Australian National University

Acoustic Communication and Collective Decision-making in Social Animal Groups



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April 2026

A thesis submitted for the degree of Doctor of Philosophy of
The Australian National University

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Declaration

This thesis and the work presented in it are the result of my own original research. No part of this thesis has been submitted for any other degree. Chapters 2, 3, and 6 have been published, and I am the first and corresponding author on all three, with primary or sole responsibility for conceptualization, data collection, analysis, writing, and manuscript preparation. All chapters, except Chapter 2, include contributions from Robert D. Magrath, Robert Heinsohn, and Andrew N. Radford to conceptualization, review, and editing. Chapter 2 includes contributions from Robert D. Magrath, Marta B. Manser, and Damien R. Farine to conceptualization, review, and editing. To the best of my knowledge, this thesis contains no material previously published or written by another person, except where reference is made in the text. This research was approved by the Australian National University Ethics Committee (protocol A2022/35), the Institutional Animal Care and Use Committee of Kaohsiung Medical University (IACUC-110049), and the Forestry Bureau, Council of Agriculture, Executive Yuan of Taiwan (No. 1105165388).

Chun-Chieh Liao

April 2026

Acknowledgements

First and foremost, I would like to express my deepest gratitude to my three wonderful supervisors, Rob Magrath, Rob Heinsohn, and Andy Radford, whose guidance, support, and encouragement made this thesis possible.

My deepest thanks go to my primary supervisor, Rob Magrath. I first met Rob at the 2018 International Ornithological Congress in Vancouver, Canada, where I gathered the courage to approach you after a talk and share my work on mixed-species flocks. Although our conversation was brief, your kindness left a lasting impression on me. About two years later, during a difficult and uncertain period of life, I reached out to you. That email opened the door to a rich and meaningful new chapter in my life. During the two years I was stranded in Taiwan because of the COVID pandemic, you regularly checked in on me and even supervised one chapter of my PhD remotely over Zoom. Throughout my time in Canberra, you gave me the freedom to follow my curiosity, while always offering thoughtful guidance and steady support. You patiently rehearsed presentations with me time and again, and your comments on my manuscripts were always insightful. I will deeply miss those conversations outdoors under the trees, coffee in hand, where ideas could wander freely and grow into something exciting—especially beneath the golden ginkgo trees in autumn. I will always remember the birdwatching trips we took in search of target species, especially the night we spent in the middle of nowhere looking for a White-throated Nightjar: under a star-filled sky, we searched for hours and heard only one or two calls, yet felt completely delighted and satisfied. As you said, we were truly a group of “Bird Nerds.” It is really hard to imagine a better supervisor. Thank you, Rob!

I am also deeply grateful to Rob Heinsohn for co-supervising my PhD and supporting my application, even though we had not known each other before. During the application stage, you gave me the opportunity to consider different study species and directions, and I feel incredibly fortunate that I ultimately chose White-winged Choughs as the focus of my PhD. It has been a privilege to build on the strong foundation of

research that you and your team established on this species and to explore the story of choughs through such fascinating questions. Thank you for so generously sharing your knowledge, experience, and enthusiasm for choughs. I am especially grateful that you joined me in the field during the early stages of the project for chough banding and taught me many of the practical details involved. I also sincerely appreciate your help with animal ethics and project administration, which allowed me to focus more fully on understanding these remarkable birds. It has been a real joy and honour to become part of the “Chough Team.”

I am likewise deeply grateful to Andy Radford. Although most of our interactions took place by email and online meetings, from our very first conversation you made me feel completely at ease with your humour, energy, and enthusiasm. Rather than feeling nervous when discussing research plans, I found myself genuinely enjoying the process. Andy consistently brought brilliant and insightful perspectives to our discussions, helping me sharpen the core questions behind each study and strengthen both the design and execution of my research. I also greatly appreciated the remarkable efficiency and clarity with which you reviewed my manuscripts and responded to my questions. It was a real pleasure to finally meet you in person at Behaviour 2025 in Kolkata, where I came to appreciate even more fully your warmth and support. I will always remember how you encouraged me immediately after my presentation; that moment eased my nerves, boosted my confidence, and made me feel genuinely supported. It was also a pleasure and an honour to meet your wonderful research group.

My sincere thanks also go to Damien Farine for all your help throughout my PhD and for inviting me to collaborate on a review paper. Completing that review in such a short time was a real breakthrough for me. Your guidance throughout that process meant a great deal, and I truly enjoyed brainstorming with you and working together to bring the paper to completion. I am equally grateful to your wonderful research group, who brought me both support and joy during my PhD.

I would also like to thank everyone in the Magrath group: You, Jessica, Natalie, Kushini, Chaminda, Tom, and Cameron. We first got to know one another through Zoom lab meetings in 2020 and, because of COVID, spent nearly two years meeting online before properly meeting in person. It was an unusual but memorable way to begin. Thank you all for your support, encouragement, and help at different stages of my PhD. I am especially grateful to You, who helped me in countless ways over the years, from experimental design and sound calibration to fieldwork, presentation rehearsals, and manuscript reading. I deeply value your friendship and will always remember your care and support. I also thank Jessica for her valuable feedback and for sharing so many wonderful bird stories, and Kushini for her warmth, optimism, and the many enjoyable conversations about Brown Thornbills.

My sincere thanks go to the wonderful Chough Team and to everyone who assisted with banding and fieldwork, especially Brendah, Lola, Esha, James, Connie, Ying, and Audrey. I am especially grateful to Brendah for always being so generous with your time and practical help throughout my PhD. You are an outstanding field researcher, someone I could always rely on, and not only a wonderful colleague but also a dear friend. Lola, it was a real pleasure to work with you on choughs and to share many unforgettable moments and stories in the field. I would also like to thank Andrew Cockburn for his warm encouragement and kindness. I always treasured our conversations, not only about choughs, but also about birding around the world and the many fascinating stories and insights you so kindly shared.

I would also like to thank my colleagues and friends for the friendship, warmth, and companionship you brought into my life over these years. Your support, encouragement, and the many conversations, shared meals, and moments of laughter along the way made my PhD journey much richer and more memorable. In particular, I would like to thank Kang-Chieh, Mina, Olga, Đorđe, Wei Wen, Alex, Meng-Han, Chenke, Fatema, Mahmud, Ivan, Edward, Yiqing, Samuele, Fran, Xingyi, Julia, Shefali, Lisa, Zheng-An, Yi-Ying, Chieh Lin, Eryn, and many others.

I am deeply grateful to Canberra Chinese Christian Church for being a second home to me during my time in Canberra. In particular, I would like to thank Pastor Mavis Kwok, Iris Wen, Hong Ming, Wei Zhang, Elaine Yao, John Lui, LuLu, Ukie, John Chang, Rachel, Rina, Wenhui, Olivia, Anthony, Chori, Xiao Yang, Jack Zhang, Shirley, Elaine Deng, Elijah, Emma, Wenshui, Binyu, Kiwi, Tracy, Evan, Richard, David, Howard, Esther, Jasmine, Emmy, and many others. Your fellowship, generous love, and prayers carried me through many seasons of my PhD and made my years in Canberra a time of joy, strength, and deep growth in life and faith.

Finally, I owe more than words can express to my lovely family, whose constant love, patience, and selfless support have carried me through every stage of this journey and given me the freedom to pursue my dreams. To my fiancée, Ying-Hsuan Lu, although we have lived more than 7,000 kilometres apart for almost all of the past nearly four years and have shared the joys and struggles of daily life from afar, I have always felt your presence close beside me.

I still vividly remember first encountering mixed-species flocks in freezing, high-elevation conifer forests in winter in Taiwan. I was captivated by the sight: how could these small birds survive in such a harsh environment, and how could different species move and act together with such coordination? That experience sparked my curiosity about social behaviour and communication and set me on the path that eventually led to this thesis. I hope to carry that original sense of wonder with me always—to remain passionate, curious, and full of awe at the beauty of the natural world.

This research was supported by the RSB International PhD Scholarship at the Australian National University (2020, 2022–2025) and by the Government Scholarship to Study Abroad from the Ministry of Education, Taiwan (2024–2026).

Abstract

Many species live in complex societies in which individuals must coordinate their behaviour to maintain cohesion and gain the benefits of social living, both within and between species. Communication plays a central role in enabling rapid coordination and reducing consensus costs when group members differ in their needs and information. In this PhD thesis, I examine how social animals use communication to coordinate behaviour, particularly in antipredator contexts. The thesis includes introductory and concluding chapters (Chapters 1 and 7), a conceptual review (Chapter 2), and four empirical studies on social birds (Chapters 3–6).

In Chapter 2, I develop a conceptual framework describing how acoustic signals and movement cues are used to coordinate behaviour in social animal groups. By integrating information masking, discrimination ability, and encoding limitations, the framework predicts that behaviours involving the timing of events or the expression of specific actions should rely more on acoustic signals, whereas decisions involving complex choices should generally rely on movement cues. This framework also highlights key future directions, including multimodal communication and decision-making in mixed-species groups.

Guided by this framework, I conducted three playback experiments on white-winged choughs (*Corcorax melanorhamphos*), a highly social cooperative breeder. In Chapter 3, I show that adult choughs possess a functionally referential alarm-call system that conveys threat type and urgency. Choughs produce three distinct alarm calls: terrestrial alarms for ground-based predators, aerial whistles for high-flying hawks, and flee alarms for high-urgency threats. Birds responded appropriately to alarm-call playbacks, typically looking around to terrestrial alarms, looking upwards to aerial whistles, and fleeing to flee alarms. In Chapter 4, I show that young choughs develop appropriate alarm-call responses slowly, remaining poor at interpreting alarm calls for several months after fledging. Most juveniles responded to all alarm types by simply looking around, even when exposed to high-urgency flee alarms, suggesting that

extended social protection and vocal complexity may shape learning in this species. In Chapter 5, I show that choughs integrate multiple components of social alarm information to coordinate collective antipredator behaviour. They assess alarm-call type to decide what action to take, and caller number to modulate both the intensity of their response and the likelihood of propagating alarm information to others. This decision rule helps reduce false alarms and unnecessary information cascades that can negatively affect group living. Together, these findings demonstrate how acoustic communication enables white-winged choughs to remain both safe and cohesive.

In Chapter 6, I extend these insights beyond single-species societies to mixed-species systems. I conducted playback experiments to examine danger information transfer in mixed-species bird flocks in Taiwan. I find strong asymmetries in predator detection and/or danger communication between leader and follower species, with leader species always initiating mobbing calls. However, mobbing calls from leaders did not elicit stronger antipredator responses than those from followers. I propose that larger conspecific group sizes and kin-selected behaviours may favour the evolution of superior antipredator signalling in leader species, leading to asymmetric information transfer about danger between species. These results further suggest that mutual antipredator benefits are common in mixed flocks, promoting positive interspecific interactions and enhancing flock cohesion.

Together, these findings suggest that sociality not only increases animals' reliance on social information, but also favours communication systems that allow information about danger to be encoded, assessed, and shared in ways that support effective antipredator behaviour.

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Chapter 1

General Introduction



White-winged choughs (*Corcorax melanorhamphos*) are highly social, obligate cooperative breeders living in stable groups year-round. Taken at the Australian National Botanic Gardens on 8 March 2020, this photograph captures the first chough group I encountered after arriving in Canberra. Even this brief encounter sparked a fascination with their social lives that ultimately shaped this thesis.

My PhD thesis examines how social animals use communication to coordinate behaviour, particularly in antipredator contexts. It is structured as a compilation of chapters prepared as independent papers, and each empirical chapter therefore includes its own introduction to the relevant literature. Chapter 2 also provides a broader conceptual review of communication and collective behaviour. Accordingly, this General Introduction does not review the literature in detail, but instead outlines the main ideas and concepts that link the thesis chapters and provides an overview of the chapters that follow.

Benefits and costs of living in social groups

Group living is widespread across the animal kingdom and occurs in many different forms, ranging from small family groups to complex multilevel societies composed of conspecifics (Grueter et al., 2020; Papageorgiou et al., 2019). Living in groups can provide a range of benefits, including reduced predation risk (Sosna et al., 2019), improved foraging efficiency (Kern et al., 2016; Thiebault et al., 2014), enhanced breeding opportunities (Ebensperger et al., 2019; O'Brien, 1991), facilitated social learning (Aplin et al., 2025; Griffin, 2004; Whiten, 2000), and buffering against harsh environments (Cornwallis et al., 2017; Shen et al., 2017). In many social species, group living can also provide protection and nutritional support to young individuals, thereby buffering them from immediate risks and reducing the costs of responding inappropriately to environmental challenges (Dezecache et al., 2019; Hollén & Manser, 2006; Seyfarth & Cheney, 1980). Such social buffering, commonly reported in social mammals and non-human primates, can also influence behavioural development, with juveniles sometimes acquiring adult-like behaviours only gradually (Fichtel, 2008; Fischer et al., 2000; Hollén & Manser, 2006). On the other hand, group living can also impose costs on individuals. For example, individuals in larger groups may face increased competition, greater conspicuousness to predators, and a higher risk of parasite or disease transmission (Ward & Webster, 2016). Signalling within groups presents an additional challenge, as the rapid spread of social information can enhance collective benefits but also amplify costly

errors when signals are inaccurate or dishonest (Gray & Webster, 2023; McCormick et al., 2024).

