihood of attack by a predator, and they may be the last individuals to get to cover (e.g. Rasa, 1987; Ridley et al., 2013). There are also hypothesised opportunity costs of carrying out sentinel behaviour in terms of lost foraging time (a hypothesis which I test in Chapter 3).

By being a public good, anti-predator behaviour may experience social problems. The fundamental problem for all public goods is their vulnerability to free-loading by individuals who receive the group-level benefits without contributing themselves. Therefore, because there are selective benefits to free-loading, the persistence of stable cooperation, and continued contribution to public goods, appears to be a paradox. Multiple theories have been presented to explain the evolution of cooperation. Most importantly, kin selection provides a powerful explanation for cooperation and even altruism (Hamilton 1964). However, conflict over cooperative contributions can still exist between group mates (Bshary et al., 2016), even when interacting with relatives: kinship reduces the intensity of conflict, but public goods problems still remain (Trivers, 1971). Therefore, separate mechanisms must have evolved to *stabilise* cooperation.

Theoretical analyses have identified several mechanisms that may explain why stable cooperation persists - all of which involve individuals monitoring the behaviour of others and responding in such a way that the benefits of free-loading are nullified. These mechanisms include partner choice (Sherratt & Roberts, 1998; McNamara et al., 2008); punishment of defectors (Boyd & Richerson, 1992; Clutton-Brock & Parker, 1995; Raihani et al., 2012); reward of co-operators (Oliver, 1980), with reward suggested as a better strategy than punishment (Rand et al., 2009); and reciprocity, which can be further sub-divided into direct (Axelrod & Hamilton, 1981), indirect (Nowak & Sigmund, 1998), or generalised (Pfeiffer et al., 2005; Barta et al., 2011).

The above mechanisms all depend on information from previous encounters, but individuals may also benefit from using knowledge of how readily others may be able to contribute in the future. One mechanism that can take into account past behaviour and possible future behaviour of collaborators is negotiation, which allows individuals to make consensus decisions over individual contributions to a public good irrespective of whether individuals are in a kin-related group or not (Houston & Davies, 1985; McNamara et al., 1999; Johnstone & Hinde, 2006; Quiñones et al., 2016). It also allows individuals to make informed decisions as to whether they should alter their contributions because of the behaviour of others, with the adaptive response possibly requiring individuals to increase their personal effort, and thus incur short-term costs (McNamara et al., 1999; Hinde, 2006).

Evidence exists for negotiation stabilising cooperation by two different methods. The first of these is for individuals to incompletely compensate for the lost effort of selfish collaborators when they reduce their workload (Houston & Davies, 1985; McNamara et al., 1999). Alternatively, if there is a lack of information available to individuals about required levels of contribution, they may be selected to match collaborator behaviour (Johnstone & Hinde, 2006). Empirical evidence exists showing that both incomplete compensation (e.g. Wright & Cuthill, 1989; van Breukelen & Itzkowitz, 2011) and behavioural matching (e.g. Hinde, 2006) occurs in parental care systems. Bell et al. (2010) also provided evidence to suggest negotiation could occur in anti-predator behaviour by manipulating a) an individual’s contribution to sentinel behaviour, and b) how groups perceive others’ ability to contribute in the future. However, manipulating only one individual does not fully test whether and how individuals may negotiate, because negotiation requires individuals reacting to the behaviour of one another; and so if multiple individuals aren’t manipulated, negotiation hasn’t fully been tested. Therefore, following from Bell et al. (2010), I decided to further test whether negotiation occurs in anti-predator behaviour, by manipulating two individuals within a group (Chapter 3).

1.2.2 Reliability Variation

The public goods problem may lead to the evolution of mechanisms for individuals to monitor the quantity of effort of collaborators. However, it may be adaptive for individuals to also monitor the quality of effort, and information, being provided by others. In doing so they may avoid being cheated by poor quality, unreliable collaborators, and can alter their response to certain individuals based on their past behaviour (e.g. cleaner-client fish mutualism, Bshary, 2002; Pinto et al., 2011).

Unreliable anti-predator information can be detrimental. For instance, if an individual cannot correctly identify threats and fails to alarm at predators, this may lead to the death of group members. At the other end of the spectrum, there may be an ultra-sensitive individual that incorrectly alarms at many things which are not threats (see Hare & Atkins, 2001; Blumstein et al., 2004). If group members react by fleeing to all of this individual's alarms, then they could lose a large amount of time from other profitable behaviours, such as reproduction and foraging. Therefore individuals may be selected to alter their response to an alarm depending on the reliability of the caller. Empirical evidence confirms this because vervet monkeys (*Chlorocebus pygerythrus*) and ground squirrels (*Spermophilus richardsonii*) show reduced response to less reliable callers (Cheney & Seyfarth, 1988; Hare & Atkins, 2001). Marmots (*Marmota flaviventris*), however, show an increased response to less reliable callers, though this is due to receivers making a personal assessment of threat (Blumstein et al., 2004).

Because of the costs of unreliable anti-predator information, if reliability develops with age and experience, a range of behaviours possibly may evolve to counteract this issue. As discussed above (Cheney & Seyfarth, 1988; Hare & Atkins 2001) individuals may counteract unreliable individuals by ignoring them, and so if juveniles are, as a whole, more unreliable than adults then selection may favour individuals to just ignore all anti-predator information from juveniles until they reach adulthood. However, in areas of high predation risk it may be maladaptive to ignore an alarm just because of caller identity (e.g. Schibler & Manser, 2007). In such an instance, if a less experienced, juvenile individual were to act as sentinel it may be adaptive for another, more experienced individual to act as sentinel simultaneously. This individual may then be able to provide their own anti-predator information which may "confirm" any information given by the juvenile.

The idea of experienced individuals accompanying inexperienced individuals also raises the possibility that the experienced individuals might be selected to teach naïve ones, so as to improve naïve individuals' reliability. For a behaviour to be classified as teaching, three key assumptions need to be verified (Caro & Hauser, 1992). These are; a) an experienced individual alters its behaviour in the presence of a naïve individual, b) doing this is costly, and c) this facilitates faster learning by the inexperienced individual (Caro & Hauser, 1992). Teaching has been shown to be widespread (Thornton & Raihani, 2008), especially with regard to feeding of juveniles and foraging behaviour (e.g. Thornton & McAuliffe, 2006; Raihani & Ridley, 2008; Hoppitt et al., 2008). However, to the best of my knowledge, my test of teaching of anti-predator behaviour in Chapter 4 is the first of its kind.

1.2.3 Spatial Issues

Monitoring the quantity and reliability of others' anti-predator behaviour requires individuals to be in close proximity of one another. However, when living in groups it is possible that individuals may be separated by some distance, which may create problems.

For group living species where individuals are patchily distributed there may be difficulties in passing information between group members who are some distance away. A scenario where this might occur is when a group has nestlings, or less mobile juveniles, located away from the main group. In such a case one or more adults may periodically move from the main group to join the juveniles in order to provision or guard the young, before returning to the main group (e.g. Clutton-Brock et al., 1998; Raihani et al., 2010) - possibly with no knowledge of predation threat at either location. Not only does this pose a possible problem for the provisioning adult, but also when feeding vulnerable individuals, such as nestlings, provisioners are selected to trade off offspring need against a predation threat (Skutch, 1949; Martin et al., 2000). Nest visits may provide the young with food, but may also draw the attention of predators to the presence of less mobile prey. Therefore, when faced with predator presence near the nest, group members may be expected to make fewer nest visits in order to reduce the probability of nest predation (Skutch, 1949; Martin et al., 2000).

Information about predator presence can be collected personally, inferred by others' behaviour, or actively signalled by group members. Personally gathering information on predation threat may not be adaptive for some species, because individuals may only infrequently visit the nest, and thus not collect sufficient information (e.g. Renton & Salinas-Melgoza, 1999). Additionally, inference of predator presence using collaborator feeding rate as a cue can be highly unreliable, because there are many different factors affecting provisioning behaviour – primary of which is offspring need (e.g. Kilner & Johnstone, 1997; Smiseth et al., 2003). Thus, it may be adaptive for individuals to actively communicate about risk levels at the nest when they return to the main part of a group. However, while it may appear adaptive for such a behaviour to be present, individuals actively communicating about conditions in a different location has in fact very rarely been documented. The clearest example of this behaviour occurring in nature comes from von Frisch's study of the waggle dance of bees (von Frisch, 1967); whereby individuals signal to others about possible food sources using a series of "dance" movements, when they return to the colony. Given the lack of documented examples of active communication about distant locations, I therefore set out to test whether individuals may actively communicate about risks at a nest when they return to the foraging group (Chapter 5).

1.3 Heterospecific Information Use

Public information, such as anti-predator signalling, is not necessarily only received by the intended recipients. Not only can unintended conspecifics eavesdrop on signallers, but heterospecifics will do this too. These may be predators or parasites eavesdropping on their victims to locate them more easily (e.g. Allan et al., 1996), or may be intra-guild heterospecifics when the signaller is providing relevant and reliable information (see Magrath et al., 2015a). Intra-guild heterospecifics may even be a more appropriate information source than conspecifics, because they may provide less niche competition than conspecifics (Seppänen et al., 2007; see Goodale et al., 2010; Westrip & Bell, 2015, for why it may be more complicated than this).

Heterospecific information use occurs within and between taxonomic groups (Rasa, 1983; Ito & Mori, 2010; Magrath et al., 2015a), with species commonly utilising heterospecific alarm calls (e.g. Shriner, 1998; Fichtel, 2004; Müller & Manser, 2008; Ridley et al., 2014; Magrath et al., 2015a). Heterospecific information use is not restricted to anti-predator information, however, because species will use other kinds of heterospecific information, including using heterospecific foraging signals to locate food (e.g. Goulson et al., 1998; Stout & Goulson, 2001; Lichtenberg et al., 2011; Koda, 2012).

Furthermore, heterospecific information use can have knock-on consequences for community spatial dynamics, and patterns of species associations (Goodale et al., 2010). Signals degrade over distance (see Forrest, 1994; Murray & Magrath, 2015), therefore, species may be drawn together as individuals attempt to eavesdrop on heterospecifics. Additionally, individuals may use heterospecific signals to inform habitat choices with individuals either eavesdropping on (e.g. Diego-Rasilla & Luengo, 2004; Pupin et al., 2007; Mukhin et al., 2008), or actively recruited to locations by heterospecific signals (e.g. Windfelder, 2001; Goodale & Kotagama, 2006). I examine how heterospecific information use may influence community dynamics in Chapter 6.

1.4 Specific Aims

In this thesis I shall examine various intra- and inter-specific aspects of anti-predator behaviour in the Southern Pied Babbler, *Turdoides bicolor*. Two of my experimental chapters will focus on anti-predator behaviour within pied babbler groups; one chapter will investigate whether pied babblers relay heterospecific information to other group members; and my final experimental chapter will examine heterospecific use of pied babbler information.

Chapters 3 and 4 focus solely on pied babbler anti-predator behaviour. In Chapter 3, I investigate whether individuals monitor the quantity of sentinel effort by group mates, using a feeding experiment to alter individual sentinel contributions, and ascertain whether anti-predator behaviour is truly a public good in my study species. In Chapter 4, I ask whether individuals monitor group mate alarm call reliability, and ascertain whether the presence of multiple, simultaneous sentinels - a previously uninvestigated behaviour - is involved in this. I do this by manipulating individual reliability using playback experiments. I then investigate whether this behaviour may be related to teaching of predator recognition.

Chapters 5 and 6, to varying extents, investigate inter-specific anti-predator information use. In Chapter 5, I use playbacks of heterospecific calls to examine whether pied babblers relay information to group mates about possible threats near the nest when they return to the foraging group from provisioning the nestlings. I do this by recording the time interval between nest visits after different playback types. Finally, in Chapter 6, I look at avian species presence across my field site in the presence and absence of pied babbler groups, and with a playback experiment I then investigate whether species may be attracted to locations by eavesdropping on public information signalled by pied babblers.

Chapter 2: General Methods

Individual methods are outlined within their respective chapters. Here I overview the study site, study population and general methods I used throughout the study. Ethical approval for this work was granted by the Edinburgh University Ethical Review Committee, ERC no: OS-02-12.

2.1 Study Site

2.1.1 Climate & Habitat

Field work was conducted in the South African Kalahari on the Kuruman River Reserve (KRR), Van Zylsrus, Northern Cape, South Africa (26º58′S, 21º49′E) and surrounding farmland, near the Botswana border. The Southern African Kalahari is classed as a semi-arid region (see van Rooyen, 2001). Daily weather data collected on the KRR shows rainfall is biased to a warm, wet summer (September to April) with average maximum/minimum daily temperatures of 33.4 and 13.9°C and average rainfall of 253.8ml in this period. Winter (May to August) is cold and dry with average maximum/minimum daily temperatures of 23.9 and 1.8°C and average rainfall of 22.3ml within this period (Figure 2.1). All three summers encompassing my field work were drier than average but my 1st (2012-2013) and 3rd (2014-2015) breeding seasons were part of especially dry periods to hit the area (1st Sept 2012-30th Apr 2013 114.2ml rainfall; 1st Sept 2013-30th Apr 2014 196.4ml rainfall; 1st Sept 2014-24th Mar 2015 104.4ml rainfall).

The reserve encompasses a section of the dry Kuruman River and adjacent land. The most common vegetation on the reserve is sour grass (*Schmidtia kalihariensis*), which is found throughout habitat types. The dry riverbed generally has little vegetation but contains some bushy species such as *Ziziphus mucronata*, in addition to the ubiquitous sour grass.

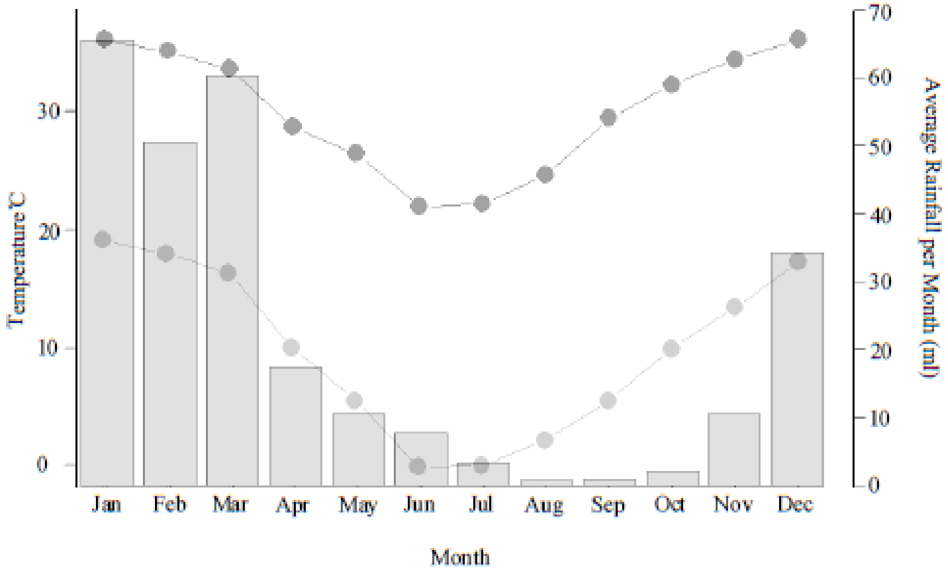


Figure 2.1 Showing weather data for the Kuruman River Reserve (10/12/2009 – 24/03/2015). Bars indicate average monthly rainfall (mm, z axis), dots indicate average maximum (darker) and minimum (lighter) temperatures (ºC, y axis)

Other habitats found on the reserve are flat areas adjacent to large dune systems, and undulating shallow dune systems. On the flats, large trees such as camel thorn (*Acacia erioloba*) as well as bushy species such as black thorn (*Acacia mellifera*) are found along with the invasive mesquite (*Prosopis glandulosa*). Smaller bushy species such as driedoring (*Rhigozum trichotomum*) and ganna (*Salsola* sp.) are also present.

The dune systems contain black thorn and occasionally camel thorn but shepherd's tree (*Boscia albitrunca*) is more usual. In the dune systems other grass species may be found including those of the genera *Eragrostis* and *Stipagrostis*. These two genera dominate the vegetation in the undulating shallow dunes that are predominantly found towards the north of the reserve. The sparsely distributed grey camel thorn (*Acacia haematoxylon*) is more commonly found there as well.

A variety of other flowering plants and herbaceous species can be found across the reserve. These, however, do not form a large proportion of the vegetation apart from after periods of sustained rainfall when they are more likely to emerge.

2.1.2 Reserve Animal Species

The land of the reserve had previously been stock farmland prior to its purchase to form the KRR. After the formation of the reserve the land continued to be managed, as stock were removed from the land apart from in a small enclosed area in the north of the reserve and native large game re-introduced. The game inhabiting the reserve now includes springbok (*Antidorcus marsupialis*), red hartebeest (*Alcelaphus buselaphus*), blue wildebeest (*Connochaetes taurinus*), eland (*Taurotragus oryx*) and gemsbok (*Oryx gazelle*). Recently a herd of Nguni cattle (*Bos taurus*) have been re-introduced onto the land as well. Smaller diurnal mammals such as meerkat (*Suricata suricatta*), cape-ground squirrel (*Xerus inauris*), yellow and slender mongoose (*Cynictis penicillata* and *Herpestes sanguineus* respectively) can be found as well as the nocturnal aardvark (*Orycteropus afer*), aardwolf (*Proteles cristata*), bat-eared and cape foxes (*Otocyon megalotis* and *Vulpes chama* respectively) amongst others. Reptiles are represented by a variety of snakes including puff adder (*Bitis arietans*) and cape cobra (*Naja nivea*) as well as by skink species (Scincidae; Squamata), and geckos (Gekkota; Squamata). Additionally there is a vast array of invertebrate species, which can be prey for many of the birds that inhabit the reserve (*pers. obs.*).

Many bird species can be found in the area (see Appendix A for a full list of species personally seen on the reserve and surrounding farms). Nocturnal species are limited, but include Verreaux's Eagle-Owl (*Bubo lacteus*), Pearl-Spotted Owlet (*Glaucidium perlatum*) and Rufous-Cheeked Nightjar (*Caprimulgus rufigena*). Commonly seen diurnal species include Fork-Tailed Drongo (*Dicrurus adsimilis*), White-Browed Sparrow-Weaver (*Plocepasser mahali*), Southern Grey-Headed Sparrow (*Passer diffusus*) and the focus of this thesis, the Southern Pied Babbler (*Turdoides bicolor*).

2.2 Study Species

Figure 2.2 A foraging pied babbler group.

2.2.1 General Behaviour

Southern Pied Babblers, *Turdoides bicolor*, (henceforth pied babbler or babbler) are medium-sized passerines found in semi-arid conditions in Southern Africa. They are facultative cooperative breeders, with groups usually consisting of a dominant pair that monopolise reproduction (Nelson-Flower et al., 2011), and varying numbers of subordinates and current fledglings living on relatively stable territories. Subordinates may be the philopatric offspring of one or both of the dominant pair, and rarely may be an immigrant individual. All group members contribute to cooperative behaviours such as sentinel activity, territory defence, and offspring rearing; and individuals may conduct such behaviours alone or accompanied by group members (Ridley & Raihani, 2007a & b; Golabek, 2010; Raihani et al., 2010; Chapter 4).

Pied babblers are predominantly ground foragers (Ridley & Raihani, 2007a), feeding on a variety of invertebrates, such as "buried insect larvae…, grasshoppers…, scarab beetles…and arachnids" (Child et al., 2012). However, they will eat vertebrates including small lizards, such as skinks (Child et al., 2012; *pers. obs.*). While foraging, individuals give a distinctive contact "chuck call". This allows individuals to maintain spacing between one another as they forage (Radford & Ridley, 2008), and may also indicate the profitability of a certain food resource (Golabek, 2010).

Other pied babbler calls may be involved with offspring care and development. When feeding older nestlings and fledglings, provisioners give a call resembling a purr. This call acts as a teaching mechanism, and is used by adults to move juveniles away from potentially dangerous areas, because they associate the call with food (Raihani & Ridley, 2007a, 2008). Nestlings and fledglings, meanwhile, give a very distinctive begging call, which may be used to blackmail adults into feeding them, because the call is so loud it would attract predators (Thompson et al., 2013). A final vocalisation that may be related to offspring care is a call given when an adult returns to the foraging group after feeding the nestlings. This call is very similar to one that pied babblers give when concluding a sentinel bout, and has been hypothesised to convey information about the urgency for another individual to contribute to that behaviour. However, as of yet there has been no evidence for this (Hollén et al., 2011).

Figure 2.3 A pied babbler conducting sentinel behaviour.

Babbler groups also gather together to give choruses, with individuals within groups giving a distinct call within these choruses dependent on individual dominance status and sex (Golabek & Radford, 2013). These calls are used in a variety of contexts, but are very noticeable during inter-group interactions where two or more groups may produce these choruses, usually at territorial boundaries (Golabek & Radford, 2013).

2.2.2 Anti-Predator Behaviour

Pied babblers are exposed to a severe predation threat in the Kalahari (see Table 2.1 for a list of possible threats). As such, they have evolved several behaviours and vocalisations to help combat this threat.

Table 2.1 List of species that Pied Babblers may consider an appropriate predation threat, commonly found on the Kuruman River Reserve. Species with * may be nest predators only.

Common Name	Scientific Name
White-Backed Vulture	*Gyps africanus*
Lappet-Faced Vulture	*Torgos tracheliotus*
Black-Chested Snake-Eagle	*Circaetus pectoralis*
Brown Snake-Eagle	*Circaetus cinereus*
Gabar Goshawk	*Micronisus gabar*
Pale Chanting Goshawk	*Melierax canorus*
Tawny Eeagle	*Aquila rapax*
Martial Eagle	*Polemaetus bellicosus*
Lanner Falcon	*Falco biarmicus*
Pygmy Falcon*	*Polihierax semitorquatus*
Red-Necked Falcon	*Falco chicquera*
African Grey Hornbill*	*Tockus nasutus*
Southern Yellow-Billed Hornbill*	*Tockus leucomelas*
African Scops Owl	*Otus senegalensis*
Barn Owl	*Tyto alba*
Southern White-Faced Owl	*Ptilopsis granti*
Verreaux's Eagle-Owl	*Bubo lacteus*
Pearl-Spotted Owlet	*Glaucidium perlatum*
Slender Mongoose	*Herpestes sanguineus*
Yellow Mongoose	*Cynictis penicillata*
Puff Adder	*Bitis arietans*
Cape Cobra	*Naja nivea*
Cape Fox	*Vulpes chama*
Bat-Eared Fox	*Otocyon megalotis*
Meerkat	*Suricata suricatta*

Pied babbler groups frequently have a group member acting as a sentinel (approximately 59% of the time; Bell et al., 2009). Contribution to sentinel behaviour may be determined by satiation state (Bell et al., 2010), and individuals contribute despite an associated increase in predation threat by being further from cover and being targeted more often by predators (Ridley et al., 2013).

The sentinel takes up an elevated position to scan for predators, and individuals are more likely to act as sentinel when predation risk is greater (e.g. due to environmental factors, or when there is perceived predator presence; Ridley et al., 2010; Hollén et al., 2011). When environmental conditions may hinder communication with group mates (e.g. in high wind), sentinels may select perches that are closer to the group to improve the likelihood that group mates will receive their vocal signals (Hollén et al., 2011).

Amongst the vocal signals that sentineling individuals give is a sentinel call. Sentinels generally give this when there is no observed threat, and this allows foragers to decrease personal vigilance and increase foraging efficiency (Hollén et al., 2008; Bell et al., 2009). This call also encodes information about individual satiation state, which may allow individuals to coordinate contributions to sentinel behaviour (Bell et al., 2010). If there is possible evidence of predator presence the sentinel may alter the characteristics of their sentinel call (e.g. fundamental frequency and calling rate) (Bell et al., 2009) to alert group members, who then increase their personal vigilance (Bell et al., 2009). Alternatively, if a possible threat is identified, individuals can give an alarm call, which allows group mates to flee and avoid predation (Ridley & Raihani, 2007a; Bell et al. 2009; Ridley et al., 2010). Pied babblers also take part in mobbing events to drive off predators (e.g. see Ridley et al., 2010), for which they have a separate call (A.R. Ridley, unpublished data).

Pied babblers do not only use conspecific information about threats. They will also react to alarm calls of other species, join mobs initiated by heterospecifics, and avian heterospecifics will do the same with babbler information (Bell et al., 2009; Ridley et al., 2014; *pers. obs.*). Additionally, the sentinel calls of fork-tailed drongos, *Dicrurus adsimilis*, have similar effects on the vigilance of foraging pied babblers as babbler sentinel calls (Radford et al., 2011).

2.2.3 Avian Heterospecific Interactions

Pied babblers are one component of a diverse avian community in the South African Kalahari. Of the 171 different species of bird personally sighted in the study area, many interact with pied babblers (see Appendix A). By interacting with pied babblers, avian heterospecifics may be able to use pied babbler information. Pied babblers have been shown to be used as an information source by scimitarbills, *Rhinopomastus cyanomelas* (Ridley et al., 2014), and in Chapter 6 I investigate to what degree information generated by pied babblers may be being used by the avian community of the area.

Avian heterospecifics can also provide a threat to pied babblers. In addition to the variety of birds of prey present on the KRR (see Table 2.1), species within the same trophic level may also provide a threat. Fork-tailed drongos will kleptoparasitise foraging pied babblers using false, frequently mimicked, alarm calls (Ridley et al., 2007; Flower, 2011; Flower et al., 2014), and my study population is the first documented site where jacobin cuckoos, *Oxylophus jacobinus*, brood parasitise pied babblers (Ridley & Thompson, 2012).

2.3 Study Population

2.3.1 Pied Babbler Research Project

This study was carried out as part of the Pied Babbler Research Project, which was given permission to conduct research on pied babblers by the Northern Cape Conservation Authority. The Pied Babbler Research Project (PBRP) was set up in 2003 by Associate-Professor Amanda Ridley with the assistance of Dr. Nichola Raihani. The number of habituated study groups fluctuates according to weather conditions, but at time of writing there were 18 groups. Group size ranges from 2-15 individuals.

2.3.2 Habituation & Identification

At 11 days old nestlings are ringed with a unique colour ring combination for identification (SAFRING licence number 1263). Individuals are habituated to allow for close access to group life and ease of observation - individuals generally allow human presence to within 2m. Groups are followed to roost so that they may be found easily in the morning, but if that is not possible then the babblers have been habituated to a distinct whistle, which they associate with food. Individuals may approach an observer who uses this whistle, and they receive a mealworm (*Tenebrio molitor*) reward for doing so. Body mass data can be easily collected without capture as individuals are habituated to a balance scale. Birds are enticed onto the scale using crumbled egg yolk, and receive a mealworm reward once their mass has been recorded.

Figure 2.4 Collecting body mass data.

2.3.3 General Work for the PBRP

As part of the PBRP, general daily data collection takes place. Body mass data are collected in the morning within 15 minutes of the birds waking at dawn, at the end of a morning session (at least 90 minutes after first mass data are collected), and within 15 minutes of the birds going to roost at dusk. Tracks of a group's movements during a session are collected by recording GPS points approximately every 15 minutes using a handheld Garmin eTrex or eTrex10 GPS device, which are later saved onto Mapsource version 6.13.7 (all: Garmin Ltd. Or its subsidiaries, Schaffhausen, Switzerland). The sites of roost and nest trees and where inter-group-interactions (IGIs) take place are also recorded using a GPS device. Major life history events such as the dispersal or immigration of individuals or the start of a breeding event are also logged.

2.4 Data Collection

2.4.1 Collection Periods

Data collection took place in 4 separate visits to the KRR. Collection periods were 15th December 2012 – 22nd April 2013, 11th September 2013 – 5th May 2014, 24th September 2014 – 28th October 2014 and 8th January 2015 – 27th March 2015.

2.4.2 Work Conducted

2.4.2a Focal Watches and ad libitum *Data*

The different methods I used to collect observational data were focal watches of individuals, bird occurrence surveys, and *ad libitum* observations. Focal watches consisted of recording a focal bird's foraging behaviour using a Samsung HMX-F80 Video Recorder (Samsung, Seoul, South Korea) under different sentinel combinations (Chapter 4). The videos were blind coded for later analyses of the vigilance of foraging birds in response to the different sentinels.

My work on avian heterospecific interactions with babblers included surveys of avian heterospecific occurrence in the presence and absence of babblers (Chapter 6). I collected data on avian heterospecific occurrence in the presence of babblers when recording GPS points as part of the general work for the PBRP. In the absence of babblers, I collected bird occurrence data at waypoints located on transects set up to run parallel to the boundaries of the KRR using Mapsource version 6.13.7. In order to control for transect location in my analyses I noted the overlap of babbler group home foraging ranges (identified as locations where babblers were recorded when taking GPS points for PBRP) with transects using Basecamp version 4.4.2 (Garmin Ltd. Or its subsidiaries, Schaffhausen, Switzerland).

My *ad libitum* data predominantly consisted of behavioural observations. These were; a) recording what individual babblers give an alarm to, in order to determine reliability scores for individual alarm callers (Chapter 4), and b) hour watches of babbler groups to ascertain the amount of sentinel behaviour individuals conducted, and the proportion of time sentinels overlapped with other sentinels (Chapters 3 & 4).

My *ad libitum* data collection also involved collected sound recordings. I collected recordings using a Sennheiser directional microphone (Sennheiser, Wedemark, Germany) connected to a Marantz PMD660 recorder with a sampling rate of 44.1 kHz, 16-bit resolution (Marantz, Kanagawa, Japan) and stored in WAV format. The babbler calls I collected throughout this study were foraging chuck calls (Chapter 4 & 6), sentinel calls (Chapter 6) and alarm calls (Chapter 4). Additionally, I took background noise recordings for Chapters 4-6, and I collected avian heterospecific context-neutral and mobbing calls for Chapter 5.

2.4.2b Experimental Work

I conducted a number of playback experiments (Chapters 4-6) over the course of this study using the sound recordings I collected. I built and standardised playback tracks using the Raven Pro 1.4 (The Cornell Lab of Ornithology, Ithaca, NY) and Cool Edit Pro 2.0 (Syntrillium Software Corporation, P.O.Box 6255, Phoenix, AZ 85082, USA) softwares. I played back tracks using standardised Jambox (Jawbone, San Francisco, USA) or Shoqbox speakers (Phillips, Amsterdam, Netherlands) connected to either a Samsung R519 laptop (Samsung, Seoul, South Korea) or an Archos 604 Wifi MP4 player (Archos, Igny, France). For the playbacks I conducted in Chapters 4 and 5 I inserted 1-2 seconds of background noise either side of the relevant calls to be played back. I did this for ease of playback, because the playback devices used in the experiment could skip onto the next track on the device and so the background noise was there to act as a buffer to give the experimenter time to pause the track.

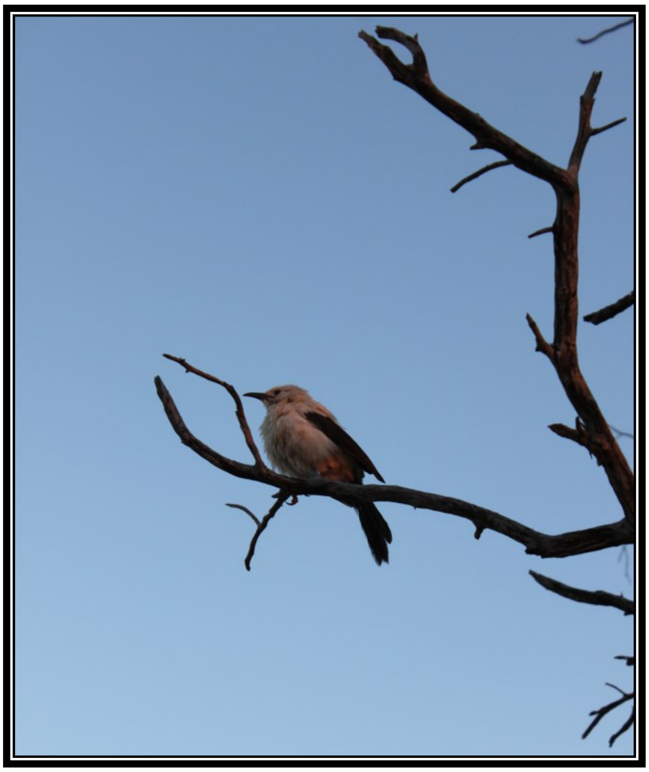
An additional type of experiment I conducted as part of this thesis was a supplementary feeding experiment (Chapter 3). This allowed me to manipulate contributions to sentinel behaviour, because an individual's sentinel behaviour contribution can be influenced by individual satiation state (Bell et al., 2010). I present the individual set-ups and aims for all of my experiments in their relevant chapters.

2.5 Statistical Analyses

I conducted data analysis in R version 2.15.2 (R Core Team, 2012) using the R Commander interface (Fox, 2005) – statistical tests and variables used for individual analyses are placed in their respective chapters. However, the main format for analysing data was using mixed-effects models using the lmerTest package (Kuznetsova et al., 2013) for linear mixed-effects models (LMM) and the lme4 package (Bates et al., 2012) for generalised mixed-effects models (GLMM). These allow for the co-analysis of both fixed and random effects on a response variable when making repeat measurements at groups and with individuals. I selected final models using backwards stepwise elimination, retaining fixed effects that explained significant (or near significant) variation in the response variable (terms with a p value of ≤ 0.10 were retained), and all random terms irrespective as to whether they were deemed to significantly affect the variance of the response variable or not.

In the statistical tables presented throughout this thesis values are presented to 2 decimal places apart for values that are so close to 0 they may be <0.001 or <0.01, which are presented as such. Where negative values this close to zero are present, in case the use of '>' may create confusion, the values are presented to 1 significant figure. One of the values I present in statistical tables is an 'estimate' value which, for categorical fixed effects, is relative to the 'estimate' value of an 'intercept'. I do not, however, present in these tables any 'estimate' values for my non-retained terms, because the 'intercept' value will change depending on the terms in the model, and so any 'estimate' for a non-retained term will not be relative to my presented 'intercept'.

Chapter 3: Are Individual Contributions to a Public Good Influenced by the State of Others?



3.1 Abstract

Animals can use negotiation to stabilise contributions to public goods by altering their behaviour based on the previous behaviour of other contributors, or others' ability to contribute in the future. Adaptive responses to behavioural alterations by others may involve individuals increasing their personal contributions, even if this incurs personal costs. In group-living pied babblers, *Turdoides bicolor*, sentinel behaviour is state-dependent and may be classed as a public good; with individuals advertising their ability to contribute in their call characteristics. Therefore, I investigated whether babblers alter their behaviour when others receive supplementary feeding; both when they themselves have and have not been fed. Additionally, I investigated whether increasing sentinel effort incurred any costs, by observing whether individuals that conducted more sentinel behaviour gained less mass. Individuals conducted relatively more sentinel behaviour when they received more supplementary food. However, I found individuals also sentineled more when others were fed, even if they themselves were not; despite sentinel behaviour carrying costs - individuals that sentineled more had reduced body mass gain. This may be due to individuals stabilising cooperation by negotiation, but to show this more clearly would require further investigations, and I suggest alternative selective pressures that may explain my observed results.

3.2 Introduction

The question of why cooperation and contribution to public goods persists in societies when there are selective advantages to defecting has attracted much attention (Trivers, 1971; Axelrod & Hamilton, 1981; West et al., 2007). Modelling techniques have generated possible mechanisms to explain the maintenance of stable cooperation (e.g. Trivers, 1971; Oliver, 1980; Axelrod & Hamilton, 1981; Houston & Davies, 1985; Clutton-Brock & Parker, 1995; Nowak & Sigmund, 1998; Sherratt & Roberts, 1998), and all of these mechanisms require individuals to monitor the behaviour of others and respond by modifying their own behaviour to negate the benefits of free-loading.

Negotiation is one of these mechanisms, and it allows not only for individuals to react to the previous behaviour of others (e.g. Houston & Davies, 1985; McNamara et al., 1999; Johnstone & Hinde, 2006), but also incorporates the ability for individuals to modify their behaviour based on the perceived ability of others to contribute in the future (e.g. Bell et al., 2010). Using this information about others, individuals are capable of making informed decisions as to whether they should alter their contributions, even if it involves increasing their effort - which may incur short-term costs - because doing so is adaptive (e.g. McNamara et al., 1999; Hinde, 2006).

Identifying negotiation initially requires the study of a system whereby two or more individuals contribute to a public good, and so conflict may be generated by individuals altering their contributions. The main system of study, to date, has been bi-parental care, but results have been equivocal over how individuals may react to alterations in the behaviour of others; with different species and sexes showing different responses to changes in the behaviour of others (e.g. Wright & Cuthill, 1989; Osorno & Székely, 2004; Hinde, 2006; van Breukelen & Itzkowitz, 2011), and even separate studies on the same species showing different responses (e.g. starlings have been shown to completely and incompletely compensate for the reduction in effort by a partner; Wright & Cuthill 1989, 1990). Therefore, I set out to identify an alternative candidate behaviour that can be classified as a public good, that can be easily manipulated, and where other individuals may alter their behaviour in response to this manipulation - even if it incurs a short-term cost.

Sentinel behaviour appears to fit this classification. Despite sentinel behaviour being frequently considered either kin-selected altruism (Hamilton, 1964; Griesser, 2003) or a selfish act (Bednekoff, 1997), it fulfils the criteria of a public good. Sentinel behaviour provides a group-wide benefits by sentinels providing alarm calls when they observe a predator, and sentinel calls that allow for increased foraging success of group members (Hollén et al., 2008; Bell et al., 2009). Additionally, it incurs costs to the actor, both because of an increased predation threat (Ridley et al., 2013), and there may be opportunity costs in terms of lost foraging time.