Beyond single-species groups, many animals also form mixed-species groups, in which individuals of different species move or forage together in a coordinated manner (Carlson et al., 2023; Goodale et al., 2020). Like single-species groups, these associations can reduce predation risk and improve foraging efficiency (Goodale et al., 2020; Sridhar et al., 2012). In addition, because participating species often differ in ecological niches, morphology, and behaviour, mixed-species groups may allow individuals to gain complementary information or other benefits while reducing the direct competition and social aggression often found in single-species groups (Seppänen et al., 2007; Goodale et al., 2010, 2020; Sridhar et al., 2012). However, these associations also involve costs, including kleptoparasitism, interspecific aggression, disease or parasite transmission, and the risk of false or dishonest social information (González et al., 2014; Goodale et al., 2020; Satischandra et al., 2010; Sridhar & Guttal, 2018). Thus, whether groups are composed of conspecifics or heterospecifics, a central challenge of social living is to balance the benefits of association against its potential costs.

Social life relies on communication

To realise the benefits of group living, individuals must coordinate their activities in order to function as a cohesive group (Byrne, 2000; Conradt & Roper, 2005). Such coordination generally depends on the ability of group members to transfer information about their environment, behaviour, and intentions (Conradt & Roper, 2005; Liao et al., 2024; Strandburg-Peshkin et al., 2015). However, coordinating behaviour can be difficult because group members often differ in their needs, capabilities, and access to information, creating potential conflicts and increasing the costs of consensus decisions (Davis et al., 2022). Having some means of communication, therefore, often plays a critical role in reducing consensus costs among group members by allowing them to rapidly coordinate their behaviours (Fichtel & Manser, 2010; Liao et al., 2024; Strandburg-Peshkin et al., 2015).

Communication entails the use of signals that have evolved because senders benefit from the responses of intended receivers, while receivers are selected to respond only when those responses are also beneficial to themselves (Bradbury & Vehrencamp, 2011; Magrath et al., 2020; Smith, 1965). Animals communicate using multiple modalities, including chemical (Thienen et al., 2014), tactile (Simpson et al., 2001), visual (Ballerini et al., 2008; Bleichman et al., 2023) and acoustic signals (Fichtel & Manser, 2010), each with different strengths and limitations depending on the ecological and social context. Among these, acoustic communication is especially important in many birds and mammals because it can transmit information rapidly, reach multiple receivers at once, and remain effective even when group members are out of sight of one another (Fichtel & Manser, 2010; Liao et al., 2024). This makes it particularly useful for coordinating behaviour in social groups, including maintaining group cohesion, coordinating departures and movements, facilitating foraging, and coordinating collective responses to danger (Bouchard & Zuberbühler, 2022; Bousquet et al., 2011; Clay et al., 2012; Coomes et al., 2019; Engesser & Manser, 2022).

Communication about danger

Predation is a major selective pressure in the evolution of social living. Information about danger can spread through both cues and signals (Beauchamp & Ruxton, 2007; Lima, 1995b; Murray et al., 2017). For example, individuals may flee immediately upon detecting a threat, providing passive cues to nearby group members that danger may be imminent and thereby triggering escape responses (Beauchamp & Ruxton, 2007; Lima, 1995a). Alarm calls, which are warning vocal signals produced in response to a threat, are particularly effective because they can rapidly alert multiple group members, even when receivers are out of sight or not currently vigilant (Caro, 2005; Devereux et al., 2008; Magrath et al., 2015). Broadly, alarm calls in many birds and mammals include two main types: mobbing calls, which promote approach or harassment of predators that do not pose an immediate threat (Curio, 1978; Dutour et al., 2017), and flee alarm calls, which trigger escape or freezing when immediate action is required (McLachlan & Magrath, 2020; Zuberbühler, 2009). In some species, alarm calls also encode specific information about

predator type, urgency, or other aspects of danger, allowing receivers to respond more appropriately without directly detecting the predator themselves (Gill & Bierema, 2013; Leavesley & Magrath, 2005; Manser, 2001; Seyfarth et al., 1980; Suzuki, 2011; Townsend & Manser, 2013). Alarm-call communication therefore plays an important role in coordinating collective antipredator behaviour and provides a useful framework for understanding how social animals transfer and use information about danger.

Information use in antipredator coordination

Animals often rely on information provided by others to guide behaviour, which can have both benefits and costs (Dall et al., 2005; Giraldeau et al., 2002; Ward & Webster, 2016). In antipredator contexts, individuals can acquire information directly by detecting a predator themselves (i.e., personal information), or indirectly through the alarm calls and behaviour of others (i.e., social information) (Caro, 2005; Dall et al., 2005). Personal information is typically more accurate (Barrera et al., 2011; Van Bergen et al., 2004), but obtaining it can be costly because it may require increased vigilance or reduced foraging time (Hollén et al., 2008; Templeton & Giraldeau, 1996). In contrast, social information can often be obtained more quickly and relatively cheaply (Giraldeau et al., 2002), allowing individuals to allocate more time to other activities, such as foraging. However, alarm calls are not always reliable, and false alarms appear to be surprisingly common in animal societies (Blumstein et al., 2004; Giraldeau et al., 2002; Gray & Webster, 2023; Searcy & Nowicki, 2005). Responding to or spreading false alarms can be costly, leading to unnecessary energy expenditure, lost foraging opportunities, and false information cascades (Beauchamp, 2010; Beauchamp & Ruxton, 2007; McCormick et al., 2024; Ridley & Raihani, 2007). These trade-offs create a central challenge for animals living in groups: individuals must decide how to use and integrate multiple sources of information in order to coordinate optimal antipredator responses.

Thesis overview

My PhD thesis focuses on how social animals use acoustic communication to coordinate antipredator behaviour, and includes introductory and concluding chapters (Chapters 1 and 7), a conceptual review (Chapter 2) and four empirical studies on social species of birds (Chapters 3–6).

In Chapter 2, I develop a conceptual framework describing how acoustic signals and movement cues are used to coordinate collective behaviour in social animal groups. By integrating information masking, discrimination ability and encoding limitations, the framework predicts that behaviours involving the timing of events or the expression of specific actions should rely more on acoustic signals, whereas decisions involving complex choices (e.g., direction or destination) should generally rely on movement cues. This framework also highlights key future directions, including multimodal communication and collective decision-making in mixed-species groups. This work is published in *Philosophical Transactions of the Royal Society B: Biological Sciences* (https://doi.org/10.1098/rstb.2023.0184).

Although Chapter 2 considers both acoustic signals and movement cues in collective behaviour, the empirical chapters focus on the framework's acoustic component in antipredator contexts. Specifically, in Chapters 3–5, I conducted three playback experiments on white-winged choughs (*Corcorax melanorhamphos*), a highly social, cooperatively breeding species, to investigate alarm communication, the development of alarm responses and collective antipredator decision-making. Chapter 6 extends this focus to acoustic information transfer and antipredator coordination in mixed-species bird flocks.

In Chapter 3, I show that adult choughs possess a functionally referential alarm-call system that conveys threat type and urgency, enabling context-specific responses. Choughs produce three distinct alarm calls in response to different threats: terrestrial alarms for ground-based predators, aerial whistles for high-flying hawks, and flee alarms for immediate, high-urgency threats. Birds responded appropriately to playbacks of

alarm calls alone, typically looking around in response to terrestrial alarms, looking upwards to aerial whistles, and fleeing in response to flee alarms. This work is published in *Animal Behaviour* (https://doi.org/10.1016/j.anbehav.2025.123330).

In Chapter 4, I show that young choughs develop appropriate alarm-call responses slowly, remaining poor at interpreting alarm calls for several months after fledging. Most juveniles respond in a largely generalised manner, typically looking around regardless of alarm-call type, suggesting limited discrimination of threat-specific information early in development. This prolonged developmental period suggests that extended social protection may relax selection for the early acquisition of accurate antipredator responses, allowing juveniles to rely on group members while gradually learning to interpret alarm calls.

In Chapter 5, I show that choughs integrate multiple components of social alarm information to coordinate collective antipredator behaviour. They assess both alarm call type and the number of callers, to decide what action to take and to modulate both the intensity of their response and the likelihood of propagating alarm information to others. This propagation decision rule should reduce false alarms and unnecessary information cascades that can negatively affect group living. Together, these findings demonstrate how acoustic communication facilitates coordinated antipredator responses while contributing to the maintenance of group cohesion in white-winged choughs.

In Chapter 6, I extend these insights beyond single-species societies to mixed-species systems. I find strong asymmetries in predator detection and/or danger communication between leader and follower species, with leader species always initiating mobbing calls. However, mobbing calls from leader species did not elicit stronger antipredator responses than those from follower species. I propose that larger conspecific group sizes and associated kin-selected behaviours may favour the evolution of more effective antipredator signalling in leader species, potentially generating asymmetric information transfer about danger between species. These results further suggest that mutual antipredator benefits are common in mixed-species bird flocks,

promoting positive interspecific interactions and enhancing flock cohesion. This work is published in *Animal Behaviour* (https://doi.org/10.1016/j.anbehav.2024.01.014).

References

Aplin, L., Crates, R., Flack, A., & McGregor, P. (2025). Social learning and culture in birds: emerging patterns and relevance to conservation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *380*(1925), 20240128. https://doi.org/10.1098/rstb.2024.0128

Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., Lecomte, V., Orlandi, A., Parisi, G., Procaccini, A., Viale, M., & Zdravkovic, V. (2008). Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(4), 1232–1237. https://doi.org/10.1073/pnas.0711437105

Barrera, J. P., Chong, L., Judy, K. N., & Blumstein, D. T. (2011). Reliability of public information: Predators provide more information about risk than conspecifics. *Animal Behaviour*, *81*(4), 779–787. https://doi.org/10.1016/j.anbehav.2011.01.010

Beauchamp, G. (2010). Determinants of false alarms in staging flocks of semipalmated sandpipers. *Behavioral Ecology*, *21*(3), 584–587. https://doi.org/10.1093/beheco/arq032

Beauchamp, G., & Ruxton, G. D. (2007). False alarms and the evolution of antipredator vigilance. *Animal Behaviour*, *74*(5), 1199–1206. https://doi.org/10.1016/j.anbehav.2007.02.014

Bleichman, I., Yadav, P., & Ayali, A. (2023). Visual processing and collective motion-related decision-making in desert locusts. *Proceedings of the Royal Society B: Biological Sciences*, *290*(1991), 20221862. https://doi.org/10.1098/rspb.2022.1862

Blumstein, D. T., Verneyre, L., & Daniel, J. C. (2004). Reliability and the adaptive utility of discrimination among alarm callers. *Proceedings of the Royal Society B: Biological Sciences*, *271*(1550), 1851–1857. https://doi.org/10.1098/rspb.2004.2808

Bouchard, A., & Zuberbühler, K. (2022). An intentional cohesion call in male chimpanzees of Budongo Forest. *Animal Cognition*, *25*(4), 853–866. https://doi.org/10.1007/s10071-022-01597-6

Bousquet, C. A. H., Sumpter, D. J. T., & Manser, M. B. (2011). Moving calls: A vocal mechanism underlying quorum decisions in cohesive groups. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1711), 1482–1488. https://doi.org/10.1098/rspb.2010.1739

Bradbury, J. W., & Vehrenkamp, S. L. (2011). *Principle of animal communication*. Sinauer Associates.

Byrne, R. W. (2000). How monkeys find their way: leadership, coordination, and cognitive maps of African baboons. In S. Boinski & P. A. Garber (Eds.), *On the*

Move: How and Why Animals Travel in Groups, pp. 491–518. University of Chicago Press.

Carlson, N. V, Freeberg, T. M., Goodale, E., Theo, A. H., & Goodale, E. (2023). Mixed-species groups and aggregations: shaping ecological and behavioural patterns and processes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *378*(1878), 20220093. https://doi.org/10.1098/rstb.2022.0093

Caro, T. (2005). *Antipredator defenses in birds and mammals*. University of Chicago Press.

Clay, Z., Smith, C. L., & Blumstein, D. T. (2012). Food-associated vocalizations in mammals and birds: What do these calls really mean? *Animal Behaviour*, *83*(2), 323–330. https://doi.org/10.1016/j.anbehav.2011.12.008

Conradt, L., & Roper, T. J. (2005). Consensus decision making in animals. *Trends in Ecology and Evolution*, *20*(8), 449–456. https://doi.org/10.1016/j.tree.2005.05.008

Coomes, J. R., McIvor, G. E., & Thornton, A. (2019). Evidence for individual discrimination and numerical assessment in collective antipredator behaviour in wild jackdaws (*Corvus monedula*). *Biology Letters*, *15*(10), 20190380. https://doi.org/10.1098/rsbl.2019.0380

Cornwallis, C. K., Botero, C. A., Rubenstein, D. R., Downing, P. A., West, S. A., & Griffin, A. S. (2017). Cooperation facilitates the colonization of harsh environments. *Nature Ecology and Evolution*, *1*, 0057. https://doi.org/10.1038/s41559-016-0057

Curio, E. (1978). The adaptive significance of avian mobbing: I. teleonomic hypotheses and predictions. *Zeitschrift Für Tierpsychologie*, *48*(2), 175–183. https://doi.org/10.1111/j.1439-0310.1978.tb00254.x

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. *Trends in Ecology and Evolution, 20*(4), 187–193. https://doi.org/10.1016/j.tree.2005.01.010

Davis, G. H., Crofoot, M. C., & Farine, D. R. (2022). Using optimal foraging theory to infer how groups make collective decisions. *Trends in Ecology and Evolution*, *37*(11), 942–952. https://doi.org/10.1016/j.tree.2022.06.010

Devereux, C. L., Fernàndez-Juricic, E., Krebs, J. R., & Whittingham, M. J. (2008). Habitat affects escape behaviour and alarm calling in Common Starlings *Sturnus vulgaris*. *Ibis*, *150*, 191–198. https://doi.org/10.1111/j.1474-919X.2008.00835.x

Dezecache, G., Crockford, C., & Zuberbühler, K. (2019). The development of communication in alarm contexts in wild chimpanzees. *Behavioral Ecology and Sociobiology*, *73*, 104. https://doi.org/10.1007/s00265-019-2716-6

Dutour, M., Léna, J. P., & Lengagne, T. (2017). Mobbing calls: a signal transcending species boundaries. *Animal Behaviour*, *131*, 3–11. https://doi.org/10.1016/j.anbehav.2017.07.004

Ebensperger, L. A., Correa, L. A., Ly Prieto, Á., De Arce, F. P., Abades, S., & Hayes, L. D. (2019). Multiple mating is linked to social setting and benefits the males in a

communally rearing mammal. *Behavioral Ecology*, *30*(3), 675–687. https://doi.org/10.1093/beheco/arz003

Engesser, S., & Manser, M. B. (2022). Collective close calling mediates group cohesion in foraging meerkats via spatially determined differences in call rates. *Animal Behaviour*, *185*, 73–82. https://doi.org/10.1016/j.anbehav.2021.12.014

Fichtel, C. (2008). Ontogeny of conspecific and heterospecific alarm call recognition in wild Verreaux's sifakas (*Propithecus verreauxi verreauxi*). *American Journal of Primatology*, *70*, 127–135. https://doi.org/10.1002/ajp

Fichtel, C., Manser, M. (2010). Vocal communication in social groups. In: Kappeler, P. (eds) *Animal Behaviour: Evolution and Mechanisms*, pp. 29–54. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-02624-9_2

Fischer, J., Cheney, D. L., & Seyfarth, R. M. (2000). Development of infant baboons' responses to graded bark variants. *Proceedings of the Royal Society B: Biological Sciences*, *267*(1459), 2317–2321. https://doi.org/10.1098/rspb.2000.1285

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*(6), 449–461. https://doi.org/10.1111/eth.12097

Giraldeau, L. A., Valone, T. J., & Templeton, J. J. (2002). Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *357*(1427), 1559–1566. https://doi.org/10.1098/rstb.2002.1065

González, A. D., Matta, N. E., Ellis, V. A., Miller, E. T., Ricklefs, R. E., & Gutiérrez, H. R. (2014). Mixed species flock, nest height, and elevation partially explain avian haemoparasite prevalence in Colombia. *PLoS ONE*, *9*(6), e100695. https://doi.org/10.1371/journal.pone.0100695

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C., & Ruxton, G. D. (2010). Interspecific information transfer influences animal community structure. *Trends in Ecology and Evolution*, *25*(6), 354–361. https://doi.org/10.1016/j.tree.2010.01.002

Goodale, E., Sridhar, H., Sieving, K. E., Bangal, P., Colorado Z., G. J., Farine, D. R., Heymann, E. W., Jones, H. H., Krams, I., Martínez, A. E., Montaño-Centellas, F., Muñoz, J., Srinivasan, U., Theo, A., & Shanker, K. (2020). Mixed company: a framework for understanding the composition and organization of mixed-species animal groups. *Biological Reviews*, *95*(4), 889–910. https://doi.org/10.1111/brv.12591

Gray, L., & Webster, M. M. (2023). Quorum decision making coordinates group departure decisions in Eurasian oystercatchers, *Haematopus ostralegus*. *Animal Behaviour*, *202*, 29–38. https://doi.org/10.1016/j.anbehav.2023.05.012

Gray, L., & Webster, M. M. (2023). False alarms and information transmission in grouping animals. *Biological Reviews*, *98*(3), 833–848. https://doi.org/10.1111/brv.12932

Griffin, A. S. (2004). Social learning about predators: A review and prospectus. *Learning and Behavior*, *32*(1), 131–140. https://doi.org/10.3758/BF03193188

Grueter, C. C., Qi, X., Zinner, D., Bergman, T., Li, M., Xiang, Z., Zhu, P., Migliano, A. B., Miller, A., Krützen, M., Fischer, J., Rubenstein, D. I., Vidya, T. N. C., Li, B., Cantor, M., & Swedell, L. (2020). Multilevel organisation of animal sociality. *Trends in Ecology and Evolution*, *35*(9), 834–847. https://doi.org/10.1016/j.tree.2020.05.003

Hollén, L. I., Bell, M. B. V., & Radford, A. N. (2008). Cooperative sentinel calling? Foragers gain increased biomass intake. *Current Biology*, *18*(8), 576–579. https://doi.org/10.1016/j.cub.2008.02.078

Hollén, L. I., & Manser, M. B. (2006). Ontogeny of alarm call responses in meerkats, *Suricata suricatta*: the roles of age, sex and nearby conspecifics. *Animal Behaviour*, *72*(6), 1345–1353. https://doi.org/10.1016/j.anbehav.2006.03.020

Kern, J. M., Sumner, S., & Radford, A. N. (2016). Sentinel dominance status influences forager use of social information. *Behavioral Ecology*, *27*(4), 1053–1060. https://doi.org/10.1093/beheco/arv240

Leavesley, A. J., & Magrath, R. D. (2005). Communicating about danger: Urgency alarm calling in a bird. *Animal Behaviour*, *70*(2), 365–373. https://doi.org/10.1016/j.anbehav.2004.10.017

Liao, C.-C., Magrath, R. D., Manser, M. B., & Farine, D. R. (2024). The relative contribution of acoustic signals versus movement cues in group coordination and collective decision-making. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *379*(1905), 20230184. https://doi.org/10.1098/rstb.2023.0184

Lima, S. L. (1995a). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, *49*(1), 11–20. https://doi.org/10.1016/0003-3472(95)80149-9

Lima, S. L. (1995b). Collective detection of predatory attack by social foragers: fraught with ambiguity? *Animal Behaviour*, *50*(4), 1097–1108. https://doi.org/10.1016/0003-3472(95)80109-X

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on heterospecific alarm calls: From mechanisms to consequences. *Biological Reviews*, *90*(2), 560–586. https://doi.org/10.1111/brv.12122

Magrath, R. D., Haff, T. M., & Igic, B. (2020). *Interspecific Communication: Gaining Information from Heterospecific Alarm Calls.* In: Aubin, T., Mathevon, N. (eds) *Coding Strategies in Vertebrate Acoustic Communication. Animal Signals and Communication* (vol 7), pp. 287–314. Springer, Cham. https://doi.org/10.1007/978-3-030-39200-0_12

Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society B: Biological Sciences*, *268*(1483), 2315–2324. https://doi.org/10.1098/rspb.2001.1773

McCormick, J. S., White, T. E., Middleton, E. J. T., & Latty, T. (2024). Information cascades spread adaptive and maladaptive behaviours in group-living animals. *Animal Behaviour*, *209*, 53–62. https://doi.org/10.1016/j.anbehav.2023.12.007

McLachlan, J. R., & Magrath, R. D. (2020). Speedy revelations: How alarm calls can convey rapid, reliable information about urgent danger. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1921). https://doi.org/10.1098/rspb.2019.2772

Murray, T. G., Zeil, J., & Magrath, R. D. (2017). Sounds of modified flight feathers reliably signal danger in a pigeon. *Current Biology*, *27*(22), 3520–3525. https://doi.org/10.1016/j.cub.2017.09.068

O'Brien, T. G. (1991). Female-male social interactions in wedge-capped capuchin monkeys: benefits and costs of group living. *Animal Behaviour*, *41*, 555–567. https://doi.org/10.1016/S0003-3472(05)80896-6

Papageorgiou, D., Christensen, C., Gall, G. E. C., Klarevas-Irby, J. A., Nyaguthii, B., Couzin, I. D., & Farine, D. R. (2019). The multilevel society of a small-brained bird. *Current Biology*, *29*, 1105–1121. https://doi.org/10.1016/j.cub.2019.09.072

Ridley, A. R., & Raihani, N. J. (2007). Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. *Behavioral Ecology*, *18*(2), 324–330. https://doi.org/10.1093/beheco/arl092

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. *Behavioral Ecology*, *21*(2), 396–403. https://doi.org/10.1093/beheco/arp203

Searcy, W. A., & Nowicki, S. (2005). *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton University Press.

Seppänen, J., 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. https://doi.org/10.1890/06-1757.1

Seyfarth, R. M., & Cheney, D. L. (1980). The ontogeny of vervet monkey alarm calling behavior: a preliminary report. *Zeitschrift Für Tierpsychologie*, *54*(1), 37–56. https://doi.org/10.1111/j.1439-0310.1980.tb01062.x

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. *Science*, *210*(4471), 801–803. https://doi.org/10.1126/science.7433999

Shen, S. F., Emlen, S. T., Koenig, W. D., & Rubenstein, D. R. (2017). The ecology of cooperative breeding behaviour. *Ecology Letters*, *20*(6), 708–720. https://doi.org/10.1111/ele.12774

Simpson, S. J., Despland, E., Hägele, B. F., & Dodgson, T. (2001). Gregarious behavior in desert locusts is evoked by touching their back legs. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(7), 3895–3897. https://doi.org/10.1073/pnas.071527998

Smith, J. M. (1965). The evolution of alarm calls. *American Naturalist*, *99*(904), 59–63. http://www.journals.uchicago.edu/t-and-c

Sosna, M. M. G., Twomey, C. R., Bak-Coleman, J., Poel, W., Daniels, B. C., Romanczuk, P., & Couzin, I. D. (2019). Individual and collective encoding of risk in animal groups. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(41), 20556–20561. https://doi.org/10.1073/pnas.1905585116

Sridhar, H., & Guttal, V. (2018). Friendship across species borders: Factors that facilitate and constrain heterospecific sociality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1746), 20170014. https://doi.org/10.1098/rstb.2017.0014

Sridhar, H., Srinivasan, U., Askins, R. A., Canales-Delgadillo, J. C., Chen, C.-C., Ewert, D. N., Gale, G. A., Goodale, E., Gram, W. K., Hart, P. J., Hobson, K. A., Hutto, R. L., Kotagama, S. W., Knowlton, J. L., Lee, T. M., Munn, C. A., Nimnuan, S., Nizam, B. Z., Péron, G., Robin, V. V., Rodewald, A. D., Rodewald, P. G., Thomson, R. L., Trivedi, P., Van Wilgenburg, S. L., & Shanker, K. (2012). Positive relationships between association strength and phenotypic similarity characterize the assembly of mixed-species bird flocks worldwide. *American Naturalist*, *180*(6), 777–790. https://doi.org/10.1086/668012

Strandburg-Peshkin, A., Farine, D. R., Couzin, I. D., & Crofoot, M. C. (2015). Shared decision-making drives collective movement in wild baboons. *Science*, *348*(6241), 1358–1361. https://doi.org/10.1126/science.aaa5099

Suzuki, T. N. (2011). Parental alarm calls warn nestlings about different predatory threats. *Current Biology*, *21*(1), R15–R16. https://doi.org/10.1016/j.cub.2010.11.027

Templeton, J. J., & Giraldeau, L.-A. (1996). Vicarious sampling: the use of personal and public information by starlings foraging in a simple patchy environment. *Behavioral Ecology and Sociobiology*, *38*, 105–114. https://doi.org/10.1007/s002650050223

Thiebault, A., Mullers, R. H. E., Pistorius, P. A., & Tremblay, Y. (2014). Local enhancement in a seabird: Reaction distances and foraging consequence of predator aggregations. *Behavioral Ecology*, *25*(6), 1302–1310. https://doi.org/10.1093/beheco/aru132

Thienen, W. Von, Metzler, D., Choe, D.-H., & Witte, V. (2014). Pheromone communication in ants: A detailed analysis of concentration-dependent decisions in three species. *Behavioral Ecology and Sociobiology*, *68*(10), 1611–1627. https://doi.org/10.1007/s00265-014-1770-3

Townsend, S. W., & Manser, M. B. (2013). Functionally referential communication in mammals: The past, present and the future. *Ethology*, *119*(1), 1–11. https://doi.org/10.1111/eth.12015

Van Bergen, Y., Coolen, I., & Laland, K. N. (2004). Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proceedings*

of the Royal Society B: Biological Sciences, *271*(1542), 957–962. https://doi.org/10.1098/rspb.2004.2684

Ward, A., & Webster, M. (2016). *Sociality: The Behaviour of Group-Living Animals*. Springer International Publishing.

Whiten, A. (2000). Primate culture and social learning. *Cognitive Science*, *24*(3), 477–508. https://doi.org/10.1207/s15516709cog2403_6

Zuberbühler, K. (2009). Survivor signals: The biology and psychology of animal alarm calling. *Advances in the Study of Behavior*, *40*, 277–322. https://doi.org/10.1016/S0065-3454(09)40008-1

Chapter 2

The Relative Contribution of Acoustic Signals Versus Movement Cues in Group Coordination and Collective Decision-Making



Great cormorants (*Phalacrocorax carbo*) stream back to a communal roost on Kinmen Island, Taiwan, on 16 November 2020. Watching thousands of these birds leave their roosts at dawn, forage in groups and return together at dusk sparked my curiosity about how animals coordinate their activities and make collective decisions.