Therefore, I set out to study whether negotiation takes place in the sentinel system of the Southern Pied Babbler, *Turdoides bicolor* (henceforth babbler). Babblers are cooperatively breeding passerines of the Southern African Kalahari found in groups of 2-12 (Ridley & Raihani, 2007a). Babblers are predominantly ground foragers, and their foraging efficiency is negatively affected by temperature – when temperatures are sufficiently high, individuals may not gain enough body mass to counteract the loss of mass overnight – and so conducting any other behaviours aside from foraging may be costly (Ridley et al., 2007; du Plessis et al., 2012). However, individuals frequently act as a sentinel (there may be at least one individual on guard up to 59%

of the time), giving alarm calls to alert the group to predators, and sentinel calls that increase group member foraging success (Hollén et al., 2008; Bell et al., 2009). Sentinel behaviour is easily manipulated because it is state dependent: the probability an individual is the next sentinel and time that individual spends as sentinel is increased by supplementary feeding (Bell et al., 2010). Such feeding also alters the vocal characteristics of the individual's contact and sentinel calls, and so other group members are able to recognise the ability of others to contribute (Bell et al., 2010). The work by Bell et al. (2010) suggests negotiation takes place in this system, but that work only simulated state changes of one individual at a time. However, negotiation involves individuals reacting to the behaviour of one another; and so to fully test whether negotiation occurs, multiple individuals should be manipulated. Here I actively manipulated the state of multiple individuals within groups, using a feeding experiment, to explicitly test whether negotiation over contributions to sentinel behaviour is occurring within groups, and I assess whether individuals alter their behaviour even if this alteration leads to costs in terms of reduced body mass gain.

I specifically asked: a) does feeding influence personal and group member contributions to sentinel behaviour?, and b) does conducting sentinel behaviour impact the amount of body mass an individual gains? I predicted that supplementary feeding would lead to an increase in the sentinel effort made by an individual, because previous work has shown how sentinel behaviour is state-dependent (e.g. Bell et al., 2010). The response I would then expect from the rest of the group would be for a decrease in their sentinel effort because of the extra effort being conducted by the fed individual. When multiple individuals were fed, again, I expected those individuals to increase their sentinel effort, and the rest of the group to reduce theirs accordingly. I predicted that individuals that spend longer acting as sentinel would gain less body mass than individuals who conduct less sentinel behaviour, because by conducting sentinel behaviour the individuals are reducing the amount of time they are able to forage.

3.3 Methods

3.3.1 Study Site & Population

Data collection took place 19th March to 18th April 2013 and 23rd September 2013 to 8th April 2014 on the Kuruman River Reserve and surrounding farmland, southern Kalahari desert, Northern Cape, South Africa (26º58'S, 21º49'E) (see du Plessis et al., 2012 for climate details). The study population consists of colour ringed, habituated pied babblers trained to jump on electric weighing scales (see Ridley & Raihani, 2007a).

3.3.2 Data Collection

To explicitly test whether feeding influences personal and group member contributions to sentinel behaviour I carried out a feeding experiment with three different experimental treatments. For each trial I recorded all sentinel events for an hour after arriving at a group. I then fed two birds that had been randomly pre-selected before the start of a trial, and again all sentinel events were recorded for another hour. I defined a sentinel event as when a bird took up a position >1m above the ground, scanning the environment whilst giving the sentinel call (Bell et al., 2009; Ridley et al., 2010).

The different treatment types were for experimental individuals to be fed either asymmetric amounts of mealworms, *Tenebrio molitor*, (one bird receiving 10 and the other 1) or symmetric amounts (both birds fed 10 or 1). Feeding babblers 10 mealworms increases their contribution to sentinel behaviour, whereas 1 mealworm does not (Bell et al., 2010), and so feeding individuals 1 mealworm acted as a control. The trial of both birds receiving 1 mealworm therefore was my control treatment. The other two treatments then allowed me to investigate to what degree individuals alter their own behaviour based on the relative state of others compared to themselves. This is because in one treatment they have both received a large amount of supplementary feeding, thus their relative state should be kept at a similar level. However, in the other treatment only one received the larger number of mealworms, and so their relative states have been altered.

For each group I studied, trial order was randomised and a minimum of 2-3 days was left between trials. I conducted a total of 35 trials; eight 1:1 trials, ten 10:10 trials and 17 asymmetric feeding trials. I originally planned to conduct a balanced number of trials of each type, but the loss of experimental individuals (by dispersal or death) hindered the conducting of all planned trials. I manipulated 28 different birds throughout the experiment across dominance levels and sexes. This was because group sizes dropped to low levels during the experiment and I was unable to match birds based on sex, age or dominance status. However, I retained the same experimental individuals within a group, where possible.

To ascertain whether conducting sentinel behaviour conferred a cost in terms of reduced body mass gain, I collected experimental individuals' body mass data at the beginning and end of the trial and mid-way through, before feeding. This data allowed me to generate 54 body mass gain data points before, and 47 after, feeding (out of the 70 potential data points – 35 trials; 2 experimental individuals per trial). There was a discrepancy between the two sample sizes for body mass data because I would not handle the birds and could not force them to jump on the scales to be weighed every time I collected body mass data. Therefore, I could not be certain to collect every individual's mass every time.

3.3.3 Analyses

Data were analysed by linear mixed effects models using the lmerTest package version 1.2-0, (Kuznetsova et al., 2013) using the R Commander interface (Fox, 2005) in R version 2.15.2 (R Core Team, 2012). I determined minimal models by conducting backwards stepwise elimination. Throughout, if referring to both manipulated individuals, I shall use the terminology "experimental individuals"; however, for analyses where the two experimental individuals within a trial were analysed separately, I shall refer to the manipulated individuals as the "focal" and "partner" individuals (note that an individual will be both a focal and a partner individual for analyses).

3.3.3a Does feeding influence personal and group member contributions to sentinel behaviour?

To determine whether individual contributions to sentinel behaviour may be influenced by the behaviour of group members I analysed the factors that may influence the change in time as sentinel by each focal bird after feeding supplementation. Model parameters tested included the feeding regime (number of mealworms fed to the focal individual compared to the number fed to the experimental partner), focal individual dominance (see Raihani, 2008, for how dominance was assigned) and sex, the time a focal individual spent as sentinel in the 1st hour of the trial, data collection season, group size and random effects of focal individual, partner and group identity (see Appendix B for details of each parameter).

However, because babblers live in groups, rather than as isolated pairs, I also investigated how the total group sentinel time was affected by my experiment. Fixed effects were feeding regime in an interaction term with trial stage (before or after feeding), group size and data collection season. The model's random effects were experimental individuals' partnership (a single term encapsulating the identity of the 2 manipulated individuals), and group ID.

Because the total group sentineling includes the experimental individuals I ran a separate analysis to investigate what may influence the change in collective time spent as sentinel between hours by non-manipulated birds. This term was transformed by taking the highest raw value + 1 and then subtracting the original raw values from this (Munro, 2005). The square root of the subsequent output was then used for analysis. The factors I tested were data collection season, feeding regime, and group size, along with the random effects of experimental individuals' partnership, and group ID.

3.3.3b Does conducting sentinel behaviour impact the amount of body mass an individual gains?

To determine whether sentinel behaviour impacts an individual's ability to gain mass, I investigated the terms influencing body mass gain per hour in my experiment. My model contained random effects of group ID, focal individual and partner bird. I included fixed effects of focal bird dominance, group size, data collection season, bird's mass at the start of trial, the time an individual spent as sentinel (secs), and feeding regime in an interaction term with trial stage (before or after feeding).

3.4 Results

3.4a Does feeding influence personal and group member contributions to sentinel behaviour?

Compared to trials where both experimental individuals were fed 1 mealworm, individuals conducted more sentinel effort after eating 10 mealworms irrespective of whether the other manipulated individual was fed 1 ($t=2.83$, $p=0.01$) or 10 mealworms ($t=3.04$, $p<0.01$). Individuals also conducted relatively more sentinel effort when they were only fed 1 mealworm yet the other manipulated individual was fed 10 mealworms, compared to when both experimental individuals were fed 1 mealworm ($t=2.59$, $p=0.01$) (see Fig. 3.1). Individuals that spent longer acting as a sentinel prior to manipulation conducted relatively less sentinel behaviour after feeding (t= -4.95, p<0.001), and, across treatment types, in the 2nd data collections season individuals trended towards conducting more sentinel behaviour after feeding compared to the 1st data collection season (t=1.85, p=0.07). Focal individual sex and dominance status, and group size did not affect individual responses to the treatments and were not retained in the final model (see Table 3.1).

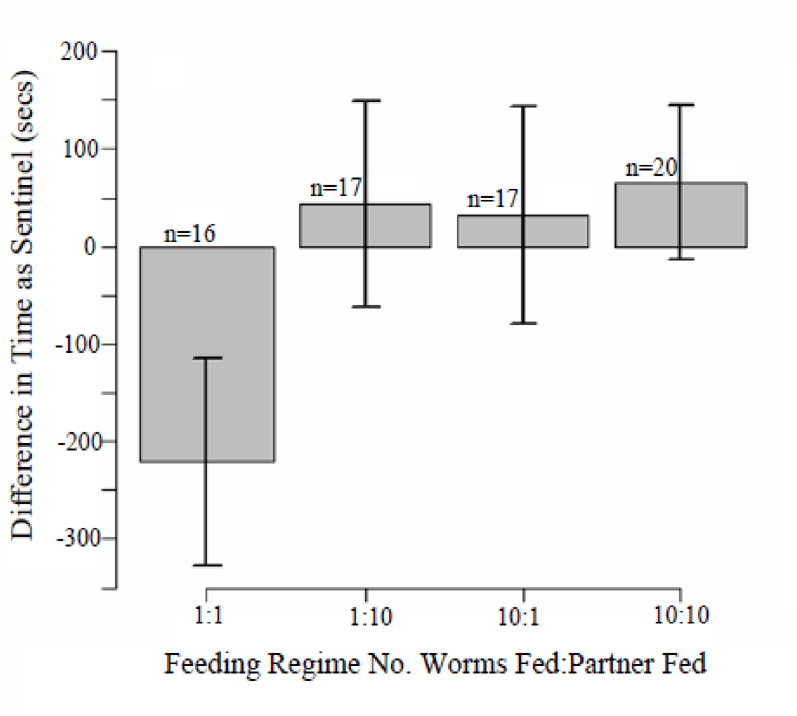


Figure 3.1 The raw mean ± standard error change in time (secs) as sentinel by a focal bird over the course of an hour after food supplementation, by feeding regime (no. mealworms fed to focal bird: no. fed to partner).

When investigating the effect trials had on the whole group, there was a trend for less sentinel behaviour to be done by the group after feeding when the experimental individuals were both fed 1 mealworm (t=2.03, p=0.05). However, there was no effect on total group sentinel activity in asymmetric feeding trials (t= -1.14, p=0.26), and when both individuals received 10 mealworms there was a trend for the whole group to invest more in sentinel behaviour after feeding (t= -1.97, p=0.05) (Fig. 3.2). Group size and data collection season did not influence how groups responded to the treatments, and were not retained in the final model (see Table 3.2).

Table 3.1 Output of linear mixed model to investigate the parameters influencing focal birds' change in time on sentinel over an hour after supplemental feeding. Data from 70 focal individuals in 35 different feeding trials (feeding trial type 1 mealworm fed to both individuals n=8, 10 mealworms fed to both n=10, asymmetric amounts of mealworms fed to individuals - 1:10/10:1 n=17).

Fixed Effects	Estimate	Standard Error	t	p
Intercept	-80.61	148.07	-0.54	0.59
Feeding Regime: [1:1vs1:10]	348.25	134.37	2.59	0.01
[1:1vs10:1]	387.21	136.69	2.83	0.01
[1:1vs10:10]	454.83	149.76	3.04	<0.01
Season	216.30	117.21	1.85	0.07
Time Guarding in 1st Hour	-0.56	0.11	-4.95	<0.001
Non-Retained Terms	**t**	**p**		
Dominance	-0.10	0.92		
Group Size	0.33	0.74		
Sex: [M]	1.40	0.17		
[Unknown]	-0.09	0.93		
Random Effects	**Variance**	**Standard Deviation**		
Individual	<0.001	<0.001		
Partner	<0.001	<0.001		
Group ID	<0.001	<0.001		

Table 3.2 Output of linear mixed model to investigate the parameters influencing the total sentineling time all of individuals in the trials. Data from 35 trials (1:1 n=8, 10:10 n=10, asymmetric 1:10/10:1 n=17).

Fixed Effects	Estimate	Standard Error	t	p
Intercept	1821.30	315.00	5.78	<0.001
Feeding Regime: [1&1vs10&1]	307.40	368.50	0.83	0.41
[1&1vs10&10]	606.30	402.00	1.51	0.14
Stage	834.00	411.20	2.03	0.05
Feeding Regime*Stage: [10&1]	-570.00	498.60	-1.14	0.26
[10&10]	-1088.30	551.70	-1.97	0.05
Non-Retained Terms	**t**	**p**		
Group Size	-0.35	0.73		
Season	-0.30	0.76		
Random Effects	**Variance**	**Standard Deviation**		
Partnership	146243	382.42		
Group ID	0.00	0.00		

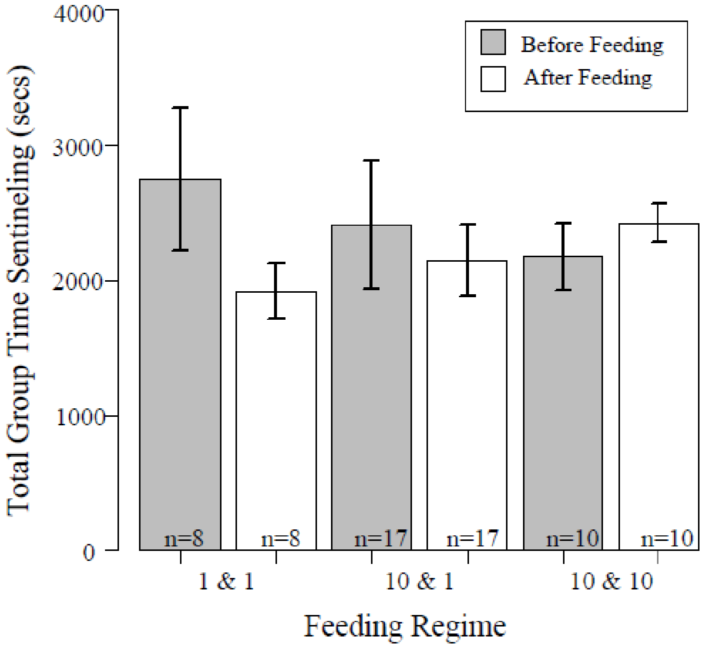


Figure 3.2 The raw mean ± standard error total sentineling time (secs) in an hour at groups before and after feeding separated by feeding regime (No. mealworms fed to experimental individuals). As 1:10 & 10:1 trials make no difference in quantity of worms fed to experimental individuals these categories were lumped together.

When manipulated birds were excluded from analyses of group sentinel effort, there was no difference in the group response to supplemental feeding of experimental individuals between trials where both experimental birds were fed 1 mealworm (Δ -392.8±216.0secs after feeding) and asymmetric feeding trials (Δ -339.1±200.0secs) (t= -1.46, p=0.16); but the group did conduct more sentinel effort when both experimental birds were fed 10 mealworms (Δ 122.9±117.6secs; t= -2.59, p=0.02) relative to when both were fed 1 mealworm (see Fig. 3.3). Non-manipulated individuals trended towards conducting more sentinel effort after feeding in the 2nd

data collection season (t= -2.07, p=0.05) and larger groups conducted relatively more sentinel behaviour after manipulation (t= -2.89, p=0.01) (see Table 3.3).

Table 3.3 Output of linear mixed model to investigate the parameters influencing the change in non-experimental individuals' total time on sentinel over an hour after food supplementation. The response variable was transformed using a reflected square root transformation. Data from 35 trials (1:1 n=8, 10:10 n=10, asymmetric 1:10/10:1 n=17).

Fixed Effects	Estimate	Standard Error	t	p
Intercept	64.02	9.14	7.01	<0.001
Group Size	-3.92	1.35	-2.89	0.01
Feeding Regime: [1&1vs10&1]	-6.17	4.21	-1.46	0.16
[1&1vs10&10]	-3.92	1.35	-2.89	0.02
Season	-8.06	3.89	-2.07	0.05
Random Effects	**Variance**	**Standard Deviation**		
Partnership	0.00	0.00		
Group ID	43.31	6.58		

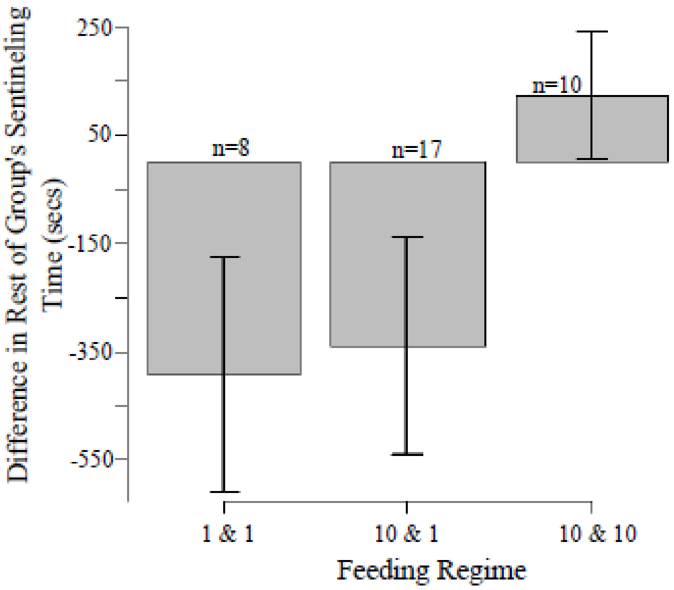


Figure 3.3 The raw mean ± standard error change in sentineling time (secs) conducted by non-manipulated birds in an hour, after supplemental feeding by experimental bird feeding regimes (No. mealworms fed to experimental birds). As 1:10 & 10:1 trials make no difference in quantity of worms fed to experimental birds these categories were lumped together.

3.4b Does conducting sentinel behaviour impact the amount of body mass an individual gains?

When both birds were fed 1 mealworm, supplemental feeding did not affect individual body mass gain (0.98±0.46g before, 1.33±0.52g after; t= -0.33, p=0.74), nor when the focal individual was fed 10 mealworms and the other experimental individual was fed 1 (2.32±0.47g, before, 0.95±0.34g after, t=1.54, p=0.13). The feeding regime did influence mass gain in the other 2 treatment types. When the focal individual was fed 1 mealworm and the other manipulated individual was fed 10 mealworms, individuals gained less mass after feeding (2.33±0.39g before, 0.76±0.48g after, t=2.01, p=0.05). Focal individual mass gain was also reduced after feeding when both of the experimental individuals were fed 10 mealworms (2.27±0.49g, before, 0.68±0.30g after, t=2.14, p=0.04) (see Fig. 3.4a). When looking at the direct impact of sentinel behaviour on body mass gain, there was a negative relationship between sentinel behaviour and mass gain such that individuals that increased their sentinel effort put on less mass (t= -2.15, p=0.03) (Fig. 3.4b). The mass of the focal bird at the start of the trial also influenced body mass gain with individuals that were heavier at the start of trials gaining less mass (t= -3.09, p<0.01). The dominance status of the focal bird, data collection season and group size did not influence body mass gain and were not retained in the final model (see Table 3.4).

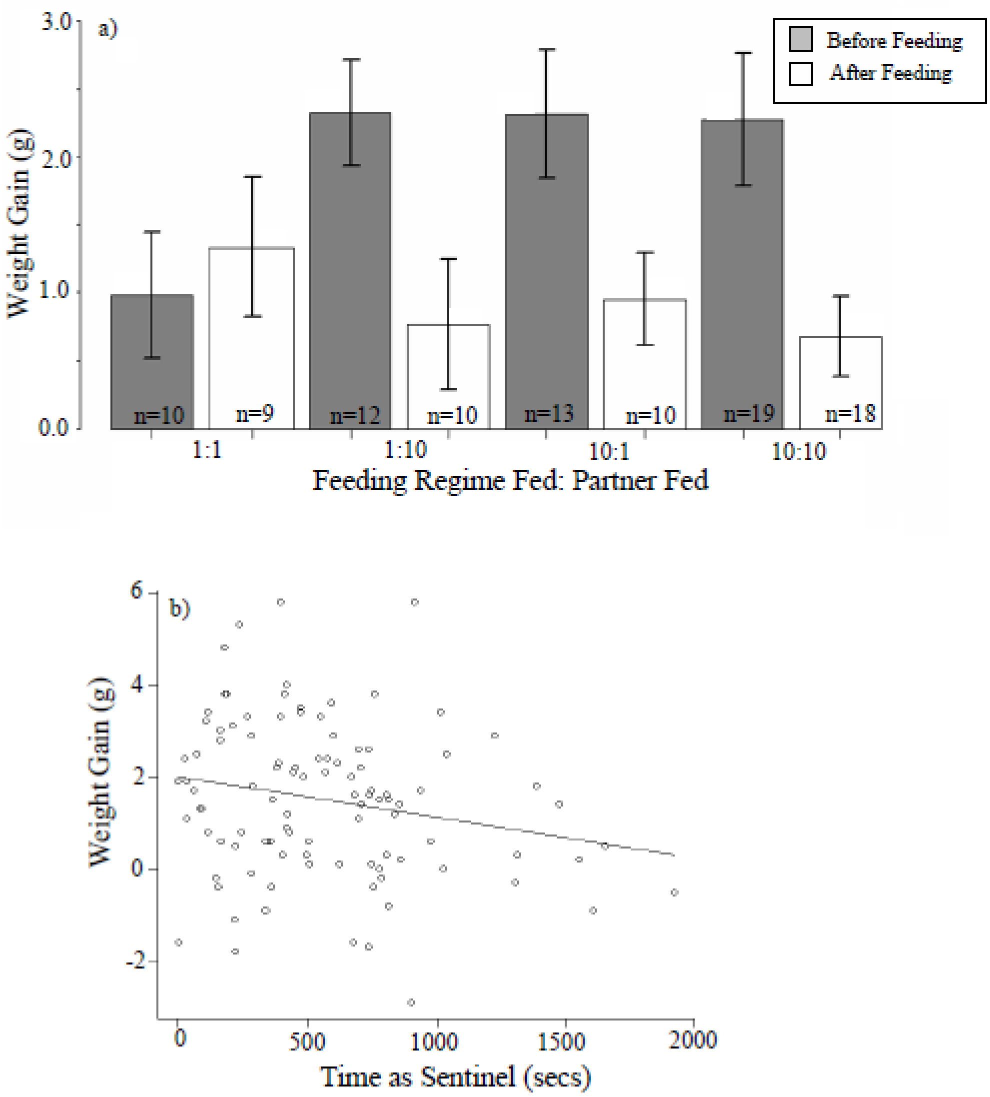


Figure 3.4 a) The raw mean ± standard error mass gain (g) by a focal bird by feeding regime (No. mealworms fed to fed to focal bird: No. fed to partner) before (grey bars) and after (white bars) feeding b) raw mass gain (g) by focal birds by time on spent as sentinel (g). Line of best fit shown is generated by least squares.

3.5 Discussion

Babblers conducted relatively more sentinel behaviour when they received supplementary feeding, compared to trials when both individuals received only 1 mealworm; and by contributing relatively more sentinel behaviour they put on less body mass. Despite this, individuals conducted more sentinel behaviour when other individuals received supplementary feeding, even if they themselves were not fed. Why then are individuals doing this? I shall now suggest some possible explanations, but key to possible explanations of my results is that in babblers, sentinel behaviour is state-dependent and individual state is advertised in call characteristics (Bell et al., 2010). Therefore, individuals may use both this indirect information to predict future effort by group members, as well as direct information about previous collaborator effort through observation of past and current sentinel effort, and they may alter their behaviour accordingly.

Table 3.4 Output of linear mixed model to investigate what influences body mass gain before and after supplemental feeding. Data consist of 101 observations; 54 before feeding and 47 after (1:1 before n=10, after n=9; 1:10 before n=12, after n=10; 10:1 before n=13, after n=10; 10:10 before n=19, after n=18).

Fixed Effects	**Estimate**	**Standard Error**	**t**	**p**
Intercept	11.52	3.22	3.58	<0.001
Feeding Regime: [1:1vs1:10]	-0.57	0.68	-0.83	0.41
[1:1vs10:1]	0.25	0.7	0.36	0.72
[1:1vs10:10]	-0.27	0.61	-0.44	0.66
Stage	-0.23	0.68	-0.33	0.74
Body Mass at Start of Trial	-0.13	0.04	-3.09	<0.01
Time on Guard	-0.0008	<0.001	-2.15	0.03
Feeding Regime*Stage: [1:10]	1.87	0.93	2.01	0.05
[10:1]	1.43	0.93	1.54	0.13
[10:10]	1.81	0.84	2.14	0.04
Non-Retained Terms	**t**	**p**		
Group Size	0.38	0.72		
Dominance	-0.40	0.69		
Season	-0.71	0.48		
Random Effects	**Variance**	**Standard Deviation**		
Individual	0.00	0.00		
Partner	0.00	0.00		
Group ID	0.00	0.00		

By reacting to the behaviour of others, and the perceived ability of others to contribute in the future, individuals may be negotiating over contributions to sentinel behaviour. A matching of the behaviour of others follows the Johnstone & Hinde (2006) negotiation model, which suggested that individuals should match the behaviour of collaborators when there is limited information available. This does, however, assume that there is only limited information available. Babblers are predominantly ground foraging (Ridley & Raihani, 2007a), and as such spend much time digging with their view of group mates obstructed. Thus, it might be assumed that the best level of information that individuals can receive is the perceived ability of others to contribute, based on call characteristics, rather than observations of absolute behaviour (Bell et al., 2010). However, whether this information can be considered incomplete is not certain. Babblers provide a lot of information in their sentinel and contact calls, encoded in their rate of calling and the fundamental frequency of their calls (Bell et al., 2009, 2010); and group members respond accordingly to this information (Bell et al., 2009, 2010). This makes it unlikely that this information may be classed as ‘limited’. However, to examine more fully whether this information is limited or not would require further observations of individuals’ vocal behaviour (in particular call rate) and how this relates to their contributions to sentinel behaviour over a more extended period of time than in Bell et al. (2010); and possibly the use of additional playback experiments.

If my results are not due to individuals negotiating contributions to sentinel behaviour there are several alternative possible selective drivers that might explain what I found. Firstly, if there are consequences for perceived failure to cooperate (e.g. Mulder & Langmore, 1993; Bshary, 2002; Fischer et al., 2014) there may be selection for individuals to increase their own contributions when others are able to contribute more. Individuals would then be able to maintain relative rates of contribution, and maintain their perceived quality (e.g. Pinto et al., 2011) in order to avoid the possible sanctions (e.g. physical aggression, Mulder & Langmore, 1993). However, if this was the case then it might be expected that subordinates may be more likely to match the behaviour of others to avoid sanctions from dominant individuals. Instead, I found no effect of dominance status on the behaviour of individuals, and while this does not preclude the possibility that individuals may be behaving in this way to avoid sanctions, it does make it less likely.

An alternative explanation for my results is that reproductive conflict may influence sentinel behaviour in this system. Reproduction is usually monopolised by dominant individuals in babbler groups, but when possible competitors for reproductive positions are present, there may be conflict (Nelson-Flower et al., 2011, 2013). To avoid physical conflict individuals may be selected to advertise their quality using costly behaviour (Zahavi, 1975). Here, I showed sentinel behaviour negatively impacts body mass gain, adding to the evidence provided by Ridley et al. (2013) that sentinel behaviour is costly in this species. Additionally, sentinel behaviour has been suggested to be, in part, a sexually selected trait in other systems (e.g. white-browed sparrow-weaver; Walker, 2014). However, I observed the same pattern for all group members, not just individuals in conflict with one another, making reproductive conflict a less likely explanation for the observed behaviours.

Another alternative explanation is that individuals may use their time as sentinel to monitor the foraging success of other group members (Hollén et al., 2011). From their elevated position sentinels may perceive the location of well-fed individuals. They may then decide to forage where well-fed individuals have been, because there may be a profitable food source in that location. In pied babblers, an individual's call may indicate it is satiated (Bell et al., 2010), and so individuals might respond to this by sentineling more in order to locate where the fed bird was foraging. A group-wide response to only one well-fed individual may be unlikely, because the prey that gives only one individual temporary satiation may not be divisible, and thus not profitable to the whole group. However, if multiple birds appear well-fed quickly (i.e. when I fed both of the focal individuals 10 mealworms) then a group-wide response may be more likely because this may indicate that there is a profitable, divisible prey source available. The results of my analyses of group sentinel effort do appear to support this suggestion.

Whatever the selective pressure for increasing contributions to sentinel behaviour, individuals do so despite reducing their ability to gain body mass. When both focal birds received 1 mealworm, experimental individuals maintained their rate of body mass gain. However, in trials where individuals increased their contribution to sentinel behaviour, individuals gained less mass post-feeding. While this may be an artefact of body mass gain being generally lower pre-feeding in trials where both individuals were fed 1 mealworm, there was still a direct negative relationship between the amount of sentinel activity conducted and an individual's body mass gain. This suggests there may be a cost for carrying out more sentinel behaviour, and this is confirmed by the direct negative correlation between individual mass gain and time devoted to sentinel behaviour.

The Johnstone & Hinde (2006) model suggested that negotiation can stabilise cooperative behaviour if individuals increase personal effort to match partner effort when there is insufficient information available to individuals. Here, I show that individuals may increase their contributions to a public good when other individuals are able to contribute more too, but there is no definitive evidence to show that this is directly related to individuals using incomplete information about the ability of group members to contribute. However, I suggest there must be a selective advantage in behaving in this manner, because individuals will increase their contribution to a public good despite it carrying costs in terms of reduced body mass gain. Other possible explanations for my observed results include sanctions avoidance, sexual competition and observing group members to find profitable foraging patches.

Chapter 4: Multi-individual Sentineling: Reliability Recognition and Anti-Predator Teaching?

4.1 Abstract

When individuals make anti-predator decisions they may be influenced by information signalled by others. However, there may be individual variation in signaller reliability. Therefore, when costs arise from the presence of unreliable signallers, individuals should monitor others and mediate their behaviour based on signaller identity. Furthermore, if reliability is based on experience, individuals may be selected to teach unreliable signallers to improve their reliability. I examined the possibility of anti-predator teaching by investigating a previously unrecognised behaviour in the cooperative Southern Pied Babbler (*Turdoides bicolor*), which involved the presence of multiple individuals acting as sentinel simultaneously. Juveniles were less reliable alarm-callers and were accompanied more than adults. Playbacks confirmed individual reliability may influence multi-individual sentineling rates. Manipulating individuals' perceived reliability by playing inappropriate alarms led to increased accompaniment of experimental individuals when acting as sentinel, when control playbacks did not, suggesting individuals are capable of monitoring others' reliability. However, the rate juveniles were accompanied did not influence reliability development, and adult alarm call playbacks brought about group-wide increases in multi-individual sentineling. This suggests multi-individual sentineling may not be related to teaching, and may instead be a response to increased possible predation threat, as well as being related to reliability monitoring.

4.2 Introduction

How individuals in social species behave can be influenced by information provided by group-mates (see Dall et al., 2005). Receivers will use the information provided by signallers in order to make appropriate behavioural decisions, e.g. fleeing to an alarm call (see Bradbury & Vehrencamp, 2011). However, the information conveyed by the signaller may not be correct, and there is often considerable individual variation in the reliability of such public information (e.g. Cheney & Seyfarth, 1988; Hare & Atkins, 2001; Bshary & Grutter, 2002; Blumstein et al., 2004; Dall et al., 2005; Polnaszek & Stephens, 2014). Alarm calling is one form of public information that could vary with individual reliability. This variation can be as a consequence of: i) developmental effects (e.g. Seyfarth & Cheney, 1986); ii) strategic manipulation by individuals deliberately signalling incorrectly to draw a response from receivers (e.g. Flower, 2011; Polnaszek & Stephens, 2014); and iii) environmental variation (e.g. Polnaszek & Stephens, 2014). Such variation may then select for individuals to monitor the reliability of alarm callers and alter their responses based on caller reliability (Cheney & Seyfarth, 1988; Hare & Atkins, 2001; Blumstein et al., 2004; Pollard, 2011).

Sentinel behaviour is one form of anti-predator behaviour that may show individual variation based on the reliability of information signalled by the sentinel (e.g. Radford et al., 2009, 2011). Sentinels provide benefits to groups in terms of predator detection and increased foraging success (Hollén et al., 2008; Bell et al., 2009; Bednekoff, 2015). However, these benefits depend on the sentineling individual's reliability, because group members are likely to adjust their responses based on how reliable individual sentinels are (Radford et al., 2009, 2011). The presence of an unreliable alarm caller as sentinel can have pronounced implications for group mates, due to; i) costs of reacting to incorrect alarm calls; ii) costs of not being informed about genuine predator threats and; iii) costs of having to increase personal vigilance to compensate for the unreliability of the sentinel; with these costs affecting survival, foraging efficiency and reducing the time individuals spend on other behaviours (e.g. Ydenberg & Dill, 1986; Lima & Dill, 1990; Bednekoff, 1997; Hare & Atkins, 2001). Therefore, where variation in the reliability of anti-predator information is associated with age and experience (e.g. Seyfarth & Cheney, 1986; see Hollén & Radford, 2009), individuals may be selected to alter their behaviour in the presence of juvenile, inexperienced sentinels. This may involve individuals ignoring the anti-predator information given by such juveniles (akin to Cheney & Seyfarth, 1988; Hare & Atkins, 2001); or experienced individuals may be selected to accompany juvenile sentinels so as to provide their own anti-predator information or even to accelerate the acquisition of reliable anti-predator behaviour of these naïve individuals to improve their reliability, by teaching them.

Recognising teaching requires that we identify that; A) Individuals alter their behaviour in the presence of naïve individuals. B) This change in behaviour must be costly for the actor. C) This change in behaviour speeds up the learning process by naïve individuals (Caro & Hauser, 1992). Despite considerable attention, unambiguous identification of teaching behaviour in the wild is rare, (see Thornton & Raihani, 2008; Kline, 2015). Also, to my knowledge, there are no current reports of teaching of anti-predator behaviour in any species so far, although teaching has been reported for foraging-related behaviours (e.g. Franks & Richardson, 2006; Thornton & McAuliffe, 2006; Raihani & Ridley, 2008; Hoppitt et al., 2008). Sentinel behaviour and alarm calling in cooperative groups seem to be good candidates for teaching because; adult direct fitness is strongly and immediately affected by the quality of anti-predator information; and anti-predator behaviour frequently has a strong socially learned component (Curio et al., 1978; Mineka & Cook, 1988; Brown & Laland, 2001; Griffin & Evans, 2003; Griffin, 2004; Magrath et al., 2015a & b). Therefore, species that employ such behaviours may be appropriate for studying the possibility of anti-predator teaching.

The Southern Pied Babbler, *Turdoides bicolor*, (henceforth pied babbler or babbler) a cooperatively breeding passerine of semi-arid Southern Africa, is a good species to investigate the possibility of teaching of sentinel behaviour and alarm calling. They are appropriate because, in this species, all group members periodically contribute to sentinel behaviour, adopting an exposed position >1m above ground level, scanning for threats whilst giving a quiet sentinel call (which can inform foraging birds of reduced threat level, and so allow foragers to be less vigilant and increase foraging efficiency; Hollén et al., 2008; Bell et al., 2009) and giving alarm calls in response to predators (Bell et al., 2009). However, individuals can be error-prone, with up to 57% of alarms observed in this study (n=615 alarm calls with identified threat) being given to innocuous threats; although true threats are rarely missed (up to 98.4% of all true threats may be alarmed at; Ridley et al. 2010). Therefore, individuals may have been selected to teach others in order to improve the reliability of these other individuals, and so reduce the number of incorrect alarms calls given.

I observed that pied babblers would frequently overlap in their sentinel behaviour, especially adults appearing to accompany juveniles. This raised the question of why multi-individual sentinel behaviour (MIS) occurred, when there are costs associated with conducting sentinel behaviour (Ridley et al., 2013; Chapter 3 of this thesis), and one individual is sufficient to provide effective protection (Hollén et al., 2008; Bell et al., 2009; Ridley et al., 2010). I hypothesised that this behaviour represented adults adaptively accompanying less reliable individuals (in particular juveniles because they would be more naïve and so less reliable alarm callers due to a lack of experience) in order to teach them to be better sentinels.

To investigate whether MIS represents anti-predator teaching I asked whether MIS fitted with Caro & Hauser's (1992) three features of teaching. This work did not investigate the 2nd feature – whether there is a cost involved in the behaviour – because this has been previously shown (Ridley et al., 2013; Chapter 3). Therefore the questions I specifically asked were 1) do experienced individuals modify their behaviour in the presence of naïve individuals? and 2) does reliability change due to MIS? For MIS to represent teaching, I predicted that adults would accompany juvenile sentinels more than other adults and that this would be because juveniles were less reliable alarm callers, and thus I expected that an experimental reduction of perceived individual reliability would lead to that individual being accompanied more when acting as a sentinel. I then predicted that juveniles that were accompanied by other individuals more when acting as sentinel would be more reliable alarm callers once adult. If MIS was not involved in anti-predator teaching, I hypothesised MIS may be an adaptation to reduce the foraging costs for group members caused by unreliable sentinels. I therefore asked a final question: 3) do foragers alter their behaviour when a less reliable bird is sentinel and when that individual is accompanied by other individuals? I predicted that foragers would be more vigilant in the presence of naïve sentinels, but they would reduce their vigilance when the naïve individual was accompanied by another individual.

4.3 Methods

4.3.1 Study Site & Population

I studied a colour-ringed, habituated population of pied babblers (total group size 2-12 individuals) in the Southern Kalahari, on the Kuruman River Reserve and surrounding farmland, Van Zylsrus, Northern Cape, South Africa (26º58′S, 21º49′E) (see du Plessis et al., 2012 for climate details). The study took place between Jan-May 2014, Sept-Oct 2014 and Jan-Mar 2015. During each data collection period I classified individuals as juveniles if they had hatched within that current breeding season (usual breeding season Sept-Apr).

4.3.2 Data Collection

4.3.2a Do experienced individuals modify their behaviour in the presence of naïve individuals?

To assess whether there was a change in behaviour when juveniles (assumed more naïve than adults) were sentineling rather than adults I investigated individual differences in being accompanied when acting as sentinel. To ascertain individual levels of being accompanied, I followed groups for an hour and recorded all sentinel bouts, where sentinel bout duration could be accurately recorded, along with the amount of overlap between individuals on guard (2242 sentinel bouts from 114 observation hours at 15 groups, amounting to 557 observation hours of 110 individuals; average sentinel bout length 108.3 ± 2.7s). I recorded timings using the stopwatch function on either a Nokia 6300 mobile telephone (Nokia, Espoo, Finland) or Garmin etrex 10 (Garmin Ltd. Or its subsidiaries, Schaffhausen, Switzerland).

I also investigated whether there were any differences in alarm call reliability, which might support the idea that juveniles were more naïve. To identify alarm call reliability levels, and so identify if there may be a difference in reliability between adults and juveniles, I recorded caller identity (to at least age class – adult or juvenile) and threat type whenever possible when an alarm was given, excluding any alarms elicited by a group all at once (615 alarms with appropriate data, collected at 18 groups out of >1400 observed alarms). Of those alarms where I could record threat type and caller ID I classed threat type as correct (n=152), incorrect (n=353) or mid (n=110). Correct alarms were those given to an appropriate species – these may be species that are predators of pied babblers and also large birds of prey which may not attack babblers. Incorrect alarms were those given to things that do not pose a threat to pied babblers such as doves and grass blowing in the wind as well as alarms given during play. Mid-level alarms were those given to species that can pose a threat but can also be tolerated by babblers; for instance fork-tailed drongos (*Dicrurus adsimilis*) can act as kleptoparasites of pied babblers, but also will act as honest sentinels (Flower, 2011; Radford et al., 2011; Flower et al., 2014).

To investigate whether reliability may be the driver of how much individuals are accompanied as sentinel, I conducted a playback experiment to determine whether group-mates reacted to a decrease in perceived sentinel reliability (i.e. an individual appearing more naïve), and this of course may apply to both adults and juveniles. For this experiment sound recordings were taken of alarm calls, and foraging contact calls as a control, from both adults and juveniles. Alarm calls fall on a spectrum from low-high intensity, assumed to relate to the urgency for a response to counteract the threat. The alarm calls I selected for playback were those of at least a medium intensity, with categorisation made in real time by observers. The exact threat was not always known for each alarm, but the calls that were used had a similar structure when viewed as spectrograms in Raven Pro 1.4 (The Cornell Lab of Ornithology, Ithaca, NY) or given in a high urgency situation (i.e. a predator was nearby), and so were assumed to convey the same information. Considering instead foraging contact calls, these calls are given very frequently by individuals (c.8-13 calls per minute, Radford & Ridley, 2008), and are used to regulate spacing, as well as indicating the profitability of a food resource (Radford & Ridley, 2008; Golabek, 2010). Therefore, my contact call playback should not have an influence on the sentinel behaviour of group-mates.

Calls were collected using a Sennheiser directional microphone (Sennheiser, Wedemark, Germany), saved in WAV format (Marantz, Kanagawa, Japan) onto a Marantz recorder with sampling rate of 44.1 kHz (16-bit resolution). I built and standardised tracks using Raven Pro 1.4 to average dB levels (alarm calls at 95.3dB; foraging calls at 85.5dB, both at 2m distance from recorder) using the Max Power function. Each track consisted of a single repeat element of a call – a single alarm or contact call – surrounded by 1-2 seconds of background noise from the respective group's territory.

For the experiment, after I located a group, I initially followed them for an hour, recording all sentinel events and the amount of MIS. I then played back 2 calls (either alarm or foraging contact call) while there were no observable threats in the vicinity, with the 2nd playback within 30 minutes of the 1st (optimally within 15 minutes). This should represent a high rate of incorrect alarm calling, because pied babbler sentinels in a group only give 3.6 alarms per hour on average (Bell et al., 2009). If any natural alarms occurred, or a predator was seen by the experimenter, I left at least 5 minutes for the group to return to normal behaviour or the predator to leave the area. After the playback, I followed the group for another hour, again recording sentinel event duration and the amount of MIS, so as to ascertain how the group altered their behaviour following manipulation.

I played back tracks using a standardised Shoqbox (Phillips, Amsterdam, Netherlands) or Jambox speaker (Jawbone, San Francisco, USA) connected to either an Archos 604 Wifi MP4 player (Archos, Igny, France) or Samsung R519 laptop (Samsung, Seoul, South Korea). Pied babblers have been shown to have individually distinct calls (although possibly not stable; Humphries et al., 2016), and this species may be capable of individual recognition by vocal characteristics (Humphries, 2013). To control for the possibility of individual recognition I hid the playback speaker in vegetation in the direction of the experimental bird from the rest of the group, while that bird was slightly distant so that it would appear to the rest of the group that the experimental individual gave the alarm. To further reduce the impact of possible vocal individual recognition, the calls selected to be played back were originally elicited by the respective experimental individuals.

4.3.2b Does reliability change due to multi-individual sentineling?

To answer whether reliability changes due to MIS I, again, used observational data of individual reliability scores and individual rates of being accompanied when acting as sentinel. I used the same data collected as above.

4.3.2c Do foragers alter their behaviour when a less reliable bird is sentinel and when that individual is accompanied by others?

To ascertain the level of personal vigilance under different sentinel conditions, I conducted paired focals on foraging individuals, a) with an adult on guard, b) with a juvenile on guard (an assumed naïve individual), and c) with a juvenile sentinel accompanied by an adult. Paired observations involved separate focal watches on the same focal forager during the same observation session. I videoed foraging individuals using a Samsung HMX-F80 Video Recorder (Samsung, Seoul, South Korea), and reviewed video data later for accurate blind coding of behaviours. I intended to collect focals of foraging individuals when there were two adults acting as sentinel, but, unfortunately by stochastic chance there were insufficient opportunities to gather video recordings under this condition when collecting these data.

4.3.3 Analyses

Across all analyses, I calculated an individual's rate of being accompanied as the proportion of an individual's time acting as sentinel when there was an experienced bird acting as sentinel simultaneously (see Appendix C for why I selected this measure). I excluded any sentinel activity that was a direct response to a perceived threat or part of a group movement, whereby group-members take up an elevated position to scan for threats before the group flies to a new location (*pers. obs.*). I did this because such data might distort my results by increasing the amount of observed sentinel overlap in the dataset that was not a result of sentinel reliability.

When I conducted analyses incorporating caller reliability, I calculated reliability as the proportion of alarms given that were correct. In order to retain as much of the data I collected as possible, and for my response variable to take a binomial distribution, I ran separate analyses that treated mid-level alarms as either correct or incorrect. I found no qualitative difference in the results generated by most of these separate analyses, and so I arbitrarily present only the cases where mid-level alarms are considered incorrect. Model outputs where mid-level alarms were considered correct, and any differences in final model outputs are presented in Appendix C.

I analysed data using lmerTest package version 1.2-0, (Kuznetsova et al., 2013) for linear mixed effects models (LMM) and lme4 for generalised mixed effects models (GLMM: Bates et al., 2012), using the R Commander interface (Fox, 2005) in R version 2.15.2 (R Core Team, 2012). I generated final models by conducting backwards stepwise elimination, and retained random effects throughout.

4.3.3a Do experienced individuals modify their behaviour in the presence of naïve individuals?

To assess whether experienced individuals modified their behaviour in the presence of juveniles, I investigated whether juveniles (i.e. individuals assumed to be more naïve) were more or less likely to have another individual acting as sentinel at the same time as them than adults. I ran a LMM with the response variable of the rate an individual was accompanied. The fixed effects in the model were age of the individual (adult or juvenile) and group size (defined here as the number of individuals in the group contributing to cooperative behaviours; see Appendix C for discussion of this), and random effects were individual and group ID. To confirm that any results were not biased by individual differences I ran a GLMM with a Poisson distribution response, using only the individuals I observed both as juveniles and adults. The terms used in this model were the same as for the above model.

Because I hypothesised that individual rates of being accompanied were driven by individual reliability, I then examined whether there was a difference in reliability between adults and juveniles. I ran GLMMs with a binomial response term of whether an alarm was correct or incorrect. I pooled all alarms given by adults and all alarms given by juveniles together and used age as a fixed effect. The random effect in the model was group ID.

To then test to what degree MIS was related to individual reliability, I used my experimental data to analyse how group mates respond to a reduction in reliability of individuals. I used LMMs to investigate how much experimental individuals' rate of being accompanied changed after manipulation. Fixed effects were the year I collected the data in, playback trial type (alarm or foraging contact call), group size (again defined as the number of individuals in the group contributing to cooperative behaviours; see Appendix C), and the experimental individual's rate of being accompanied in the 1st hour of the trial. Random effects were group and individual ID. I ran separate models for adult and juvenile experimental individuals.

I also investigated if experiments caused group-wide effects by investigating whether experiments affected the rate all non-experimental individuals were accompanied by another individual when acting as sentinel. Fixed effects were trial type, group size (again defined as the number of individuals in the group contributing to cooperative behaviours; see Appendix C), data collection year and the combined rate of accompaniment for all non-experimental sentinels in the 1st hour of the trial. Random effects were group ID and experimental individual ID. Again, I analysed juveniles and adults separately. However, for the juvenile model in this analysis, the fixed effect of the rate of being accompanied in the 1st hour was negatively skewed and so I transformed this term by "reflecting" the data (Munro, 2005). This involved taking the largest value and adding 1 to it and then subtracting the raw data from this value (Munro, 2005). The resulting values were then $\log_{10}$ transformed.

4.3.3b Does reliability change due to multi-individual sentineling?

To investigate whether accompanying juvenile sentinels influenced their rate of development of anti-predator recognition I ran models with the response variable of an individual's change in reliability from when they were juvenile to when they were adult. The fixed effects of the model were an individual's average rate of being accompanied when they were juvenile, and individual reliability when juvenile. The random effect was group ID. When mid-level alarms were considered incorrect I used a GLMM with a Poisson distribution (although note when mid-level alarms were considered correct I used a LMM). Because using a Poisson distribution requires values to be ≥ 0, I transformed the response variable by adding $^{1}/_{3}$ (the lowest negative value in the dataset) to each value.

4.3.3c Do foragers alter their behaviour when a less reliable bird is sentinel and when that individual is accompanied by others?

To investigate whether foragers alter their personal vigilance based on the category of sentinel (adult, juvenile or accompanied juvenile) I ran Friedman tests using paired observations. For comparisons involving MIS, the individuals involved in the MIS event were also the individual sentinels for the lone adult or juvenile sentinel conditions. When there were multiple possible focals to select from for a given focal forager, then the focal that was longest was selected. Multiple paired observations could result from the same observation session if there were multiple focal foragers.

Then to investigate whether the reliability of the main sentinel affects forager vigilance, I ran LMMs with a response term of the proportion of time a forager spent vigilant. This term was normalised by square root transformation and then the subsequent value +1 was $\log_{10}$ transformed. Fixed effects were the reliability of the main sentinel and the number of adults in the group. Random effects were focal forager ID, group ID and the ID of the main sentinel. When only one individual was acting as sentinel they were automatically the main sentinel, but in a MIS event, the main sentinel was assumed to be the adult.

4.4 Results

The tables I present in the main text are only those relevant to the figures. The tables of the final outputs of all other models are in Appendix C.

4.4a Do experienced individuals modify their behaviour in the presence of naïve individuals?

Adults are more reliable alarm callers than juveniles (adult 31.9%, juvenile 8.5% correct; z=5.77, p<0.001) (Table 4.1 & Appendix C; see Figure 4.1a), and juvenile sentinels were accompanied for a greater proportion of time than adults (juveniles 47.3 ± 2.7%; adults 16.7 ± 1.5%; t=11.63, p<0.001; Table 4.2; Figure 4.1b). Additionally, as individuals aged into adulthood they were accompanied for a smaller proportion of the time when acting as sentinel (10.5 ± 3.1%) than when juvenile (38.0 ± 4.3%; z=2.67, p=0.01) (see Appendix C). Group size did not significantly influence how much an individual was accompanied and the term was not retained in final outputs.

Table 4.1 Table showing the final output of a GLMM with a binomial distribution response investigating whether juveniles are less reliable than adults, when mid-level alarms are considered incorrect. 615 alarms collected at 18 groups.

Fixed Effect	Estimate	Standard Error	z	p
Intercept	0.76	0.10	7.29	<0.001
Age	1.62	0.28	5.77	<0.001
Random Effect	**Variance**	**Standard Deviation**		
Group ID	<0.001	<0.001		

In playback experiments juvenile sentinels were accompanied for a greater proportion of time after playback of alarm calls (0.37 ± 0.10) compared to foraging call playbacks (-0.17 ± 0.13; t=2.86, p=0.01) (Table 4.3). This was the same for adult individuals (alarm call, 0.28 ± 0.07; foraging call, -0.04 ± 0.04; t=4.25, p<0.01; Table 4.4; see Figure 4.2). Juvenile sentinels in larger groups were also more likely to be accompanied more after manipulation, and if they had been accompanied for a smaller proportion of time before playbacks (Table 4.3). This was not the case for adults, and these terms were not retained in the final adult model (Table 4.4). Data collection year had no effect on either juvenile or adult experiments and the term wasn't retained (Tables 4.3 & 4.4).

Table 4.2 Table showing the final output of a LMM investigating whether juveniles are accompanied more than adults. 557 observations of 118 individuals from 114 observation hours at 15 groups.

Fixed Effect	Estimate	Standard Error	t	p
Intercept	0.17	0.02	7.14	<0.001
Age	0.31	0.03	11.63	<0.001
Non-Retained Term	**t**	**p**		
Group Size	0.31	0.76		
Random Effects	**Variance**	**Standard Deviation**		
Individual	<0.001	<0.001		
Group ID	<0.001	<0.001		

Groups showed a relative increase in the overall rate of MIS after adults' alarm call playbacks (0.17 ± 0.06) compared to adult foraging call playbacks (-0.12 ± 0.06; t=2.51, p=0.02; see Appendix C). This was not significantly the case for trials where juveniles were manipulated (change in MIS rate after alarm calls, 0.03 ± 0.05; change in MIS rate after foraging calls, -0.08 ± 0.04; t=1.78, p=0.09; see Appendix C). Data collection year, the overall rate of MIS prior to playback and group size all did not significantly affect responses to adult and juvenile trials, and group size and collection year were not retained final models (see Appendix C).

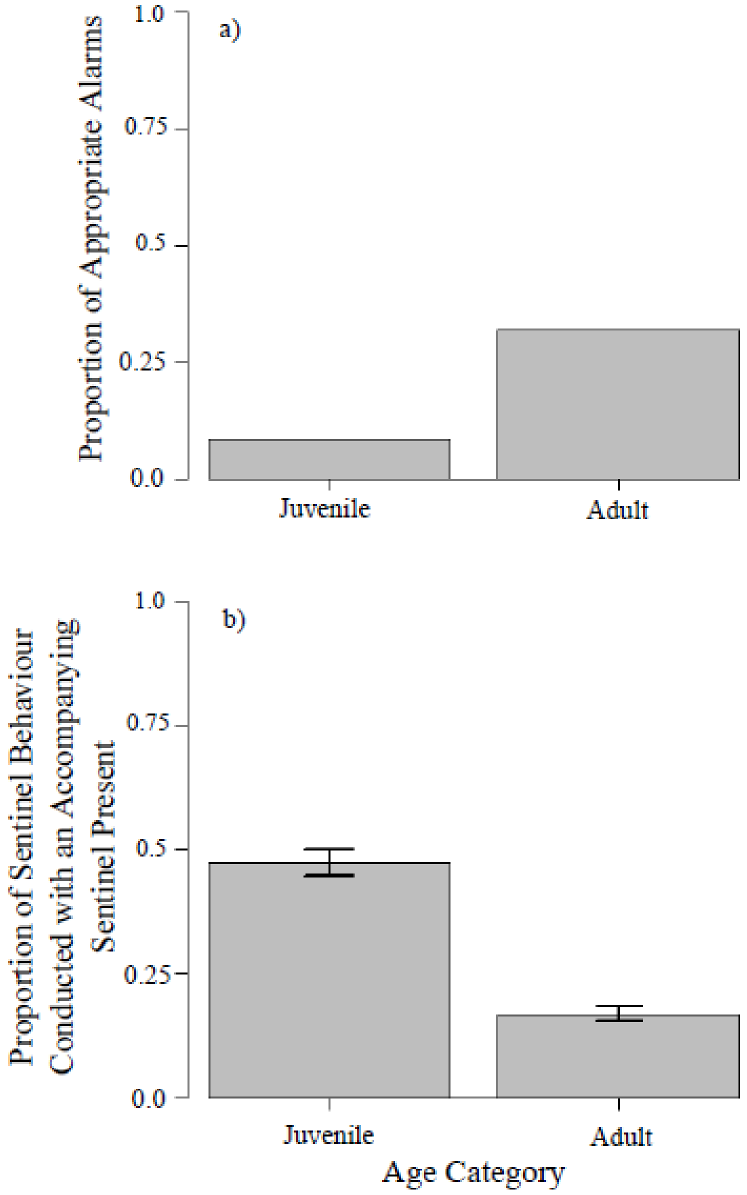


Figure 4.1 Figure showing a) the proportion of all alarm calls given by either juveniles or adults that are given to an appropriate threat (when mid-level alarms are considered incorrect) and b) the raw mean ± standard error proportion of time juvenile or adult sentinels were accompanied.

4.4b Does reliability change due to multi-individual sentineling?

There was no correlation between the average rate a juvenile sentinel was accompanied and the change in their reliability as they age, with the term for the rate a juvenile sentinel was accompanied not being retained in final models (see Appendix C). When mid-level alarms were considered incorrect, the reliability of an individual when they were juvenile also had no effect in the change of an individual's reliability as they age (z= -0.59, p=0.56; see Appendix C).

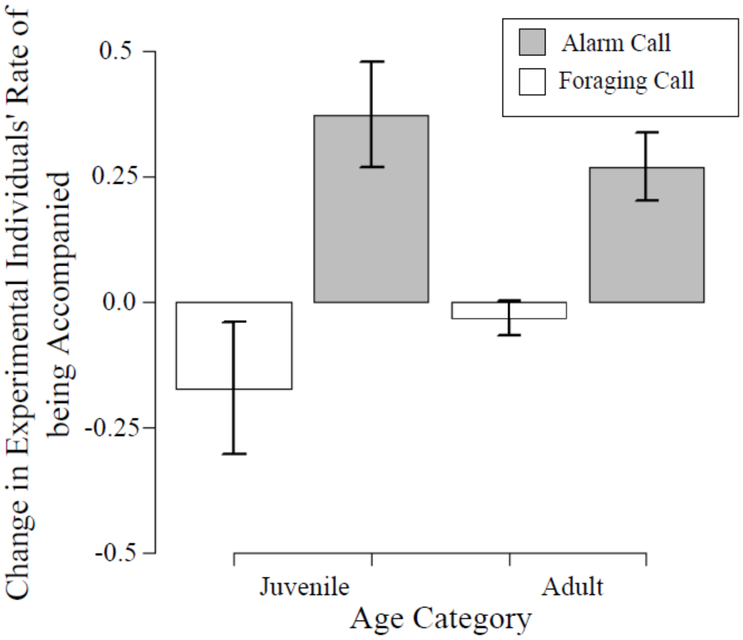


Figure 4.2 Figure showing the raw mean ± standard error change in the proportion of time that an experimental individual is accompanied by others when acting as sentinel, following either foraging call (white bars) or alarm call (grey bars) playbacks, by age category.

4.4c Do foragers alter their behaviour when a less reliable bird is sentinel and when that individual is accompanied by others?

When an adult acted as sentinel, forager vigilance was no different from when a juvenile acted as sentinel (median proportion of time vigilant with adult sentinel 0.03, IQR 0.04; median proportion of time vigilant with juvenile sentinel 0.02, IQR 0.07; Friedman $\chi^2=0.05$, df=1, p=0.82, n=21 pairs). MIS also did not affect forager vigilance, because when juveniles sentineled alone forager vigilance was no different from when juveniles were accompanied (median proportion of time vigilant with juvenile sentinel 0.01, IQR 0.02; median proportion of time vigilant under MIS 0.01, IQR 0.04; Friedman $\chi^2=0.09$, df=1, p=0.76, n=11 pairs); and when adults sentineled alone forager vigilance was no different from when adults accompanied a juvenile (median proportion of time vigilant with adult sentinel 0.03, IQR 0.03; median proportion of time vigilant under MIS 0.01, IQR 0.05; Friedman $\chi^2=1.14$, df=1, p=0.29, n=17 pairs).

Table 4.3 Table showing the final output of a LMM investigating the effect of alarm and foraging call playback on the rate of accompaniment of an experimental juvenile individual when acting as a sentinel. 23 trials, 12 alarm call playbacks and 11 foraging call playbacks. Data collected at 8 groups.

Fixed Effects	**Estimate**	**Standard Error**	**t**	**p**
Intercept	-0.37	0.29	-1.29	0.21
Trial Type	0.37	0.13	2.86	0.01
Rate Accompanied in 1st Hour	-0.86	0.20	-4.20	<0.001
Group Size	0.16	0.07	2.25	0.04
Non-Retained Term	**t**	**p**		
Data Collection Year	0.87	0.40		
Random Effects	**Variance**	**Standard Deviation**		
Individual	0.00	0.00		
Group ID	0.00	0.00		

There was no evidence that main sentinel reliability influenced forager vigilance (t=1.40, p=0.18). The number of adults in the group did not influence forager vigilance either, and the term was not retained in final models (see Appendix C).

Table 4.4 Table showing the final output of a LMM investigating the effect of alarm and foraging call playback on the rate of accompaniment of an experimental adult individual when acting as sentinel. 23 trials, 11 alarm call playbacks and 12 foraging call playbacks. Data collected at 12 groups.

Fixed Effect	**Estimate**	**Standard Error**	**t**	**p**
Intercept	-0.03	0.05	-0.53	0.60
Trial Type	0.30	0.07	4.25	<0.01
Non-Retained Terms	**t**	**p**		
Rate Accompanied in 1st Hour	0.01	1.00		
Group Size	0.33	0.75		
Data Collection Year	1.57	0.13		
Random Effects	**Variance**	**Standard Deviation**		
Individual	<0.001	<0.001		
Group ID	<0.001	<0.001		

4.5 Discussion

My results show juveniles produced fewer appropriate alarm calls than adults and were accompanied more than adults when acting as sentinel. The results also suggest that group members accompanied sentinels more when they were made to appear less reliable. However, how much a juvenile sentinel is accompanied did not influence the development of alarm-calling reliability, and sentinel reliability did not affect forager vigilance.

By Caro & Hauser's (1992) definition, three features of a behaviour must be confirmed for it to represent teaching. The first of these is that experienced individuals alter their behaviour in the presence of naïve individuals. This work implies this because juvenile sentinels are more likely to be accompanied by adults when acting as sentinel. My observations suggest that this may be being driven by alarm call reliability, because juveniles were more likely to give incorrect alarm calls than adults. My experiment gave further evidence for the relationship between individual reliability and the rate an individual sentinel was accompanied because sentinels were accompanied more after being manipulated to appear less reliable. This in itself gives further evidence to suggest that pied babblers may be capable of individual recognition and might be able to monitor the reliability of group-mates (see also Appendix C, Humphries, 2013). Individual recognition is a complex trait that is now widely recognised in many taxa (see Tibbetts & Dale, 2007) and this work adds to a burgeoning number of studies to have previously shown its existence (e.g. Godard, 1991; Tibbetts, 2002; for review see Tibbetts & Dale, 2007).

The next feature of teaching is that the behaviour is costly to the actor. While this work has not investigated it, previous work by Ridley et al. (2013) and my work in Chapter 3 has shown that sentinel behaviour is costly to individuals in this system in terms of increased predation risk and reduced body mass gain. Therefore, increasing one's contribution to sentinel behaviour may be assumed to be costly.

The final point from Caro & Hauser (1992) to show that teaching is present is that the behaviour in question leads to increased learning. In this study I did not find evidence for a relationship between a juvenile sentinel's rate of being accompanied and the change in their reliability as they age. I should note, however, that there may have been difficulties with the data when trying to analyse this. For instance, it is very difficult to recognise when an individual in the wild is truly naïve, and unless individuals are followed constantly, it is impossible to know what experience each one will receive. Additionally, I had to use long-term measures of reliability because I could not be guaranteed sufficient numbers of alarm calls from an individual on any given day. This, in itself, may actually be a poor measurement of reliability because individuals' reliability is probably a very plastic trait, varying day-to-day; and my experimental manipulations of individual reliability show how there can be such short-term responses to reliability alterations. In the absence of such data though, the available results do suggest that MIS is not related to teaching, and my forager vigilance work showed no evidence that MIS was an adaptive way to increase group foraging success. What role does MIS play then?

While accompanying an individual may not represent teaching, individuals may still be selected to actively accompany certain individuals – in particular juveniles – because they may be at particular risk. In this species, sentinel behaviour does carry a cost in terms of increased predation risk (Ridley et al., 2013), and evidence from this chapter shows that juveniles are particularly unreliable at identifying predators (however, more work should be done to provide evidence to show that juveniles fail to alarm at true predators, in addition to the work I have done that suggests they alarm frequently at things that do not pose a threat). MIS may, therefore, represent a form of sentinel "babysitting".

Babysitting has been recorded in several species, with individuals spending some of their time, possibly away from the rest of the group, guarding young that may not be their own (e.g. Clutton-Brock et al., 1998; Cant, 2003; White & Cameron, 2011); and there may be consistent differences between individuals in how much they contribute to such cooperative behaviours (e.g. Sanderson et al., 2015). Individuals in a cooperative species may also increase their contributions to sentinel behaviour when there are vulnerable, dependent young present (e.g. Santema & Clutton-Brock, 2013). Thus, MIS may represent a similar form of protection for more vulnerable individuals. My experimental results in part support this, with experimental individuals being accompanied more after playbacks to make them appear less reliable, and so possibly more vulnerable to predation (although, again, it should be checked to what extent individuals may fail to recognise true predators as well as alarming at non-threats). Further investigation of this would require more work and analyses, such as whether all juveniles are accompanied more after alarm calls, as they may be the most vulnerable individuals, and further investigations into to what extent certain individuals are targeted for accompaniment (see Appendix C for preliminary analyses towards this). However, there remains the question of "why are there group-wide increases in accompaniment of sentinels after an adult alarm playback?".

Following the above logic, an increase in accompaniment for all individuals may be due to a perceived increase in vulnerability for all individuals. However, alternatively, with increased threat, individuals may independently act as sentinel more often leading to increased sentinel overlap, or more individuals may be required to scan for predators. The difference in effects of adult and juvenile playbacks on overall group MIS may support this hypothesis. Because adults are generally more reliable sentinels than juveniles, there may be a greater likelihood that groups may consider an adult alarm playback to be correct even though they did not see a predator, when they may not do so for unreliable individuals (i.e. juveniles). The group response may then be to have more individuals acting as sentinels to scan for possible threats after adult alarm playbacks but not juvenile playbacks. This is what occurred (see Appendix C for further discussion on this point). Additionally, because unreliable sentinels may increase predation risk for the group, it may be adaptive for other group members to act as sentinel at the same time as unreliable sentinels so as to reduce predation risk. This may then also manifest itself in the age category difference between adults and juveniles, given that juveniles are generally less reliable than adults, and juveniles are accompanied more when acting as sentinel. Therefore, MIS may be an anti-predator behaviour to reduce predation risk.

In this work I provide evidence that individuals can effectively monitor the reliability of other individuals, and alter their behaviour based on this knowledge. This study identifies a new behaviour – multi-individual sentineling – and I find that this behaviour is particularly driven towards unreliable individuals. This work does not provide sufficient evidence for this behaviour to represent teaching; and alternatively multi-individual sentineling may represent alternative anti-predator behaviours, although further work may be needed to investigate these possibilities. However, while I do not find evidence that predator recognition teaching takes place in wild populations, I suggest that such anti-predator teaching should be adaptive, and I encourage future studies to attempt to see how wide-ranging it may be.

Chapter 5: Do Pied Babblers Relay Information from the Nest to the Foraging Group?

5.1 Abstract

To optimise reproductive output, individuals must trade-off offspring growth with predation risk. Returning to a nest too often alerts predators to the nest's presence; therefore, if a threat is nearby, provisioners should return to the nest less frequently. As such, provisioners should be selected to use information about nest threats and mediate their behaviour accordingly. This information can be gathered personally; by observing others' behaviour; or by individuals actively communicating. In Southern Pied Babblers, *Turdoides bicolor*, gathering information about nest threats personally, and observing others' behaviour may not be possible. If, instead, individuals communicate about nest threats, then information provided to one individual should affect group-mates' behaviour. Therefore, I played back heterospecific mobbing or context neutral calls to lone nest provisioners. Once that individual left the nest to return to the foraging group I recorded the time until the next feeding event. However, playback type did not influence nest visit rates, suggesting individuals did not communicate about possible nest threats. I suggest offspring need may be a greater driver of provisioning effort instead. Additionally, babblers have evolved other mechanisms to reduce nest predation, including multi-individual nest visits and early fledging age, making the evolution of other mechanisms less likely.

5.2 Introduction

In order to optimise reproductive output, it is adaptive for individuals to make trade-offs (see Alonso-Alvarez & Velando, 2012). These trade-offs include those between the size and number of offspring (Sinervo & Licht, 1991), current and future reproduction (e.g. Williams, 1966b; Trivers, 1972), or offspring growth and predation (e.g. Skutch, 1949; Martin et al., 2000; 2015; Martin, 2015). The trade-off between offspring growth and predation threat involves the rate of provisioning by adults. By returning more often to a nest, individuals can increase the amount of food delivered to dependent juveniles, which increases the quality of the young (Eggert et al., 1998). However, while in the nest the juveniles are not mobile, and so by returning to the same location more often, predators may be alerted to the presence of the juveniles (Skutch, 1949; Martin et al., 2000). Therefore, the optimal rate of return will be determined by offspring need and the relative predation risk.

To determine the optimal rate of nest visits, individuals require information about the conditions at the nest, and the condition of the nestlings. This information can be derived from three different sources. The first of these is that individuals can gather information personally (e.g. Redondo & Castro, 1992; Kilner, 1995). This is a very simple idea that would involve an individual personally observing conditions at the nest; for instance observing whether there is a predator nearby and then altering their behaviour accordingly. There are, however, issues with using such a method. For this to be a viable method individuals should be returning to the nest frequently, which would thus negate the benefit of minimising nest visits to reduce nest predation risk. Additionally, in species where there are multiple individuals contributing to nestling provision, such as cooperative breeders, individuals will visit the nest less often and have fewer opportunities to gather information personally. Therefore, gathering information about conditions at the nest personally may not be viable.

An alternative method individuals can use to gather information about conditions at the nest would be to use indirect information from other individuals by observation of collaborator effort (e.g. Hinde, 2006). Here an individual observes the amount of effort another individual gives and decides how much personal effort is required based on this amount. However, using this method has many shortfalls. All individuals cannot use only this method to collect information, because it requires at least one individual to be personally assessing the nest conditions. Additionally, conditions at the nest are not the only factors that can affect collaborator effort. Individual contributions to cooperative behaviours can be state dependent (Clutton-Brock et al., 1999; 2001; Bell et al., 2010; Chapter 3) and so basing decisions on the behaviour of others may lead to a maladaptive rate of nestling provisioning. Therefore, other methods of gathering information may be more adaptive.

The final method is for individuals to actively communicate about nest conditions, something that has not been previously investigated. In fact, despite the possibility that active communication about distant locations may be adaptive, there has been very little documented evidence to suggest that it occurs in any context - the clearest example of animals using active communication comes from bees using their dance language to inform colony members about the possible food sources (von Frisch, 1967). Therefore, I set out to investigate whether such a behaviour may occur when individuals are assessing risk at a nest. I tested whether individuals actively communicate to group members about predation risk at the nest when they return from feeding the nestlings in the Southern Pied Babbler, *Turdoides bicolor* (henceforth pied babbler or babbler). The pied babbler is particularly appropriate for investigating the possibility of active communication about nest threats. This is because foraging individuals can be a long way away from the nest (up to 1km. away, *pers. obs.*) and pied babblers can live in groups of up to 15 individuals, limiting the number of nest visits per individual if all group members contribute to nestling provisioning. Thus, there should be few opportunities for collecting personal information. Using collaborator effort may not be the viable either, because individual contributions to cooperative behaviours can be state dependent (Bell et al., 2010; Chapter 3) and so the rate an individual returns to feed the nestlings may not be directly related to the conditions at the nest. Therefore, I proposed that pied babblers may instead actively communicate about conditions at the nest. This would involve individuals relaying information to group mates about possible nest threats when they return to the foraging group from the nest, and pied babblers do give a distinct call when they either return from the nest or conclude a sentinel bout (see Hollén et al., 2011; *pers. obs.*). Active communication about predator presence near to the nest may be especially beneficial, because not only would the nestlings be at greater risk if adults returned too frequently (Skutch, 1949; Martin et al., 2000), but the adults themselves would also be putting themselves at greater risk by approaching an area containing a predator.

To test whether individuals do actively communicate about possible nest threats I conducted a playback experiment. If pied babblers were capable of active communication about nest conditions, then I expected that providing information to only one bird would influence the behaviour of its group mates too. Therefore, I conducted playbacks of heterospecific mobbing or context neutral calls near to nest trees when selected individuals returned alone to feed the nestlings. Foraging pied babblers respond to heterospecific alarms and mobbing calls (Ridley & Raihani, 2007a; Flower, 2011; Flower et al., 2014; Ridley et al., 2014 & *pers. obs.*) so I could be confident that individuals are able to recognise the information conveyed in these calls. I predicted that the time until the next nest visit would be greater when playing back mobbing calls compared to those playbacks when context-neutral calls were played. I predicted this, because if individuals were to communicate about nest conditions, then the other group members would know about the perceived threats after a mobbing call playback. Their response should then be to reduce their nest visit rate in order to avoid drawing predators' attention to the nest location.

5.3 Methods

5.3.1 Study Site & Focal Species

I carried out this study on the Kuruman River Reserve and surrounding farmland, in the Southern Kalahari Desert, Northern Cape Province, South Africa (26º58′S, 21º49′E; see du Plessis et al., 2012, for climate details) on a habituated population of pied babblers. Pied Babblers are cooperatively breeding, medium-sized passerines found predominantly in semi-arid conditions of Southern Africa. All group members contribute to a variety of cooperative behaviours, including nestling feeding (Ridley & Raihani, 2007b), with the nestling stage lasting approximately 14-18 days (Raihani & Ridley, 2007a). Offspring provisioning may be conducted by lone birds, or multiple individuals returning to the nest (Raihani et al., 2010). Nests suffer high predation rates, and young fledglings can be particularly vulnerable due to poor motor skills (Raihani & Ridley, 2007a; Raihani et al., 2010). Therefore, communication about possible predator threats near the nest may be adaptive.

5.3.2 Experimental Procedure

I collected mobbing and context neutral calls ad libitum from bird species on the Kuruman River Reserve and surrounding farmland using a Sennheiser directional microphone (Sennheiser, Wedemark, Germany) connected to a Marantz recorder and saved in WAV format (Marantz, Kanagawa, Japan) (sampling rate of 44.1 kHz, 16-bit resolution). Each recording did not include pied babbler calls.

Calls were extracted from recordings and ten second playback tracks were built using Raven Pro 1.4 (The Cornell Lab of Ornithology, Ithaca, NY), with 1-2 secs of background noise from the test group's territory inserted either side of the selected calls. I collected average amplitudes for individual calls using the Max Power function in Raven Pro 1.4 (context-neutral 85.7dB from 20 separate call units; mobbing 81.6dB from 20 separate call units; at 10m from the calling individuals) and I set tracks to playback with a maximum amplitude of these values. A total of 12 mobbing tracks were used from 5 different recordings, and 14 context neutral tracks from 5 separate recordings. I played back each track only once.

When nestlings were between 7 & 11 days old, I set up a Shoqbox speaker (Phillips, Amsterdam, Netherlands) approximately 10m away from the nest tree, connected to an Archos MP4 player (Archos, Igny, France). Over the course of an hour I played back up to 3 ten second tracks of heterospecific calls (either mobbing or context neutral) to a randomly selected provisioner, one for each of the first 3 times that individual returned to feed the nestlings alone. I then recorded the time until the next nest visit after the selected individual had left to return to the group. I repeated this structure in the following hour, using the opposite playback call type. I aimed to make 3 playbacks of each call type, but was not able to perfectly counter balance the experiment because frequently other individuals would be in the vicinity of the nest at the same time as the focal individual, or the focal individual would only make one or two nest visits over the course of an hour, and so I could not always conduct all 3 playbacks. I structured the experiment so that there would be an equal number of groups that would receive mobbing playbacks first as groups receiving mobbing playbacks second, and randomised which group would be exposed to the mobbing playbacks first.

5.3.3 Analyses

In order to investigate pied babblers' responses to my experiment, I conducted analyses using the R Commander interface (Fox, 2005) in R version 2.15.2 (R Core Team, 2012). I selected my final model using backwards stepwise elimination and retained random effects throughout. I used the package lmerTest version 1.2-0, (Kuznetsova et al., 2013) to conduct a linear mixed-effects model to investigate what affects the time between nest visits. As a fixed effect, I used playback type in an interaction term with playback order (whether the respective playback type was used first or second in the trial). I also use a fixed effect of group size and a random effect of group ID. Experimental individual ID was not used in the model because only one individual was tested per group and so this term would contain the same information as group ID. Because only 4 of my 12 mobbing call playbacks were conducted in the 2nd hour of trials, I also ran an analysis of only the playbacks that took place in the first hour of trials with fixed effects of playback type and group size, and random effect of group ID. This latter model gave qualitatively similar results to the other, and so in the main chapter I only present the results from the first model (a table of the results of the second model are presented in Appendix D).