This chapter has been published as:

Liao, C.-C., Magrath, R. D., Manser, M. B., & Farine, D. R. (2024). The relative contribution of acoustic signals versus movement cues in group coordination and collective decision-making. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 379(1905), 20230184. https://doi.org/10.1098/rstb.2023.0184

Abstract

To benefit from group living, individuals need to maintain cohesion and coordinate their activities. Effective communication thus becomes critical, facilitating rapid coordination of behaviours and reducing consensus costs when group members have differing needs and information. In many bird and mammal species, collective decisions rely on acoustic signals in some contexts but on movement cues in others. Yet, to date there is no clear conceptual framework that predicts when decisions should evolve to be based on acoustic signals versus movement cues. Here, we first review how acoustic signals and movement cues are used for coordinating activities. We then outline how information masking, discrimination ability (Weber's Law), and encoding limitations, as well as trade-offs between these, can identify which types of collective behaviours likely rely on acoustic signals or movement cues. Specifically, our framework proposes that behaviours involving the timing of events or expression of specific actions should rely more on acoustic signals, whereas decisions involving complex choices with multiple options (e.g. direction, destination) should generally use movement cues because sounds are more vulnerable to information masking and Weber's Law effects. We then discuss potential future avenues, including multimodal communication and collective decision-making by mixed-species animal groups.

Keywords: collective behaviour, group cohesion, movement, quorum, vocalisation

Introduction

To maximise the benefits of group living, social animals must maintain cohesion and coordinate their activities. This necessitates mechanisms that allow groups to express the same level of behavioural flexibility as individuals, yet in a coordinated manner. Group behaviours can include small-scale shifts, such as switching from resting to foraging (Rands, 2011), through to large-scale movements, such as collective migration (Berdahl et al., 2018). Understanding how social animals maintain cohesion, coordinate their actions, and influence the group for their own needs—especially while navigating dynamic environments and changing circumstances—is fundamental to unravelling the evolution of animal societies (Conradt & Roper, 2005).

What actions should we take? Where and when should we go? As humans, we constantly engage in consensus decision-making. And we are not alone in facing the challenges of making consensus decisions; many other group-living animals also rely on making consensus decisions and coordinating their actions in order to function as a group. One of the major challenges associated with reaching consensus is that groups generally comprise individuals with differing needs and capabilities (Davis et al., 2022). Having some means of communication, therefore, often plays a critical role in reducing consensus costs among group members by allowing them to rapidly coordinate their behaviours (Demartsev et al., 2023). For instance, before making group movements, communicating information about 'when to go' among members can allow individuals to coordinate departure times (Dibnah et al., 2022; Walker et al., 2017); such coordination can reduce the risk of predation and enhance energetic efficiency by allowing individuals to avoid false starts. During activities, such as foraging, communicating spatial information about the current positions can minimize the chance of an individual becoming separated from the group (Radford & Ridley, 2008; Toni et al., 2020). The same information can also help regulate spacing of potential foraging competitors, thereby reducing conflicts (Engesser & Manser, 2022; Radford & Ridley, 2008). These examples highlight the significant role that communication plays in coordinating behaviours within groups.

Two central and related questions in collective behaviour are: (i) when is the use of signals as active communication, as opposed to cues as passive communication, necessary, and (ii) which of these forms of communication is most effective? While it seems obvious that acoustic signals should evolve as a means of communication when making collective decisions, movement-based signals or cues (here we focus on movement cues) still play an important role (Strandburg-Peshkin et al., 2013). For example, humans often acquire social information by observing the movements or behaviours of others that subsequently impact collective decisions (Dachner et al., 2022; Dyer et al., 2008, 2009). In some primates, the direction of departures is often determined by individuals 'voting with their feet' (Byrne, 2000; Strandburg-Peshkin et al., 2015), with individuals coordinating movements following in the footsteps of others (Farine et al., 2016; Strandburg-Peshkin et al., 2017). In starling murmurations, individuals coordinate their flying direction and speed by copying the behaviour of nearby individuals, rather than relying on acoustic communication (Ballerini et al., 2008; Cavagna et al., 2010).

What dictates the use of acoustic signals versus movement cues? A group of mammals resting on a hot day would avoid unnecessary activity if they could communicate their preference to leave using acoustic signals rather than movements. By contrast, in highly dynamic flocking birds, using vocalisations to communicate intentions like 'I want to turn right' or 'I want to turn left' is likely to be unsuitable, being prone to errors due to signal interference (if many individuals communicate simultaneously), low efficacy (if the sound of flight adds noise), and difficulties in locating the source individual (as the flock is moving fast). Thus, while in some contexts animals can use acoustic signals to communicate contextual information (Engesser et al., 2016; Manser, 2001; Suzuki, 2011; Suzuki et al., 2019), in other contexts, movement cues may be more efficient for coordinating actions. To date, there is no clear conceptual framework that we can draw upon to make predictions about when group-living animals should evolve to use acoustic signals versus movement cues as a means of reaching a consensus and making collective decisions.

Here, we first review how acoustic signals and movement cues are used for coordinating activities in group-living vertebrates, with a specific focus on terrestrial birds and mammals. In this review, we define social behaviour as the extended spatial proximity among individuals, social interactions as any behaviour by one individual that affects or changes the behaviour of another individual, and collective behaviour as the behaviour and movement of groups of animals that result from, or emerge from, social behaviour (maintaining cohesion) and social interactions (the effect of the behaviour of individuals on others). Our emphasis is on collective behaviours in foraging, anti-predator, and movement contexts. We then outline a framework that aims to make predictions on whether animals should use acoustic signals versus movement cues when making collective decisions. In developing this framework, we consider informational masking, discrimination ability (e.g. the ability to discriminate small differences), and encoding limitations, as well as trade-offs between these. We also highlight the importance of quorum and quorum-like thresholds in reaching collective decisions. Finally, we discuss potential future avenues, including multimodal communication and collective decision-making by mixed-species animal groups.

The role of acoustic communication in coordinating behaviours

Acoustic communication is often used during coordination of vertebrate groups. Through modifications in frequency, amplitude, and call rate, acoustic signals are flexible, allowing them to be used to convey a wide array of information—from the caller's identity and internal motivations to specific details about external events or objects. Depending on the situation, acoustic signals can either span long distances, reaching all group members almost simultaneously (global communication), or be limited to short-range interactions with neighbouring members (local communication) (Conradt & Roper, 2005; Fichtel & Manser, 2010). Specifically, if active space spans the entire spatial extent of the group, as in the case of travel calls and alarm calls, a signaler can directly communicate with all group members. Conversely, acoustic signals that reach only nearby group members, such as soft contact calls, can mediate local interactions and contribute to group coordination.

In this section, we review the literature on acoustic communication used for coordinating activities in social animals, ranging from internal motivational calls, such as contact calls and travel calls, to external referential calls, such as food-associated calls and alarm calls (Manser, 2010). We also highlight the common use of acoustic communications by group-living animals in maintaining group cohesion during foraging, initiating changes in group behaviours, and coordinating cooperative anti-predator responses.

(a) Acoustic signals for maintaining and coordinating current behaviour

'What to do now?' A crucial decision in synchronising animal activities is whether to continue current behaviour or switch to a different one. Many socially living animals produce 'contact' calls during group foraging, movement, and even during resting (Bouchard & Zuberbühler, 2022; Fichtel & Manser, 2010; Radford & Ridley, 2008). These acoustic signals are believed to facilitate coordinated activities and maintain group cohesion by conveying information about the caller's location and current motivation to the receivers. For example, southern pied babblers *Turdoides bicolor*, which cooperate to raise young, maintain cohesion and coordinate their foraging by emitting 'chuck' calls (Radford & Ridley, 2007). These calls are used to spatially organise foragers by maintaining spacing among group members but also keeping the group members together (Radford & Ridley, 2008), while the rate of call production provides information on the greater need to forage and/or the availability of food (Radford & Ridley, 2007). Doing so allows individuals to function effectively as a group, increasing their breeding success (Raihani et al., 2010). Similarly, meerkats *Suricata suricatta* continuously produce 'close' calls during foraging, adjusting the call rates to communicate spatial information between group members, thereby mediating the cohesion of progressively moving groups (Engesser & Manser, 2022; Gall & Manser, 2017). Moreover, chimpanzees *Pan troglodytes* use 'rest hoos' to communicate whether they should resume travelling after a brief stop-over or initiate a prolonged rest period (Bouchard & Zuberbühler, 2022). When the intensity of these vocalisations increases and more individuals respond, they tend to rest for longer durations (Bouchard & Zuberbühler, 2022). Taken together, such calls not only function as 'location markers'—signalling the caller's location, regulating

spacing between individuals, and thereby maintaining group cohesion (Fichtel & Manser, 2010; Radford & Ridley, 2008)—but they also play a crucial role in conveying an individual's preferences (i.e. internal motivation) to continue their current behaviour (e.g. foraging and resting) rather than switching to another one (Figure 2.1a), thereby facilitating the coordination of group behaviour.

Acoustic communication is also used in another coordinated group activity, sentinel behaviour, which has evolved in some social mammals and birds (Bednekoff, 2015). Sentinels are individuals stationed in a prominent position that scan for predators and frequently emit specific acoustic signals while the other group members are foraging (Hollén et al., 2008; Manser, 1999; Ostreiher & Heifetz, 2020; Radford et al., 2009). Sentinels often give soft surveillance calls, providing information about their presence (Hollén et al., 2008). For example, during sentinel duty, meerkats use sentinel calls to help coordinate their guarding rotation, which substantially increases the foraging time for the other group members (Manser, 1999). Similarly, in foraging groups of southern pied babblers, sentinels give constant 'watchman's calls' to announce their presence, which allows group members to invest more time in foraging and less time in vigilance (Hollén et al., 2008; Radford et al., 2009). Sentinel calls, therefore, not only coordinate vigilance behaviour during foraging but also allow group members to fully focus on foraging without the need for constant vigilance.

(b) Travel calls in collective departures

'When to go?' is one of the most frequent collective decisions that social animals face. Coordinating the timing of departures from a resting site, or moving toward a new foraging patch, is crucial for individuals to maintain the benefits of living in a group (Gray & Webster, 2023; Radford, 2004). Many social animals produce acoustic signals to indicate readiness to travel or to initiate group movements (Sperber et al., 2017). Recently, empirical studies suggested that timing decisions are mediated often by acoustic communication (Bousquet et al., 2011; Dibnah et al., 2022; Walker et al., 2017). These decisions frequently operate under a type of quorum-like process, where a specific acoustic signal has to reach a certain threshold of intensity before the group changes

activity (Bousquet et al., 2011; Dibnah et al., 2022; Walker et al., 2017). For instance, among group-living birds, green woodhoopoes *Phoeniculus purpureus* emit calls to initiate group movement and recruit group mates (Radford, 2004), while jackdaws *Coloeus monedula* use vocalisations to coordinate mass departures from communal roosts (Dibnah et al., 2022). Among mammals, African wild dogs *Lycaon pictus* emit specific 'sneeze' sounds to switch from resting to moving (Walker et al., 2017), and meerkats produce 'moving' calls to initiate group departure from a foraging patch (Bousquet et al., 2011). In primates, white-faced capuchins *Cebus imitator* make 'trill' calls to initiate group movement in stationary troops (Boinski, 1993), mountain gorillas *Gorilla beringei beringei* increase their 'grunt' rate and more group members call before the transition from resting to moving (Stewart & Harcourt, 1994), and similar behaviours are also found in chacma baboons *Papio ursinus* (Fischer & Zinner, 2011). These studies all highlight the crucial role of acoustic communication in coordinating the timing of transitions from one group behaviour to another (Figure 2.1b) and suggest that the increasing intensity of acoustic signals, or having more individuals vocalise simultaneously, can act as a 'voting' process (Bousquet et al., 2011; Walker et al., 2017).

(c) Food-associated calls for attracting group members to food patches

Many social bird and mammal species produce distinctive 'food-associated' calls when they encounter food, thereby advertising their location to other group members (Clay et al., 2012). In some species, such acoustic signals can even convey specific information about the type, quality, or quantity of food, and are hence considered functionally referential (Di Bitetti, 2003; Evans & Evans, 1999; Kitzmann & Caine, 2009). Although most research on food-associated calls in animals has focused on their referential functions (Di Bitetti, 2003; Evans & Evans, 1999) and audience effects (Kalan & Boesch, 2015; Roush & Snowdon, 2000), these acoustic signals can also play a pivotal role in synchronising and coordinating group foraging (Clay et al., 2012; King & Janik, 2015). Food-associated calls in social bird species can be used to trigger foraging behaviours in others, and such vocalisations are more likely to be produced when individuals cannot exploit the entire resource themselves (Elgar, 1986; Suzuki, 2012a). For example, southern pied babblers produce 'purr' calls when they find a rich foraging patch. These

calls attract conspecifics, particularly fledglings, to food sources (Radford & Ridley, 2006). Willow tits *Poecile montanus* frequently produce long-distance calls when they discover a food source. They use these calls to attract flockmates to foraging patches, especially when separated from conspecifics, suggesting this vocalisation helps individuals in coordinating foraging activities, thereby maintaining cohesion (Suzuki, 2012b). Studies on mixed-species bird flocks support the primary function of these calls being to attract conspecifics when beneficial (Hillemann et al., 2019), rather than conveying specific details about the food itself (Hillemann et al., 2020). In primates, spider monkeys emit 'whinny' vocalisations to attract conspecifics to feeding trees (Chapman & Lefebvre, 1990), and chimpanzees produce 'rough grunts' when they discover food (Fedurek & Slocombe, 2013). Unlike in birds, the food-associated calls of chimpanzees can convey information about not only the presence of food but also the size of the food patch and possibly the type of food (Kalan et al., 2015; Slocombe & Zuberbühler, 2005; Watson et al., 2015), thereby influencing the foraging decisions of the receivers (Fedurek & Slocombe, 2013). Finally, bottlenose dolphins *Tursiops truncatus* produce food-associated acoustic signals during social foraging presumably to coordinate with certain individuals in the group (King & Janik, 2015). Taken together, food-associated calls not only recruit conspecifics to food patches but also trigger and synchronise foraging (Figure 2.1c).