5.4 Results

There was no difference in the time between nest visits between mobbing call (318.4 ± 72.7 secs) and context-neutral (286.2 ± 54.5 secs) playbacks irrespective of the playback order, with the terms not being retained in the final model (see Figure 5.1; Table 5.1). There was a trend for a positive correlation between group size and the time between nest visits, such that larger groups tended to have longer gaps between nest visits (t=2.22, p=0.06) (Table 5.1).

Table 5.1 Table showing the output of a linear mixed-effects model investigating the time between manipulated individuals leaving the nest and the next nest visit by any individual. Sample size 26 playbacks at 8 groups, 12 mobbing call playbacks (8 in first hour, 4 in second), and 14 context-neutral playbacks (8 in first hour, 6 in second).

Fixed Effect	Estimate	Standard Error	z	p
Intercept	-150.65	221.37	-0.68	0.52
Group Size	94.91	42.84	2.22	0.06
Non-Retained Terms	**z**	**p**		
Playback Type*Playback Position	0.47	0.66		
Playback Position	0.00	1.00		
Playback Type	0.29	0.78		
Random Effect	**Variance**	**Standard Deviation**		
Group ID	15865.00	125.96		

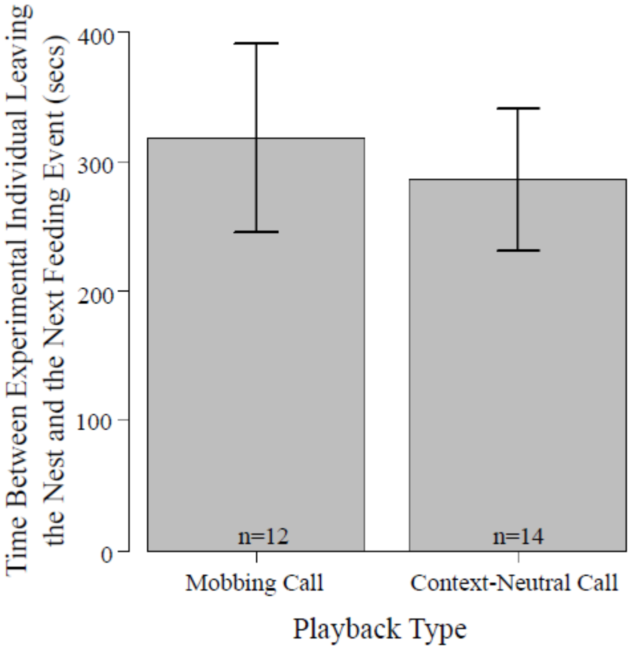


Figure 5.1 Raw mean ± standard error time between an experimental individual leaving the nest after a playback and the next feeding event at the nest by any individual (secs); for playbacks of either mobbing or context-neutral calls.

5.5 Discussion

My results show no difference in the time between nest visits by pied babblers following playbacks of either heterospecific mobbing or context neutral calls to an individual before they return to the foraging group. This suggests that pied babblers may not pass on information about predation threat at the nest to the rest of the group. This is despite the expected benefits of reducing nest detection by delaying returning to the nest when predators are nearby, in order to prevent nest predation. Why then did I not find evidence for it in this experiment?

I may not have found evidence for pied babblers passing on anti-predator information from the nest to the rest of the group because other behaviours have evolved to reduce predation at the nest instead. One of these that has been previously studied is having multiple birds return to the nest simultaneously (Raihani et al., 2010). This follows the same selective pressure as for why active communication about risk at the nest might evolve. By having multiple individuals return to the nest simultaneously fewer nest visits are required and this draws less attention to the nest, thus reducing predation risk (Raihani et al., 2010). Additionally, having multiple individuals return to the nest together reduces the likelihood that communication will be needed, because more individuals will be present at the nest to observe whether there is a predator present or not.

Another feature that has evolved in pied babblers to reduce predation risk at the nest is for juveniles to fledge very young, with group size determining how early they fledge (Raihani & Ridley, 2007b). With a high predation risk in the Kalahari, juveniles are selected to leave the nest very young because the longer individuals stay in the nest, the longer they are in one location, and this increases the risk that a predator may find this location (Raihani & Ridley, 2007b). By leaving the nest, juveniles are then mobile and, while still at risk because they are relatively immobile, adults may be able to move individuals away from more risky locations (e.g. Raihani & Ridley, 2007a).

If babblers are not using active communication between provisioners, what is the most likely system that they use to determine the rate of feeding at the nest?

Offspring need has been shown to determine parental resource provisioning (see Kilner & Johnstone, 1997 for a review). From personal observation, offspring need may predominate in this species because more nest visits were made in the first hour of trials than in the second. Trials commenced at first light, thus the chicks would not have been fed for several hours, and so would have been hungry. As the day proceeds they will be fed, becoming more satiated and will therefore require less provisioning. The trend for larger groups to have longer gaps between feeding (supporting previous evidence for this, Raihani et al., 2010) may also support this hypothesis, because if larger groups satiate nestlings quickly (e.g. by having more simultaneous nest visits (Raihani et al., 2010)) then nestlings are likely to beg less, as long as begging is an honest signal for this species.

Provisioners may determine offspring need by personal assessment, but there is still the possibility that individuals may be directly communicating to the foraging group about chick need. Pied babblers do sometimes give a distinctive call when they return to the group from the nest. This call is similar to that which may be given when an individual ends a sentinel bout (Hollén et al., 2011). There has been no conclusive evidence that the call is related to urgency of need for a follow-up sentinel (Hollén et al., 2011), and the lack of any results for this experiment may suggest that it may not be involved in the relaying of urgency information at the nest, with relevance to anti-predator behaviour. While the call may still play a role in conveying information about chick need, the definitive function of this vocalisation is still currently unknown. To confirm if this call influences nest visitation rate, playbacks of the call at the foraging group are required in the future.

A separate issue that may have led to my results is that the experimental set-up and amount of data available may not have been correct or sufficient for showing active communication from the nest to the foraging group. First of all, sample sizes were very small, and so any true, significant differences in responses to playbacks may have been masked by statistical noise. Also, individuals may not use indirect heterospecific anti-predator signals as a cue for predator presence, instead relying on direct personal observation of predators, and so the absence of an actual predator may have led to individuals not reacting to my playback. This seems unlikely, because pied babblers do react to heterospecific alarm calls and playbacks, and will join mobs that have been instigated by heterospecifics (Ridley & Raihani, 2007a; Flower, 2011; Flower et al., 2014; *pers. obs.*). Additionally, 10 seconds may have been too short a playback. However, I selected this length of time a) for ethical reasons, because I did not want to draw too much attention to the nest tree, and thus possibly aid predators in locating the nest; and b) for experimental reasons, because with a longer playback there would have been a greater chance that an individual other than the experimental bird would hear the playback. This would have then nullified the testing of whether individuals communicate about the nest state.

Another problem may be that the time between nest visits could have been influenced by how far groups were from the nest, and individuals not directly returning to the foraging group. However, I set a limit for how close a group could be before I conducted the playback, which hopefully kept any travel times trivially different; and individuals not returning directly to the foraging group might have been part of a response to the playback (see Appendix D). I have only limited data for individuals delaying their return to the group, and it is still possible that travel time may have had an effect, but I do not have the available data to investigate this. Therefore, I suggest that future studies take these factors into consideration.

Individuals can coordinate feeding visits to offspring in order to optimise the trade-off between offspring provisioning and possible predation threat. While it may appear adaptive for individuals to provide information to other provisioners about possible predation threats near to the nest, I found no evidence to support the existence of this behaviour in pied babblers. Instead the stronger driver on the rate of feeding at the nest may be offspring need and separate behavioural adaptations may have evolved to reduce the possibility of nest predation.

Chapter 6: Following the Caller: Do Avian Heterospecifics Associate with Pied Babblers, *Turdoides bicolor*?

6.1 Abstract

Species utilise heterospecific information to make adaptive decisions, which may influence species' movements and community dynamics. One behaviour that may influence heterospecific location choice is sentinel behaviour, because it provides information that many species find beneficial, and it likely degrades with distance. Thus, individuals should approach as close as possible to receive the information. I therefore investigated whether pied babbler, *Turdoides bicolor*, sentinel behaviour influences heterospecific location choice. Observations confirmed that bird species were more prevalent in the presence of babbler groups than when an observer was alone, and I tested whether this was because heterospecifics use pied babbler information. I conducted playbacks of babbler foraging calls with and without sentinel calls; background noise; and silence. Background noise and silence attracted fewer heterospecifics than babbler calls. However, there was no difference in the number of heterospecifics attracted, or the time they were present, between playbacks including sentinel calls and foraging calls alone. While this does not confirm that pied babbler sentinel behaviour drives interspecific interactions, it does show species distributions, and hence community dynamics, may be influenced by interspecific eavesdropping.

6.2 Introduction

Adaptive decision making requires access to accurate information (Dall et al., 2005). Individuals may collect this information personally, or from others if the cost of collecting personal information is high (Dall et al., 2005; Danchin et al., 2004). Conspecifics provide the most relevant information but they also compete for resources (Seppänen et al., 2007). Therefore, if heterospecifics provide relevant and reliable information without increasing competition, then it may be beneficial for an individual to attend to them instead (Seppänen et al., 2007).

Heterospecific information use is widespread throughout taxa. For instance, some species attend to heterospecific anti-predator information (e.g. Shriner, 1998; Fichtel, 2004; Magrath et al., 2015a) and use heterospecific foraging signals (e.g. Goulson et al., 1998; Stout & Goulson, 2001; Lichtenberg et al., 2011) in order to make adaptive decisions. Yet, by using heterospecific information, individuals' spatial and temporal positioning choices may be affected, because beneficial heterospecific signals may degrade over distance (see Forrest, 1994; Murray & Magrath, 2015), and so individuals should approach heterospecifics more readily to ensure they receive the information. Additionally, species may eavesdrop on heterospecific signals to make habitat choices (e.g. Diego-Rasilla & Luengo, 2004; Pupin et al., 2007; Mukhin et al., 2008), and species may even produce or receive signals that allow them to attract or locate other individuals to associate with, whether hetero- or conspecific (e.g. Windfelder, 2001; Goodale & Kotagama, 2006). Therefore, species' distributions may converge as a result of heterospecific information use.

If species are drawn together because of active association with heterospecific signallers, then community structure and patterns of association may be driven by heterospecific eavesdropping (see Goodale et al., 2010). To test whether this occurs I identified a candidate signalling system that may attract heterospecifics – the foraging and sentinel behaviour of Southern Pied Babblers, *Turdoides bicolor* (henceforth pied babbler or babbler). Sentinels provide public information in the form of alarm calls when a threat is spotted, and sentinel calls that allow for decreased personal vigilance of foragers and increased foraging success (Hollén et al., 2008; Bell et al., 2009). Alarms can also be given by foragers, but sentinels are usually positioned in an elevated position and so the presence of a sentinel increases the likelihood of predator detection (e.g. McGowan & Woolfenden, 1989; Manser, 1999; Ridley et al., 2010). The foragers also provide a foraging contact call, appearing to coordinate group spacing and also giving some information about food source divisibility (Radford & Ridley, 2008; Golabek, 2010). There is evidence that other species can use such information generated by pied babblers as an information source. Scimitarbills, *Rhinopomastus cyanomelas*, have been shown to actively associate with pied babblers, responding to their anti-predator information and altering their foraging behaviour in the presence of pied babblers (Ridley et al., 2014); showing that pied babbler generated public information can be valuable to heterospecifics.

Therefore, I set out to investigate whether species distributions (and as such interspecific associations) within the avian community which the pied babbler is a part of may be influenced by heterospecific eavesdropping. Specifically, I asked a) are avian heterospecifics more prevalent in the presence rather than the absence of a babbler group. Then, to confirm that any observed patterns of association may be being driven by interspecific eavesdropping, I used a playback experiment to ask b) are heterospecifics attracted by pied babblers' signals, and are they more likely to be attracted by calls that suggest the potential for greater predator detection? To do this, I investigated whether there is a greater response to playbacks that included babbler calls (either foraging contact calls or foraging calls and sentinel calls) rather than playbacks of background noise and silence. I expected that heterospecifics would be more prevalent in the presence of pied babblers. I hypothesised that this may be due to heterospecifics eavesdropping on one another to gain foraging and anti-predator benefits. Thus I predicted that playbacks including babbler calls should attract more heterospecifics, in particular those including sentinel calls because of the perceived additional anti-predator benefit.

6.3 Methods

6.3.1 Study Site & Population

I carried out this study on the Kuruman River Reserve (KRR) and surrounding farmland, Southern Kalahari Desert, South Africa (26º58'S, 21º49'E; see du Plessis et al., 2012, for habitat and climate details), using a population of colour-ringed pied babblers and their sympatric avian heterospecifics (171 bird species identified on the reserve, of which pied babblers interacted with 57 identified and 2 unknown species; see Appendix A). Pied babblers are cooperatively breeding, medium-sized passerines found in semi-arid areas of Southern Africa. They are predominantly ground foraging but frequently have at least one bird acting as a sentinel for the group providing anti-predator information (59% of the time; Bell et al., 2009). The population of pied babblers used in this study is habituated to human presence, allowing observers to follow groups and approach individuals closely (to within 2m).

6.3.2 Identifying Species Seen with Pied Babblers

In order to ascertain which species may be found with pied babblers I carried out scans for heterospecifics whilst in the presence of pied babblers. I located babbler groups by listening for their choruses or I attracted them using a whistle, which they associate with a food reward. When following a pied babbler group I conducted one minute scans for avian heterospecific presence every 10 to 20 minutes. I recorded all birds present within a 20m radius of the centre of the pied babbler group and the habitat characteristics of the area - including vegetation types to the nearest 10% cover of the area. I also recorded the amount of time that the pied babbler group had spent within that area. I recorded the location of observations using a Garmin eTrex or eTrex 10 GPS device (Garmin Ltd. or its subsidiaries, Schaffhausen, Switzerland). I conducted a total of 1126 scans at a total of 19 pied babbler groups over two collection periods (23rd January 2013 to 18th April 2013 and 21st September 2013 to 3rd May 2014). Two birds of prey (3 GPS points) and the Jacobin cuckoo (2 GPS points), *Clamator jacobinus* (a brood parasite of pied babblers; Ridley & Thompson, 2012), were observed within 20m of a babbler group, but were excluded from analyses because their presence was assumed to be solely as to act as a threat to the group.

6.3.3 Avian Sightings without Babbler Presence

To determine whether the avian community differs in the absence of babblers, I walked 12 individual transects, attempting to keep my behaviour as similar as possible to my behaviour when following a pied babbler group. I used transects instead of re-using routes previously visited by babblers because babblers are highly territorial (Ridley et al., 2008) and may be found in similar locations on a daily basis

– thus my transect data could have been affected by the presence of babblers if I had re-used pied babbler foraging routes. However, my transects did cross through pied babbler foraging home ranges so that I could make a fair comparison to data collected in the presence of babblers. I did this because babblers may make use of habitats that are beneficial to many species, and so the presence of avian heterospecifics when a babbler group is present may be more indicative of the habitat rather than the presence of a babbler group. Each transect was visited once between 24th October 2013 and 16th April 2014. I set up my transects using Mapsource (Garmin Ltd. Or its subsidiaries, Schaffhausen, Switzerland) to run parallel to the sides of the Kuruman River Reserve (6 parallel to the North-to-South boundary and 6 parallel to the East-to-West boundary). Each transect was approximately 1km apart, and waypoints were placed every 200 ± 5m along each transect. At each waypoint I recorded vegetation and avian presence data within 20m of myself, the same as for observations with babbler groups. I collected data at a total of 349 waypoints.

6.3.4 Playback Experiment

I conducted a playback experiment to ascertain whether heterospecifics are attracted to locations because of pied babbler derived public information, and investigate if they are more likely to do this when there is perceived greater predator detection. I conducted playbacks in 14 different pied babbler group home foraging ranges. I used two speakers to playback foraging calls, foraging calls + sentinel calls, background noise or silence. Each playback lasted 3 minutes. One speaker was delegated as the "sentinel", which played back sentinel calls, silence or background noise; and the other speaker was delegated as the "foragers", which played back foraging calls, silence or background noise (see Table 6.1 for playback combinations). I randomly assigned one of the 24 different combinations of the four playback types to each of the 14 playback locations, with each combination used only once. However, because I was only able to use 14 group foraging home ranges, and there are 24 different combinations of the four playback types, I was not able to counter-balance the experiment.

Table 6.1 Showing the different playback combinations from a speaker mounted at approximately head height (c.1.8m) – a 'quasi' sentinel – and a speaker placed on the ground – 'quasi' foragers – for different playback types.

Playback Type	Sentinel Speaker	Foraging Speaker
Foraging + Sentinel	Sentinel Call	Foraging Call
Foraging	Silence	Foraging Call
Silence	Silence	Silence
Background Noise	Background Noise	Background Noise

Playbacks took place at a location that would be a viable foraging location for a babbler group with a sentinel. The "sentinel" playback speaker - either a Jambox (Jawbone, San Francisco, USA) or Shoqbox speaker (Phillips, Amsterdam, Netherlands) - was attached to a wooden pole approximately 1.8m above the ground, and the "foragers" speaker placed at the bottom of the pole. Speakers were either connected to an Archos 604 Wifi MP4 player (Archos, Igny, France) or a Samsung R519 laptop (Samsung, Seoul, South Korea). To prevent equipment biases, the system used for playback at either sentinel or foraging position were split equally between trials. Each 3 minute playback was separated by 5 minutes, and playback order was randomised. I commenced trials when there were no birds in the vicinity. I then recorded any bird arriving within a 20m radius of the speaker set up, along with how long they remained within the area. If the resident pied babbler group arrived within 50-100m of the playback area I paused the trial and resumed 5 minutes after they left.

Pied babbler foraging and sentinel calls were recorded using a Sennheiser directional microphone (Sennheiser, Wedemark, Germany) and saved on a Marantz recorder in WAV format (Marantz, Kanagawa, Japan) (sampling rate of 44.1 kHz, 16-bit resolution). Background noise was also recorded from within a group's territory close to where the playback experiment would take place. I built tracks of silence and inserted standardised calls using Raven Pro 1.4 (The Cornell Lab of Ornithology, Ithaca, NY) and Cool Edit Pro 2.0 (Syntrillium Software Corporation, P.O.Box 6255, Phoenix, AZ 85082, USA). I standardised foraging and sentinel calls to average dB levels (foraging calls 65 calls from 22 individuals, 85.5±0.7dB; sentinel calls 72 calls from 12 individuals, 81.8±0.4dB; at 2m distance) shown by the Max Power function in Raven Pro 1.4.

For each group, I built eight separate 3 minute tracks (see Table 6.1). To make background noise tracks I edited a minimum of 1 minute of a background noise recording to remove artificial sound (such as car noise), and then looped this to fill a full 3 minute track. Playback treatments that used pied babbler vocalisations contained the same number of calls evenly spaced throughout the track (102 calls per track). This was calculated by the average number of calls given by foragers per 30 secs (17±3.2, n=11 groups). For trials that included sentinel calls, 48 of these were sentinel calls roughly evenly distributed between foraging calls, calculated from the average rate of calling per 30 secs (8±1.0, n=16 individuals). To create each individual track I used a minimum of 8 call exemplars to make up an individual "set" of calls. For each track I repeated the "set" enough times that would be sufficient to provide the required number of calls. I randomised the order of playback of call exemplars within in each repetition of the "set", with no two repetitions containing the same calls in the same order.

6.3.5 Analyses

I conducted my analyses in the R Commander interface (Fox, 2005) of R version 2.15.2 (R Core Team, 2012), using the package lme4 (Bates et al., 2012) for generalised mixed effects models.

6.3.5a Are avian heterospecifics more prevalent in the presence rather than the absence of a babbler group?

To investigate if heterospecifics are more prevalent in the presence of babblers I analysed whether there was a difference in the proportion of GPS points with at least one heterospecific present between data collected in the presence and absence of babbler groups. I used my transect data to calculate expected proportions of heterospecific presence and absence at GPS points. These were then used to calculate expected values for the data collected in the presence of babblers, which was analysed in comparison to observed values using chi-squared tests, using the chi-squared table from Fisher & Yates (1963). For this analysis, I controlled for the amount of time spent at a location by using GPS points where the babbler group had been present for ≤1 minute, because I did not spend longer than this at any transect waypoint. Also, I used only the transect points that were located within habituated babbler groups' home foraging ranges, identified using Basecamp version 4.4.2 (Garmin Ltd. Or its subsidiaries, Schaffhausen, Switzerland), so that my transect data provided a fair comparison with the data collected in the presence of babblers. Because the transects were only on the KRR, I did not use any data collected in the presence of babblers on land outside of the reserve.

Using my full dataset, I also fitted a generalized mixed effects model (GLMM) with a binomial response term of whether there was at least one heterospecific present or not, and the fixed effect of whether babblers were present or not and time (AM/PM). I also used the percentage vegetation cover of taller species, smaller species, bare ground (including collapsed dead vegetation) and man-made structures, and in the maximal model, each of these vegetation cover terms was used as a fixed effect in an interaction with the term for whether the data were collected in the presence of a babbler group or not. Random effects used in this model were date and babbler home foraging range. Because there was some fluidity of territory (and so home foraging range) ownership during the course of this study, each separate home foraging range was named after the 1st dominant babbler group in that area during data collection, for data collected both in the presence and absence of babblers. For transect locations without a known habituated babbler group, the home foraging range was classified as "other". The final model was selected using backwards stepwise elimination, with random effects terms retained throughout. A separate GLMM with a Poisson error structure was also run to investigate the number of different heterospecific species observed at each location. The fixed and random effects used in this model were the same as for the model investigating heterospecific presence/absence. For these

GLMMs investigating heterospecific presence/absence and species richness, only points with complete vegetation data (1470 total – 347 transect points & 1123 with babblers) were used.

6.3.5b Are heterospecifics attracted by pied babblers' signals, and are they more likely to be attracted by calls that suggest the potential for greater predator detection?

To investigate whether birds are attracted to the location of pied babbler groups due to the public information provided by them I conducted Friedman tests on the data collected in playback experiments (paired by group). I tested for differences between trial types in i) the number of heterospecifics arriving during playback periods, and ii) the time with at least one avian heterospecific present. Holm-Bonferroni corrections were made to alter significance levels due to repeat comparisons (Holm, 1979). I wanted to control for playback order, however, a lack of statistical power meant this was not completely possible; but I present preliminary analyses of this in Appendix E.

6.4 Results

6.4a Are avian heterospecifics more prevalent in the presence rather than the absence of a babbler group?

Data only from pied babbler foraging ranges on the KRR showed heterospecifics were more prevalent when in the presence of babbler groups (29/51 points) than in the absence of babblers (40/119) (chi-squared test: $\chi^2=12.4$, df=1, $p<0.01$; Figure 6.1).

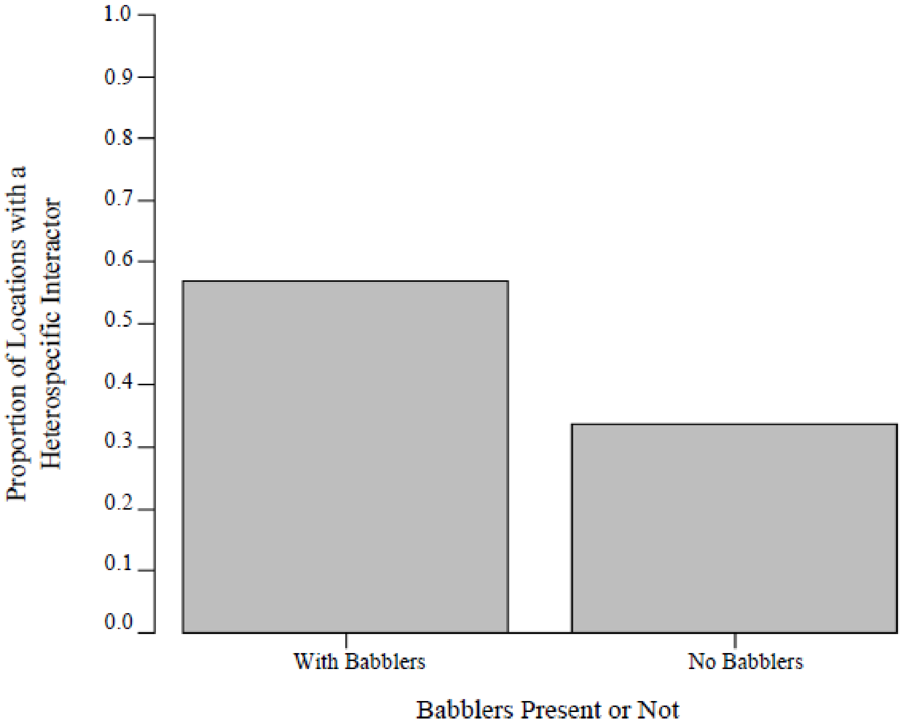


Figure 6.1 Figure showing the proportion of GPS points where there is at least one avian heterospecific present within 20m of a human observer; where the observer is either in the presence of a babbler group or the observer is alone.

Data from the complete study area showed heterospecifics were more likely to be seen, and a larger number of species were present, when babblers were present (GLMM: babblers present n=1123; babblers absent n=347; heterospecific presence/absence z=6.26, p<0.001; species number z=6.21, p<0.001; Tables 6.2 & 6.3). In the absence of babblers the amount of taller vegetation positively correlated with interactor presence (z = 3.42, p<0.001) and species number (z=2.93, p<0.01; see Tables 6.2 & 6.3), but the effect of taller vegetation presence was less strong when babblers were present (heterospecific presence/absence z= -2.53, p=0.01; species number z= -2.15, p=0.03; Tables 6.2 & 6.3). The amount of bare ground negatively correlated with heterospecific presence (z= -3.40, p<0.001), and species number (z= -3.64, p<0.001; see Tables 6.2 & 6.3). Shorter vegetation and man-made structures had no effect on heterospecific presence or species richness whether in the presence of babblers or not, and these terms were not retained in the final models (see Tables 6.2 & 6.3).

Table 6.2 Minimal model output of generalized mixed effects model investigating how vegetation characteristics and babbler group presence affect the presence of heterospecifics. Data from 1470 GPS points 1123 with babbler groups, 347 when a researcher was alone.

Fixed Effects	**Estimate**	**Standard Error**	**z**	**p**
Intercept	-1.24	0.19	-6.40	<0.001
Babbler Present	1.48	0.24	6.26	<0.001
Taller Vegetation %	0.03	0.01	3.42	<0.001
Bare ground %	-0.01	<0.01	-3.40	<0.001
Babbler Present*Taller Vegetation %	-0.03	0.01	-2.53	0.01
Non-Retained Terms	**z**	**p**		
Babbler Present*Bare ground %	-0.07	0.94		
Babbler Present*Man Made %	0.77	0.44		
Babbler Present*Smaller Vegetation %	0.81	0.42		
Session Time	-0.34	0.74		
Smaller Vegetation%	-0.68	0.50		
Man Made %	-0.54	0.59		
Random Effects	**Variance**	**Standard Deviation**		
Date	0.02	0.15		
Territory	0.01	0.08		

6.4b Are heterospecifics attracted by pied babblers' signals, and are they more likely to be attracted by calls that suggest the potential for greater predator detection?

Playbacks of foraging calls, and foraging calls with sentinel calls, attracted more heterospecifics than either background noise (foraging calls Friedman χ^2=12, df=1, p<0.001; foraging + sentinel calls Friedman χ^2=12, df=1, p<0.001; Figure 6.2) or silence (foraging calls Friedman χ^2=7.36, df=1, p=0.01; foraging + sentinel calls Friedman χ^2=7.36, df=1, p=0.01; Figure 6.2). The time with at least one interactor was also greater for playbacks of foraging calls, and foraging calls with sentinel calls, compared to background noise (foraging calls Friedman χ^2=12, df=1, p<0.001; foraging + sentinel calls Friedman χ^2=12, df=1, p<0.001; Figure 6.3) and silence (foraging call Friedman χ^2=9.31, df=1, p<0.01; foraging + sentinel call Friedman χ^2=8.33, df=1, p<0.01; Figure 6.3). However, playback of foraging calls with sentinel calls did not attract significantly more heterospecifics than foraging calls alone (Friedman χ^2=0.4, df=1, p=0.53; Figure 6.2), and the time of interaction was not different either (Friedman χ^2=0.69, df=1, p=0.41; Figure 6.3). There were also no differences between background noise and silence playbacks for the number of heterospecifics attracted (Friedman χ^2=0.2, df=1, p=0.65; Figure 6.2) and time of interaction (Friedman χ^2=0, df=1, p=1.00; Figure 6.3). All significant results held after Holm-Bonferroni correction.

Table 6.3 Minimal model output of generalized mixed effects model investigating how vegetation characteristics and babbler group presence affect the number of heterospecific bird species present. Data from 1470 GPS points 1123 with babbler groups, 347 when a researcher was alone.

Fixed Effects	Estimate	Standard Error	z	p
Intercept	-1.25	0.15	-8.38	<0.001
Babbler Present	1.04	0.17	6.21	<0.001
Taller Vegetation %	0.02	0.01	2.93	<0.01
Bare ground %	-0.01	<0.01	-3.64	<0.001
Babbler Present*Taller Vegetation %	-0.02	0.01	-2.15	0.03
Non-Retained Terms	**z**	**p**		
Babbler Present*Smaller Vegetation %	-0.11	0.91		
Babbler Present*Bare ground %	-0.6	0.55		
Babbler Present*Man Made %	0.97	0.33		
Session Time	-0.52	0.60		
Man Made %	-0.72	0.47		
Smaller Vegetation%	-0.46	0.65		
Random Effects	**Variance**	**Standard Deviation**		
Date	<0.001	<0.001		
Home Foraging Range	<0.001	<0.001		

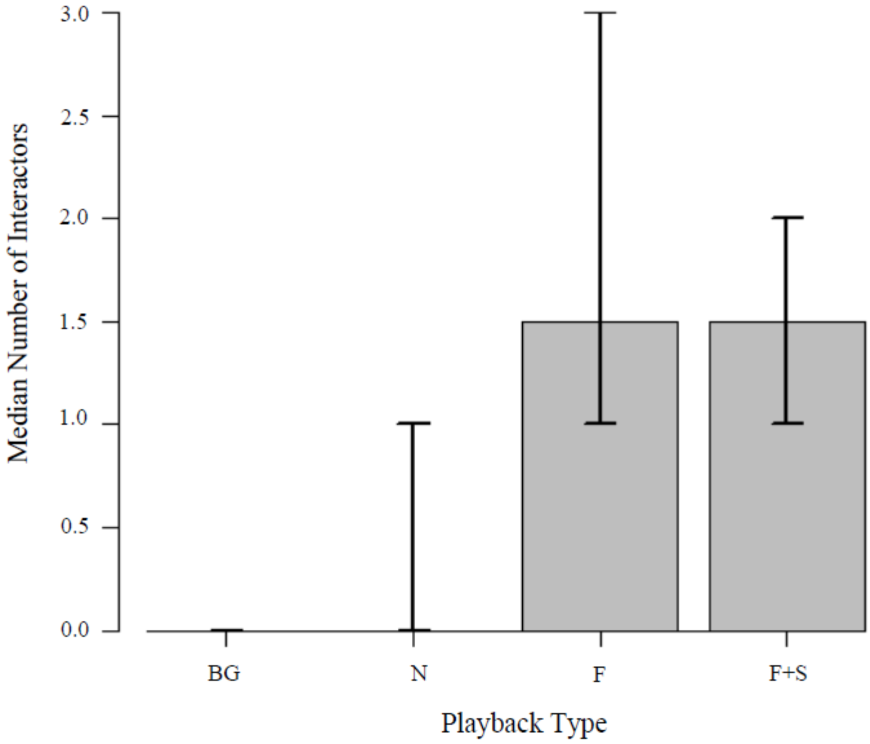


Figure 6.2 Showing the median, with IQR, number of heterospecific interactors to approach within 20m of the playback speakers during each playback type. BG = background noise, N = silence, F = foraging contact calls, F + S = foraging contact calls with sentinel calls.

6.5 Discussion

In this study avian heterospecifics were more likely to be observed when in the presence of pied babblers than when an observer was alone. Additionally, playbacks of pied babbler calls attracted heterospecifics more so than background noise and silence. I shall now discuss these results and their possible implications for community dynamics.

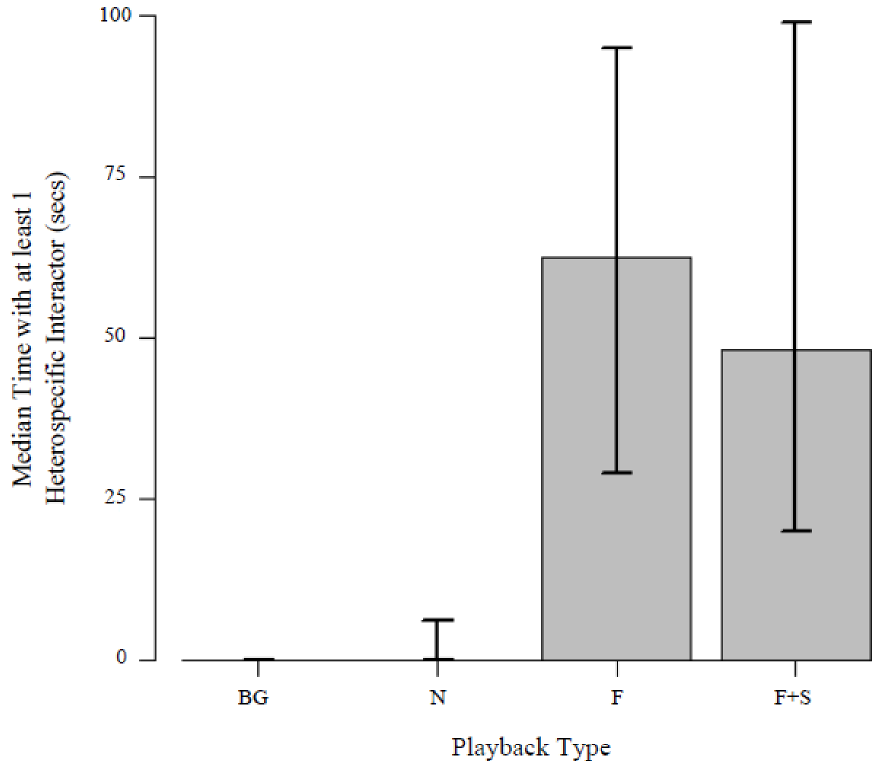


Figure 6.3 Showing the median, with IQR, time (secs) with at least one avian heterospecific interactor present within 20m of the playback speakers during each playback type. BG = background noise, N = silence, F = foraging contact calls, F + S = foraging contact calls with sentinel calls.

When following babbler groups, avian heterospecifics were more likely to approach a human observer than when the observer was alone. One initial explanation for this observed result could be that the areas where pied babblers were found were profitable for a variety of species (e.g. Scimitarbills will forage in the same locations as babblers; Ridley et al., 2014). Therefore, other species may have been present in these areas because the habitat was profitable for them. However, I did control for this in my chi-squared analysis, by using transect data only collected in areas where babblers have been known to forage; and still heterospecifics were more commonly observed when a babbler group was present rather than absent. Therefore, while it is still possible that certain habitat types or locations at the study site were more profitable for more species, my observed results may not have been driven by this.

Alternatively, my observations may have resulted from species deliberately associating with others, which they might do for possible anti-predator or foraging benefits. Joining a group (even if it does contain heterospecifics) will have a general anti-predator effect for individuals for a variety of reasons; including by the dilution effect, by reducing an individual's 'domain of danger', or by increased levels of total vigilance compared to when an individual is alone (e.g. Williams, 1966a; Hamilton 1971; Bertram 1980). Joining with heterospecifics can also increase an individual's available anti-predator information (e.g. Goodale & Kotagama, 2005); because different species will provide different anti-predator information (e.g. Goodale & Kotagama, 2005), and conduct different behaviours to generate anti-predator information (e.g. in this system pied babblers and fork-tailed drongos, *Dicrurus adsimilis*, conduct sentinel behaviour; e.g. Ridley & Raihani, 2007a; Bell et al., 2009; Ridley et al., 2010; Radford et al., 2011). Therefore, as long as competition over resources such as food are not significantly affected, it may be valuable to locate and associate with heterospecifics. There may be conflict over resources because species may locate profitable foraging sites by eavesdropping on heterospecific signals (e.g. Coolen et al., 2003; Lichtenberg et al., 2011). However, interacting with other species, particularly those of different foraging guilds or with different foraging techniques, need not create competition over food, because, compared to conspecifics, these heterospecifics may be less likely to impose competitive costs (Seppänen et al., 2007). Associating with heterospecifics with alternative foraging techniques can additionally create foraging benefits. For instance, species which sally to catch prey may benefit from prey flushed by species with other foraging techniques (e.g. Sridhar & Shanker, 2014); and many of the species observed with babbler groups in this study have different a foraging technique from one another (e.g. drongos [when not acting as a kleptoparasite], and some flycatchers may sally from a perch to hawk prey or pounce on terrestrial prey, while babblers are usually ground-foragers; e.g. del Hoyo et al., 2006; Child et al., 2012; *pers. obs.*). Therefore, it is possible that species may have been interacting with others in this system for foraging or anti-predator benefits. I shall now explore to what extent pied babblers themselves may have influenced my results, and potentially may influence community dynamics.

Pied babblers are a very vocal species (e.g. Bell et al., 2009; Hollén et al., 2008; Radford & Ridley, 2008; Raihani & Ridley, 2008; Thompson et al., 2013) and convey a lot of information that may easily be detected by heterospecifics. The presence of a babbler group itself can signal a profitable foraging site, with their ubiquitous foraging contact calls acting as a public signal of the profitability and divisibility of food sources (Golabek, 2010), which may be useful for other species too. There is also direct evidence for babblers being a source of anti-predator information for heterospecifics, with scimitarbills eavesdropping on babbler anti-predator signals (e.g. Ridley et al., 2014). Thus, babbler signals may indeed be possible cues for other species to eavesdrop on.

My experiment suggests that species may be attracted to an area by pied babbler calls not for anti-predator benefits, but instead as a way to locate profitable foraging patches - heterospecifics preferably foraged near a human when there are babbler calls, but there was no observable difference between playbacks that included sentinel calls and those that did not. However, it is still possible that species may be associating with one another in this system for anti-predator benefits.

In addition to the general anti-predator benefits of joining groups (e.g. Williams, 1966a; Hamilton 1971; Bertram 1980) there are a range of other factors that could mean that interspecific interactions in this system may be, in part, a result of anti-predator behaviour. For instance, sentinelling species can provide useful anti-predator information for other species (e.g. Sharpe et al., 2010; Radford et al., 2011; Baigrie et al., 2014). There is evidence that species in this community will deliberately alter their behaviour to recruit to areas where heterospecific sentinels are e.g. sociable weavers, *Philetarius socius*, are attracted by fork-tailed drongos, despite the possible costs of being kleptoparasitised by them (Baigrie et al. 2014). Of course there may not be a sentinel present all the time, but they may be present relatively frequently (babbler groups may employ a sentinel 59% of the time; Bell et al., 2009). Heterospecifics may, therefore, attend to any calls of sentineling species, such as pied babblers, because of the high probability that soon there will be a sentinel present. This might then explain why there is no observable difference between playbacks containing only foraging contact calls and those containing sentinel calls as well.

Additionally, the presence of the observer for this study may show evidence that anti-predator behaviour may have played a role in my observed results – although this evidence is only anecdotal. The pied babblers on the study site are habituated to human presence (see Ridley & Raihani, 2007a) and so do not alarm at humans while many other species will alarm at lone human observers (*pers. obs.*). Therefore, we may assume that humans may be considered as a threat by much of the Kalahari avian community. The lack of an alarm from a sentinelling species, such as the pied babbler, may then indirectly signal to heterospecifics that the human is not a threat, and so they are more likely to approach. The vegetation data also support the idea that anti-predator behaviour to avoid the observer may be a factor behind my results. Heterospecifics were more likely to be within 20m of an observer when there was taller vegetation present if there are no babblers around, and less likely to do so when there was open space. Therefore, it is still possible that anti-predator behaviour played a role in my observed results.

While this work shows that species may associate with pied babbler groups and can locate them by eavesdropping on their vocalisations, it is not conclusive about the definitive role that pied babblers play in their community. In order to ascertain this, more experiments would be required, playing back the vocalisations of other species that can be found in the ecosystem (see Westrip & Bell, 2015). This will then show whether the observed response, in my experiment, is specific to babblers or part of a general response that species give to all heterospecifics. Other studies have found very fine-tuned levels of eavesdropping, with species utilising motivational and referential information conveyed in heterospecific calls (Fichtel, 2004; Kirchhof &

Hammerschmidt, 2006; Fallow & Magrath, 2010), yet my study showed no difference in response to two different call types. By conducting such additional experiments using a range of species with different life-histories, this may then provide a greater perspective on the inter-specific dynamics that occur within communities, and possibly allow us to elucidate the conditions required for fine-tuned eavesdropping to evolve.

In summary, bird species are more commonly seen when an observer is with babblers than when an observer is alone, and species are attracted to locations by playback of pied babbler calls. This supports the idea that interspecific eavesdropping within communities can affect community spatial dynamics in an ecosystem. Conducting multiple similar studies on many different species within a community may be able to show to what degree there may be information sharing networks within communities, or whether select species are being eavesdropped on.

Chapter 7: Discussion

Part of this chapter has been published in Ethology: **Westrip, J.R.S. & Bell, M.B.V. (2015)** Breaking down the species boundaries: selective pressures behind interspecific communication in vertebrates. *Ethology*, **121**, 725-732.

In this thesis I have shown that anti-predator behaviour, in particular sentinel behaviour, is a public good, and individuals in groups are able to monitor the behaviour of collaborators within their group. Firstly, they are able to monitor the quantity of effort individuals make in contribution to a public good, and match the behaviour of their collaborators. Secondly, individuals will monitor the quality of the behaviour of collaborators in terms of the reliability of the information they provide – in this case the information about predator presence. Individuals may then alter their behaviour when a less reliable individual acts as sentinel. I found no evidence for pied babblers actively communicating about predator threat at the nest to the rest of the group, when predation threat is implied through heterospecific mobbing. On the other hand, avian heterospecifics appear to use pied babbler public information as they will approach playbacks of pied babbler calls.

7.1 Sentinel Behaviour as a Public Good

The public goods dilemma is one of the key problems to study in social behaviour. Many behaviours are considered public goods, yet within cooperative breeders, anti-predator behaviour has not. Instead it has been suggested to be a selfish act (Bednekoff, 1997) or kin-selected altruism (Hamilton, 1964; Griesser, 2003). I argue that it is indeed a public good because:

1. It provides benefits to multiple individuals. While my work has not explicitly investigated this, previous work has shown that sentinel behaviour provides a benefit to the group as a whole (Hollén et al., 2008; Bell et al., 2009). Sentinels provide benefits in two separate ways; a) they scan for threats and

alert the rest of the group when one is observed (see Bednekoff, 2015); and b) they provide sentinel calls which allow group members to decrease personal vigilance and thus increase personal foraging, increasing foraging success (Hollén et al., 2008; Bell et al., 2009).

2. Sentinel behaviour is costly to the actor. My work as part of this thesis has shown for the first time that there is an opportunity cost to individuals that act as sentinel. This is because individuals that spend longer acting as sentinel spend less time foraging and so gain less mass than those that spend less time as sentinel and more time foraging. Additionally, Ridley et al. (2013) showed that there may be increased predation threats for sentinels, thus creating extra costs for acting as sentinel.

Identifying sentinel behaviour as a public good means that it may become a useful behaviour for studying the dynamics of cooperation in nature, because of the ease of manipulation and its relative simplicity compared to other behaviours. Much of the previous work on public goods in nature have focussed on parental care (e.g. Wright & Cuthill, 1989; Hinde, 2006; van Breukelen & Itzkowitz, 2011). However, parental care is complex, because other factors distinct from the behaviour of collaborators can influence the system e.g. there may be active manipulation by offspring (amplified by brood parasitic offspring e.g. Redondo, 1993). Thus sentinel behaviour may be a more beneficial system to use.

7.2 Collaborator Monitoring

As a public good, sentinel behaviour may be vulnerable to exploitation by individuals that do not contribute. I argue that, of the mechanisms proposed to stabilise contributions to public goods, negotiation (Houston & Davies, 1985; McNamara et al., 1999; Johnstone & Hinde, 2006) is the most likely to act in pied babblers. In chapter 3 I showed that individuals appear to monitor and match the behaviour of collaborators. The amount of sentinel effort an individual conducts is related to satiation state (Bell et al., 2010), but I observed that when an individual increases its contribution to sentinel behaviour due to supplementary feeding, there is an increase in the amount sentinel work conducted by other members of the group, irrespective of their own satiation state. This provides some tentative evidence for the theory indicating that negotiation can lead to individuals matching the behaviour of collaborators (Johnstone & Hinde, 2006); and behaving in such a manner can stabilise contributions to a public good (Johnstone & Hinde, 2006), although confirmation of this may require further work.

While chapter 3 investigated how individuals monitor the effort of collaborators, chapter 4 examined whether individuals monitor others' quality. Cheney & Seyfarth (1988), Hare & Atkins (2001) and Blumstein et al. (2004) have all shown that individuals are capable of monitoring the quality of anti-predator information provided by collaborators; by altering their responses to alarms based on caller reliability. I found evidence that pied babblers may also monitor alarm-caller reliability. While investigating a previously unrecognised behaviour – "multi-individual sentineling" – I showed that juvenile babblers are less reliable at correctly identifying predators, and they were more likely to have a second bird acting as sentinel with them than adults. To confirm that this was because individuals monitor the reliability of others, I conducted a playback experiment to make individuals appear less reliable. The response was for sentinels to be accompanied more after they were made to appear less reliable. Thus, pied babblers are capable of recognising less reliable callers and altering their behaviour accordingly.

There are other ways that individuals may moderate their behaviour according to sentinel ID. Pied babblers reduce their personal vigilance when an individual is acting as sentinel (Hollén et al., 2008; Bell et al., 2009), and so I predicted that this would be an additional area where individuals may alter their behaviour based on the reliability of the individual on guard. There was, however, no evidence for individuals altering their personal vigilance based on the identity of the individual conducting sentinel behaviour. Work on meerkats on the same field site (Schibler & Manser, 2007) has shown that they also don't alter their anti-predator behaviour based on the identity of the alarm-caller. This was suggested to be because there is such a high predation risk in the Kalahari that individuals will have been selected to react to all alarms because the costs of not reacting to a true alarm are overwhelmingly so high that any costs of incorrectly reacting to an incorrect alarm become trivial (Schibler & Manser, 2007). Thus, under constant threat of predation, pied babblers may have been selected to maintain a minimum level of personal vigilance however reliable the sentinel is.

This work in chapters 3 & 4 gives additional possible evidence to a range of studies that show that individuals in social groups may be capable of using vocalisations to inform their decision making based on the behaviour of others, and negotiating individual investment (e.g. Cheney & Seyfarth, 1988; McNamara et al., 1999; Johnstone & Hinde, 2006; Bell et al., 2010). Negotiation may play a role in many different social settings, with vocal communication being used to negotiate a) contributions to parental care (e.g. Boucaud et al., 2016), b) outcomes of competitive interactions between siblings (e.g. Johnstone & Roulin, 2003), and c) contributions to anti-predator behaviour (e.g. Bell et al., 2010; this study). Are there any other areas where vocal negotiation may take place?

One other situation where vocal negotiation may take place is cooperative hunting. Species have been shown across taxa to take place in cooperative hunting and foraging patch choice (Packer & Ruttan, 1988; Anderson & Franks, 2001). While some species do not appear to use social information regarding patch choice (e.g. Leadbeater & Florent, 2014), there is a large history of studies that have shown species use social and public information to make foraging patch choices (e.g. von Frisch, 1967; Brown et al., 1991; Giurfa, 1993; Valone, 2007). Additionally, there is evidence that species – in particular marine fish – may use gestures to coordinated cooperative hunts, both with conspecifics and heterospecifics (Bshary et al., 2006; Vail et al., 2013; Lönnstedt et al., 2014), which may represent a form of negotiation. Therefore, investigations on species that take part in cooperative hunting (see Anderson & Franks, 2001), especially those that give calls during hunts (such as chimpanzees, Crockford & Boesch, 2005) may prove fruitful in discovering further vocal negotiation systems.

7.3 Anti-Predator Teaching?

Because multi-individual sentineling (MIS) was a response to a reduction in reliability, in Chapter 4, I decided to test whether MIS may represent teaching. Teaching may be especially prevalent for species when having a less reliable individual acting as sentinel is costly for others, and sentinel reliability increases with age and experience. Thus teaching would be beneficial, in order to accelerate learning.

Caro & Hauser (1992) set out three features that are required to show teaching takes place. Of Caro & Hauser's three features, I found evidence for the first two aspects of teaching:

i. Knowledgeable individuals alter their behaviour in the presence of naïve individuals - chapter 4 showed that juveniles are less reliable alarm callers than adults, and individuals are more likely to accompany a juvenile sentinel rather than an adult.

ii. This alteration in behaviour carries a cost - chapter 3 showed that acting as a sentinel (and therefore accompanying another individual when they are already acting as sentinel) reduces individual body mass gain.

I did not, however, find evidence for the third and final feature to show a behaviour represents teaching, which is for there to be a relationship between the presence of the behaviour and learning by the naïve individual.

While I did not show evidence for MIS increasing learning, I would argue that behaviours that do not show evidence for this may still represent teaching. One reason for this is there is an assumption that all individuals will respond the same way to teaching, i.e. there is an absence of individual variation in response to teaching - and as such a lack of variation in cognitive abilities. It is unlikely that this is the case because individual variation occurs in nearly every characteristic including cognitive ability (Thornton & Lukas, 2012) and as such is the basis for natural selection (Darwin, 1859). While the first of Caro & Hauser's features of teaching (knowledgeable individuals alter their behaviour in the presence of naïve individuals) does account for some level of individual variation (Caro & Hauser, 1992), I argue Caro & Hauser's features do not fully account for large amounts of variation. Imagine a population with two types of individual: highly intelligent individuals, and individuals with very low cognitive abilities. In this species experienced individuals are selected to attempt to improve the abilities of naïve individuals. However, intelligent individuals may learn at a very fast pace without requiring teaching; but by contrast, individuals with very low cognitive capabilities may receive a large amount of teaching, and still not improve in their ability (see Pearson, 1989; discussed in Caro & Hauser, 1992). This then would follow the first of Caro & Hauser's features, yet fall short of the 3rd, despite teaching being present. While this may not be the case in my study, this does highlight that Caro & Hauser's criteria may be a good benchmark from which to initially identify teaching in the wild, but they may need to be altered to recognise the fact that some cases of teaching may be incorrectly ignored.

Currently, the only studies that have shown clear evidence of teaching in the wild have been related to foraging behaviour, one of which is in the pied babbler (Raihani & Ridley, 2008). Pied babblers give a distinctive purr call when feeding offspring and this call has been shown to teach juveniles that an impending food delivery is about to occur (Raihani & Ridley, 2008). This can then be used to move young which have left the nest away from dangerous areas (Raihani & Ridley, 2007a). There are several other studies showing putative evidence for Caro & Hauser's criteria, including teaching of begging "passwords" in fairy-wrens (Kleindorfer et al., 2014), and prey handling skills in bats (Geipel et al., 2013). However, the most convincing studies to show teaching in the wild have shown that meerkats will teach pups how to handle dangerous prey (Thornton & McAuliffe, 2006) and *Temnothorax albipennis* ants use a behaviour called "tandem running" to teach other colony members where to find profitable food patches (Franks & Richardson, 2006).

These studies only show teaching in the context of foraging, and so I would encourage future studies to try to identify other candidate behaviours for teaching in alternative scenarios. Anti-predator behaviour appears, to me, to be the best possible alternative scenario to identify teaching. There are obvious benefits from accelerating naïve individuals' learning about predator threats; both from a selfish point of view if living in a group because it increases the number of reliable individuals that can identify possible threats, and from an inclusive fitness point of view for the genetic parents of naïve individuals (Hamilton, 1964). Not only this, but also anti-predator behaviour has frequently been shown to have a socially learnt component (Curio et al., 1978; Mineka & Cook, 1988; Brown & Laland, 2001; Griffin & Evans, 2003; Griffin, 2004; Magrath et al., 2015a & b), and so this lays the platform for teaching to be based on.

To further investigate the possibility of anti-predator teaching will require the identification of more candidate species in which it is likely to have evolved. Foremost of these should be species that employ sentinel behaviour, which can be found throughout animal classes (e.g. McGowan & Woolfenden, 1989; Clutton-Brock et al., 1999; Ridley et al., 2010; Fox & Donelson, 2014; see Bednekoff, 2015 for a full summary). Sentinels can play an important role in identifying threats, and increasing foraging success (Hollén et al., 2008; Bell et al., 2009; Bednekoff, 2015). With an unreliable sentinel these benefits will be lost, and additionally group mates may receive costs – the most severe of which would be losing their life if the sentinel did not identify a predator. Therefore, if individual anti-predator recognition ability is related to age and experience, which I provide evidence for in chapter 4, experienced individuals may be selected to invest in teaching less able individuals. In addition to this, sentinel behaviour is conspicuous (see Bednekoff, 2015), allowing for ease of identification of the individuals involved, and can be easily manipulated (e.g. Bell et al., 2010; Ridley et al., 2010; see Bednekoff, 2015). Thus it can be a useful behaviour to start with, when attempting to find anti-predator teaching.

Broadening our view of which species may participate in anti-predator teaching may then next lead to cooperative breeders. In these species, relatedness can be high (e.g. see Hatchwell, 2009), and so there can be inclusive fitness benefits (Hamilton, 1964) of improving the predator detection abilities of group members. There has also been a recent suggestion that cooperative breeding can drive the evolution of higher cognitive capabilities, and teaching appears to be biased towards these species (Burkart et al., 2009). Therefore, cooperative breeders may be a good group of species to select from when looking for anti-predator teaching. However, Thornton & McAuliffe (2015) argue that this need not be the case. The observed bias towards teaching being shown in cooperative breeders may be related to how easy it is to work with these species rather than cooperative breeding being a trait that leads to the evolution of teaching (Thornton & McAuliffe, 2015). Therefore, if studies are restricted to cooperative breeders then many viable candidate species for anti-predator teaching may be ignored.

The social intelligence hypothesis, suggests that brains may be under more selective pressures generated by the social surroundings of a species rather than environmental conditions (e.g. Jolly, 1966; Dunbar, 1998). Thus, studies may be broadened to investigate species that live in social groups, which need not be cooperative breeders. However, teaching need not be related to cognitive ability, because non-human teaching can be governed by simple processes (Caro & Hauser, 1992; Thornton & McAuliffe, 2012). Therefore, we can broaden the search for anti-predator teaching even more to encompass any species where the costs of conducting teaching are outweighed by the benefits that arise once the originally naïve individuals have learnt the behaviour (Thornton & Raihani, 2008; Fogarty et al., 2011; Thornton & McAuliffe, 2015).

While, the benefits of teaching may be assumed to only be relevant within species, could it still be plausible that inter-specific teaching might take place? For this to happen, there would have to be an interaction whereby individuals of different species spend a high level of time together for the benefits of teaching to be felt by the teacher. It might, in deed, be that there is such a system: that of the relationship between pied babblers and fork-tailed drongos, *Dicrurus adsimilis*. Pied babblers are accompanied by fork-tailed drongos for approximately 12% of the time (Ridley & Raihani, 2007a), and both species have relatively stable territories, increasing the likelihood that individuals will interact with each other more frequently than at random. Drongos act as sentinels for pied babbler groups (Ridley & Raihani, 2007a), but also give false alarm calls in order to kleptoparasitise the babblers. The kleptoparasitic nature of drongos poses the interesting possibility that drongos may teach pied babblers to respond to their alarm calls in honest circumstances, in order to later use this for kleptoparasitism. This, therefore, demonstrates how anti-predator teaching need not be confined to only a limited set of species, it may be occurring in and between a wide variety of species.

7.4 Location-Specific Information

Monitoring and teaching of individuals requires these individuals to be in direct contact with each other. However, in group living species there can be some distance between group members. The most obvious case of this is when there are dependent young in a nest. In birds, chick provisioning is usually conducted by more than one individual, and so there is a situation where one individual has knowledge about the conditions in a location and the other(s), that may require that information, does not.

It may then be adaptive for provisioners to actively communicate about these conditions when they interact, i.e. when one returns to a foraging patch from the nest.

I found no evidence that pied babblers did actively communicate about the perceived threat level at the nest, despite the apparent adaptive advantages of doing so. Returning to the nest too frequently can draw more attention to the nest, increasing predation risk (Skutch, 1949; Martin et al., 2000), and so species should be selected to alter their behaviour and return less frequently when there is evidence for predator activity nearby. However, the time between nest visits when playing back heterospecific mobbing calls (a proxy for predator presence) was no different from the response to heterospecific context neutral call playbacks.

The lack of a tactic of active communication about risk may be in part due to pied babblers already having evolved alternative tactics to combat nest predation. Firstly, pied babblers fledge at a very young age (Raihani & Ridley, 2007b). When chicks are in a nest they are, intrinsically, in a single location, and so the longer they stay there the greater the chance that a predator may locate them. Therefore, by fledging early they are able to reduce this risk of being located as they are mobile, but at the cost of having very immobile, vulnerable fledglings (Raihani & Ridley, 2007a). Secondly, pied babblers have a tactic of multiple birds returning to the nest simultaneously. In doing this they reduce the chance that a predator can locate the nest because there are fewer total visits to the nest for the amount of food that is delivered (Raihani et al., 2010).

An alternative explanation is that pied babblers do not use anti-predator information from heterospecifics. This is very unlikely because pied babblers frequently react to the alarm and mobbing calls of heterospecifics (Ridley & Raihani, 2007a; Flower, 2011; Flower et al., 2014; Ridley et al., 2014, *pers. obs.*) and their willingness to react to alarm calls generated by other species is key to the kleptoparasitic behaviour of fork-tailed drongos (Ridley & Raihani, 2007a; Flower, 2011; Flower et al., 2014). It could be, however, that pied babblers may not utilise heterospecific anti-predator information in this context specifically. Instead pied babblers may make personal observations to confirm that a predator is nearby, rather than infer predator presence by eavesdropping on public information.

7.5 Information Use beyond Species Boundaries

While my work in chapter 5 was inconclusive about pied babblers' use of heterospecific information, chapter 6 provided evidence for heterospecifics using pied babbler information. General avian observations showed that species are more prominent when an observer is with pied babblers rather than when they are alone. Playback experiments revealed that a variety of species are attracted to an area by babbler calls, with background noise and silence attracting very few if any individuals. Why then are heterospecifics actively associating with members of other species?

Individuals may join mixed-species groups because of anti-predator benefits. Just as when in a group consisting of only conspecifics, when an individual joins a group it reduces the probability that will be attacked by a predator by the dilution effect

(Williams, 1966a; Hamilton, 1971), and there are more individuals to look out for threats, thus bringing about mutual benefits.

The anti-predator benefit, however, need not be mutual. Certain species can also appear to parasitise the anti-predator behaviour of interactors. Species that employ a sentinel system, such as pied babblers, may provide information that is beneficial for every species in the group, while others may not have such a sentinel system and so do not appear able to repay the sentineling species. Greig-Smith (1981) demonstrated that species may have their anti-predator behaviour parasitised by others, with alarm-calling stonechats not receiving reciprocal benefits from birds that actively associate with them.

Another reason for joining mixed-species groups is for foraging benefits. Kleptoparasitic species, such as drongos, use heterospecifics as a source of food, allowing their victims to catch a prey item before they attack them and steal the food (e.g. Satischandra et al., 2010; Flower, 2011). Mixed species groups are also beneficial foraging locations when individuals are not kleptoparasiting others. Species may actively associate with heterospecifics of alternative foraging strategies because they may flush out prey items that would otherwise be unattainable (e.g. Sridhar & Shanker, 2014).

This all shows that species can provide benefits to heterospecifics in different contexts, for instance foraging or anti-predator. However, all previous work on interspecific communication has only taken into account one aspect of a species' niche at a time. Incorporating multiple aspects of a species' niche into studies is therefore one of several key areas for future work that will advance our knowledge of heterospecific information use.

7.6 Possible Future Work

To date, the study of heterospecific communication has been primarily descriptive, simply cataloguing situations where one species reacts to information provided by another. These interactions then fall on a cost-benefits continuum of interspecific communication from very beneficial communication to very costly (Danchin et al., 2004). Intuitively, where heterospecific responses provide high benefits, active signalling will be selected for (e.g. grouper-eel relationship; Bshary et al., 2006; Vail et al., 2013). Conversely, when there are high costs, such as when there are high levels of competition or predator eavesdropping (Page & Ryan, 2008), signals may be suppressed (Dapper et al., 2011). When the net payoffs of an interspecific interaction are near zero for the signaller, there may be little selection for or against signalling to heterospecifics (Danchin et al., 2004), while the benefits of signalling to conspecifics remain high (e.g. Charnov & Krebs, 1975; Sherman, 1977; Curio et al., 1978; Gehlbach & Leverett, 1995; Hogstad, 1995). Therefore heterospecific eavesdropping will persist as long as the signal provides beneficial information for the eavesdroppers.

Studies showing the direction of information flow can be informative, but it is analyses of selective pressures that may be able to show whether the communication we observe is truly mutualistic or possibly parasitic. It is now necessary to develop a more formal analytical framework based on robust quantification of the payoffs to both partners (e.g. Radford et al., 2011; Flower et al., 2013), and identify key areas for research in this field.

7.6.1 Accurate Quantification of Costs and Benefits of Communication to Both Signallers and Receivers

Classification of signalling interactions requires robust measurement of the payoffs to both parties. This in turn requires that we identify the proximate currency affected on both sides (weight gain, survival, foraging success etc.). For example, the work on fork-tailed drongos has measured the costs and benefits of communication for both parties by recording food intake. By acting as sentinels for their hosts, drongos increase host biomass intake (Radford et al., 2011). Drongos will then attempt to kleptoparasitise their hosts. This is a strategy that is more beneficial for the drongos, in terms of biomass intake, than self-foraging (Flower et al., 2013). By showing that it is more beneficial to signal to heterospecifics than to self-forage Flower et al. have shown how signalling to heterospecifics has been selected for in this system.

Quantifying the payoffs of signalling poses problems because signallers and receivers may be benefiting via very different – and sometimes quite cryptic – currencies. For example, evidence showing species A gains ‘x’ amount of anti-predator information from species B while species B gets no anti-predator information in return does not mean A is purely parasitizing information from B. As a species’ niche is made of n-dimensions (Hutchinson, 1957) multi-dimensional analyses are required. Vitousek et al., (2007) and Ito & Mori (2010) have shown there are interactions between species where one party is non-vocal, and so the signalling species is unlikely to receive any predator vocal warnings from the receiver. It may prove interesting to investigate whether there is another, as yet untested, benefit to the signaller from such interactions. This may be information based in another context (such as foraging) or a direct benefit of association e.g. Zenaida doves do not show aggression to carib grackles on their territory and the doves use grackle alarms (Griffin et al., 2005).

Ultimately, the only robust way to resolve problems with identifying and converting the relevant proximate currencies is to quantify the effect of cross-species association and communication on individual fitness. The logistics of actually doing this will not be trivial. It will require long term studies of individually marked animals of both species involved in an eavesdropping or signalling relationship. It will also require measurement of the effect of individual variation in the capacity to use heterospecific information on variation in reproductive success. A profitable avenue may be to deploy the logic and techniques starting to be used to investigate the fitness consequences of variation in social competence (Taborksy & Oliveira, 2012; Sih et al., 2014).

7.6.2 Identifying Reliability Discrimination at Species and Individual Level

Reacting to unreliable signals can be costly (Cheney & Seyfarth, 1988; Hare & Atkins, 2001; Blumstein et al., 2004). Therefore, individuals should be selected to adjust their responses in relation to signaller reliability. This may be both between (e.g. Magrath et al., 2009) and within species, which would require a degree of individual recognition.

Intra-specific individual recognition is observed throughout taxa (Tibbetts & Dale, 2007), and several species are observed to alter their anti-predator responses to the reliability of the signaller (e.g. Cheney & Seyfarth, 1988; Hare & Atkins, 2001; Blumstein et al., 2004). There is limited evidence for cross-species individual recognition (Proops et al., 2009), but Flower et al. (2014) have shown that victims of drongo kleptoparasitism will reduce their response to repeated drongo false alarms, suggesting inter-specific individual recognition may be present in this system. Experimental manipulation of individual reliability may allow for empirical testing of cross-species reliability monitoring.

7.6.3 Ontogeny of Heterospecific Communication

Some studies have briefly touched upon the development of heterospecific communication (e.g. Kitchen et al., 2010; Magrath & Bennett, 2012; Haff & Magrath, 2013). More thorough investigations in a wider range of species will allow for more general trends to be observed. The ontogeny of the adaptive recognition of heterospecific signals can be done using longitudinal studies with individuals. By testing their ability to respond to heterospecific signals as individuals' age may show whether they learn or have an innate ability (e.g. Haff & Magrath, 2013). Alternatively separate populations of the same species can be studied where there is heterospecific presence or not (e.g. Magrath & Bennett, 2012). The best way to then show that there is no genetic effect on recognition ability would be to conduct cross-fostering experiments between populations. If there is no such easy divide between populations, then it may still be possible to test this by creating artificial communities in laboratories or aviaries, both with and without heterospecific presence.

7.6.4 Conclusions for Future Work

Moving the study of interspecific communication away from descriptive studies and instead focussing on more adaptive and mechanistic questions will allow the field to grow. In doing so it will move the study of interspecific communication more into line with more general studies of conspecific communication and creates the possibility of studying selection and its role in moulding the behaviour of species in the context of its entire community rather than just as a lone entity.

References

Allan, R.A., Elgar, M.A. & Capon, R.J. (1996) Exploitation of an ant chemical alarm signal by the zodariid spider *Habronestes bradleyi* Walckenaer. *Proc. R. Soc. B*, **263**, 69-73

Alonso-Alvarez, C. & Velando, A. (2012) Benefits and costs of parental care. In *The evolution of parental care* (Eds. N.J. Royle, P.T. Smiseth & M. Kölliker), pp 40-61. Oxford University Press, Oxford

Anderson, C. & Franks, N.R. (2001) Teams in animal societies. *Behav. Ecol.*, **12**, 534-540

Andersson, M. & Wicklund, C.G. (1978) Clumping versus spacing out: experiments on nest predation in fieldfares (*Turdus pilaris*). *Anim. Behav.*, **26**, 1207-1212

Axelrod, R. & Hamilton, W.D. (1981) The evolution of cooperation. *Science*, **211**, 1390–1396.

Baigrie, B.D., Thompson, A.M. & Flower, T.P. (2014) Interspecific signalling between mutualists: food-thieving drongos use a cooperative sentinel call to manipulate foraging partners. *Proc. R. Soc. B*, **281**, 20141232

Barta, Z., McNamara, J.M., Huszár, D.B. & Taborsky, M. (2011) Cooperation among non-relatives evolves by state-dependent generalized reciprocity. *Proc. R. Soc. B*, **278**, 843-848.

Bates, D., Maechler, M. & Bolker, B. (2012) lme4: linear mixed-effects models using S4 classes, R package version 0.999999-0. http://CRAN.R-project.org/package=lme4

Bednekoff, P.A. (1997) Mutualism among safe, selfish sentinels: a dynamic game. *Am. Nat.*, **150**, 373-392

Bednekoff, P.A. (2015) Chapter Four - Sentinel behaviour: a review and prospectus. *Adv. Study Behav.*, **47**, 115-145

Bell, M.B.V., Radford, A.N., Rose, R., Wade, H.M. & Ridley, A.R. (2009) The value of constant surveillance in a risky environment. *Proc. R. Soc. B*, **276**, 2997–3005

Bell, M.B.V., Radford, A.N., Smith, R.A., Thompson, A.M. & Ridley, A.R. (2010) Bargaining babblers: vocal negotiation of cooperative behaviour in a social bird. *Proc. R. Soc. B*, **277**, 3223–3228

Bertram, B.C.R. (1980) Vigilance and group size in ostriches. *Anim. Behav.*, **28**, 278-286

Blumstein, D.T., Verneyre, L. & Daniel, J.C. (2004) Reliability and the adaptive utility of discrimination among alarm callers. *Proc. R. Soc. B*, **271**, 1851-1857

Boucaud, I.C.A., Mariette, M.M., Villain, A.S. & Vignal, C. (2016) Vocal negotiation over parental care? Acoustic communication at the nest predicts partners' incubation share. *Biol. J. Linn. Soc.*, **117**, 322-336

Boyd, R. & Richerson, P.J. (1992) Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethol. Sociobiol.*, **13**, 171-195

Bradbury, J.W. & Vehrencamp, S.L. (2011) Environmental Signals. In *Principles of Animal Communication*, Second Edition. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts pp561-610

Brown, C. & Laland, K. (2001) Social learning and life skills training for hatchery reared fish. *J. Fish Biol.*, **59**, 471-493

Brown, C.R., Brown, M.B. & Shaffer, M.L. (1991) Food-sharing signals among socially foraging cliff swallows. *Anim. Behav.*, **42**, 551-564

Bshary, R. (2002) Biting cleaner fish use altruism to deceive image-scoring client reef fish. *Proc. R. Soc. B*, **269**, 2087–2093.

Bshary, R. & Grutter, A.S. (2002) Asymmetric cheating opportunities and partner control in a cleaner fish mutualism. *Anim. Behav.*, **63**, 547–555

Bshary, R., Hohner, A., Ait-el-Djoudi, K. & Fricke, H. (2006) Interspecific communicative and coordinated hunting between groupers and giant moray eels in the Red Sea. *PLoS Biol.*, **4**, e431

Bshary, R., Zuberbühler, K. & van Schaik, C.P. (2016) Why mutual helping in most natural systems is neither conflict-free nor based on maximal conflict. *Philos. Trans. R. Soc. B.*, **371**, 20150091

Burkart, J.M., Hrdy, S.B. & van Schaik, C.P. (2009) Cooperative breeding and human cognitive evolution. *Evol. Anthropol.*, **18**, 175-186

Cant, M.A. (2003) Patterns of helping effort in co-operatively breeding banded mongoose (*Mungos mungo*). *J. Zool*, **259**, 115-121

Caraco, T., Martindale, S. & Pulliam, H.R. (1980) Avian flocking in the presence of a predator. *Nature*, **285**, 400-401

Caro, T.M. & Hauser, M.D. (1992) Is there teaching in nonhuman animals? *Q. Rev. Biol.*, **67**, 151-174.

Carroll, L. (1871) *Through the Looking-Glass, and What Alice Found There*. Macmillan Publishers, London

Charnov, E.L. & Krebs, J.R. (1975) The evolution of alarm calls: altruism or manipulation? *Am. Nat.*, **109**, 107-112

Cheney, D.L. & Seyfarth, R.M. (1988) Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Anim. Behav.*, **36**, 477-486

Cheney, D.L. & Seyfarth, R.M. (1990) *How monkeys see the world*. University of Chicago Press, Chicago.