(d) Mobbing calls for collective mobbing threat

In many social animals, group members come together to repel external threats. This collective action, known as mobbing, involves two or more individuals synchronously approaching or harassing a threat and is commonly initiated by acoustic signals (Templeton et al., 2005). Synchronising mobbing actions is crucial for group-living animals because it can enhance their anti-predator benefits (Griesser, 2009; Wheatcroft & Price, 2018). Specifically, the more individuals that participate, the better they can repel potential predators and the lower risk for each individual (Wheatcroft & Price, 2018).

Mobbing calls, similar to food-associated calls, primarily function for recruitment but prompt receivers to switch from their normal states (e.g. foraging and movement) to

anti-predator behaviours (e.g. approaching and mobbing calling; Figure 2.1d). In many species, the acoustic structure of mobbing calls varies depending on the type or level of predation risk, and can thereby elicit appropriate anti-predator responses in conspecifics (Carlson et al., 2020; Griesser, 2009; Suzuki, 2012c). Although mobbing behaviours have been extensively studied, more recent studies indicate that collective mobbing responses seem to be significantly influenced by the number of calling individuals—the greater the number of simultaneous callers, the more likely it is for group members to participate in the mob (Coomes et al., 2019; Dutour et al., 2021). This implies that collective mobbing might involve quorum-like decision-making. For example, jackdaws assess the number of conspecifics involved in initiating mobbing events by recognising individually distinctive recruitment calls (Coomes et al., 2019; Woods et al., 2018). Playback simulations found that three or five callers attracted more individuals than a single caller, showing that jackdaws can recognise the number of callers from these vocalisations and use that information in deciding their participation in the mobbing events (Coomes et al., 2019). Similarly, in great tits *Parus major*, the decision on whether to respond to conspecific mobbing calls—like approaching threat signals or emitting their own mobbing calls—is influenced by the number of callers (Dutour et al., 2021). Specifically, great tits respond more strongly to the mobbing calls of three callers than to one caller, although the mobbing calls of five callers did not elicit an even stronger response. Additionally, spotted hyenas *Crocuta crocuta* use long-range recruitment vocalisations, known as 'whoops,' to coordinate their collective defense of resources, territories, and against threats (Lehmann et al., 2022; Montgomery et al., 2023). Although no direct playback experiments indicate that a greater number of callers intensify mobbing responses, the number of hyenas, presence of social allies, and kin are shown as important factors in their decision to mob predators. In conclusion, mobbing calls play an important role in coordinating collective anti-predator behaviours in social animals, but sensory limitations (following Weber's Law, see section 4a-ii) might constrain the ability for individuals to perceive the complete gradient of information available as the number of callers increases (Coomes et al., 2019; Dutour et al., 2021).

(e) Alarm signals for avoiding predators

Flee alarm calls, commonly used to coordinate anti-predator behaviours, often prompt receivers to shift from their current activities to vigilance or flee (Figure 2.1e). In social animals, collective vigilance and coordinated anti-predator responses are key benefits of group living (Carere et al., 2009; Elgar, 1989; Lima, 1994, 1995). These benefits are amplified when individuals can efficiently communicate and transfer information about danger. Alarm calling, the production of specific acoustic signals upon detecting a predator, is particularly effective because it can quickly alert all nearby group members, even if other individuals are not currently vigilant or out of sight (Manser, 2010; Marler, 1967). For example, common starlings Sturnus vulgaris are more likely to emit alarm calls in long-grass habitats than in short-grass habitats, suggesting that their alarm calls are crucial for coordinating group anti-predator responses when visual cues are impractical (Devereux et al., 2008). Additionally, in some species lacking vocal alarm calls, specific sounds can be acoustic alarm signals. For instance, crested pigeons *Ocyphaps lophotes* produce distinct 'whistle' alarm signals using their modified wing feathers, triggering rapid fleeing behaviours in foraging groups (Hingee & Magrath, 2009; Murray et al., 2017).

Referential alarm call systems, which represent a more complex form of alarm communication, enable receivers to respond more effectively and appropriately, even in the absence of direct cues from the threat itself (Evans et al., 1993). These types of alarm calls can convey predator-specific information, such as predator type (LaPergola et al., 2023; Seyfarth et al., 1980), size (Carlson et al., 2020; Templeton et al., 2005), behaviour (Cunningham & Magrath, 2017), and urgency level (Leavesley & Magrath, 2005; Soltis et al., 2014), thereby prompting fine-scale coordinated anti-predator responses. Such systems have been documented in a variety of group-living mammal and bird species (Evans et al., 1993; Gill & Bierema, 2013; Townsend & Manser, 2013). A classic example is vervet monkeys *Chlorocebus pygerythrus*, which give different types of alarm calls to snakes, leopards, and eagles, and other group members respond appropriately to playback of those calls, such as running into trees after leopard alarms and looking up and running into cover after eagle alarms (Seyfarth et al., 1980). Such specific information can prompt fine-scale coordinated anti-predator responses among group members,

enhancing their chances of survival, as escaping in the wrong direction or responding inappropriately can potentially lead to fatal mistakes (Quinn & Cresswell, 2005; Shifferman & Eilam, 2004). Similar behaviours can be found in many social primates, such as Diana monkeys *Cercopithecus diana* (Zuberbühler, 2000), Campbell's monkeys *Cercopithecus campbelli* (Ouattara et al., 2009; Zuberbühler, 2001), and non-primate mammals, e.g. meerkats (Manser, 2001) as well as birds, e.g. chickens *Gallus gallus* (Evans & Evans, 1999). Furthermore, referential alarm calls in some species can simultaneously convey more than one type of predator-related information. For instance, meerkats combine information by producing alarm calls depending on predator type as well as varying acoustic structure to convey urgency information (Manser, 2001; Manser et al., 2002), and Siberian jays *Perisoreus infaustus* produce alarm calls that encode predator behaviour and not just taxonomic categories (Griesser, 2008). These examples illustrate that social animals commonly evolve complex alarm call systems and possess the capacity to produce a wide variety of acoustic signals that convey referential information, ultimately coordinating fine-scale anti-predator behaviours within groups.

The role of movement cues in coordinating behaviours

Once on the move, individuals within a group have to constantly coordinate their directions, speed, and next destination. Understanding how these individuals coordinate their movements can be challenging, particularly when there are no clear starting and stopping points during their traveling. Although mammals and birds commonly use acoustic communication to coordinate activities, empirical research suggests that directional decisions, such as those made by groups on the move or when choosing a destination, are predominantly mediated by movement cues (Averly et al., 2022; Fischer & Zinner, 2011; Papageorgiou & Farine, 2020; Strandburg-Peshkin et al., 2015). For example, olive baboons *Papio anubis* use a simple rule, 'voting with their feet' by making directed movement initiations, to decide on movement direction. Specifically, individuals make a short, directed movement towards their preferred movement direction, and group members tend to follow the direction with the most initiators (i.e. votes) (Strandburg-Peshkin et al., 2015). These types of movements are likely to be widespread and appear to provide an important cue for others to follow. For example,

while mountain gorillas increase 'grunt' vocalisations to reflect a readiness to move (Stewart & Harcourt, 1994), dominant silverbacks always take the lead in a certain direction, after which other group members follow (Watts, 2000). Similarly, meerkats use 'moving' calls to increase movement speed; however, these calls have not been associated with changes in direction, suggesting that influencing movement direction may require an additional cue (likely visual) to specify the intended direction (Averly et al., 2022; Bousquet et al., 2011).

While animals can communicate their intentions through directed movements (often a straight movement at intermediate speed) (Strandburg-Peshkin et al., 2015), there is also a growing body of evidence that decisions can emerge through simple, local interactions among neighbours. For example, in flocks of starlings, individuals pay attention to around eight local neighbours, coordinating their speed and turn to maintain consistent spacing (Ballerini et al., 2008). Simulations propose that such topological (or zonal—where individuals avoid, align, and are attracted to conspecifics at different distances) interaction rules can allow groups to make effective collective decisions, such as choosing between two foraging patches, even when only a fraction of group members are knowledgeable (Couzin et al., 2005). Thus, there is significant scope for collective decisions—especially those such as simple navigational tasks—to be reached without any active communication, but instead based on simple rule-based responses to cues.

Our understanding is limited about how and when animals make consensus decisions regarding a specific destination, and it remains unclear whether (or when) all group members become aware of the final destination. For example, how often do particular paths lead to specific resources, and do animals learn these associations? If animal groups repeatedly re-use the same locations—for example for foraging, drinking, or resting—then it is likely that directional movements are interpreted not only in terms of their direction, but also the ultimate goal of the movement. In certain instances, the movement direction and destination can be also determined by specific group members. For example, older African elephants play a key role in coordinating group movements (Allen et al., 2020; McComb et al., 2001), and killer whales heavily rely on older females

to lead collective movements in hunting grounds (Brent et al., 2015) when conditions are poor and resources are scarce. Thus, there is much to be discovered in terms of how much information is encoded about movement objectives and in who is engaging in these actions.

More broadly, the importance of non-acoustic cues in coordinating social behaviours remains much less studied than acoustic signals, likely due to the more challenging task of quantifying and recording visual cues. Yet visual signals are widely used in a range of other social behaviours. For example, many mammals and birds use facial signals, such as teeth-baring (de Waal, 1986) or beak gaping (Dehnen et al., 2022), as a low-cost display of subordinance or dominance. In chimpanzees, one such display—lip smacking—has been shown to increase the length of grooming bouts and the probability that grooming would be reciprocated (Fedurek et al., 2015). In canids, play bows have been shown to promote playful interactions, which could otherwise be misinterpreted as aggressive interactions (Bekoff, 1995). While in most of these examples the signals are used in dyadic interactions, the importance of movements as a trigger for responses by others is likely to have been under-appreciated. For example, walking out from the core of a social group represents an unusual behaviour that catches the attention of others. Thus, movements can be very strong signals, and these can represent clear intentions.

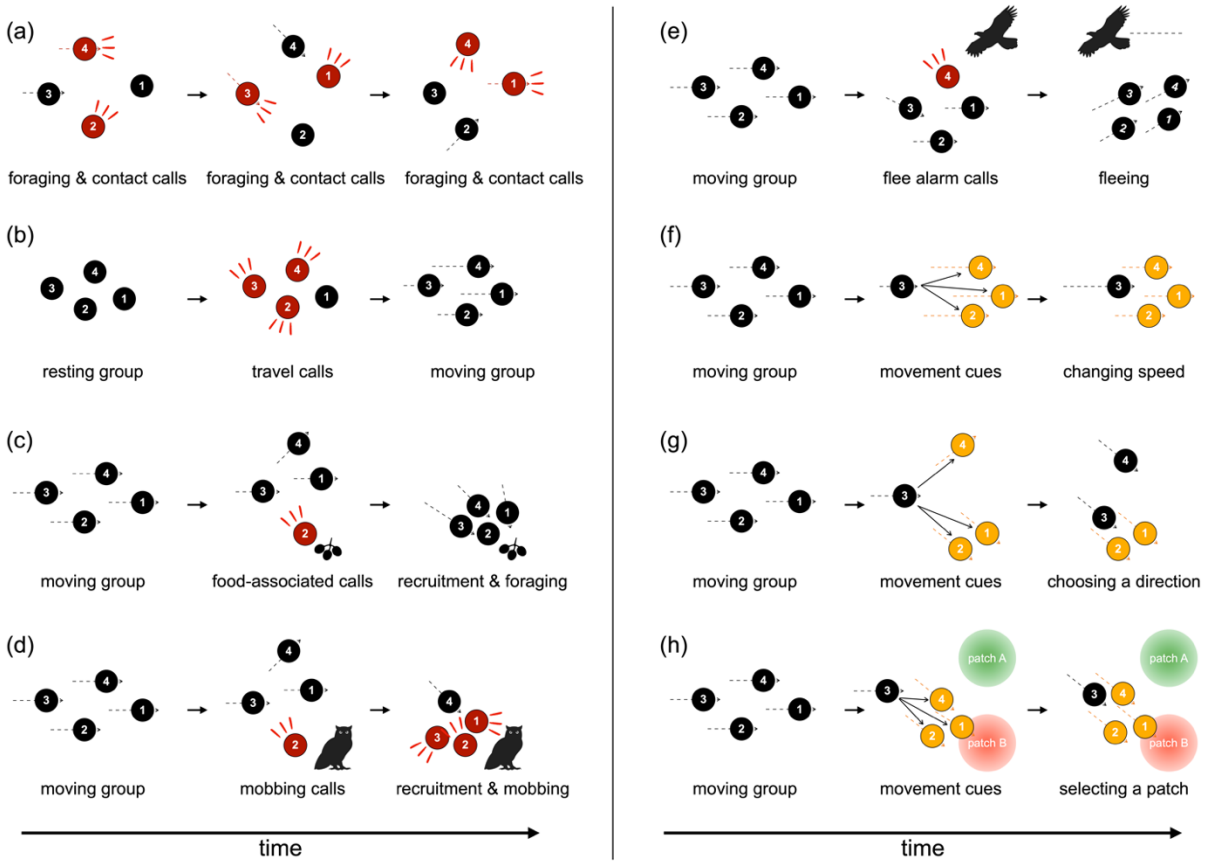


Figure 2.1. Schematic diagrams illustrating the role of acoustic signals (red circles) and movement cues (yellow circles) in coordinating activities in group-living animals. Behaviours involving the expression of specific actions or the timing of events tend to rely more on acoustic communication for coordination, whereas behaviours related to directional decisions are typically mediated by movement cues. a) Contact calls communicate the location and current state of callers, helping to synchronise individuals' current behaviours, regulate spacing between them, and maintain group cohesion; b) travel calls communicate the timing of transitions from one group behaviour to another, primarily coordinating departures from a sedentary state; c) food-associated calls recruit group members to food sources and initiate foraging behaviours; d) mobbing alarm calls rally group members to collectively mob low-urgency predators, prompting a shift from their normal states to anti-predator actions; e) flee alarm calls prompt a collective flee response within the group in response to high-urgency predators; Once on the move, individuals rely more heavily on movement cues to coordinate their f) speed, g) direction, and h) destination. Black circles indicate individuals, red circles indicate individuals giving acoustic signals, and yellow circles indicate movement cues from individuals. Dashed lines indicate movement direction and speed, red lines indicate an individual gives acoustic signals in a specific direction, and black thin arrows indicate an individual gains information from the movement cues of other individuals. Gradient-filled red and green circles indicate different patches.

Predicting the relative roles of acoustic signals and movement cues in collective behaviours

Within a group, individuals rely on different forms of social information to coordinate their behaviours across a range of contexts. Understanding the modalities used to produce and acquire signals or cues that coordinate collective actions is crucial for identifying the mechanisms underlying the evolution of social groupings. Here, we outline a framework to determine the types of collective behaviours that are more likely to use acoustic communication or movement cues for coordinating actions, and to assess their significance and limitations.

Our review identified that acoustic signals are likely to be more prevalent for some decisions, and in some environments, than visual movement cues. For instance, behaviours involving the timing of events or expression of specific actions, such as deciding when to depart (Figure 2.1b) or whether to mob a predator (Figure 2.1d), likely rely more on acoustic signals. Furthermore, acoustic signals are valuable in situations where intended receivers are engaged in other activities (McLachlan et al., 2019; Reber et al., 2013), like foraging or resting, or to convey urgent information about the caller's intentions or nearby threats. Similarly, sounds are more effective in environments where visual signals might be difficult to be perceived because of the habitat or poor lighting conditions. In contrast to acoustic signals, movement cues are likely to be important for decisions involving complex choices with multiple options, when more individuals involved in making the decision, and when dynamic spatial and direction information is critical (Byrne, 2000; Strandburg-Peshkin et al., 2015). Our framework, below, captures how these patterns reflect the limitations in producing and acquiring signals and cues, different trade-offs that individuals face during decision-making, and ways in which signals and cues can be aggregated.

(a) Sensory limitations

(i) Informational masking

As the number of individuals simultaneously contributing to a given collective decision increases, it becomes increasingly challenging to recognize and extract information from the signals or cues. Acoustic signals are vulnerable to interference from environmental noises (Brumm & Slabbekoorn, 2005; Zhou et al., 2019), which in social groups includes sounds from conspecifics (Bee & Micheyl, 2008; Hulse, 2002). In noisy social environments, for example, humans frequently face the 'cocktail party problem,' which refers to the difficulty humans encounter when recognising speech, as acoustic signals in such settings often overlap in frequency and timing, resulting in direct acoustic interference and informational masking (Bee & Micheyl, 2008; Cherry, 1953). Group-living animals communicating acoustically in social aggregations also encounter cocktail-party-like challenges, particularly when group members produce different types of acoustic signals simultaneously (Aubin & Jouventin, 1998; Beleyur & Goerlitz, 2019; Quick & Janik, 2008; Wyman et al., 2017). For example, when bottlenose dolphins are in groups larger than 15 individuals, their whistle rates decrease (Quick & Janik, 2008). Similarly, when many bats emit echolocation calls simultaneously, detecting and recognising the echoes generated by one's own calls becomes more challenging (Amichai et al., 2015; Beleyur & Goerlitz, 2019). In meerkats, adults reduce their close call production when pups are foraging with the group. This reduction is likely due to the loud begging calls from pups, which can mask the adults' softer close calls (Wyman et al., 2017). These examples show that while animals can adapt their acoustic behaviours to solve cocktail-party-like problems, the number of individuals emitting acoustic signals simultaneously will influence the efficiency of acoustic communication. Thus, there is likely to be a potential upper limit of how many acoustic signals can transmit information effectively at any one time, because when acoustic signaling increases, the potential for interference from other signals also rises (Quick & Janik, 2008).

Movement cues appear not to suffer as severely as acoustic signals from information masking. They can be used to coordinate movement in very large groups,

such as in murmurations of starlings, because the interactions are limited to a local set of neighbouring individuals, with the collective behaviour scaling up from these dyadic interactions to affecting the behaviour globally of the entire group. While local visual perception can limit the ability for single individuals to broadcast a signal to entire groups (in large, dense, or widely distributed groups), studies of schooling fish have found that relatively few individuals are needed to lead very large groups (Couzin et al., 2011). Thus, as groups become larger and more individuals are involved in making any given decision, we predict that movement cues will become more important than acoustic signals (with some exceptions, see section 4c).

(ii) Assessment of number and intensity

As the absolute number of signals or cues increases, individuals also face the challenge of distinguishing the relative differences in stimuli, as revealed by Weber's Law. Weber's Law suggests that animals usually compare stimuli based on proportional differences in stimulus magnitude rather than absolute differences (Akre & Johnsen, 2014; Arganda et al., 2012). That is, as the quantity of different stimuli increases, the comparison of absolute differences between these becomes more difficult. This means that the difference needs to be greater in order for individuals to identify which is the larger amount when there are more stimuli (Figure 2.2). Thus, even without information masking, animals can show limitations in distinguishing the difference in the number or intensity of stimuli as the number of contributors to a decision increases.

Acoustic signals appear to be more susceptible to 'Weber's Law' effects than visual cues and signals. Many bird and mammal species have been shown to possess considerable numerical abilities, at least when assessing visual cues (Aïn et al., 2009; Benson-Amram et al., 2018; Bogale et al., 2011; Ditz & Nieder, 2016; Hauser et al., 2000; Jaakkola et al., 2005). For instance, jungle crows *Corvus macrorhynchos* consistently choose the larger quantity whether in familiar smaller sets (e.g. 3 versus 5) or in novel larger comparisons (e.g. 5 versus 7) (Bogale et al., 2011). Semi-free-ranging rhesus monkeys *Macaca mulatta* can naturally discriminate and choose containers with more apple slices in comparisons up to three versus five slices, but struggle with higher

quantities (Hauser et al., 2000). However, acoustic stimuli appear more vulnerable to Weber's Law than visual stimuli. For instance, in jackdaws, a single mobbing caller recruited fewer individuals than more callers, but there was no significant difference in numbers recruited to three compared to five callers (Coomes et al., 2019). Similar patterns occur in playback experiments of great tits' mobbing calls, meerkats' moving calls, and female lions' roaring vocalisations (Bousquet et al., 2011; Dutour et al., 2021; McComb et al., 1994). These findings imply cognitive limitations in distinguishing the number acoustic signals above a certain threshold (Coomes et al., 2019), although there may also be a role for informational masking (above) or the cost borne by group members if they do not accurately select the majority. The difficulty in discriminating small differences as quantities become larger (or the number of options become greater) suggests a role for Weber's Law in predicting the relative importance of acoustic versus visual signals and cues in coordinating behaviours.

In addition to increased visual discrimination ability of animals (relative to acoustic discrimination), movement-based decisions can also act to reduce the total number of individuals that one group member can perceive (e.g. its local neighbours). Doing so reduces the effect of Weber's Law faced by individuals involved in a decision using movement cues, with the individual-level decisions being aggregated up through the collective to identify the majority decision even in very large groups (Couzin et al., 2005).

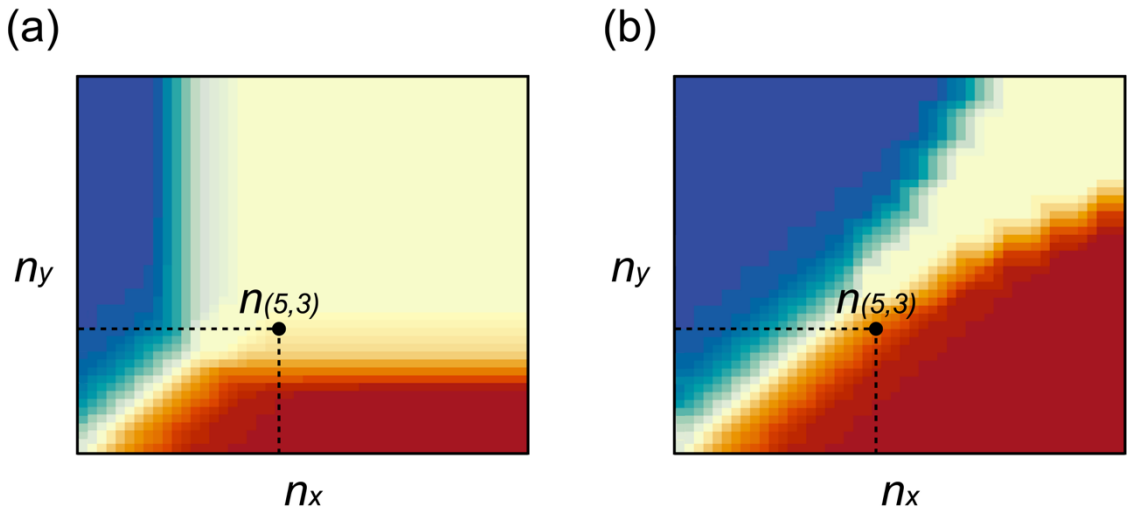


Figure 2.2. Schematic diagrams depicting the discrimination ability for a) acoustic signals and b) visual cues, as a function of the difference in the number of individuals communicating each of two preferences (i.e. Weber's Law). Dark red and dark blue represent high probabilities of selecting either option X or option Y, corresponding to which option has the highest number of 'votes'. The yellow area represents where individuals cannot reliably discriminate between the relative number of 'votes' and choose at random. In the illustrated example, the greater discrimination ability allows the group to select option X when there are 5 vs. 3 visual cues for X vs. Y, but choose at random when there are 5 vs. 3 acoustic signals, as they cannot discriminate which option has the most votes. The design of this figure is based on Arganda et al., 2012.

(iii) Encoding limitations

Acoustic signals often convey information about an animal's state or motivation, or external objects and events, but movement cues appear better at conveying specific information about direction and speed. Acoustic signals can often communicate about the state of the caller, such as fear or hunger, and motivation, such as intent to fight or defend a territory (Fichtel & Manser, 2010). Referential calls can also communicate about external objects or events. For example, Japanese tits emit alert calls to warn conspecifics about predators, while they produce recruitment calls to attract conspecifics in non-dangerous situations (Suzuki, 2014; Suzuki et al., 2016). These two types of calls are combined into alert-recruitment call sequences when mobbing predators, a capability similarly also observed in southern pied babblers (Engesser et al., 2016). Referential alarm calls can, for example, indirectly convey directional and distance information. Vervet monkeys look 'up' when they hear eagle alarms and look

'down' for snake alarms (Seyfarth et al., 1980), showing that these calls provide information about the direction of threat. White-browed scrubwrens *Sericornis frontalis* vary their aerial alarm calls depending on the distance to a predator in flight, which conveys information about the proximity of danger to conspecifics (Leavesley & Magrath, 2005). However, even though acoustic referential signals convey limited directional and distance information, there is no evidence that acoustic signals can communicate specific directional information, such as 'left' or 'right'. Movement cues, by contrast, can provide detailed information about specific directions. Aside from dynamic movements in mobbing groups (above), an individual making initiating movement along a particular animal track provides unambiguous information about its directional preference. The speed and directedness of the movement may also encode information about the strength of this preference (Strandburg-Peshkin et al., 2015). However, whether particular movement cues can convey broader contextual information, such as a preference to follow a given path to reach water versus a food patch, remains largely unknown.

(b) Key trade-offs underpinning the use of different modalities in collective behaviours

Animal collective behaviour, specifically decision-making, is largely governed by two key trade-offs: salience (conspicuousness) versus complexity and speed versus accuracy (Chittka et al., 2009; Farine, 2022). Understanding how sensory limitations contribute to these trade-offs can also provide insight into the relative importance of acoustic signals versus movement cues in animal collectives.

(i) The salience-complexity trade-off

Effective communication requires precision in the information being conveyed, but precision increases the complexity of a signal or cue. For example, distinguishing preferences between different types of food requires more different signals relative to simply communicating a preference for feeding (Clay et al., 2012). As complexity increases, signals or cues need to be (a) more distributed across the communication space (e.g. across the frequency spectrum) and (b) become more different from one-

another. This not only requires greater cognitive ability (potentially increasing decoding errors), but it also means that the salience of these signals or cues are necessarily decreased. Consider the difference between shouting "stop" versus "please finish eating". The latter contains more information but is less salient, and would be more difficult to discern in a busier acoustic environment by increasing the potential for information masking. By contrast, "stop" is easy to receive and interpret, but conveys no specific information. Thus, the salience of acoustic signals will decrease if they are used to convey more information, and at some point, will become lower than movement cues or signals.