Child, M.F., Flower, T.P. & Ridley, A.R. (2012) Investigating a link between bill morphology, foraging ecology and kleptoparasitic behaviour in the fork-tailed drongo. *Anim. Behav.*, **84**, 1013–1022

Clutton-Brock, T.H., Brotherton, P.N.M., O'Riain, M.J., Griffin, A.S., Gaynor, D., Kansky, R., Sharpe, L. & McIlrath, G.M. (2001) Contributions to cooperative rearing in meerkats. *Anim. Behav.*, **61**, 705-710

Clutton-Brock, T.H., Gaynor, D., Kansky, R., MacColl, A.D.C., McIlrath, G., Chadwick, P., Brotherton, P.N.M., O'Riain, J.M., Manser, M. & Skinner, J.D. (1998) Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proc. R. Soc. B*, **265**, 185-190

Clutton-Brock, T.H., O'Riain, M.J., Brotherton, P.N.M., Gaynor, D., Kansky, R., Griffin, A.S. & Manser, M. (1999) Selfish sentinels in cooperative mammals. *Science*, **284**, 1640–1644

Clutton-Brock, T.H. & Parker, G.A. (1995) Punishment in animal societies. *Nature*, **373**, 209-216

Coolen, I., van Bergen, Y., Day, R.L. & Laland, K.N. (2003) Species difference in adaptive use of public information in sticklebacks. *Proc. R. Soc. Lond. B*, **270**, 2413-2419

Crockford, C. & Boesch, C. (2005) Call combinations in wild chimpanzees. *Behaviour*, **142**, 397-421

Curio, E., Ernst, U. & Vieth, W. (1978) Cultural transmission of enemy recognition: one function of mobbing. *Science*, **202**, 899-901

Dall, S.R.X., Giraldeau, L.-A., Olsson, O., McNamara, J.M., & Stephens, D.W. (2005) Information and its use by animals in evolutionary ecology. *TREE*, **20**, 187–193

Danchin, É., Giraldeau, L.-A., Valone, T.J. & Wagner, R.H. (2004) Public information: from nosy neighbours to cultural evolution. *Science*. **305,** 487-491

Dapper, A.L., Baugh, A.T. & Ryan, M.J. (2011) The sounds of silence as an alarm cue in túngara frogs, *Physalaemus pustulosus*. *Biotropica*, **43**, 380-385

Darwin, C. (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray, London

De Vos, A. & O'Riain, M.J. (2010) Sharks shape the geometry of a selfish seal herd: experimental evidence from seal decoys. *Biol. Lett.*, **6**, 48-50

del Hoyo, J., Elliott, A. & Christie, D.A. (2006) *Handbook of the Birds of the World. Vol. 11. Old World Flycatchers to Old World Warblers.* Lynx Edicions, Barcelona

Diego-Rasilla, F.J. & Luengo, R.M. (2004) Heterospecific call recognition and phonotaxis in the orientation behavior of the marbled newt, *Triturus marmoratus*. *Behav. Ecol. Sociobiol.*. **55,** 556–560

du Plessis, K.L., Martin, R.O., Hockey, P.A.R., Cunningham, S.J. & Ridley, A.R. (2012) The costs of keeping cool in a warming world: implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. *Global Change Biology*, **18**, 3063-3070

Dumbacher, J.P., Menon, G.K. & Daly, J.W. (2009) Skin as a toxin storage organ in the endemic New Guinean genus *Pitohui*. *Auk*, **126**, 520-530

Dunbar, R.I.M. (1998) The social brain hypothesis. *Evol. Anthropol.*, **6**, 178-190

Eggert, A.-K., Reinking, M. & Müller, J.K. (1998) Parental care improves offspring survival and growth in burying beetles. *Anim. Behav.*, **55**, 97-107

Fallow, P.M., & Magrath, R.D. (2010) Eavesdropping on other species: mutual interspecific understanding of urgency information in avian alarm calls. *Anim. Behav.*, **79**, 411–417

Fichtel, C. (2004) Reciprocal recognition of sifaka (*Propithecus verreauxi verreauxi*) and redfronted lemur (*Eulemur fulvus rufus*) alarm calls. *Anim. Cogn.*, **7**, 45-52

Fischer, F. & Linsenmair, K.E. (2007) Changing social organization in an ungulate population subject to poaching and predation – the kob antelope (*Kobus kob kob*) in the Comoé National Park, Côte d'Ivoire. *Afr. J. Ecol.*, **45**, 285-292

Fischer, S., Zöttl, M., Groenewoud, F. & Taborsky, B. (2014) Group-size-dependent punishment of idle subordinates in a cooperative breeder where helpers pay to stay. *Proc. R. Soc. B*, **281**, 20140184

Fisher, R.A. & Yates, F. (1963) Table IV in *Statistical tables for biological, agricultural and medical research*, 6th edition. Oliver & Boyd, Edinburgh & London

Flower, T. (2011) Fork-tailed drongos use deceptive mimicked alarm calls to steal food. *Proc. R. Soc. B*, **278**, 1548-1555

Flower, T.P., Child, M.F. & Ridley, A.R. (2013) The ecological economics of kleptoparasitism: pay-offs from self-foraging versus kleptoparasitism. *J. Anim. Ecol.*, **82**, 245-255

Flower, T.P., Gribble, M. & Ridley, A.R. (2014) Deception by flexible alarm mimicry in an African bird. *Science*, **344**, 513-516

Fogarty, L., Strimling, P. & Laland, K.N. (2011) The evolution of teaching. *Evolution*, **65**, 2760-2770

Forrest, T.G. (1994) From sender to receiver: propagation and environmental effects on acoustic signals. *Am. Zool.*, **34**, 644-654

Foster, W.A. & Treherne, J.E. (1981) Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature*, **293**, 466-467

Fox, J. (2005) The R Commander: A Basic Statistics Graphical User Interface to R. *J. Stat. Softw.*, **14**, 1-42

Fox, R.J. & Donelson, J.M. (2014) Rabbitfish sentinels: first report of coordinated vigilance in conspecific marine fishes. *Coral Reefs*, **33**, 253

Franks, N.R. & Richardson, T. (2006) Teaching in tandem-running ants. *Nature*, **439**, 153

Furrer, R.D. & Manser, M.B. (2009a) The evolution of urgency-based and functionally referential alarm calls in ground-dwelling species. *Am. Nat.*, **173**, 400–410

Furrer, R.D. & Manser, M.B. (2009b) Banded mongoose recruitment calls convey information about risk and not stimulus type. *Anim. Behav.*, **78**, 195–201

Gehlbach, F.R. & Leverett, J.S. (1995) Mobbing of eastern screech-owls: predatory cues, risk to mobbers and degree of threat. *Condor*, **97**, 831-834

Geipel, I., Kalko, E.K.V., Wallmeyer, K. & Knörnschild, M. (2013) Postweaning maternal food provisioning in a bat with a complex hunting strategy. *Anim. Behav.*, **85**, 1435-1441

Gill, S.A. & Bierema, A.M.-K. (2013) On the meaning of alarm calls: a review of functional reference in avian alarm calling. *Ethology*, **119**, 449-461

Giurfa, M. (1993) The repellent scent-mark of the honeybee *Apis mellifera tigustica* and its role as communication cue during foraging. *Insect. Soc.*, **40**, 59-67

Gochfeld, M. (1980) Mechanisms and adaptive value of reproductive synchrony in colonial seabirds. In *Behavior of Marine Animals. Current Perspectives in Research. Vol. 4 Marine Birds* (Ed. by J. Burger, B.L. Olla and H.E. Winn), pp. 207-270. Plenum Press, New York

Godard, R. (1991) Long-term memory of individual neighbours in a migratory songbird. *Nature*, **350**, 228-229

Golabek, K.A. (2010) Vocal communication and the facilitation of social behaviour in the southern pied babbler (*Turdoides bicolor*). PhD Thesis, University of Bristol

Golabek, K.A. & Radford, A.N. (2013) Chorus-call classification in the southern pied babbler : multiple call types given in overlapping contexts. *Behaviour*, **150**, 691–712

Goodale, E., Beauchamp, G., Magrath, R.D., Nieh, J.C. & Ruxton, G.D. (2010) Interspecific information transfer influences animal community structure. *TREE*, **25**, 354–361

Goodale, E. & Kotagama, S.W. (2005) Alarm calling in Sri Lankan mixed-species bird flocks. *Auk*, **122**, 108-120

Goodale, E. & Kotagama, S.W. (2006) Vocal mimicry by a passerine bird attracts other species involved in mixed-species flocks. *Anim. Behav.*, **72**, 471-477

Goulson, D., Hawson, S.A. & Stout, J.C. (1998) Foraging bumblebees avoid flowers already visited by conspecifics or by other bumblebee species. *Anim. Behav.*, **55**, 199-206

Greig-Smith, P.W. (1981) The role of alarm responses in the formation of mixed-species flocks of heathland birds. *Behav. Ecol. Sociobiol.*, **8**, 7-10

Griesser, M. (2003) Nepotistic vigilance behavior in Siberian jay parents. *Behav. Ecol.*, **14**, 246-250

Griesser, M. (2009) Mobbing calls signal predator category in a kin group-living bird species. *Proc. R. Soc. B*, **276**, 2887-2892

Griffin, A.S. (2004) Social learning about predators: a review and prospectus. *Learning & Behavior*, **32**, 131–140

Griffin, A.S. & Evans, C.S. (2003) Social learning of antipredator behaviour in a marsupial. *Anim. Behav.*, **66**, 485-492

Griffin, A.S., Savani, R.S., Hausmanis, K. & Lefebvre, L. (2005) Mixed-species aggregations in birds: zenaida doves, *Zenaida aurita*, respond to the alarm calls of carib grackles, *Quiscalus lugubris*. *Anim. Behav.*, **70**, 507-515

Haff, T.M. & Magrath, R.D. (2013) Eavesdropping on the neighbours: fledglings learn to respond to heterospecific alarm calls. *Anim. Behav.*, **85**, 411–418

Hamilton, W.D. (1964) The genetical evolution of social behaviour I/II. *J. Theor. Biol.*, **7**, 1–52

Hamilton, W.D. (1971) Geometry for the selfish herd. *J. Theor. Biol.*, **31**, 295-311

Hare, J.F. & Atkins, B.A. (2001) The squirrel that cried wolf: reliability detection by juvenile Richardson's ground squirrels (*Spermophilus richardsonii*). *Behav. Ecol. Sociobiol.*, **51**, 108-112

Hatchwell, B.J. (2009) The evolution of cooperative breeding in birds: kinship, dispersal and life history. *Philos. Trans. R. Soc. B*, **364**, 3217-3227

Hennessy, D.F., Owings, D.H., Rowe, M.P., Coss, R.G. & Leger, D.W. (1981) The information afforded by a variable signal: constraints on snake-elicited tail flagging by California ground squirrels. *Behaviour*, **78**, 188-226

Hinde, C.A. (2006) Negotiation over offspring care? A positive response to partner-provisioning rate in great tits. *Behav. Ecol.*, **17**, 6–12

Hogstad, O. (1995) Alarm calling by willow tits, *Parus montanus*, as mate investment. *Anim. Behav.*, **49**, 221-225

Hollén, L.I., Bell, M.B.V. & Radford, A.N. (2008) Cooperative sentinel calling? Foragers gain increased biomass intake. *Curr. Biol.*, **18**, 576–579

Hollén, L.I., Bell, M.B.V., Russell, A., Niven, F., Ridley, A.R. & Radford, A.N. (2011) Calling by concluding sentinels: coordinating cooperation or revealing risk? *PLoS one*, **6**, e25010

Hollén, L.I. & Radford, A.N. (2009) The development of alarm call behaviour in mammals and birds. *Anim. Behav.*, **78**, 791-800

Holm S. (1979) A simple sequentially rejective multiple test procedure. *Scand. J. Stat.*, **6**, 65-70

Hoppitt, W.J.E., Brown, G.R., Kendal, R., Rendell, L., Thornton, A., Webster, M.M. & Laland, K.N. (2008) Lessons from animal teaching. *TREE*, **23**, 486-493

Houston, A.I. & Davies, N.B. (1985) Evolution of cooperation and life history in dunnocks, *Prunella modularis*. In *Behavioural Ecology* (Ed. by R. Sibly and R. H. Smith), pp. 471-487. British Ecological Society Symposium. Blackwell Scientific Publication, Oxford

Huang, P., Sieving, K.E. & St. Mary, C.M. (2012) Heterospecific information about predation risk influences exploratory behavior. *Behav. Ecol.*, **23**, 463-472

Humphries, D.J. (2013) The mechanisms and function of social recognition in the cooperatively breeding southern pied babbler, *Turdoides bicolor*. PhD thesis Macquarie University

Humphries, D.J., Finch, F.M., Bell, M.B.V. & Ridley, A.R. (2016) Vocal cues to identity: pied babblers produce individually distinct but not stable loud calls. *Ethology*, **122**, 609-619

Hutchinson, G.E. (1957) Concluding Remarks. *Cold Spring Harb. Symp. Quant. Biol.*, **22**, 415–427

Ito, R. & Mori, A. (2010) Vigilance against predators induced by eavesdropping on heterospecific alarm calls in a non-vocal lizard *Oplurus cuvieri cuvieri* (Reptilia: Iguania). *Proc. R. Soc. B*, **277**, 1275-1280

Johnstone, R.A. & Hinde, C.A. (2006) Negotiation over offspring care – how should parents respond to each other's efforts? *Behav. Ecol.*, **17**, 818-827

Johnstone, R.A. & Roulin, A. (2003) Sibling negotiation. *Behav. Ecol.*, **14**, 780-786

Jolly, A. (1966) Lemur social behaviour and primate intelligence. *Science*, **153**, 501-506

Kilner, R. (1995) When do canary parents respond to nestling signals of need? *Proc. R. Soc. B*, **260**, 343-348

Kilner, R. & Johnstone, R.A. (1997) Begging the question: are offspring solicitation behaviours signals of need? *TREE*, **12**, 11-15

Kirchhof, J. & Hammerschmidt, K. (2006) Functionally referential alarm calls in tamarins (*Saguinus fuscicollis* and *Saguinus mystax*) – evidence from playback experiments. *Ethology*, **112**, 346-354

Kitchen, D.M., Bergman, T.J., Cheney, D.L., Nicholson, J.R. & Seyfarth, R.M. (2010) Comparing responses of four ungulate species to playbacks of baboon alarm calls. *Anim. Cogn.*, **13**, 861-870

Kleindorfer, S., Hoi, H., Evans, C., Mahr, K., Robertson, J., Hauber, M.E., & Colombelli-Négrel, D. (2014) The cost of teaching embryos in superb fairy-wrens. *Behav. Ecol.*, **25**, 1131-1135

Kline, M.A. (2015) How to learn about teaching: an evolutionary framework for the study of teaching behaviour in humans and other animals. *Behav. Brain Sci.*, **38**, e31

Koda, H. (2012) Possible use of heterospecific food-associated calls of macaques by sika deer for foraging efficiency. *Behav. Proc.*, **91**, 30-34

Kruuk, H. (1964) Predators and anti-predator behaviour of the black headed gull (*Larus ridibundus* L.). *Behaviour (Suppl.)*, **11**, 1-129

Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. (2013) lmerTest: tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 1.2-0. http://CRAN.R-project.org/package=lmerTest

Leadbeater, E. & Florent, C. (2014) Foraging bumblebees do not rate social information above personal experience. *Behav. Ecol. Sociobiol.*, **68**, 1145-1150

Leavesley, A.J., & Magrath, R.D. (2005) Communicating about danger: urgency alarm calling in a bird. *Anim. Behav.*, **70**, 365–373

Li, Z., Jiang, Z. & Beauchamp, G. (2009) Vigilance in Przewalski's gazelle: effects of sex, predation risk and group size. *J. Zool.*, **277**, 302-308

Lichtenberg, E.M., Hrncir, M., Turatti, I.C. & Nieh, J.C. (2011) Olfactory eavesdropping between two competing stingless bee species. *Behav. Ecol. Sociobiol.*, **65**, 763-774

Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, **68**, 619-640

Lönnstedt, O.M., Ferrari, M.C.O. & Chivers, D.P. (2014) Lionfish predators use flared fin displays to initiate cooperative hunting. *Biol. Lett.*, **10**, 20140281

Lüning, J. (1992) Phenotypic plasticity of *Daphnia pulex* in the presence of invertebrate predators: morphological and life-history responses. *Oecologia*, **92**, 383-390

Magrath, R.D. & Bennett, T.H. (2012) A micro-geography of fear: learning to eavesdrop on alarm calls of neighbouring heterospecifics. *Proc. R. Soc. B*, **279**, 902–909

Magrath, R.D., Haff, T.M., Fallow, P.M. & Radford, A.N. (2015a) Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biol. Rev.*, **90**, 560-586

Magrath, R.D., Haff, T.M., McLachlan, J.R. & Igic, B. (2015b) Wild birds learn to eavesdrop on heterospecific alarm calls. *Curr. Biol.*, **25**, 2047-2050

Magrath, R.D., Pitcher, B.J., & Gardner, J.L. (2009) An avian eavesdropping network: alarm signal reliability and heterospecific response. *Behav. Ecol.*, **20**, 745–752

Manser, M.B. (1999) Response of foraging group members to sentinel calls in suricates, *Suricata suricatta. Proc. R. Soc. B*, **266**, 1013-1019

Manser, M.B., Bell, M.B., & Fletcher, L.B. (2001) The information that receivers extract from alarm calls in suricates. *Proc. R. Soc. B*, **268**, 2485–2491

Manser, M.B. & Fletcher, L.B. (2004) Vocalize to localize: a test on functionally referential alarm calls. *Interaction Studies*, **5**, 327–344

Manser, M.B., Seyfarth, R.M. & Cheney, D.L. (2002) Suricate alarm calls signal predator class and urgency. *Trends Cog. Sci.*, **6**, 55–57

Martin, T.E. (2015) Age-related mortality explains life history strategies of tropical and temperate songbirds. *Science*, **349**, 966-970

Martin, T.E., Martin, P.R., Olson, C.R., Heidinger, B.J. & Fontaine, J.J. (2000) Parental care and clutch sizes in North and South American birds. *Science*, **287**, 1482-1485

Martin, T.E., Oteyza, J.C., Boyce, A.J., Lloyd, P. & Ton, R. (2015) Adult mortality probability and nest predation rates explain parental effort in warming eggs with consequences for embryonic development time. *Am. Nat.*, **186**, 223-236

McGowan, K.J. & Woolfenden, G.E. (1989) A sentinel system in the Florida scrub jay. *Anim. Behav.*, **37**, 1000-1006

McNamara, J.M., Barta, Z., Fromhage, L. & Houston, A.I. (2008) The coevolution of choosiness and cooperation. *Nature*, **451**, 189-192

McNamara, J.M., Gasson, C.E., & Houston, A.I. (1999) Incorporating rules for responding into evolutionary games. *Nature*, **401**, 368–371

Mineka, S. & Cook, M. (1988) Social learning and the acquisition of snake fear in monkeys. In *Social Learning: Psychological and Biological Perspectives* (Eds T.R. Zentall & B.G. Galef Jnr.), pp. 51-73. Lawrence Erlbaum Associates, Hillsdale, New Jersey, Hove & London

Morrison, E.B. (2011) Vigilance behaviour of a tropical bird in response to indirect and direct cues of predation risk. *Behaviour*, **148**, 1067-1085

Mukhin, A., Chernetsov, N. & Kishkinev, D. (2008) Acoustic information as a distant cue for habitat recognition by nocturnally migrating passerines during landfall. *Behav. Ecol.*, **19**, 716-723

Mulder, R.A. & Langmore, N.E. (1993) Dominant males punish helpers for temporary defection in superb fairy-wrens. *Anim. Behav.*, **45**, 830-833

Müller, C.A. & Manser, M.B. (2008) The information banded mongooses extract from heterospecific alarm calls. *Anim. Behav.*, **75**, 897-904

Munro, B.H. (2005) *Statistical Methods for Health Care Research,* Fifth Edition. Lippincott Williams & Wilkins, Philadelphia, PA, USA

Murphy, T.G. (2006) Predator-elicited visual signal: why the turquoise-browed motmot wag-displays its racketed tail. *Behav. Ecol.*, **17**, 547-553

Murray, T.G. & Magrath, R.D. (2015) Does signal deterioration compromise eavesdropping on other species' alarm calls? *Anim. Behav.*, **108**, 33-41

Neill, S.R.St.J. & Cullen, J.M. (1974) Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. *J. Zool.*, **172**, 549-569

Nelson, X.J. (2014) Evolutionary implications of deception in mimicry and masquerade. *Curr. Zool.*, **60**, 6-15

Nelson-Flower, M.J., Hockey, P.A.R., O'Ryan, C., English, S., Thompson, A.M., Bradley, K., Rose, R. & Ridley, A.R. (2013) Costly reproductive competition between females in a monogamous cooperatively breeding bird. *Proc. R. Soc. B*, **280**, 20130728

Nelson-Flower, M.J., Hockey, P.A.R., O'Ryan, C., Raihani, N.J., du Plessis, M.A. & Ridley, A.R. (2011) Monogamous dominant pairs monopolize reproduction in the cooperatively breeding pied babbler. *Behav. Ecol.*, **22**, 559–565

Nowak, M.A. & Sigmund, K. (1998) Evolution of indirect reciprocity by image scoring. *Nature*, **393**, 573-577

Oliver, P. (1980) Rewards and punishments as selective incentives for collective action: theoretical investigations. *Am. J. Sociol.*, **85**, 1356-1375

Osorno, J.L. & Székely, T. (2004) Sexual conflict and parental care in magnificent frigatebirds: full compensation by deserted females. *Anim. Behav.*, **68**, 337–342

Packer, C. & Ruttan, L. (1988) The evolution of cooperative hunting. *Am. Nat.*, **132**, 159-198

Page, R.A. & Ryan, M.J. (2008) The effect of signal complexity on localization performance in bats that localize frog calls. *Anim. Behav.*, **76**, 761-769

Pavey, C.R. & Smyth, A.K. (1998) Effects of avian mobbing on roost use and diet of powerful owls, *Ninox strenua*. *Anim. Behav.*, **55**, 313-318

Pearson, A.T. (1989) *The teacher: theory and practice in teacher education*. Routledge, New York

Pfeiffer, T., Rutte, C., Killingback, T., Taborsky, M. & Bonhoeffer, S. (2005) Evolution of cooperation by generalized reciprocity. *Proc. R. Soc. B*, **272**, 1115-1120

Pinto, A., Oates, J., Grutter, A. & Bshary, R. (2011) Cleaner wrasses *Labroides dimidiatus* are more cooperative in the presence of an audience. *Curr. Biol.*, **21**, 1140–1144

Polnaszek, T.J. & Stephens, D.W. (2014) Receiver tolerance for imperfect signal reliability: results from experimental signalling games. *Anim. Behav.*, **94**, 1-8

Pollard, K.A. (2011) Making the most of alarm signals: the adaptive value of individual discrimination in an alarm context. *Behav. Ecol.*, **22**, 93-100

Proops, L., McComb, K. & Reby, D. (2009) Cross-modal individual recognition in domestic horses (*Equus caballus*). *PNAS*, **106**, 947–951

Pupin, F., Sacchi, R., Gentilli, A., Galeotti, P. & Fasola, M. (2007) Discrimination of toad calls by smooth newts: support for the heterospecific attraction hypothesis. *Anim. Behav.*, **74**, 1683–1690

Quiñones, A.E., van Doorn, G.S., Pen, I., Weissing, F.J. & Taborksy, M. (2016) Negotiation and appeasement can be more effective drivers of sociality than kin selection. *Philos. Trans. R. Soc. B*, **371**, 20150089

R Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Radford, A.N., Bell, M.B.V., Hollén, L.I. & Ridley, A.R. (2011) Singing for your supper: sentinel calling by kleptoparasites can mitigate the cost to victims. *Evolution*, **65**, 900–906

Radford, A.N., Hollén, L.I. & Bell, M.B.V. (2009) The higher the better: sentinel height influences foraging success in a social bird. *Proc. R. Soc. B.*, **276**, 2437-2442

Radford, A.N. & Ridley, A.R. (2008) Close calling regulates spacing between foraging competitors in the group-living pied babbler. *Anim. Behav.*, **75**, 519–527

Raihani, N.J. (2008) Cooperation and conflict in pied babblers. PhD Thesis, Cambridge University

Raihani, N.J., Nelson-Flower, M.J., Moyes, K., Browning, L.E. & Ridley, A.R. (2010) Synchronous provisioning increases brood survival in cooperatively breeding pied babblers. *J. Anim. Ecol.*, **79**, 44–52

Raihani, N.J. & Ridley, A.R. (2007a) Adult vocalizations during provisioning: offspring response and postfledging benefits in wild pied babblers. *Anim. Behav.*, **74**, 1303–1309

Raihani, N.J. & Ridley, A.R. (2007b) Variable fledgling age according to group size: trade-offs in a cooperatively breeding bird. *Biol. Lett.*, **3**, 624-627

Raihani, N.J. & Ridley, A.R. (2008) Experimental evidence for teaching in wild pied babblers. *Anim. Behav.*, **75**, 3–11

Raihani, N.J., Thornton, A. & Bshary, R. (2012) Punishment and cooperation in nature. *TREE*, **27**, 288-295

Rand, D.G., Dreber, A., Ellingsen, T., Fundenberg, D. & Nowak, M.A. (2009) Positive interactions promote public cooperation. *Science*, **325**, 1272-1275

Rasa, O.A.E. (1983) Dwarf mongoose and hornbill mutualism in the Taru Desert, Kenya. *Behav. Ecol. Sociobiol.*, **12**, 181-190

Rasa, O.A.E. (1987) Vigilance behaviour in dwarf mongooses: selfish or altruistic? *South African Journal of Science*, **83**, 587-590

Redondo, **T. (1993)** Exploitation of host mechanisms for parental care by avian brood parasites. *Etología*, **3**, 235-297

Redondo, T. & Castro, F. (1992) Signalling of nutritional need by magpie nestlings. *Ethology*, **92**, 193-204

Reichstein, T, von Euw, J., Parsons J.A. & Rothschild M. (1968) Heart poisons in the monarch butterfly. *Science*, **161**, 861-866

Renton, K. & Salinas-Melgoza, A. (1999) Nesting behaviour of the lilac-crowned parrot. *Wilson Bull.*, **111**, 499-493

Ridley, A.R., Child, M.F. & Bell, M.B.V. (2007) Interspecific audience effects on the alarm-calling behaviour of a kleptoparasitic bird. *Biol. Lett.*, **3**, 589–591

Ridley, A.R., Nelson-Flower, M.J. & Thompson, A.M. (2013) Is sentinel behaviour safe? An experimental investigation. *Anim. Behav.*, **85**, 137–142

Ridley, A.R. & Raihani, N.J. (2007a) Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. *Behav. Ecol.*, **18**, 324–330

Ridley, A.R. & Raihani, N.J. (2007b) Variable postfledging care in a cooperative bird: causes and consequences. *Behav. Ecol.*, **18**, 994–1000

Ridley, A.R., Raihani, N.J. & Bell, M.B.V. (2010) Experimental evidence that sentinel behaviour is affected by risk. *Biol. Lett.*, **6**, 445-448

Ridley, A.R., Raihani, N.J. & Nelson-Flower, M.J. (2008) The cost of being alone: the fate of floaters in a population of cooperatively breeding pied babblers *Turdoides bicolor*. *J. Avian Biol.*, **39**, 389-392

Ridley, A.R. & Thompson, A.M. (2012) The effect of Jacobin Cuckoo *Clamator jacobinus* parasitism on the body mass and survival of young in a new host species. *Ibis*, **154**, 195–199

Ridley, A.R., Wiley, E.M. & Thompson, A.M. (2014) The ecological benefits of interceptive eavesdropping. *Funct. Ecol.*, **28**, 197–205

Sanderson, J.L., Stott, I., Young, A.J., Vitikainen, E.I.K., Hodge, S.J. & Cant, M.A. (2015) The origins of consistent individual differences in cooperation in wild banded mongooses, *Mungos mungo*. *Anim. Behav.*, **107**, 193-200

Santema, P. & Clutton-Brock, T. (2013) Meerkat helpers increase sentinel behaviour and bipedal vigilance in the presence of pups. *Anim. Behav.*, **85**, 655-661

Satischandra, S.H.K., Kodituwakku, P., Kotagama, S.W. & Goodale, E. (2010) Assessing "false" alarm calls by a drongo (*Dicrurus paradiseus*) in mixed-species bird flocks. *Behav. Ecol.*, **21**, 396-403

Schibler, F. & Manser, M.B. (2007) The irrelevance of individual discrimination in meerkats alarm calls. *Anim. Behav.*, **74**, 1259-1268

Seeley, R.H. (1986) Intense natural selection caused a rapid morphological transition in a living marine snail. *PNAS*, **83**, 6897-6901

Seppänen, J.-T., Forsman, J.T., Mönkkönen, M. & Thomson, R.L. (2007) Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology*, **88**, 1622-1633

Seyfarth, R.M. & Cheney, D.L. (1986) Vocal development in vervet monkeys. *Anim. Behav.*, **34**, 1640-1658

Sharpe, L.L., Joustra, A.S. & Cherry, M.I. (2010) The presence of an avian co-forager reduces vigilance in a cooperative mammal. *Biol. Lett.*, **6**, 475-477

Sherratt, T.N. & Roberts, G. (1998) The evolution of generosity and choosiness in cooperative exchanges. *J. Theor. Biol.*, **193**, 167-177

Sherman, P.W. (1977) Nepotism and the evolution of alarm calls. *Science*, **197**, 1246-1253

Shriner, W.M. (1998) Yellow-bellied marmot and golden-mantled ground squirrel responses to heterospecific alarm calls. *Anim. Behav.*, **55**, 529-536

Sih, A., Chang, A.T. & Wey, T.W. (2014) Effects of behavioural type, social skill and the social environment on male mating success in water striders. *Anim. Behav.*, **94**, 9-17

Sinervo, B. & Licht, P. (1991) Proximate constraints on the evolution of egg size, number, and total clutch mass in lizards. *Science*, **252**, 1300-1302

Skelhorn, J., Rowland, H.M., Speed, M.P. & Ruxton, G.D. (2010) Masquerade: camouflage without crypsis. *Science*, **327**, 51

Skutch, A.F. (1949) Do tropical birds rear as many young as they can nourish? *Ibis*, **91**, 430-455

Smiseth, P.T., Bu, R.J., Eikenæs, A.K. & Amundsen, T. (2003) Food limitation in asynchronous bluethroat broods: effects on food distribution, nestling begging and parental provisioning rules. *Behav. Ecol.*, **14**, 793-801

Sridhar, H. & Shanker, K. (2014) Using intra-flock association patterns to understand why birds participate in mixed-species foraging flocks in terrestrial habitats. *Behav. Ecol. Sociobiol.*, **68**, 185–196

Stout, J.C. & Goulson, D. (2001) The use of conspecific and interspecific scent marks by foraging bumblebees and honeybees. *Anim. Behav.*, **62,** 183-189

Sweeney, B.W. & Vannote, R.L. (1982) Population synchrony in mayflies: a predator satiation hypothesis. *Evolution*, **36**, 810-821

Taborsky, B. & Oliveira, R.F. (2012) Social competence: an evolutionary approach. *TREE*, **27**, 679-688

Teichroeb, J.A. & Sicotte, P. (2012) Cost-free vigilance during feeding in folivorous primates? Examining the effect of predation risk, scramble competition, and infanticide threat on vigilance in ursine colobus monkeys (*Colobus vellerosus*). *Behav. Ecol. Sociobiol.*, **66**, 453-466

Templeton, C.N. & Greene, E. (2007) Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *PNAS*, **104**, 5479-5482

Tennyson, A. (1850) *In Memoriam A.H.H.* Edward Moxon, London, UK

Thompson, A.M., Raihani, N.J., Hockey, P.A.R., Britton, A., Finch F.M. & Ridley, A.R. (2013) The influence of fledgling location on adult provisioning: a test of the blackmail hypothesis. *Proc. R. Soc. B*, **280**, 20130558

Thornton, A. & Lukas, D. (2012) Individual variation in cognitive performance: developmental and evolutionary perspectives. *Philos. Trans. R. Soc. B*, **367**, 2773-2783

Thornton, A. & McAuliffe, K. (2006) Teaching in wild meerkats. *Science*, **313**, 227-229

Thornton, A. & McAuliffe, K. (2012) Teaching can teach us a lot. *Anim. Behav.*, **83**, e6-e9

Thornton, A. & McAuliffe, K. (2015) Cognitive consequences of cooperative breeding? A critical appraisal. *J. Zool.*, **295**, 12-22

Thornton, A. & Raihani, N.J. (2008) The evolution of teaching. *Anim. Behav.*, **75**, 1823-1836

Tibbetts, E.A. (2002) Visual signals of individual identity in the wasp *Polistes fuscatus*. *Proc. R. Soc. B*, **269**, 1423–1428

Tibbetts, E.A. & Dale, J. (2007) Individual recognition: it is good to be different. *TREE*, **22**, 529–537

Trivers, R.L. (1971) The evolution of reciprocal altruism. *Q. Rev. Biol.*, **46**, 35-57

Trivers, R.L. (1972) Parental investment and sexual selection. In *Sexual selection and the descent of man 1871-1971* (Ed. by B. Campbell), pp. 136-179. Adline Publishing Company, Chicago, IL

Vail, A.L., Manica, A. & Bshary, R. (2013) Referential gestures in fish collaborative hunting. *Nat. Commun.*, **4**, 1765

Valone, T.J. (2007) From eavesdropping on performance to copying the behaviour of others: a review of public information use. *Behav. Ecol. Sociobiol.*, **62**, 1-14

van Breukelen, N.A., & Itzkowitz, M. (2011) Mate removal leads to increase in parental defence behaviour in free-ranging convict cichlids. *Anim. Behav.*, **82**, 1023–1026

van Rooyen, N. (2001) *Flowering plants of the Kalahari dunes*. Ekotrust CC, South Africa

Van Valen, L. (1973) A new evolutionary law. *Evol. Theory*, **1**, 1-30

Vitousek, M.N., Adelman, J.S., Gregory, N.C. & St. Clair, J.J.H. (2007) Heterospecific alarm recognition in a non-vocal reptile. *Biol. Lett.*, **3**, 632-634

von Frisch, K. (1967) *The dance language and orientation of bees*. Harvard University Press, Cambridge MA

Walker, L.A. (2014) Sexually-selected sentinels: experimental evidence from a cooperatively breeding songbird. *Talk presented at International Society for Behavioral Ecology 2014 conference, New York, USA*

Welbergen, J.A. & Davies, N.B. (2008) Reed warblers discriminate cuckoos from sparrowhawks with graded alarm signals that attract mates and neighbours. *Anim. Behav.*, **76**, 811-822

West, S.A., Griffin, A.S. & Gardner, A. (2007) Evolutionary explanations for cooperation. *Curr. Biol.*, **17**, R661-R672

Westrip, J.R.S. & Bell, M.B.V. (2015) Breaking down the species boundaries: selective pressures behind interspecific communication in vertebrates. *Ethology*, **121**, 725-732

White, A.M. & Cameron, E.Z. (2011) Evidence of helping behaviour in a free-ranging population of communally breeding warthogs. *J. Ethol*, **29**, 419-425

Williams, G.C. (1966a) *Adaptation and natural selection.* Princeton University Press, NJ.

Williams, G.C. (1966b) Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.*, **100**, 687-690

Windfelder, T.L. (2001) Interspecific communication in mixed-species groups of tamarins: evidence from playback experiments. *Anim. Behav.*, **61**, 1193-1201

Wright, J. & Cuthill, I. (1989) Manipulation of sex differences in parental care. *Behav. Ecol. Socbiol.*, **25**, 171-181

Wright, J. & Cuthill, I. (1990) Biparental care: short-term manipulation of partner contribution and brood size in the starling, *Sturnus vulgaris*. *Behav. Ecol.*, **1**, 116–124

Ydenberg, R.C. & Dill, L.M. (1986) The economics of fleeing from predators. *Adv. Study Behav.*, **16**, 229-249

Zahavi, A. (1975) Mate selection – a selection for a handicap. *J. Theor. Bio.*, **53**, 205-214

Appendices

Appendices: Appendix A – Bird List

Table of the 171 species personally observed on the Kuruman River Reserve and surrounding farmland using nomenclature from Sinclair et al. (2011) (apart from emu – taken from BirdLife International (2016). * Denotes that this species was observed within 20m of a pied babbler group as part of data collection, but this species is a bird of prey and hence assumed to be present as a predator. Species included that were only observed "Ad. Lib." may have been seen with babbler groups, just they were not observed as part of data collection. Species marked as "X" are those kept as farm stock or pets and have been seen whilst accompanying babbler groups, but not interacting with them.

Common Name	Latin binomial	With Babblers & on Transect	With Babblers	On Transect	Only Ad. Lib.	Total Obs.
Ostrich	Struthio camelus				Yes	X
Emu	Dromaius novaehollandiae				Yes	X
Darter African	Anhinga rufa				Yes	1
Heron Grey	Ardea cinerea				Yes	1
Egret Yellow-Billed	Egretta intermedia				Yes	1
Egret Cattle	Bubulcus ibis				Yes	1 to 10
Heron Black-Crowned Night	Nycticorax nycticorax				Yes	1
Stork Abdim's	Ciconia abdimii				Yes	1
Ibis Hadeda	Bostrychia hagedash				Yes	>10
Shelduck South African	Tadorna cana				Yes	1 to 10
Teal Red-Billed	Anas erythrorhyncha				Yes	1
Kite Black	Milvus migrans				Yes	1 to 10
Kite Yellow-Billed	Milvus parasitus				Yes	1 to 10
Vulture White-Backed	Gyps africanus				Yes	>10
Vulture Cape	Gyps coprotheres				Yes	1

Vulture Lappet-Faced	Torgos tracheliotus				Yes	>10
Snake-Eagle Black-Chested	Circaetus pectoralis				Yes	>10
Snake-Eagle Brown	Circaetus cinereus				Yes	1 to 10
Bateleur	Terathopius ecaudatus				Yes	1 to 10
Harrier Pallied	Circus macrourus				Yes	1
Goshawk Pale Chanting	Melierax canorus				Yes	>10
Goshawk Gabar	Micronisus gabar		Yes*			>10
Shikra	Accipiter badius				Yes	1 to 10
Buzzard Steppe	Buteo vulpinus				Yes	1 to 10
Eagle Tawny	Aquila rapax				Yes	>10
Eagle Wahlberg's	Aquila wahlbergi				Yes	1
Eagle Booted	Aquila pennatus				Yes	1 to 10
Eagle Martial	Polemaetus bellicosus				Yes	>10
Falcon Pygmy	Polihierax semitorquatus		Yes*			>10
Kestrel Rock	Falco rupicolus				Yes	1 to 10
Kestrel Greater	Falco rupicoloides				Yes	1 to 10
Falcon Red-Necked	Falco chicquera				Yes	1 to 10
Hobby	Falco subbuteo				Yes	1
Falcon Lanner	Falco biarmicus				Yes	1 to 10
Spurrfowl Red-Billed	Pternistis adspersus				Yes	>10
Peafowl Indian	Pavo cristatus				Yes	X
Guineafowl Helmeted	Numidia meleagris				Yes	>10
Buttonquail Common	Turnix sylvaticus			Yes		1 to 10
Bustard Kori	Ardeotis kori				Yes	>10
Korhaan Red-Crested	Lophotis ruficrista				Yes	>10
Korhaan Northern Black	Afrotis afraoides				Yes	>10
Thick-Knee Spotted	Burhinus capensis				Yes	>10
Courser Burchell's	Cursorius rufus				Yes	1 to 10
Courser Double-Banded	Rhinoptilus africanus				Yes	1
Lapwing Crowned	Vanellus coronatus	Yes				>10
Sandpiper Common	Actitis hypoleucos				Yes	1
Sandgrouse Namaqua	Pterocles namaqua				Yes	>10

Sandgrouse Double-Banded	Pterocles bicinctus				Yes	1 to 10
Sandgrouse Burchell's	Pterocles burchelli				Yes	>10
Pigeon Speckled	Columba guinea				Yes	>10
Dove Red-Eyed	Streptopelia semitorquata				Yes	>10
Dove Cape Turtle	Streptopelia capicola	Yes				>10
Dove Laughing	Streptopelia senegalensis		Yes			>10
Dove Namaqua	Oena capensis	Yes				>10
Go-Away-Bird Grey	Corythaixoides concolor				Yes	1
Cuckoo Jacobin	Oxylophus jacobinus		Yes			>10
Cuckoo Great Spotted	Clamator glandarius		Yes			>10
Cuckoo Black	Cuculus clamosus		Yes			>10
Cuckoo African	Cuculus gularis				Yes	>10
Cuckoo Dideric	Chrysococcyx caprius				Yes	>10
Owl Barn	Tyto alba				Yes	>10
Owl African Scops	Otus senegalensis				Yes	>10
Owl Southern White-Faced	Ptilopsis granti				Yes	1 to 10
Owl Spotted Eagle	Bubo africanus				Yes	1 to 10
Owl Verreaux's Eagle	Bubo lacteus				Yes	>10
Owlet Pearl-Spotted	Glaucidium perlatum				Yes	>10
Nightjar Rufous-Cheeked	Caprimulgus rufigena			Yes		>10
Nightjar Fiery-Necked	Caprimulgus pectoralis				Yes	1 to 10
Swift African Palm	Cypsiurus parvus				Yes	1 to 10
Swift Common	Apus apus				Yes	>10
Swift Bradfield's	Apus bradfieldi				Yes	1 to 10
Swift Little	Apus affinis				Yes	>10
Swift White-Rumped	Apus caffer				Yes	1 to 10
Mousebird White-Backed	Colius colius				Yes	1 to 10
Mousebird Red-Faced	Urocolius indicus	Yes				>10
Kingfisher Striped	Halcyon chelicuti				Yes	1
Bee-Eater Swallow-Tailed	Merops hirundineus		Yes			>10