(ii) The speed-accuracy trade-off

Faster decisions are often made using information acquired only from one or a few individuals, meaning that they are more prone to errors because they do not benefit from information pooling. By contrast, decisions involving information from more individuals can take much longer to resolve (David-Barrett, 2023). This introduces a speed-accuracy trade-off in collective decision-making. In general, in more urgent situations—such as an imminent attack by a predator—decisions can be made using information from just a few individuals, and more effectively made by global (i.e. acoustic) signals. By contrast, if the importance is that the correct decision is made (e.g. selecting a migration route), then preferences should be pooled over a larger number of individuals. The latter should favour visual modes of communication, as this maximizes individuals' abilities to discriminate smaller differences in which option has the majority of individual preferences.

(c) Quorum thresholds as a general principle for aggregating preferences in collective behaviours

Quorum decisions involve making a choice based on reaching a threshold number (or intensity) of individuals that are engaged in a activity or signaling a preference (Sumpter & Pratt, 2009). Thus, quorums are most often considered in situations where the decision involves a change in behaviour as opposed to choosing between a large number of options (e.g. directional movement decisions based on a majority rule). For example,

groups of vulturine guineafowl *Acryllium vulturinum* leave food patches when—on average and independent of group size—13 group members have initiated movements away from the patch (Papageorgiou & Farine, 2020), presumably because waiting for an absolute majority becomes too costly for group members. However, these concepts are not diametrically opposed, as majority-based decisions can also be made when a given 'sub-majority' is reached. For example, baboons will follow when there are fewer initiators if these all agree in their direction, but require more initiators if there is greater disagreement among initiators (Strandburg-Peshkin et al., 2015). Here we briefly highlight the importance of quorum and quorum-like thresholds in reaching collective decisions.

Quorum thresholds can differ based on the context, influenced by the level of urgency conveyed by the information. For example, in high-urgency situations like imminent threats, a group might have a lower quorum threshold to coordinate actions swiftly (Figure 2.3). High-urgency signals, like aerial alarm calls, from just one individual, can be sufficient to initiate collective escape actions (Figure 2.1e). By contrast, for less urgent situations like mobbing, the collective response may necessitate signals from a greater number of individuals (Figure 2.1d), resulting in a higher quorum threshold for collective action. Thus, where the threshold is set will have a major impact on the speed at which decisions are made.

Quorum thresholds can also be influenced by the reliability of information. As the group size grows, for example, false alarms can become more frequent (Beauchamp & Ruxton, 2007), thereby reducing the accuracy of decisions. This suggests an interaction between the speed-accuracy and the salience-complexity trade-offs in determining where the threshold is set. For example, using movement (e.g. a take-off flight) as a cue for an attack represents a relatively simple cue (high salience), but individuals make movements for a range of reasons (e.g. in response to social interactions), making it more inaccurate (requiring a higher threshold to avoid false positives). A more complex alarm call that is specific to a predation threat is also very salient, but less prone to false positives (requiring a lower threshold to avoid false positives). However, if alarm calls become too complex, and begin overlapping with other (e.g. social) signals, they could

also be prone to suffering from false positives or be too difficult to decode (thereby reducing accuracy). Thus, the interactions between these trade-offs warrants more detailed experimental investigations.

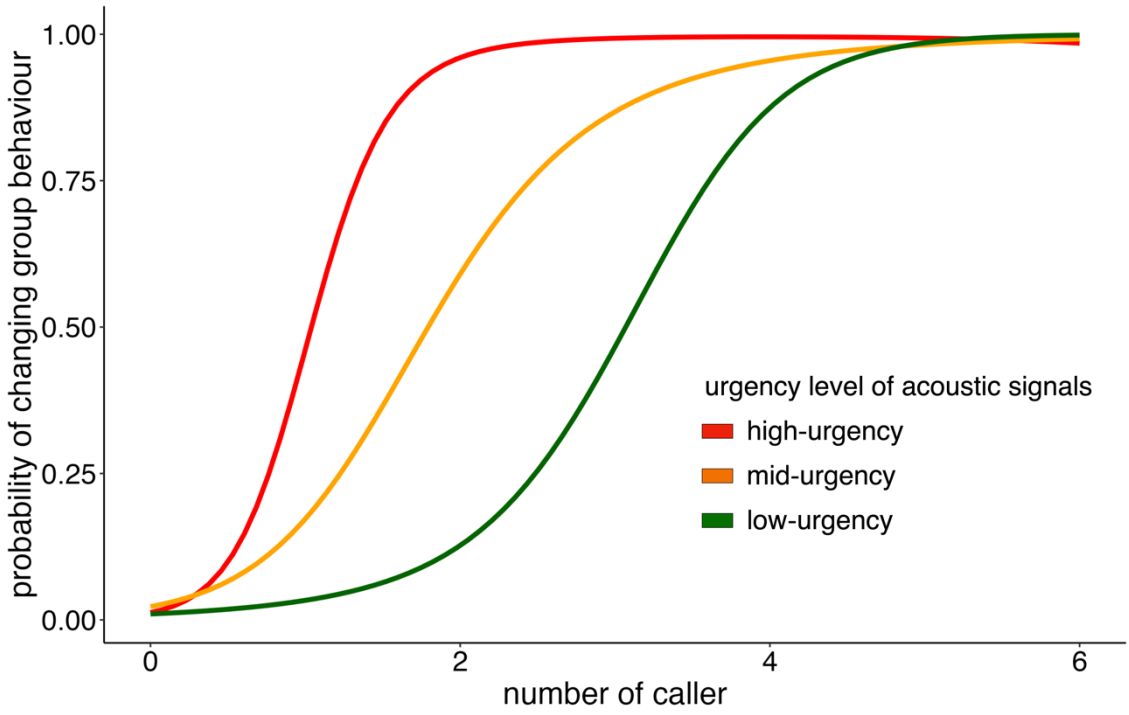


Figure 2.3. Schematic diagrams illustrating the probability thresholds for changing group behaviour based on varying levels of urgency in acoustic signals. The red line represents high-urgency acoustic signals, such as flee alarm calls; the orange line represents mid-urgency signals, such as mobbing calls; and the green line represents low-urgency signals, such as travel calls.

Collective decision-making in vertebrate vs. non-vertebrate organisms

While our focus in this paper has been on vertebrate decision-making, collective action can be expressed by most other organisms, including invertebrates and bacteria (Bazazi et al., 2008; Reid & Latty, 2016; Seeley & Buhrman, 1999). For example, plagues of locusts can move as a cohesive group over continental scales (Bazazi et al., 2008), and both invertebrates and bacteria are capable of quorum sensing (Pratt et al., 2002; Reid & Latty, 2016). These organisms can benefit from the emergent properties of collectives to most effectively exploit their environment (e.g. slime molds can solve two-armed bandit

problems (Reid et al., 2016)). While there are many distinctions between collectives of vertebrates versus those of non-vertebrates (e.g. the stratified relationships within social groups), many of the same biases are likely to be a feature of collective behaviours of both. For example, both vertebrates and non-vertebrates decrease in their ability to discriminate between numerical differences as the number of individuals involved in a collective behaviour increases (Weber's Law). One notable factor in most invertebrate and bacterial systems is that they rarely use acoustic cues or signals, and instead use very local modes of communication—such as cell-to-cell signaling in bacteria (Waters & Bassler, 2005), pheromones in ants (von Thienen et al., 2014), or physical cues in locusts (Bleichman et al., 2023; Simpson et al., 2001). The reasons for this—sensory limitations—are likely similar to why similar local cues are used in large groups of vertebrates, like starlings (Ballerini et al., 2008) and fish (Herbert-Read et al., 2011). While our review is not focused on collective decision-making in non-vertebrates, further consideration of the similarities and contrasts between vertebrate and non-vertebrate social organisms should shed more light on how ecology, cognitive and sensory limitations have shaped the evolution of collective actions.

Outstanding issues and future directions

In this review, we present a framework to identify which types of collective behaviours likely rely on acoustic signals or movement cues for coordination, while also assessing their significance and limitations. Nonetheless, the predictions mentioned necessitate further exploration, such as exploring 1) how sensory limitations, shaped by the effects of 'Weber's Law', influence coordination behaviours, and 2) how different types and reliabilities of information influence the quorum-like thresholds needed to reach a group consensus. These concepts can further be extended to more complex situations, such as multimodal signalling and collective behaviours within mixed-species animal groups.

(a) Multimodal communication

Each sensory modality has its own strengths and limitations, but combining multiple senses can enhance signal efficiency and potentially facilitate group consensus

decisions. Animals, particularly birds and mammals, commonly rely on auditory and visual senses to coordinate their immediate activities. Generally, hearing has a high temporal resolution, which is beneficial for judging timing and estimating distance. On the other hand, vision has a greater angular resolution, making it more effective for determining the number of objects, direction, and dynamic cues in groups. These attributes can supplement each other, and thus, enhancing signal and communication efficiency by senders and receivers (Ręk & Magrath, 2016, 2022). For example, when attempting to initiate a collective movement, white-faced capuchins display various behaviours, such as emitting 'trill' vocalisations, giving back-glances and/or moving at a slow speed, to increase the probability of a successful departure (Boinski, 1993; Leca et al., 2003). Also, domestic fowl produce food-associated calls are typically accompanied by a visual display, creating a multimodal signal, with each modality as a backup signals to potentially enhance signal efficiency (Smith & Evans, 2008). Alarm calls can quickly convey 'alert' information to receivers, while by observing the caller's subsequent behaviours (e.g. direction of scanning or escaping), receivers can refine the information, such as the specific direction of an approaching predator, and ultimately respond more appropriately and accurately. Thus, while acoustic signals likely function as an 'initiation,' complementary information from other senses can enhance the signal's efficiency and clarity, leading to more efficient coordinated collective actions. The integration of signals from multiple sensory modalities, like acoustic and visual, remains largely unexplored in the context of collective behaviour. Studies investigating how modalities interact within the context of, for example, making collective decision merits further research (Demartsev et al., 2023).

(b) Collective behaviours in mixed-species animal groups

Do animals use the same mechanisms to coordinate collective behaviours in mixed-species groups as they do in single-species groups? While our current understanding is still limited, the mechanisms seem to be similar (Sridhar & Guttal, 2018). Mixed-species animal groups, comprised of multiple species that forage and move together in a coordinated manner, are commonly observed across diverse taxa and habitats (Goodale et al., 2020). Individuals from different species coordinate their activities to maximize

group benefits, such as reducing predation risk and enhancing foraging efficiency. Previous studies indicate that interspecific acoustic communication can play an important role in coordinating mixed-species group behaviours, particularly in birds (Goodale et al., 2010; Magrath et al., 2015). Similar to single-species groups, contact calls maintain mixed-species group cohesion (Gayk & Mennill, 2023; Goodale & Kotagama, 2006; Zhou et al., 2021), food calls attract both conspecific and heterospecific members to food patches (Suzuki, 2012b), mobbing calls coordinate collective mobbing behaviours across species (Liao et al., 2024; Suzuki, 2016; Templeton & Greene, 2007), and aerial alarm calls elicit heterospecific escape responses (Goodale & Kotagama, 2008; Magrath et al., 2007). However, our understanding of how mixed-species groups determine departure times, movement directions, speed, and destinations is still limited. Such coordination might largely be influenced by specific species, as seen with many 'leader' species in mixed-species bird flocks (Goodale et al., 2020; Mangini et al., 2023). Future studies exploring how acoustic signals and movement cues are used for group movement coordination, and understanding how different species reach a consensus decision (e.g. through a quorum or non-shared process) can help unravel the evolutionary mechanisms driving the formation of complex mixed-species animal groups.

References

Aïn, S. A., Giret, N., Grand, M., Kreutzer, M., & Bovet, D. (2009). The discrimination of discrete and continuous amounts in African grey parrots (*Psittacus erithacus*). *Animal Cognition*, *12*(1), 145–154. https://doi.org/10.1007/s10071-008-0178-8

Akre, K. L., & Johnsen, S. (2014). Psychophysics and the evolution of behavior. *Trends in Ecology & Evolution*, *29*(5), 291–300. https://doi.org/10.1016/j.tree.2014.03.007

Allen, C. R. B., Brent, L. J. N., Motsentwa, T., Weiss, M. N., & Croft, D. P. (2020). Importance of old bulls: Leaders and followers in collective movements of all-male groups in African savannah elephants (*Loxodonta africana*). *Scientific Reports*, *10*, 13996. https://doi.org/10.1038/s41598-020-70682-y

Amichai, E., Blumrosen, G., & Yovel, Y. (2015). Calling louder and longer: How bats use biosonar under severe acoustic interference from other bats. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1821), 20152064. https://doi.org/10.1098/rspb.2015.2064

Arganda, S., Pérez-Escudero, A., & de Polavieja, G. G. (2012). A common rule for decision making in animal collectives across species. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(50), 20508–20513. https://doi.org/10.1073/pnas.1210664109

Aubin, T., & Jouventin, P. (1998). Cocktail-party effect in king penguin colonies. *Proceedings of the Royal Society B: Biological Sciences*, *265*(1406), 1665–1673. https://doi.org/10.1098/rspb.1998.0486

Averly, B., Sridhar, V. H., Demartsev, V., Gall, G., Manser, M., & Strandburg-Peshkin, A. (2022). Disentangling influence over group speed and direction reveals multiple patterns of influence in moving meerkat groups. *Scientific Reports*, *12*, 13844. https://doi.org/10.1038/s41598-022-17259-z

Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., Lecomte, V., Orlandi, A., Parisi, G., Procaccini, A., Viale, M., & Zdravkovic, V. (2008). Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(4), 1232–1237. https://doi.org/10.1073/pnas.0711437105

Bazazi, S., Buhl, J., Hale, J. J., Anstey, M. L., Sword, G. A., Simpson, S. J., & Couzin, I. D. (2008). Collective motion and cannibalism in locust migratory bands. *Current Biology*, *18*(10), 735–739. https://doi.org/10.1016/j.cub.2008.04.035

Beauchamp, G., & Ruxton, G. D. (2007). False alarms and the evolution of antipredator vigilance. *Animal Behaviour*, *74*(5), 1199–1206. https://doi.org/10.1016/j.anbehav.2007.02.014

Bednekoff, P. A. (2015). Sentinel behavior: A review and prospectus. In *Advances in the study of behavior* (eds M Naguib, HJ Brockmann, JC Mitani, LW Simmons, L Barrett, S Healy, et al.), pp. 115–145, vol. 47. Academic Press. https://doi.org/10.1016/bs.asb.2015.02.001

Bee, M. A., & Micheyl, C. (2008). The cocktail party problem: What is it? How can it be solved? And why should animal behaviorists study it? *Journal of Comparative Psychology*, *122*(3), 235–251. https://doi.org/10.1037/0735-7036.122.3.235

Bekoff, M. (1995). Play signals as punctuation: The structure of social play in canids. *Behaviour*, *132*, 419–429.