Bee-Eater Little	Merops pusillus				Yes	1 to 10
Bee-Eater European	Merops apiaster				Yes	>10
Roller Purple	Coracias naevius				Yes	>10
Roller Lilac-Breasted	Coracias caudatus	Yes				>10
Hoopoe African	Upupa africana				Yes	>10
Wood-Hoopoe Green	Phoeniculus purpureus		Yes			>10
Scimitarbill Common	Rhinopomastus cyanomelas		Yes			>10
Hornbill African Grey	Tockus nasutus		Yes			>10
Hornbill Southern Yellow-Billed	Tockus leucomelas	Yes				>10
Barbet Crested	Trachyphonus vaillantii				Yes	1
Barbet Acacia Pied	Tricholaema leucomelas		Yes			>10
Honeybird Brown-Backed	Prodotiscus regulus				Yes	1
Woodpecker Bennett's	Campethera bennettii	Yes				>10
Woodpecker Golden-Tailed	Campethera abingoni		Yes			>10
Woodpecker Cardinal	Dendropicos fuscescens		Yes			>10
Woodpecker Bearded	Dendropicos namaquus		Yes			>10
Lark Monontonous	Mirafra passerina				Yes	>10
Lark Rufous-Naped	Mirafra africana				Yes	1 to 10
Lark Eastern Clapper	Mirafra fasciolata			Yes		>10
Lark Sabota	Calendulauda sabota				Yes	1 to 10
Lark Fawn-Coloured	Calendulauda africanoides	Yes				>10
Lark Spike-Heeled	Chersomanes albofasciata				Yes	1 to 10
Sparrow-Lark Grey-Backed	Eremopterix verticalis				Yes	1 to 10
Lark Stark's	Spizocorys starki				Yes	1
Martin Brown-Throated	Riparia paludicola				Yes	>10
Swallow Barn	Hirundo rustica				Yes	>10
Swallow White-Throated	Hirundo albigularis				Yes	1 to 10
Swallow Pearl-Breasted	Hirundo dimidiata				Yes	1 to 10
Martin Rock	Ptyonoprogne fuligula				Yes	>10

Martin House	Delichon urbicum				Yes	1 to 10
Swallow Greater Striped	Cecropis cucullata				Yes	1 to 10
Pipit African	Anthus cinnamomeus				Yes	>10
Wagtail Cape	Motacilla capensis				Yes	1
Bulbul African Red-Eyed	Pycnonotus nigricans				Yes	>10
Thrush Groundscraper	Psophocichla litsitsirupa	Yes				>10
Chat Ant-Eating	Myrmecocichla formicivora		Yes			>10
Scrub-Robin Kalahari	Cercotrichas paena	Yes				>10
Wheatear Capped	Oenanthe pileata				Yes	1 to 10
Chat Familiar	Cercomela familiaris		Yes			>10
Flycatcher Chat	Bradornis infuscatus				Yes	1 to 10
Flycatcher Marico	Bradornis mariquensis	Yes				>10
Flycatcher Spotted	Muscicapa striata		Yes			>10
Batis Pririt	Batis pririt			Yes		>10
Prinia Black-Chested	Prinia flavicans	Yes				>10
Cisticola Desert	Cisticola aridulus				Yes	1 to 10
Warbler Icterine	Hippolais icterina				Yes	1 to 10
Warbler Willow	Phylloscopus trochilus		Yes			1 to 10
Eremomela Yellow-Bellied	Eremomela icteropygialis	Yes				>10
Crombec Long-Billed	Sylvietta rufescens		Yes			>10
Tit-Babbler Chestnut-Vented	Sylvia subcaeruleum	Yes				>10
Babbler Southern Pied	Turdoides bicolor	NA	NA	NA	NA	NA >10
Tit Ashy	Parus cinerascens	Yes				>10
Penduline-Tit Grey	Anthoscopus caroli				Yes	1
Penduline-Tit Cape	Anthoscopus minutus			Yes		1 to 10
Sunbird Marico	Cinnyris mariquensis	Yes				>10
Sunbird Dusky	Cinnyris fuscus		Yes			>10
White-Eye Cape	Zosterops capensis				Yes	1
White-Eye Orange River	Zosterops pallidus				Yes	1 to 10

Oriole Eurasion Golden	Oriolus oriolus			Yes	1
Oriole African Golden	Oriolus auratus			Yes	1
Shrike Red-Backed	Lanius collurio		Yes		>10
Shrike Lesser Grey	Lanius minor			Yes	>10
Fiscal Common	Lanius collaris			Yes	1 to 10
Tchagra Brown-Crowned	Tchagra australis		Yes		>10
Tchagra Black-Crowned	Tchagra senegalus			Yes	1 to 10
Shrike Crimson-Breasted	Laniarius atrococcineus	Yes			>10
Brubru	Nilaus afer	Yes			>10
Drongo Fork-Tailed	Dicrurus adsimilis	Yes			>10
Oxpecker Red-Billed	Buphagus erythrorhynchus			Yes	>10
Starling Wattled	Creatophora cinerea		Yes		>10
Mynah Indian (Common)	Acridotheres tristis			Yes	1
Starling Pale-Winged	Onychognathus nabouroup			Yes	1
Starling Red-Winged (possible pale-winged hybrid)	Onychognathus morio			Yes	1
Starling Burchell's	Lamprotornis australis		Yes		>10
Starling Cape Glossy	Lamprotornis nitens	Yes			>10
Sparrow Great	Passer motitensis			Yes	>10
Sparrow Cape	Passer melanurus		Yes		>10
Sparrow Southern Grey-Headed	Passer diffusus	Yes			>10
Weaver Red-Billed Buffalo	Bubalornis niger		Yes		>10
Sparrow-Weaver White-Browed	Plocepasser mahali	Yes			>10
Finch Scaly-Feathered	Sporopipes squamifrons	Yes			>10
Weaver Sociable	Philetarius socius	Yes			>10
Quelea Red-Billed	Quelea quelea			Yes	>10
Weaver Southern-Masked	Ploceus velatus		Yes		>10

Whydah Shaft-Tailed	Vidua regia			Yes	>10
Finch Red-Headed	Amadina erythrocephala			Yes	>10
Waxbill Black-Faced	Estrilda erythronotos			Yes	>10
Waxbill Violet-Eared	Granatina granatina		Yes		>10
Pytilia Green-Winged	Pytilia melba		Yes		>10
Firefinch Red-Billed	Lagonosticta senegala			Yes	1 to 10
Canary Black-Throated	Crithagra atrogularis			Yes	1 to 10
Canary Yellow	Crithagra flaviventris	Yes			>10
Bunting Lark-Like	Emberiza impetuani		Yes		>10
Bunting Golden-Breasted	Emberiza flaviventris		Yes		>10

Reference

BirdLife International (2016) Species factsheet: *Dromaius novaehollandiae*. Downloaded from http://www.birdlife.org on 25/05/2016

Sinclair, I., Hockey, P., Tarboton, W. & Ryan, P. (2011) Sasol Birds of Southern Africa, fourth edition. Struik Nature, Cape Town

Appendices: Appendix B – Extra Information & Analyses for Chapter 3

Details of fixed effects for mixed models

Influence on time as sentinel:

- Dominance – dominant or subordinate (see Raihani, 2008, for definitions of how dominance is reliably assigned in this species).
- Sex – can be achieved by behavioural observation, but birds are also sexed using genetic techniques. Not all individuals had been sexed yet, however, and so sex is listed as Female, Male or Unknown.
- Feeding regime: combine the terms "number of mealworms fed" and "partner fed" to form one 4 term effect (1:1, 1:10, 10:1 & 10:10)

Influence on group sentinel behaviour

- Feeding regime - the terms number of mealworms fed to the focal pair (1&1, 1&10 and 10&10).

Body mass gain model

- Feeding regime: combine the terms "number of mealworms fed" and "partner fed" to form one 4 term effect (1:1, 1:10, 10:1 & 10:10).

Data confidence – early iterations of the models contained a term for "data confidence". This was a categorical term, with less confident data including sessions where a large amount of time was spent in inter-group interactions, or a focal bird was less than a year old. There was only one case of the latter and the individual was behaving like a full subordinate individual. This term was later removed from models, but for the body mass gain model there was a significant effect of data confidence, and so the less confident data were removed from the dataset.

Extra Analyses

Sample sizes for analyses in Chapter 3 were relatively low given the number of terms in models, particularly for the analyses of group-wide effort. I, therefore, wanted to check that I would get similar results if I withdrew some of the terms from initial analyses. The simplest level of statistical analysis of the data is to use paired tests to test between sentineling rates in the hour before and after experimental feeding.

For the analysis that included all individuals within a group, I used paired t-tests. I found that there was a non-significant trend for the group to conduct less sentinel behaviour after manipulation in control trials where manipulated individuals were both fed 1 mealworm (t=1.9, df=7, p=0.09). When both fed individuals received 10 mealworms, the opposite trend occurred, but again this was not significant (t= -1.9, df=9, p=0.09); and in asymmetric feeding trials the group did not alter their total sentinel workload after manipulation (t=1.0, df=16, p=0.33). This is very similar to the results I obtained when running mixed effects models, and are presented in Chapter 3.

When the manipulated individuals were removed from the data, I instead used paired Wilcoxon Sign Rank tests, because the data was non-parametric. I again found that, in control trials where manipulated individuals were both fed 1 mealworm, the group showed a non-significant trend to reduce their total sentinel behaviour after manipulation (V=31, p=0.08). Asymmetric feeding trials (V=110, p=0.12) and trials where both experimental individuals were fed 10 mealworms (V=15, p=0.23) did not produce a significant change in group sentinel effort. However, effects sizes support the findings presented in Chapter 3. Control trials showed a median reduction of 380secs of sentinel behaviour after manipulation and asymmetric feeding trials showed a similar reduction of 309secs in sentinel behaviour; yet trials where both individuals received 10 mealworms showed a median increase in sentinel effort of 190secs.

<u>Reference:</u>

Raihani, N.J. (2008) Cooperation and conflict in pied babblers. PhD Thesis, Cambridge University

Appendices: Appendix C – Extra Information & Analyses for Chapter 4

Additional Methods Notes & Assumptions

Why Defining Multi-Individual Sentineling is Difficult

Defining multi-individual sentineling (MIS) as "the proportion of an individual's time acting as sentinel when there was an experienced bird acting as sentinel simultaneously" creates the problem that the direction of MIS is not necessarily being clearly shown (i.e. it is unclear which individual is the "main sentinel", and which is being accompanied by the main sentinel – which would be important in identifying teaching). However, I felt that this was the best available measure for MIS given the dataset.

Because MIS as a behaviour involves no additional behaviour to normal sentineling it is difficult to ascertain which individual is the main sentinel or "accompanier" and which is being "accompanied". However, when juveniles were involved it seemed unlikely that juveniles would be teaching each other, or indeed teaching adults. Therefore, I did not count individuals acting as sentinel at the same time as a juvenile as being accompanied themselves (though see the group size assumptions below).

Detecting who is the main sentinel when there are two adults as sentinel is more difficult. It could be suggested that the main sentinel could be ascertained by the order of individuals moving up to sentinel, with either the 1st or 2nd bird up being considered the main sentinel. I would argue that this is not appropriate. I frequently observed that juveniles could be either the 1st or 2nd bird to go up as sentinel, thus suggesting that the order is irrelevant. Additionally, I could not give accurate reliability scores to all individuals in the population because of limited alarm call sample sizes, and so was unable to assume whether an individual was the main sentinel or being accompanied by the main sentinel based on such scores. Therefore, I settled for my current definition which then creates the situation that adult individuals end up being counted as the main sentinel and being accompanied by the main sentinel simultaneously. It does then mean that the rate an adult sentinel is accompanied will be overestimated in my results, but despite this I still found juvenile sentinels to be accompanied more than adults. Although it is not perfect, I feel this measure is the best available, and it appears to be adequate to answer the question I set out to answer.

Group Size

The way I measured group size for these analyses could have been done in multiple different ways. I could have used the total number of individuals in a group, the number of adults, or the number of individuals that are contributing fully to cooperative behaviours. My main definition of group size for analyses in this chapter was the number of individuals that are contributing fully to cooperative behaviours. I selected this because selecting all individuals would be inappropriate if there are very young individuals present in a group that are contributing nothing to sentinel behaviour, and selecting adults only would also be inappropriate because juveniles also contribute to sentinel behaviour. I selected an age of 4 months old as the age when individuals are contributing fully to sentinel behaviour, and individuals younger than this were not included in group size measures. I selected this age because sentinels older than this tend to been accompanied less than juveniles (*unpublished data*), and begin to contribute more to group behaviours (*pers. obs.*). These individuals therefore represented "quasi-adults" and were assumed to be able to be the main sentinel as well as be accompanied by another experienced individual during a MIS event, whereas individuals younger than this were not assumed to be the main sentinel when another individual was acting as sentinel as well.

I explicitly state which metric for group size I use elsewhere in the chapter if I am not referring to this measure. Notably, this happens is in my analyses of forager vigilance. Here I used only the number of adults because I did not have any evidence to suggest any improvement in reliability of juveniles past 4 months of age. In case group members may make decisions about personal vigilance rates based on the reliability of other foragers, I decided to only use the number of adults as the metric because adults were shown to be more reliable than juveniles.

Additional Tables for the Analyses of Chapter 4

Table C.1 Table showing the final output of a GLMM with a binomial distribution response investigating whether juveniles are less reliable than adults, when mid-level alarms are considered correct. 615 alarms collected at 18 groups.

Fixed Effect	Estimate	Standard Error	z	p
Intercept	0.05	0.10	0.48	0.63
Age	0.87	0.19	4.63	<0.001
Random Effect	**Variance**	**Standard Deviation**		
Group ID	<0.001	<0.001		

Table C.2 Table showing the final output of a GLMM with a Poisson distribution for the response investigating whether as individuals age their rate of being accompanied, when acting as sentinel, changes. 119 observations from 14 individuals at 8 groups.

Fixed Effect	Estimate	Standard Error	z	p
Intercept	-2.25	0.44	-5.11	<0.001
Age	1.29	0.48	2.67	0.01
Non-Retained Term	**z**	**p**		
Group Size	0.13	0.89		
Random Effects	**Variance**	**Standard Deviation**		
Individual ID	<0.001	<0.001		
Group ID	<0.001	<0.001		

Table C.3 Table showing the final output of a LMM investigating the effect of adult alarm and foraging call playback on the total rate of MIS among all of the non-manipulated birds within a group. 24 trials, 12 alarm call playbacks and 12 foraging call playbacks. Data collected at 12 groups.

Fixed Effects	Estimate	Standard Error	t	p
Intercept	0.03	0.10	0.31	0.76
Trial Type	0.22	0.09	2.51	0.02
Rate of MIS in 1st Hour	-0.48	0.26	-1.82	0.08
Non-Retained Terms	**t**	**p**		
Group Size	0.49	0.63		
Data Collection Year	-1.09	0.29		
Random Effects	**Variance**	**Standard Deviation**		
Individual ID	0.00	0.00		
Group ID	0.00	0.00		

Table C.4 Table showing the final output of a LMM investigating the effect of juvenile alarm and foraging call playback on the total rate of MIS amongst all of the non-manipulated birds within a group. 24 trials, 12 alarm call playbacks and 12 foraging call playbacks. Data collected at 8 groups.

Fixed Effects	Estimate	Standard Error	t	p
Intercept	-0.04	0.05	-0.88	0.39
log(reflected(Rate of MIS in 1st Hour))	1.14	0.61	1.88	0.07
Trial Type	0.12	0.07	1.78	0.09
Non-Retained Terms	**t**	**p**		
Group Size	-0.36	0.72		
Data Collection Year	0.61	0.55		
Random Effects	**Variance**	**Standard Deviation**		
Individual ID	0.00	0.00		
Group ID	0.00	0.00		

Table C.5 Table showing the final output of a LMM investigating whether there is a relationship between the average rate of accompaniment a juvenile sentinel receives and the change in their reliability between when they are an adult and as a juvenile, when mid-level alarms are considered correct. Observations of 11 individuals at 7 groups.

Fixed Effect	Estimate	Standard Error	t	p
Intercept	0.46	0.15	3.08	0.01
Reliability when juvenile	-1.41	0.32	-4.46	0.01
Non-Retained Term	**t**	**p**		
Rate accompanied when juvenile	-0.37	0.72		
Random Effect	**Variance**	**Standard Deviation**		
Group ID	0.03	0.18		

Table C.6 Table showing the final output of a GLMM with a Poisson distribution for the response investigating whether there is a relationship between the average rate of accompaniment a juvenile sentinel receives and the change in their reliability between when they are an adult and as a juvenile, when mid-level alarms are considered incorrect. Observations of 11 individuals at 7 groups.

Fixed Effect	Estimate	Standard Error	z	p
Intercept	-0.56	0.49	-1.15	0.25
Reliability when juvenile	-2.51	4.27	-0.59	0.56
Non-Retained Term	**z**	**p**		
Rate accompanied when juvenile	0.10	0.92		
Random Effect	**Variance**	**Standard Deviation**		
Group ID	0.00	0.00		

Table C.7 Table showing the final output of a LMM investigating whether the reliability of the main sentinel affects forager vigilance, when mid-level alarms are considered correct. 111 observations, with 29 different main sentinels, 18 focal foragers from 9 groups.

Fixed Effect	Estimate	Standard Error	t	p
Intercept	0.04	0.01	2.54	0.02
Main sentinel reliability	0.05	0.03	1.88	0.07
Non-Retained Term	**t**	**p**		
Number of adults	-0.01	1.00		
Random Effects	**Variance**	**Standard Deviation**		
Main Sentinel	<0.001	<0.001		
Focal Individual	<0.001	<0.001		
Group ID	<0.001	<0.001		

Table C.8 Table showing the final output of a LMM investigating whether the reliability of the main sentinel affects forager vigilance, when mid-level alarms are considered incorrect. 111 observations, with 29 different main sentinels, 18 focal foragers from 9 groups.

Fixed Effect	Estimate	Standard Error	t	p
Intercept	0.04	0.01	3.83	<0.01
Main sentinel reliability	0.04	0.03	1.40	0.18
Non-Retained Term	**t**	**p**		
Number of adults	0.19	0.85		
Random Effects	**Variance**	**Standard Deviation**		
Main Sentinel	<0.001	<0.001		
Focal Individual	<0.001	<0.001		
Group ID	<0.001	<0.001		

Differences between Mid-level alarms considered as Incorrect & Correct

The only qualitative difference between analyses that considered mid-level alarms as correct or incorrect was when assessing whether reliability changes due to being accompanied when acting as sentinel. When mid-level alarms were considered incorrect, an individual's reliability when juvenile had no effect on the improvement of reliability. However, when mid-level alarms were considered correct, individuals that were more reliable when juvenile were less likely to improve their reliability (or were actually becoming less reliable) compared to those that were less reliable as juveniles. While investigating this possible relationship may be interesting, I suggest that such a difference in results may in part be a consequence of the small sample sizes used in these analyses (only 11 individuals). Additionally, because these results are not key to understanding the questions I set out, I will not discuss this idea further.

Additional Analyses not Included in the Main Text of Chapter 4

Who is accompanied?

My definition of multi-individual sentineling meant that an individual that acted as sentinel at the same time as a juvenile was not counted as being accompanied. To confirm I was not biasing analyses by not allowing juveniles to act as the main sentinel, I conducted a t-test analysis that included all sentinel activity. While this did not control for individual or group identity, it still confirmed that MIS was biased towards juveniles (adults accompanied 20.6 ± 1.3%, juveniles accompanied 51.6 ± 2.7% of the time, $t= -10.38$, $p<0.001$).

Using Total Time Accompanied rather than Proportion of Time Accompanied

My analyses used the proportion of time an individual was accompanied when acting as sentinel. However, it is possible that the total amount of accompaniment may be a better measure to investigate teaching. I therefore ran an extra analysis on the change in reliability of an individual from when they were a juvenile to when they are adult. I used fixed effects of the average amount of time an individual was accompanied as a sentinel when they were juvenile and the reliability of an individual when they were juvenile. I used a random effect of group ID, and ran different models that treated mid-level alarms as either correct or incorrect.

When I ran my models, I did not find any effect of accompaniment influencing the change in reliability of an individual as they age, and the term was not retained in the final models. Therefore the final outputs were the same as those presented in Chapter 4 – supplementary tables 5 & 6.

Preliminary Investigation to see whether Accompaniment Responses to Juvenile Alarm Playback are Targeted to the Experimental Individual

My results may suggest that the accompaniment of adult sentinels may be a form of threat response because there is a group-wide increase in MIS after adult alarm playbacks. This suggests that the increase in accompaniment of a manipulated adult may be a result of an overall group-wide effect, rather than individual monitoring of reliability. However, this is not the case for juveniles. After juvenile alarm playbacks, there is not a significant increase in overall MIS amongst the non-manipulated individuals, but the experimental juvenile is accompanied more when acting as sentinel. This, therefore, might suggest that individuals are capable of identifying unreliable juvenile sentinels and targeting them for accompaniment.

However, it is only anecdotal evidence to suggest that multi-individual sentineling is targeted to the manipulated individual after juvenile alarm playbacks, while the rate of accompaniment in the rest of the group is unaffected. Therefore, to investigate whether this is the case, I ran a paired Wilcoxon test to test whether there was a difference in the effect juvenile alarm playbacks had on group-wide levels of accompaniment and the rate the experimental individual was accompanied. This test showed that there was a difference in the two responses (V=77, p<0.01, n=12), thus suggesting the juvenile is being targeted for accompaniment. I also ran the same test for adult data. This again suggested that the response to an adult alarm playback may be a general response rather than targeted to the experimental individual as there was no difference in the effect the adult alarm playback had on group-wide levels of accompaniment and the rate the experimental individual was accompanied (V=50, p=0.15, n=11).

Testing for Differences in Playback Responses between Adults and Juveniles

To test whether the degree of response to playback experiments was different between adult and juvenile trials I conducted multi-way ANOVAs. I ran separate analyses for the total group-wide rates of accompaniment and the rate of accompaniment received by the experimental individual. I used explanatory terms of trial type (alarm or contact call playback) and experimental individual age (adult or juvenile). These tests confirm that the response towards the experimental individual was similar for adults and juveniles (F=1.79, df=1, p=0.19). The analysis of the total rate of accompaniment within a group also showed that the responses to adult and juvenile playbacks were similar (F=2.78, df=1, p=0.10). However, effects sizes (see Figure C.1) suggest that there may be indeed be a difference between the responses to adult and juvenile playbacks in terms of the total rate of accompaniment within a group.

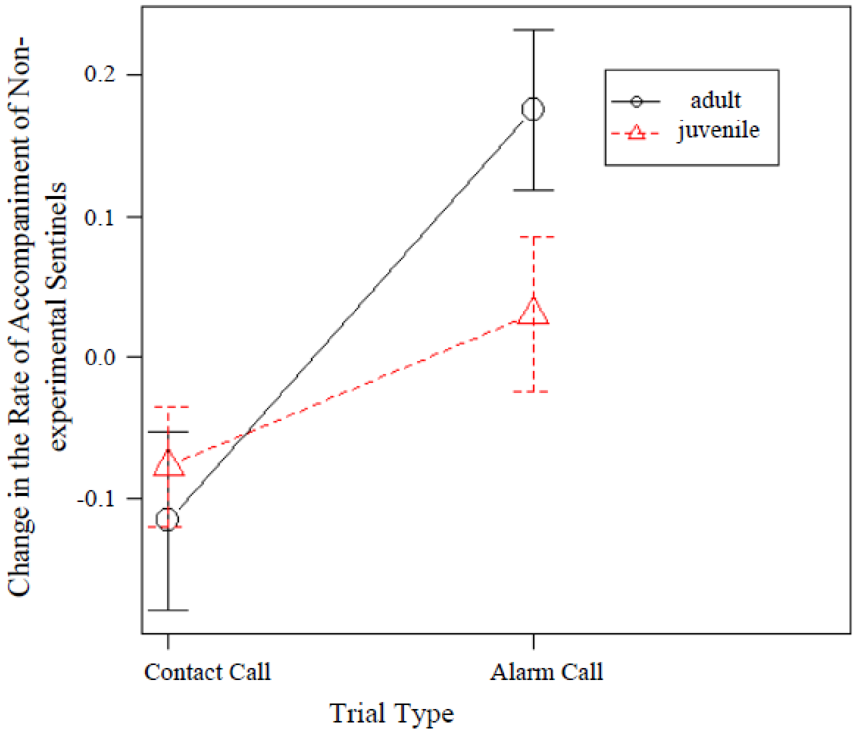


Figure C.1 Graph showing the mean ± standard error change in the rate of accompaniment of all non-experimental sentinels after playbacks of either contact, or alarm calls from either adults or juveniles. 48 trials; 12 each of adult contact call, adult alarm call, juvenile contact call and juvenile alarm call playbacks.

Appendices: Appendix D – Extra Information & Analyses for Chapter 5

Additional Table for the Analyses of Chapter 5

Table D.1 Table showing the output of a linear mixed-effects model with investigating the time between manipulated individuals leaving the nest and the next nest visit by any individual, using data only from the first playback type to be used at a group. Sample size 16 playbacks at 8 groups, 8 mobbing call playbacks, and 8 context-neutral playbacks.

Fixed Effect	Estimate	Standard Error	z	p
Intercept	-212.80	285.00	-0.75	0.48
Group Size	107.70	55.00	1.96	0.09
Non-Retained Terms	**z**	**p**		
Playback Type	-0.12	0.91		
Random Effects	**Variance**	**Standard Deviation**		
Group ID	29816.00	172.67		

Additional Analyses not Included in the Main Text of Chapter 5

Do pied babblers delay returning from the nest as a response to perceived predator presence?

Individuals did not always return immediately to the group after feeding the nestlings. I frequently observed that the provisioning individual would sit on the nest to brood the young after feeding. Therefore, I recorded whether this behaviour occurs or not after each playback to ascertain whether this was an alternative response to the playback treatment.

To ascertain whether perceived predator presence may influence a provisioner's decision over whether to brood the nestlings or not, I ran a generalised linear mixed-effects model with a binomial response of whether the experimental individual brooded the nestlings or not. I used fixed effects of playback type (heterospecific mobbing or context neutral calls) in an interaction with playback order position (whether its respective playback type was conducted first or second) and group size; in addition to a random effect of group ID. Because only 4/12 mobbing playbacks were conducted in the 2nd hour of trials, I also ran an analysis of only the data collected in the first hour of the trial. The model was the same as above, apart from the playback order position term was not used.

When using the full dataset, there were non-significant trends for mobbing calls to be more likely to elicit brooding behaviour than context neutral calls when used as the first ($z=1.81$, $p=0.07$) trial type (5/8 mobbing playbacks, 2/8 context neutral playbacks elicited brooding). When used as the second trial type this trend was reversed, with context neutral playbacks more likely to elicit brooding behaviour ($z= -1.72$, $p=0.09$) trial type at the group (2/4 mobbing playbacks, 5/6 context neutral playbacks elicited brooding). Individuals in smaller groups were also more likely to brood the nestlings ($z= -1.99$, $p=0.05$) (see Table D.2). However, when only using data from the first hour these effects were not present (see Table D.3).

The offspring should have been old enough, at date of experiment, to not require brooding from an adult. Therefore, brooding may have been a different anti-predator response to not draw attention to the nest. My results do not provide definitive evidence to suggest whether this was, or was not the case. While using the full dataset, mobbing playbacks trended towards eliciting brooding behaviour more than context neutral playbacks when used as the first playback type; however, as second playback type, there was a trend for context neutral playbacks to be more likely to elicit brooding (though sample sizes are limited). Additionally, when only analysing data from the first hour, there was no statistical difference between the two trial types in the likelihood of eliciting brooding behaviour. Therefore, I cannot conclusively state whether individuals were using brooding behaviour as a response to playbacks.

Table D.2 Table showing the output of a generalised linear mixed-effects model with a binomial response term investigating whether individuals use nestling brooding as a response to heterospecific anti-predator information. Sample size 26 playbacks at 8 groups, 12 mobbing call playbacks (8 in first hour, 4 in second), and 14 context-neutral playbacks (8 in first hour, 6 in second).

Fixed Effects	**Estimate**	**Standard Error**	**z**	**p**
Intercept	4.39	3.10	1.42	0.16
Playback Type	3.20	1.77	1.81	0.07
Playback Position	4.86	2.61	1.86	0.06
Group Size	-1.34	0.68	-1.99	0.05
Playback Type*Playback Position	-5.77	3.36	-1.72	0.09
Random Effect	**Variance**	**Standard Deviation**		
Group ID	1.24	1.11		

Table D.3 Table showing the output of a generalised linear mixed-effects model with a binomial response term investigating whether individuals use nestling brooding as a response to heterospecific anti-predator information, using data only from the first playback type to be used at a group. Sample size 16 playbacks at 8 groups, 8 mobbing call playbacks, and 8 context-neutral playbacks.

Fixed Effect	**Estimate**	**Standard Error**	**z**	**p**
Intercept	-1.10	0.82	-1.35	0.18
Playback Type	1.61	1.10	1.47	0.14
Non-Retained Term	**z**	**p**		
Group Size	-1.31	0.19		
Random Effect	**Variance**	**Standard Deviation**		
Group ID	<0.001	<0.001		

Appendices: Appendix E – Extra Analyses for Chapter 6

Is there a greater species diversity in the presence of pied babblers than in their absence?

My analyses contained within chapter 6 showed that heterospecific presence and species richness is greater in the presence rather than the absence of pied babbler groups. I conducted a further analysis to investigate whether species diversity was also different in the presence compared to the absence of babblers. To do this I used only data collected on the Kuruman River Reserve, excluding data collected on surrounding farmland because the transects did not cover this land. I only used data collected on babbler home foraging ranges where there were at least 6 data collection points on transects and at least 6 data collection points in the presence of pied babblers. There was a total of 6 foraging ranges that fitted this classification. I then calculated separate Shannon-Wiener index values (Shannon, 1948) for each foraging range in the presence and absence of pied babblers.

To analyse whether there were any differences in species diversity in the presence and absence of babbler groups I conducted a LMM with a response term of the Shannon-Wiener index values. I used a fixed effect of whether the data was collected in the presence or absence of babblers. To control for the fact that greater sampling effort can lead to the recording of additional species, and thus can bias diversity measures, I used an additional fixed effect of the number of sample points collected on each babbler home foraging range. My model contained a random effect of babbler home foraging range. Data presented are raw values ± standard error.

I found that diversity was not affected by the presence of babblers (presence, 2.05±0.25, n=6; absence, 1.02±0.30, n=6) with the term not being retained in the minimal model. Instead sampling effort was a greater predictor of the Shannon-Wiener index value, with a greater sampling effort leading to a greater diversity (est=0.02, t=5.29, p<0.001; see Table E.1).

Table E.1 Minimal model output of a linear mixed effects model investigating the predictors of species diversity measurements on babbler group home foraging ranges on the Kuruman River Reserve. Data from 6 pied babbler group home foraging ranges, collected in the presence and absence of babblers.

Fixed Effect	Estimate	Standard Error	z	p
Intercept	0.80	0.19	4.19	<0.01
Sampling Effort	0.02	<0.01	5.29	<0.001
Non-Retained Term	**z**	**p**		
Babbler Presence	-0.66	0.52		
Random Effect	**Variance**	**Standard Deviation**		
Home Foraging Range ID	0.00	0.00		

Are heterospecifics attracted by pied babblers' signals, and are they more likely to be attracted by calls that suggest the potential for greater predator detection? – Controlling for order

In the main chapter, I investigated whether birds are attracted to locations due to the public information provided by heterospecifics by using Friedman tests. I tested for differences between playback types in the number of heterospecifics arriving during playback periods, and the time with at least one avian heterospecific present. However, this did not control for the order of playback, and what playback types had occurred before (e.g. if babbler calls had been played back previously then more species may have already been attracted to a location).

Given the limited number of trials I was unable to do a thorough analysis with these factors incorporated, but I present here the results of preliminary models that do include them. I ran separate generalised linear mixed effects models (family=Poisson) with response variables of either the number of heterospecifics that arrived within a playback period, or the time with at least 1 heterospecific present. Fixed effects were playback type, the playback's position in the playback sequence and whether babbler calls had been played back before it during the experiment. I also included the random effect of the ID of the babbler group whose calls were used (and whose foraging home range was used) for the playback.

Table E.2 Minimal model output of a generalised linear mixed effects model investigating the predictors of the number of heterospecifics that arrive to different playback treatments. BG=Background Noise playback, F=Foraging call playback, F+S=Foraging call with Sentinel call playback. Data from 14 pied babbler group home foraging ranges. To allow for comparisons between all playback types I set different trial types as the baseline intercept, and present the additional data generated by these re-runnings of the model after the relevant 'Intercept' value.

Fixed Effects	Estimate	Standard Error	z	p
Intercept [Backgorund Noise]	-3.10	0.73	-4.25	<0.001
Playback Type: BG vs F	2.83	0.61	4.66	<0.001
BG vs F+S	2.42	0.62	3.90	<0.001
BG vs Silence	0.61	0.74	0.83	0.41
Playback Order	0.43	0.12	3.69	<0.001
Intercept [Silence]	-2.49	0.61	-4.07	<0.001
Playback Type: Silence vs F	2.22	0.48	4.59	<0.001
Silence vs F+S	1.80	0.49	3.65	<0.001
Intercept [Foraging+Sentinel Calls]	-0.68	0.43	-1.59	0.11
Playback Type: F+S vs F	0.41	0.25	1.65	0.10
Non-Retained Term	**z**	**p**		
Whether follows Babbler Playback	-0.33	0.74		
Random Effect	**Variance**	**Standard Deviation**		
Group ID	0.60	0.77		

As with the Friedman test in the main Chapter, foraging calls (3.42 ± 1.46 individuals) and foraging calls with sentinel calls (2.07 ± 0.53 individuals) attracted more heterospecifics that background noise (0.21 ± 0.11 individuals) (foraging calls vs. background noise, z=4.66, p<0.001; foraging + sentinel calls vs. background noise, z=3.90, p<0.001; Table E.2) and silence (0.36 ± 0.17 individuals) (foraging calls vs. silence, z=4.59, p<0.001; foraging + sentinel calls vs. silence, z=3.65, p<0.001; Table E.2). The time with at least one heterospecific was also greater for foraging call (70.21 ± 14.37 secs) and foraging call with sentinel call playbacks (61.21 ± 14.25 secs) compared to background noise (3.00 ± 1.94 secs) (foraging calls vs. background noise, z=19.35, p<0.001; foraging + sentinel calls vs. background noise, z=19.07, p<0.001, Table E.3) and silence (9.50 ± 8.07 secs) (foraging calls vs. silence, z=19.91, p<0.001; foraging + sentinel calls vs. silence, z=19.48, p<0.001, Table E.3). Silence and background noise playbacks did not attract a different number of heterospecifics (z=0.83, p=0.41; Table E.2), but during silence playbacks the time with at least one heterospecific present was greater than background noise playbacks (z=6.80, p<0.001; Table E.3). The time with at least one heterospecific present was not different between foraging call and foraging call with sentinel call playbacks (z=0.41, p=0.68; Table E.3), but there was a non-significant trend for foraging calls to attract more heterospecifics (z=1.65, p=0.10; Table E.2). Trial order affected both the number of heterospecifics attracted and the time with at least one heterospecific present, with later trials attracting more heterospecifics, which stayed for longer (number: est.=0.43, s.e.=0.12, z=3.69, p<0.001; time: est.=0.47, s.e.=0.05, z=9.42, p<0.001; Tables E.2 & E.3). Whether a playback occurred after a babbler playback did not affect the number of heterospecifics attracted, and was not retained in the final model (playback after a babbler playback, 1.73 ± 0.67 individuals; playback not after a babbler playback, 1.22 ± 0.35 individuals; see Table E.2); but it did influence the time with at least one heterospecific present, with the playbacks that were after babbler playbacks having heterospecifics stay for less time (playback after a babbler playback, 27.58 ± 7.45 secs; playback not after a babbler playback, 48.04 ± 12.02 secs; z= -10.66, p<0.001; Table E.3).

Table E.3 Minimal model output of a generalised linear mixed effects model investigating the predictors of the time with at least one heterospecific present during different playback treatments. BG=Background Noise playback, F=Foraging call playback, F+S=Foraging call with Sentinel call playback. Data from 14 pied babbler group home foraging ranges. To allow for comparisons between all playback types I set different trial types as the baseline intercept, and present the additional data generated by these re-runnings of the model after the relevant 'Intercept' value.

Fixed Effects	Estimate	Standard Error	z	p
Intercept [Backgorund Noise]	0.03	0.41	0.08	0.94
Playback Type: BG vs F	3.09	0.16	19.35	<0.001
BG vs F+S	3.07	0.16	19.07	<0.001
BG vs Silence	1.21	0.18	6.80	<0.001
Playback Order	0.47	0.05	9.42	<0.001
Whether follows Babbler Playback	-1.02	0.10	-10.66	<0.001
Intercept [Silence]	1.24	0.39	3.22	<0.01
Playback Type: Silence vs F	1.88	0.09	19.91	<0.001
Silence vs F+S	1.86	0.10	19.48	<0.001
Intercept [Foraging+Sentinel Calls]	3.10	0.37	8.30	<0.001
Playback Type: F+S vs F	0.02	0.05	0.41	0.68
Random Effect	**Variance**	**Standard Deviation**		
Group ID	1.81	1.35		

As these are preliminary results I shall not discuss them fully, and the main results regarding the effects of playbacks are similar to those in the main Chapter, the only difference being in the GLMM where the time with at least one heterospecific present was greater for silence playbacks than background noise. Trial order did seem to affect my results with more heterospecifics turning up to playbacks and there being a longer time with at least one heterospecific present in later playbacks, which is possibly an effect of the avian community becoming more used to my presence at the playback location. Whether a playback took place after a babbler playback or not did not seem to affect the number of heterospecifics arriving to playbacks, but it did influence the length of time with at least one heterospecific present. This effect was not as expected, however, with there being less time with a heterospecific present in those playbacks after babbler playbacks compared to those where there had been no babbler playbacks previously. This may, however, be a result of my small sample size, and the fact that this term is correlated with playback order (the first playback condition will obviously not be following a playback of babbler calls). Thus, I recognise this model is not perfect, but given a larger sample size I would attempt to analyse the data in a different manner (for instance not include any of the first playbacks).

Reference:

Shannon, C.E. (1948) A mathematical theory of communication. The Bell System Technical Journal, **27**, 379-423 & 623-656

Appendix F

Published Work from this Thesis

ethology international journal of behavioural biology

Ethology

PERSPECTIVES AND REVIEWS

Breaking down the Species Boundaries: Selective Pressures behind Interspecific Communication in Vertebrates

James R. S. Westrip & Matthew B. V. Bell

Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Ashworth Laboratories, Edinburgh, UK

Correspondence
James R. S. Westrip, Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Ashworth Laboratories, Charlotte Auerbach Road, Edinburgh EH9 3FL, UK.
E-mail: j.r.s.westrip@sms.ed.ac.uk

Received: December 5, 2014
Initial acceptance: January 7, 2015
Final acceptance: February 26, 2015
(M. E. Hauber)

doi: 10.1111/eth.12379

Keywords: eavesdropping, information exploitation, interspecific communication

Abstract

Studying heterospecific communication provides an opportunity to examine the dynamics of cross-species social behaviour. It allows us to ask questions about the extent to which the transfer of information is adaptive or accidental and provides an empirically tractable context for manipulating relationships. To date, most studies of heterospecific communication have focussed on receivers. However, the selective pressures on signallers can be as important in determining the dynamics of interspecific communication. Here, we propose a simple framework for thinking about cross-species information transfer, which (i) considers whether information exchange is either accidental or adaptive and (ii) whether it is unidirectional or bidirectional. To clearly classify interactions, it is necessary to quantify all of the payoffs of interspecific communication to both signallers and receivers. This requires accurate characterisation of the currency influenced by cross-species communication (e.g. weight gain, foraging success, survival). However, quantifying the payoffs may be difficult, because each side may be benefiting via different currencies. To date, studies on heterospecific communication have focussed on only one dimension of a niche (usually antipredator or foraging signals). However, because niches are multidimensional, investigations should incorporate multiple aspects of a species' niche, to get a better perspective on why we see certain patterns of information use between species.

Introduction : The Importance of Considering Both Signallers and Receivers

Interspecific communication among vertebrates is widespread (Goodale et al. 2010; Magrath et al. 2014) and provides an opportunity to understand the evolutionary dynamics of cross-species social behaviour. In common with any social behaviour, a complete understanding of an interaction requires consideration of how selection acts on both parties.

To date, most studies have focussed on receiver responses, revealing that receivers frequently gain substantial benefits via access to reliable or relevant information that is not otherwise available (Dall et al. 2005; Goodale & Kotagama 2005a; Magrath et al. 2014). Focussing on receiver responses, however, has limitations: it tends to restrict the types of interactions investigated, does not explore the possibility of bidirectional communication and does not generally consider the payoffs to signallers. This is despite the fact that the dynamics of a cross-species interaction will depend on the payoffs accruing to both signallers and receivers. It is the costs and benefits of an interaction for a signaller that determine whether public information use is parasitic, commensal or mutualistic (see Danchin et al. 2004).

We suggest that to clearly define a cross-species signalling interaction, it is necessary to (i) determine whether communication with another species is adaptive to the signaller and (ii) determine whether the flow of information is uni- or bidirectional. The first requires that we correctly identify the intended primary receiver of a signal and that we accurately quantify the costs and benefits of communication to both signaller and receiver. The second requires that we recognise both species in an interaction can act as both signaller and receiver, and so should be investigated accordingly. We build on Kostan's (2002) four-stage model for the evolution of mutualistic interspecific communication, to develop a simple framework for identifying five main categories of heterospecific communication: uni- and bidirectional eavesdropping, unidirectional signalling which may be mutually beneficial to signallers and receiver or receiver exploitation, and active reciprocal communication.

Eavesdropping: Payoffs to Signaller not Dependent on Behaviour of Heterospecific Receiver

The first step in classifying a heterospecific signalling interaction is to determine whether or not the payoffs to the signaller are contingent on the behaviour of the receiver (Fig. 1). Where a signal is recognised by heterospecifics yet the signal is adapted solely to communicate with conspecifics, heterospecific receivers are eavesdropping (see Magrath et al. 2014). Eavesdropping evolves because it increases the receiver's total information (Goodale & Kotagama 2005a), and it may be unidirectional, where one species exploits information from another, or bidirectional, where both species exploit information generated by the other.

Unidirectional Eavesdropping

Opportunistic exploitation of signals given by other species is probably the most common target of experimental investigation to date (see Magrath et al. 2014). In many cases, the signalling species appears not to gain any benefit or suffer a cost from the behaviour of the receiving species, and the roles are not reversed. For example, bird species may associate with alarm calling stonechats without the stonechats receiving any reciprocal benefit (Greig-Smith 1981). Nine-spined sticklebacks also are able to exploit heterospecific public information when making foraging decisions, when three-spined sticklebacks cannot (Coolen et al. 2003).

Bidirectional Eavesdropping

Where associating species both generate conspicuous signals, there is an opportunity for bidirectional eavesdropping. Again, signallers may be unaffected by the behaviour of receivers, but roles can be reversed, with both species attending to each other's signals.

Bidirectional eavesdropping is particularly common when signals provide information about predator threats (e.g. Shriner 1998; Magrath et al. 2007; Goodale et al. 2010), with heterospecifics apparently even able to extract referential or motivational information about threats from heterospecific sources (e.g. Fichtel 2004; Kirchhof & Hammerschmidt 2006; Templeton & Greene 2007; Müller & Manser 2008; Fallow & Magrath 2010). This stands to reason, given that alarm signals are frequently very conspicuous, and most predators are relative generalists, posing a threat to all prey species in quite a wide-size spectrum. Additionally, species will be under stronger selection to recognise and respond to heterospecific antipredator information, than they may be for other contexts of information. This is because the information is a time-dependent cue for predator presence allowing for

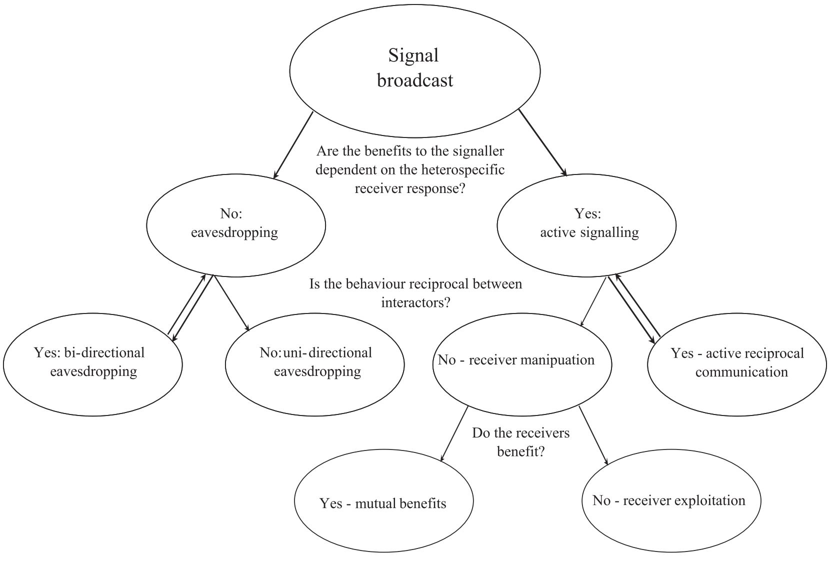


Fig. 1: Categorisation of heterospecific communication based on whether the selective benefits of signalling are based on the heterospecific response or not, and if the signaller–receiver relationship is reciprocal.

immediate antipredator responses (Magrath et al. 2014), and so is a matter of life or death, as well as providing longer term benefits (see Magrath et al. 2014), whereas the costs for not responding to signals in other contexts are not so severe.

Bidirectional eavesdropping need not be a symmetrical relationship because each species may derive different value from the same information, or place different values on different signallers (Goodale & Kotagama 2008; Magrath et al. 2009; Nolen & Lucas 2009; Martinez & Zenil 2012). This may depend upon how much relevant information the signaller provides for the receiver. For example, although pied babblers (*Turdoides bicolor*) and scimitarbills (*Rhinopomastus cyanomelas*) react to each others' alarms, scimitarbills react more strongly to pied babbler alarms than pied babblers do to scimitarbill alarms (Ridley et al. 2014). This may be because scimitarbills are usually solitary foragers. Therefore, they are more vulnerable than the group-living babblers and so they would gain more by eavesdropping (Lea et al. 2008).

The Negative Consequences of Eavesdropping: Costs to Signallers

Even where a signal is adaptive to signallers, there may often be costs imposed by eavesdroppers. Competitors, predators and parasites are all possible eavesdroppers that may exert selection for signal suppression or crypsis (e.g. Page & Ryan 2008; Goodale et al. 2010; Dapper et al. 2011). More subtly, solitary species or species lacking coordinated sentinel systems frequently accompany social species, taking advantage of the protection provided by their sentinels and alarm calls (e.g. Lea et al. 2008; Ridley et al. 2014). These species may then increase resource competition depending upon their extent of niche overlap.

Despite the risks associated with information parasitism, the existence of conspicuous, exploitable signals indicates that the benefits derived via conspecific responses outweigh the costs imposes by parasites. For example, social species continue to broadcast signals directing group-mates to food (e.g. Brown et al. 1991) or indicating that food sources are divisible (Elgar 1986; Radford & Ridley 2006), even though these signals may risk attracting competitors (see Danchin et al. 2004).

However, we have not yet been able to accurately quantify all of the payoffs involved in heterospecific associations. It may be that species which appear to be competitors actually provide additional benefits. For instance, the antipredator benefits individuals gain from group living, with con- or heterospecifics (e.g. Kruuk 1964; Hamilton 1971; Neill & Cullen 1974; Bertram 1980) may outweigh any costs imposed by information parasitism (see Future Directions, below).

The Negative Consequences of Eavesdropping: Costs to Receivers

Although receivers will be selected to respond to any relevant information generated by another species (Dall et al. 2005; Magrath et al. 2014), they are also likely to pay costs of eavesdropping, if they do so indiscriminately. In particular, variation in signaller reliability and variation in the extent of niche overlap may affect the payoffs of responding.

Signallers may vary in their reliability for a variety of reasons (see Goodale et al. 2010). For example, some species may be more prone to giving 'false' alarm calls (Magrath et al. 2009). This may be because the costs missed detections are substantially higher than the costs of false alarms (see Schibler & Manser 2007). Reacting to unreliable and irrelevant signals can be costly for individuals (see Cheney & Seyfarth 1988; Hare & Atkins 2001; Blumstein et al. 2004; Dall et al. 2005; Magrath et al. 2014) and so we might expect species to alter their responses depending on signaller identity (e.g. Magrath et al. 2009).

Even where reliability remains constant, the degree of niche overlap may alter the value of information provided by a heterospecific. Heterospecifics pose less resource competition than conspecifics because they have less niche overlap (Seppänen et al. 2007). However, it seems likely that the value of heterospecific information will increase as niche overlap increases (e.g. resource requirements and predation risks become more similar). Therefore, the heterospecifics likely to provide the most valuable information may also be the most direct competitors. Reacting indiscriminately, even to reliable signallers providing relevant information may therefore lead to conflict, with receivers needing to balance the benefits obtained via extra information against the costs of increased competition. Variation in reliability and the risk of increased competition with ecologically similar species may therefore lead to selection for discrimination between signallers; both at a species level, and even at an individual level (see Future Directions, below).

Signalling: Payoffs to Signaller are Dependent on Behaviour of Heterospecific Receiver

Eavesdropping amounts to a by-product relationship, with heterospecific receivers opportunistically utilising information generated for a different audience. By contrast, signalling occurs where a signal is specifically adapted to communicate with heterospecifics, and the benefits of signalling depend on heterospecific behaviour (e.g. grouper-eel relationship; Bshary et al. 2006; Vail et al. 2013). These signals may possibly even be used to tutor naïve heterospecifics (Gehlbach & Leverett 1995). Some species may even alter their signal or signalling behaviour to be of a greater benefit to heterospecific receivers (e.g. Rasa 1983; Ridley et al. 2007; May-Collado 2010), which may include mimicking heterospecifics (e.g. Wheatcroft & Price 2013) and this may influence signal evolution within a clade (Wheatcroft & Price 2015). Again the direction of information flow may be either unidirectional or reciprocal.

Unidirectional Signalling—Receiver Manipulation

Signallers may gain benefits from heterospecific receivers by using their signals to manipulate interactors. This may take the form of receiver exploitation where signallers manipulate receivers into inappropriate behaviour (e.g. Flower et al. 2013). Alternatively, the signaller may produce signals that manipulate heterospecific responses but also benefit the heterospecific receiver, without any reciprocal communication (e.g. Bshary et al. 2006).

Receiver Manipulation: Receiver Exploitation

Signallers may benefit from providing information to manipulate heterospecifics into acting inappropriately in a way that benefits the signaller. Several species of drongos (Dicruridae) are facultatively kleptoparasitic, and use deceptive signals to steal food from their victims (see Flower et al. 2013). For example, fork-tailed drongos (*Dicrurus adsimilis*) steal food by using false alarm calls to trick victims into fleeing for cover (Ridley & Raihani 2007; Flower 2011). Greater racket-tailed drongos (*D. paradiseus*) also use false alarm calls. These calls are more similar to aggressive calls and are hypothesised to act as a warning to hosts of aggression from drongos and so hosts flee to avoid aggression from the drongo (Satischandra et al. 2010).

Drongos are not completely parasitic, though. When associating with potential victims, fork-tailed drongos act as sentinels for their host (Radford et al. 2011) increasing the latter's foraging efficiency; they use true alarm calls they would otherwise not use (Ridley et al. 2007); they use their calls to attract foraging partners (Baigrie et al. 2014). Similarly, greater racket-tailed drongos provide true alarms (which may be mimicked) while in flocks (Goodale & Kotagama 2005a; Goodale et al. 2014) and heterospecifics preferably join flocks containing drongos (Goodale & Kotagama 2005b). Thus, the case of such drongos may not be entirely one of parasitism.

Receiver Manipulation: Mutual Benefits

Signalling to heterospecifics need not be exploitative of the receiver. Signalling may set up interactions that benefit both parties. For example, Bshary et al. (2006) showed how groupers (*Plectropomus pessuliferus*) use visual signals to induce moray eels (*Gymnothorax javanicus*) into joining hunts. Both species were more successful at catching prey when in association with the other species than when they hunted alone. Therefore, this unidirectional signalling relationship provides mutual benefits to both the signaller and the receiver.

Active Reciprocal Communication

True reciprocal communication may evolve where there is niche overlap, limited competition and repeated interactions between the same individuals. The emergence of such stable, sophisticated cross-species communication requires cognitive skills not currently thought to be common outside humans.

True reciprocal communication has been documented, but only rarely. Greater honeyguides (*Indicator indicator*) and human honey gatherers have a mutualistic communication system for locating bee colonies (Isack & Reyer 1989). Additionally, recruitment and flocking signals may encourage individuals to come together to form foraging associations (e.g. Windfelder 2001; Goodale & Kotagama 2006; Suzuki 2012). Tamarin long-calls may act as con- and heterospecific signals, as both saddle-backed (*Sanguinus fusicollis*) and emperor tamarins (*S. imperator*) respond to conspecific and heterospecific long-calls by long-calling and approaching the signal source (Windfelder 2001). This may allow both parties to locate other individuals (whether con- or heterospecific) to associate with. We emphasize that such a mutualistic relationship between interactors need not be symmetrical, as long as both parties gain a net benefit from the association, rather than acting alone, the relationship will be selected for (Kostan 2002).

Future Directions

To date, the study of heterospecific communication has been primarily descriptive, simply cataloguing situations where one species reacts to information provided by another (see Appendix S1 for examples). These interactions then fall on a cost-benefits continuum of interspecific communication from very beneficial communication to very costly (Danchin et al. 2004). Intuitively, where heterospecific responses provide high benefits, active signalling will be selected for (e.g. grouper-eel relationship; Bshary et al. 2006; Vail et al. 2013). Conversely, when there are high costs, such as when there are high levels of competition or predator eavesdropping (Page & Ryan 2008), signals may be suppressed (Dapper et al. 2011). When the net payoffs of an interspecific interaction are near zero for the signaller, there may be little selection for or against signalling to heterospecifics (Danchin et al. 2004), while the benefits of signalling to conspecifics remain high (e.g. Charnov & Krebs 1975; Sherman 1977; Curio et al. 1978; Gehlbach & Leverett 1995; Hogstad 1995). Therefore, heterospecific eavesdropping will persist as long as the signal provides beneficial information for the eavesdroppers.

Studies showing the direction of information flow can be informative, but it is analyses of selective pressures that may be able to show whether the communication we observe is truly mutualistic or possibly parasitic. It is now necessary to develop a more formal analytical framework based on robust quantification of the payoffs to both partners (e.g. Radford et al. 2011; Flower et al. 2013).

Accurate Quantification of Costs and Benefits of Communication to Both Signallers and Receivers

Classification of signalling interactions requires robust measurement of the payoffs to both parties. This in turn requires that we identify the proximate currency affected on both sides (weight gain, survival, foraging success, etc.). For example, the work on fork-tailed drongos has measured the costs and benefits of communication for both parties by recording food intake. By acting as sentinels for their hosts, drongos increase host biomass intake (Radford et al. 2011). Drongos will then attempt to kleptoparasitise their hosts. This is a strategy that is more beneficial for the drongos, in terms of biomass intake, than self-foraging (Flower et al. 2013). By showing that it is more beneficial to signal to heterospecifics than to self-forage Flower et al. have shown how signalling to heterospecifics has been selected for in this system.

Quantifying the payoffs of signalling poses problems because signallers and receivers may be benefiting via very different—and sometimes quite cryptic—currencies. For example, evidence showing species A gains 'x' amount of antipredator information from species B while species B gets no antipredator information in return does not mean A is purely parasitizing information from B. As a species' niche is made of n-dimensions (Hutchinson 1957) multidimensional analyses are required. Vitousek et al. (2007) and Ito & Mori (2010) have shown there are interactions between species where one party is non-vocal, and so the signalling species is unlikely to receive any predator vocal warnings from the receiver. It may prove interesting to investigate whether there is another, as yet untested, benefit to the signaller from such interactions. This may be information based on another context (such as foraging) or a direct benefit of association, for example Zenaida doves do not show aggression to carib grackles on their territory and the doves use grackle alarms (Griffin et al. 2005).

Ultimately, the only robust way to resolve problems with identifying and converting the relevant proximate currencies is to quantify the effect of cross-species association and communication on individual fitness. The logistics of actually doing this will not be trivial. It will require long-term studies of individually marked animals of both species involved in an eavesdropping or signalling relationship. It will also require measurement of the effect of individual variation in the capacity to use heterospecific information on variation in reproductive success. A profitable avenue may be to deploy the logic and techniques starting to be used to investigate the fitness consequences of variation in social competence (Taborsky & Oliveira 2012; Sih et al. 2014).

Identifying Reliability Discrimination at Species and Individual Level

Reacting to unreliable signals can be costly (Cheney & Seyfarth 1988; Hare & Atkins 2001; Blumstein et al. 2004). Therefore, individuals should be selected to adjust their responses in relation to signaller reliability. This may be both between (e.g. Magrath et al. 2009) and within species, which would require a degree of individual recognition.

Intraspecific individual recognition is observed throughout taxa (Tibbetts & Dale 2007), and several species are observed to alter their antipredator responses to the reliability of the signaller (e.g. Cheney & Seyfarth 1988; Hare & Atkins 2001; Blumstein et al. 2004). There is limited evidence for cross-species individual recognition (Proops et al. 2009), but Flower et al. (2014) have shown that victims of drongo kleptoparasitism will reduce their response to repeated drongo false alarms, suggesting interspecific individual recognition may be present in this system. Experimental manipulation of individual reliability may allow for empirical testing of cross-species reliability monitoring.

Ontogeny of Heterospecific Communication

Some studies have briefly touched upon the development of heterospecific communication (e.g. Kitchen et al. 2010; Magrath & Bennett 2012; Haff & Magrath 2013). More thorough investigations in a wider range of species will allow for more general trends to be observed. The ontogeny of the adaptive recognition of heterospecific signals can be performed using longitudinal studies with individuals. By testing their ability to respond to heterospecific signals as individuals' age may show whether they learn or have an innate ability (e.g. Haff & Magrath 2013). Alternatively separate populations of the same species can be studied where there is heterospecific presence or not (e.g. Magrath & Bennett 2012). The best way to then show that there is no genetic effect on recognition ability would be to conduct cross-fostering experiments between populations. If there is no such easy divide between populations, then it may still be possible to test this by creating artificial communities in laboratories or aviaries, both with and without heterospecific presence.

Conclusions

Many studies have conclusively shown how some species can interpret specific information from heterospecific signals. But, such studies have been mainly limited to one-dimensional, unidirectional testing of receiver responses. It is time that more studies began to quantify the relationship between heterospecific receivers and signallers, to ascertain what benefits each party receives from such an interactions, thus allowing for clear categorisation of interspecific communication. However, rather than a set of categories we may see a continuum from very beneficial communication to very costly. To empirically investigate where interactions lie on this continuum will require species to be observed both alone and in association with heterospecifics.

Acknowledgements

JRSW is funded by a NERC studentship, MBVB is supported by the University of Edinburgh. We would like to thank Thomas Flower, Eben Goodale and one anonymous reviewer for helpful comments in the preparation of this manuscript. The authors have no conflicts of interest to declare.

Literature Cited

Baigrie, B. D., Thompson, A. M. & Flower, T. P. 2014: Interspecific signalling between mutualists: food-thieving drongos use a cooperative sentinel call to manipulate foraging partners. Proc. R. Soc. B **281**, 20141232.

Bertram, B. C. R. 1980: Vigilance and group size in ostriches. Anim. Behav. **28**, 278—286.

Blumstein, D. T., Verneyre, L. & Daniel, J. C. 2004: Reliability and the adaptive utility of discrimination among alarm callers. Proc. R. Soc. B **271**, 1851—1857.

Brown, C. R., Brown, M. B. & Shaffer, M. L. 1991: Food-sharing signals among socially foraging cliff swallows. Anim. Behav. **42**, 551—564.

Bshary, R., Hohner, A., Ait-el-Djoudi, K. & Fricke, H. 2006: Interspecific communicative and coordinated hunting between groupers and giant moray eels in the Red Sea. PLoS Biol. **4**, e431.

Charnov, E. L. & Krebs, J. R. 1975: The evolution of alarm calls: altruism or manipulation? Am. Nat. **109**, 107—112.

Cheney, D. L. & Seyfarth, R. M. 1988: Assessment of meaning and the detection of unreliable signals by vervet monkeys. Anim. Behav. **36**, 477—486.

Coolen, I., Bergen, Y. V., Day, R. L. & Laland, K. N. 2003: Species difference in adaptive use of public information in sticklebacks. Proc. R. Soc. B **270**, 2413—2419.

Curio, E., Ernst, U. & Vieth, W. 1978: Cultural transmission of enemy recognition: one function of mobbing. Science **202**, 899—901.

Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M. & Stephens, D. W. 2005: Information and its use by animals in evolutionary ecology. TREE **20**, 187—193.

Danchin, É., Giraldeau, L.-A., Valone, T. J. & Wagner, R. H. 2004: Public information: from nosy neighbours to cultural evolution. Science **305**, 487—491.

Dapper, A. L., Baugh, A. T. & Ryan, M. J. 2011: The sounds of silence as an alarm cue in túngara frogs, *Physalaemus pustulosus*. Biotropica **43**, 380—385.

Elgar, M. A. 1986: House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. Anim. Behav. **34**, 169—174.

Fallow, P. M. & Magrath, R. D. 2010: Eavesdropping on other species: mutual interspecific understanding of urgency information in avian alarm calls. Anim. Behav. **79**, 411—417.

Fichtel, C. 2004: Reciprocal recognition of Sifaka (*Propithecus verreauxii verreauxii*) and redfronted lemur (*Eulemur fulvus rufus*) alarm calls. Anim. Cogn. **7**, 45—52.

Flower, T. 2011: Fork-tailed drongos use deceptive mimicked alarm calls to steal food. Proc. R. Soc. B **278**, 1548—1555.

Flower, T. P., Child, M. F. & Ridley, A. R. 2013: The ecological economics of kleptoparasitism: pay-offs from self-foraging versus kleptoparasitism. J. Anim. Ecol. **82**, 245—255.

Flower, T. P., Gribble, M. & Ridley, A. R. 2014: Deception by flexible alarm mimicry in an African bird. Science **344**, 513—516.

Gehlbach, F. R. & Leverett, J. S. 1995: Mobbing of eastern screech-owls: predatory cues, risk to mobbers and degree of threat. Condor **97**, 831—834.

Goodale, E. & Kotagama, S. W. 2005a: Alarm calling in Sri Lankan mixed-species bird flocks. Auk **122**, 108—120.

Goodale, E. & Kotagama, S. W. 2005b: Testing the roles of species in mixed-species bird flocks of a Sri Lankan rain forest. J. Trop. Ecol. **21**, 669—676.

Goodale, E. & Kotagama, S. W. 2006: Vocal mimicry by a passerine bird attracts other species involved in mixed-species flocks. Anim. Behav. **72**, 471—477.

Goodale, E. & Kotagama, S. W. 2008: Response to conspecific and heterospecific alarm calls in mixed-species bird flocks of a Sri Lankan rainforest. Behav. Ecol. **19**, 887—894.

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C. & Ruxton, G. D. 2010: Interspecific information transfer influences animal community structure. TREE **25**, 354—361.

Goodale, E., Ratnayake, C. P. & Kotagama, S. W. 2014: Vocal mimicry of alarm-associated sounds by a drongo elicits flee and mobbing responses from other species that participate in mixed-species bird flocks. Ethology **120**, 266—274.

Greig-Smith, P. W. 1981: The role of alarm responses in the formation of mixed-species flocks of heathland birds. Behav. Ecol. Sociobiol. **8**, 7—10.

Griffin, A. S., Savani, R. S., Hausmanis, K. & Lefebvre, L. 2005: Mixed-species aggregations in birds: zenaida doves, *Zenaida aurita*, respond to the alarm calls of carib grackles, *Quiscalus lugubris*. Anim. Behav. **70**, 507—515.

Haff, T. M. & Magrath, R. D. 2013: Eavesdropping on the neighbours: fledglings learn to respond to heterospecific alarm calls. Anim. Behav. **85**, 411—418.

Hamilton, W. D. 1971: Geometry for the selfish herd. J. Theor. Biol. **31**, 295—311.

Hare, J. F. & Atkins, B. A. 2001: The squirrel that cried wolf: reliability detection by juvenile Richardson's ground squirrels (*Spermophilus richardsonii*). Behav. Ecol. Sociobiol. **51**, 108—112.

Hogstad, O. 1995: Alarm calling by willow tits, *Parus montanus*, as mate investment. Anim. Behav. **49**, 221—225.

Hutchinson, G. E. 1957: Concluding remarks. Cold Spring Harb. Symp. Quant. Biol. **22**, 415—427.

Isack, H. A. & Reyer, H.-U. 1989: Honeyguides and honey gatherers: interspecific communication in a symbiotic relationship. Science **243**, 1343—1346.

Ito, R. & Mori, A. 2010: Vigilance against predators induced by eavesdropping on heterospecific alarm calls in a non-vocal lizard *Oplurus cuvieri cuvieri* (Reptilia: Iguania). Proc. R. Soc. B **277**, 1275—1280.

Kirchhof, J. & Hammerschmidt, K. 2006: Functionally referential alarm calls in tamarins (*Saguinus fuscicollis* and *Sanguinus mystax*) – evidence from playback experiments. Ethology **112**, 346—354.

Kitchen, D. M., Bergman, T. J., Cheney, D. L., Nicholson, J. R. & Seyfarth, R. M. 2010: Comparing responses of four ungulate species to playbacks of baboon alarm calls. Anim. Cogn. **13**, 861—870.

Kostan, K. M. 2002: The evolution of mutualistic interspecific communication: assessment and management across species. J. Comp. Psychol. **116**, 206—209.

Kruuk, H. 1964: Predators and anti-predator behaviour of the black headed gull (*Larus ridibundus* L.). Behaviour (Suppl.) **11**, 1—129.

Lea, A. J., Barrera, J. P., Tom, L. M. & Blumstein, D. T. 2008: Heterospecific eavesdropping in a nonsocial species. Behav. Ecol. **19**, 1041—1046.

Magrath, R. D. & Bennett, T. H. 2012: A micro-geography of fear: learning to eavesdrop on alarm calls of neighbouring heterospecifics. Proc. R. Soc. B **279**, 902—909.

Magrath, R. D., Pitcher, B. J. & Gardner, J. L. 2007: A mutual understanding? Interspecific responses by birds to each other's aerial alarm calls. Behav. Ecol. **18**, 944—951.

Magrath, R. D., Pitcher, B. J. & Gardner, J. L. 2009: An avian eavesdropping network: alarm signal reliability and heterospecific response. Behav. Ecol. **20**, 745—752.

Magrath, R. D., Haff, T. M., Fallow, P. M. & Radford, A. N. 2014: Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. Biol. Rev., DOI: 10.1111/brv.12122.

Martinez, A. E. & Zenil, R. T. 2012: Foraging guild influences dependence on heterospecific alarm calls in Amazonian bird flocks. Behav. Ecol. **23**, 544—550.

May-Collado, L. J. 2010: Changes in whistle structure of two dolphin species during interspecific associations. Ethology **116**, 1065—1074.

Müller, C. A. & Manser, M. B. 2008: The information banded mongooses extract from heterospecific alarms. Anim. Behav. **75**, 897—904.

Neill, S. R. St. J., & Cullen, J. M. 1974: Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. J. Zool. **172**, 549—569.

Nolen, M. T. & Lucas, J. R. 2009: Asymmetries in mobbing behaviour and correlated intensity during predator mobbing by nuthatches, chickadees and titmice. Anim. Behav. **77**, 1137—1146.

Page, R. A. & Ryan, M. J. 2008: The effect of signal complexity on localization performance in bats that localize frog calls. Anim. Behav. **76**, 761—769.

Proops, L., McComb, K. & Reby, D. 2009: Cross-modal individual recognition in domestic horses (*Equus caballus*). PNAS **106**, 947—951.

Radford, A. N. & Ridley, A. R. 2006: Recruitment calling: a novel form of extended parental care in an altricial species. Curr. Biol. **16**, 1700—1704.

Radford, A. N., Bell, M. B. V., Hollén, L. I. & Ridley, A. R. 2011: Singing for your supper: sentinel calling by kleptoparasites can mitigate the cost to victims. Evolution **65**, 900—906.

Rasa, O. A. E. 1983: Dwarf mongoose and hornbill mutualism in the Taru Desert, Kenya. Behav. Ecol. Sociobiol. **12**, 181—190.

Ridley, A. R. & Raihani, N. J. 2007: Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. Behav. Ecol. **18**, 324—330.

Ridley, A. R., Child, M. F. & Bell, M. B. V. 2007: Interspecific audience effects on the alarm-calling behaviour of a kleptoparasitic bird. Biol. Lett. **3**, 589—591.

Ridley, A. R., Wiley, E. M. & Thompson, A. M. 2014: The ecological benefits of interceptive eavesdropping. Funct. Ecol. **28**, 197—205.

Satischandra, S. H. K., Kodituwakku, P., Kotagama, S. W. & Goodale, E. 2010: Assessing "false" alarm calls by a drongo (*Dicrurus paradiseus*) in mixed-species bird flocks. Behav. Ecol. **21**, 396—403.

Schibler, F. & Manser, M. B. 2007: The irrelevance of individual discrimination in meerkat alarm calls. Anim. Behav. **74**, 1259—1268.

Seppänen, J.-T., Forsman, J. T., Mönkkönen, M. & Thomson, R. L. 2007: Social information use is a process across time, space, and ecology, reaching heterospecifics. Ecology **88**, 1622—1633.

Sherman, P. W. 1977: Nepotism and the evolution of alarm calls. Science **197**, 1246—1253.

Shriner, W. M. 1998: Yellow-bellied marmot and golden-mantled ground squirrel responses to heterospecific alarm calls. Anim. Behav. **55**, 529—536.

Sih, A., Chang, A. T. & Wey, T. W. 2014: Effects of behavioural type, social skill and the social environment on male mating success in water striders. Anim. Behav. **94**, 9—17.

Suzuki, T. N. 2012: Long-distance calling by the willow tit, *Poecile montanus*, facilitates formation of mixed-species foraging flocks. Ethology **118**, 10—16.

Taborsky, B. & Oliveira, R. F. 2012: Social competence: an evolutionary approach. TREE **27**, 679—688.

Templeton, C. N. & Greene, E. 2007: Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. PNAS **104**, 5479—5482.

Tibbetts, E. A. & Dale, J. 2007: Individual recognition: it is good to be different. TREE **22**, 529—537.

Vail, A. L., Manica, A. & Bshary, R. 2013: Referential gestures in fish collaborative hunting. Nat. Commun. **4**, 1765.

Vitousek, M. N., Adelman, J. S., Gregory, N. C. & St. Clair, J. J. H. 2007: Heterospecific alarm recognition in a non-vocal reptile. Biol. Lett. **3**, 632—634.

Wheatcroft, D. & Price, T. D. 2013: Learning and signal copying facilitate communication among bird species. Proc. R. Soc. B, **280**, 20123070.

Wheatcroft, D. & Price, T. D. 2015: Rates of signal evolution are associated with the nature of interspecific communication. Behav. Ecol. **26**, 83—90.

Windfelder, T. L. 2001: Interspecific communication in mixed-species groups of tamarins: evidence from playback experiments. Anim. Behav. **61**, 1193—1201.

Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Table showing a selection of studies that show heterospecific information use, but with only uni-directional testing/observation.

Appendix – Table showing a selection of studies that show heterospecific information use, but with only uni-directional testing/observation

Reference	Reference Details	Study Species	System	Type of Test
Bell et al. (2009)	Proc. R. Soc., B, 276, 2997-3005	Pied Babbler, Fork-tailed Drongo & Crowned Lapwing	Anti Predator	One way playback
Burger (1984)	Am. Nat., 123, 327-337	Grebe & Gulls	Anti Predator	One way observations
Carrasco & Blumstein (2012)	Ethology, 118, 243-250	Mule Deer & Marmot	Anti Predator	One way playback
Diego-Rasilla & Luengo (2004)	Behav. Ecol. Sociobiol., 55, 556-560	Amphibians	Habitat Selection	One way playback
Fallow et al. (2011)	Behav. Ecol., 22, 401-410	Superb Fairy-Wren	Anti Predator	One way playback
Ferrari & Chivers (2008)	Anim. Behav., 75, 1921-1925	Amphibians	Anti Predator	Cohabitation with one way
Forsman & Mönkkönen (2001)	Anim. Behav., 62, 1067-1073	Willow Tit & Redwing	Anti Predator	Playbacks of each species but not reciprocal trials between the 2 focal bird species
Haff & Magrath (2013)	Anim. Behav., 85, 411-418	Scrubwren, Fairy-Wren, Honeyeater	Anti Predator	One way playback
Hauser (1988)	Behaviour, 105, 187-201	Vervet Monkey & Starling	Anti Predator	One way playback
Hetrick & Sieving (2012)	Behav. Ecol., 23, 83-92	Chickadees & Tufted Titmouse	Anti Predator	One way playback
Hromada et al. (2008)	PLOS ONE, 3, e3930	Shrikes	Habitat Selection	Food Supplementation & One
Huang et al. (2012)	Behav. Ecol., 23, 463-472	Tufted Titmouse & Northern Cardinal	Anti Predator	One way playback
Hurd (1996)	Behav. Ecol. Sociobiol., 38, 287-292	Chickadees	Anti Predator	One way playback
Ito & Mori (2010)	Proc. R. Soc., B, 277, 1275-1280	Iguana & Paradise Flycatcher	Anti Predator	One way playback
Koda (2012)	Behav. Proc., 91, 30-34	Deer & Macaque	Foraging	One way playback
Lea et al. (2008)	Behav. Ecol., 19, 1041-1046	Dik-dik & Go-away Bird	Anti Predator	One way playback

Reference	Reference Details	Study Species	System	Type of Test
Magrath et al. (2009)	Proc. R. Soc., B, 276, 769-774	Scrubwren, Fairy-Wren, Honeyeater	Anti Predator	One way playback
Müller & Manser (2008)	Anim. Behav., 75, 897-904	Banded Mongoose & Plovers	Anti Predator	One way playback
Penna & Velasquez (2011)	Ethology, 117, 63-71	Frogs	Advertisement Call	One way playback
Phelps et al. (2007)	Behav. Ecol., 18, 108-114	Frogs	Anti Predator?	Predator exposure & one way playback
Pupin et al. (2007)	Anim. Behav., 74, 1683-1690	Amphibians	Habitat Selection	One way playback
Rainey et al. (2004)	Proc. R. Soc., B, 271, 755-759	Hornbills & Diana Monkey	Anti Predator	One way playback
Ramakrishnan & Cross (2000)	J. Comp. Psychol., 114, 3-12	Macaques & multiple heterospecifics	Anti Predator	One way playback
Randler (2006)	Ethology, 112, 411-416	Red Squirrel & Jay	Anti Predator	One way playback
Sullivan (1984)	Behaviour, 91, 294-311	Downy Woodpecker & avian heterospecifics	Anti Predator	One way playback
Sullivan et al. (2003)	Behaviour, 140, 553-564	Salamanders	Anti Predator	One way chemical release
Suzuki (2012)	Ethology, 118, 10-16	Willow Tit & sympatric heterospecifics	Flocking	One way playback
Templeton & Greene (2007)	PNAS, 104, 5479-5482	Nuthatch & Chickadee	Anti Predator	One way playback
Vitousek et al. (2007)	Biol. Lett., 3, 632-634	Galapagos Iguana &	Anti Predator	One way playback
Whiting & Greeff (1999)	Behav. Ecol. Sociobiol., 45, 420-423	Flat Lizard	Foraging	One way presentation of heterospecific individuals (not signal per se)
Zuberbühler (2000)	Proc. R. Soc., B, 267, 713-718	Diana & Campbell's Monkey	Anti Predator	One way playback