Beleyur, T., & Goerlitz, H. R. (2019). Modeling active sensing reveals echo detection even in large groups of bats. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(52), 26662–26668. https://doi.org/10.1073/pnas.1821722116

Benson-Amram, S., Gilfillan, G., & McComb, K. (2018). Numerical assessment in the wild: Insights from social carnivores. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1740), 20160508. https://doi.org/10.1098/rstb.2016.0508

Berdahl, A. M., Kao, A. B., Flack, A., Westley, P. A. H., Codling, E. A., Couzin, I. D., Dell, A. I., & Biro, D. (2018). Collective animal navigation and migratory culture: From theoretical models to empirical evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1746), 20170009. https://doi.org/10.1098/rstb.2017.0009

Bleichman, I., Yadav, P., & Ayali, A. (2023). Visual processing and collective motion-related decision-making in desert locusts. *Proceedings of the Royal Society B: Biological Sciences*, *290*(1991), 20221862. https://doi.org/10.1098/rspb.2022.1862

Bogale, B. A., Kamata, N., Mioko, K., & Sugita, S. (2011). Quantity discrimination in jungle crows, *Corvus macrorhynchos*. *Animal Behaviour*, *82*(4), 635–641. https://doi.org/10.1016/j.anbehav.2011.05.025

Boinski, S. (1993). Vocal coordination of troop movement among white-faced capuchin monkeys, *Cebus capucinus*. *American Journal of Primatology*, *30*(2), 85–100. https://doi.org/10.1002/ajp.1350300202

Bouchard, A., & Zuberbühler, K. (2022). An intentional cohesion call in male chimpanzees of Budongo Forest. *Animal Cognition*, *25*(4), 853–866. https://doi.org/10.1007/s10071-022-01597-6

Bousquet, C. A. H., Sumpter, D. J. T., & Manser, M. B. (2011). Moving calls: A vocal mechanism underlying quorum decisions in cohesive groups. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1711), 1482–1488. https://doi.org/10.1098/rspb.2010.1739

Brent, L. J. N., Franks, D. W., Foster, E. A., Balcomb, K. C., Cant, M. A., & Croft, D. P. (2015). Ecological knowledge, leadership, and the evolution of menopause in killer whales. *Current Biology*, *25*(6), 746–750. https://doi.org/10.1016/j.cub.2015.01.037

Brumm, H., & Slabbekoorn, H. (2005). Acoustic communication in noise. *Advances in the Study of Behavior*, *35*(05), 151–209. https://doi.org/10.1016/S0065-3454(05)35004-2

Byrne, R. W. (2000). How monkeys find their way: Leadership, coordination, and cognitive maps of African baboons. In S. Boinski & P. A. Garber (Eds.), *On the move: How and why animals travel in groups* (pp. 491–518). University of Chicago Press.

Carere, C., Montanino, S., Moreschini, F., Zoratto, F., Chiarotti, F., Santucci, D., & Alleva, E. (2009). Aerial flocking patterns of wintering starlings, Sturnus vulgaris, under different predation risk. *Animal Behaviour*, *77*(1), 101–107. https://doi.org/10.1016/j.anbehav.2008.08.034

Carlson, N. V., Greene, E., & Templeton, C. N. (2020). Nuthatches vary their alarm calls based upon the source of the eavesdropped signals. *Nature Communications*, *11*, 526. https://doi.org/10.1038/s41467-020-14414-w

Cavagna, A., Cimarelli, A., Giardina, I., Parisi, G., Santagati, R., Stefanini, F., & Viale, M. (2010). Scale-free correlations in starling flocks. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(26), 11865–11870. https://doi.org/10.1073/pnas.1005766107

Chapman, C. A., & Lefebvre, L. (1990). Manipulating foraging group size: Spider monkey food calls at fruiting trees. *Animal Behaviour*, *39*(5), 891–896. https://doi.org/10.1016/S0003-3472(05)80953-4

Cherry, E. C. (1953). Some experiments on the recognition of speech, with one and with two ears. *The Journal of the Acoustical Society of America*, *25*(5), 975–979.

Chittka, L., Skorupski, P., & Raine, N. E. (2009). Speed-accuracy tradeoffs in animal decision making. *Trends in Ecology & Evolution*, *24*(7), 400–407. https://doi.org/10.1016/j.tree.2009.02.010

Clay, Z., Smith, C. L., & Blumstein, D. T. (2012). Food-associated vocalizations in mammals and birds: What do these calls really mean? *Animal Behaviour*, *83*(2), 323–330. https://doi.org/10.1016/j.anbehav.2011.12.008

Conradt, L., & Roper, T. J. (2005). Consensus decision making in animals. *Trends in Ecology & Evolution*, *20*(8), 449–456. https://doi.org/10.1016/j.tree.2005.05.008

Coomes, J. R., McIvor, G. E., & Thornton, A. (2019). Evidence for individual discrimination and numerical assessment in collective antipredator behaviour in wild jackdaws (*Corvus monedula*). *Biology Letters*, *15*(10), 20190380. https://doi.org/10.1098/rsbl.2019.0380

Couzin, I. D., Ioannou, C. C., Demirel, G., Gross, T., Torney, C. J., Hartnett, A., Conradt, L., Levin, S. A., & Leonard, N. E. (2011). Uninformed individuals promote democratic consensus in animal groups. *Science*, *334*(6062), 1578–1580. https://doi.org/10.1126/science.1210280

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature*, *433*(7025), 513–516. https://doi.org/10.1038/nature03236

Cunningham, S., & Magrath, R. D. (2017). Functionally referential alarm calls in noisy miners communicate about predator behaviour. *Animal Behaviour*, *129*, 171–179. https://doi.org/10.1016/j.anbehav.2017.05.021

Dachner, G. C., Wirth, T. D., Richmond, E., & Warren, W. H. (2022). The visual coupling between neighbours explains local interactions underlying human 'flocking'. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1970), 20212089. https://doi.org/10.1098/rspb.2021.2089

David-Barrett, T. (2023). Human group size puzzle: Why it is odd that we live in large societies. *Royal Society Open Science*, *10*(8), 230559. https://doi.org/10.1098/rsos.230559

Davis, G. H., Crofoot, M. C., & Farine, D. R. (2022). Using optimal foraging theory to infer how groups make collective decisions. *Trends in Ecology & Evolution*, *37*(11), 942–952. https://doi.org/10.1016/j.tree.2022.06.010

de Waal, F. B. M. (1986). The integration of dominance and social bonding in primates. *The Quarterly Review of Biology*, *61*(4), 459–479. https://doi.org/10.1086/415144

Dehnen, T., Papageorgiou, D., Nyaguthii, B., Cherono, W., Penndorf, J., Boogert, N. J., & Farine, D. R. (2022). Costs dictate strategic investment in dominance interactions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *377*(1845), 20200447. https://doi.org/10.1098/rstb.2020.0447

Demartsev, V., Gersick, A. S., Jensen, F. H., Thomas, M., Roch, M. A., Manser, M. B., & Strandburg-Peshkin, A. (2023). Signalling in groups: New tools for the integration of animal communication and collective movement. *Methods in Ecology and Evolution*, *14*(8), 1852–1863. https://doi.org/10.1111/2041-210X.13939

Devereux, C. L., Fernàndez-Juricic, E., Krebs, J. R., & Whittingham, M. J. (2008). Habitat affects escape behaviour and alarm calling in Common Starlings *Sturnus vulgaris*. *Ibis*, *150*, 191–198. https://doi.org/10.1111/j.1474-919X.2008.00835.x

Di Bitetti, M. S. (2003). Food-associated calls of tufted capuchin monkeys (*Cebus apella nigritus*) are functionally referential signals. *Behaviour*, *140*(5), 565–592. https://doi.org/10.1163/156853903322149441

Dibnah, A. J., Herbert-Read, J. E., Boogert, N. J., McIvor, G. E., Jolles, J. W., & Thornton, A. (2022). Vocally mediated consensus decisions govern mass departures from jackdaw roosts. *Current Biology*, *32*(10), R455–R456. https://doi.org/10.1016/j.cub.2022.04.032

Ditz, H. M., & Nieder, A. (2016). Numerosity representations in crows obey the Weber-Fechner law. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1827), 20160083. https://doi.org/10.1098/rspb.2016.0083

Dutour, M., Kalb, N., Salis, A., & Randler, C. (2021). Number of callers may affect the response to conspecific mobbing calls in great tits (*Parus major*). *Behavioral Ecology and Sociobiology*, *75*, 29. https://doi.org/10.1007/s00265-021-02969-7

Dyer, J. R. G., Ioannou, C. C., Morrell, L. J., Croft, D. P., Couzin, I. D., Waters, D. A., & Krause, J. (2008). Consensus decision making in human crowds. *Animal Behaviour*, *75*(2), 461–470. https://doi.org/10.1016/j.anbehav.2007.05.010

Dyer, J. R. G., Johansson, A., Helbing, D., Couzin, I. D., & Krause, J. (2009). Leadership, consensus decision making and collective behaviour in humans. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1518), 781–789. https://doi.org/10.1098/rstb.2008.0233

Elgar, M. A. (1986). House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. *Animal Behaviour*, *34*, 169–174. https://doi.org/10.1016/0003-3472(86)90020-5

Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. *Biological Reviews*, *64*(1), 13–33. https://doi.org/10.1111/j.1469-185X.1989.tb00636.x

Engesser, S., & Manser, M. B. (2022). Collective close calling mediates group cohesion in foraging meerkats via spatially determined differences in call rates. *Animal Behaviour*, *185*, 73–82. https://doi.org/10.1016/j.anbehav.2021.12.014

Engesser, S., Ridley, A. R., & Townsend, S. W. (2016). Meaningful call combinations and compositional processing in the southern pied babbler. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(21), 5976–5981. https://doi.org/10.1073/pnas.1600970113

Evans, C. S., & Evans, L. (1999). Chicken food calls are functionally referential. *Animal Behaviour*, *58*(2), 307–319. https://doi.org/10.1006/anbe.1999.1143

Evans, C. S., Evans, L., & Marler, P. (1993). On the meaning of alarm calls: Functional reference in an avian vocal system. *Animal Behaviour*, *46*(1), 23–38. https://doi.org/10.1006/anbe.1993.1158

Farine, D. R. (2022). Collective action in birds. *Current Biology*, *32*(20), R1140–R1144. https://doi.org/10.1016/j.cub.2022.08.035

Farine, D. R., Strandburg-Peshkin, A., Berger-Wolf, T., Ziebart, B., Brugere, I., Li, J., & Crofoot, M. C. (2016). Both nearest neighbours and long-term affiliates predict individual locations during collective movement in wild baboons. *Scientific Reports*, *6*, 27704. https://doi.org/10.1038/srep27704

Fedurek, P., & Slocombe, K. E. (2013). The social function of food-associated calls in male chimpanzees. *American Journal of Primatology*, *75*(7), 726–739. https://doi.org/10.1002/ajp.22122

Fedurek, P., Slocombe, K. E., Hartel, J. A., & Zuberbühler, K. (2015). Chimpanzee lip-smacking facilitates cooperative behaviour. *Scientific Reports*, *5*, 13460. https://doi.org/10.1038/srep13460

Fichtel, C., & Manser, M. (2010). Vocal communication in social groups. In: P. M. Kappeler (Ed.) *Animal Behaviour: Evolution and Mechanisms*. Springer Press. https://doi.org/10.1007/978-3-642-02624-9_2

Fischer, J., & Zinner, D. (2011). Communication and cognition in primate group movement. *International Journal of Primatology*, *32*(6), 1279–1295. https://doi.org/10.1007/s10764-011-9542-7

Gall, G. E. C., & Manser, M. B. (2017). Group cohesion in foraging meerkats: Follow the moving 'vocal hot spot'. *Royal Society Open Science*, *4*(4), 170004. https://doi.org/10.1098/rsos.170004

Gayk, Z. G., & Mennill, D. J. (2023). Acoustic similarity of flight calls corresponds with the composition and structure of mixed-species flocks of migrating birds: Evidence from a three-dimensional microphone array. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *378*(1878), 20220114. https://doi.org/10.1098/rstb.2022.0114

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*(6), 449–461. https://doi.org/10.1111/eth.12097

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C., & Ruxton, G. D. (2010). Interspecific information transfer influences animal community structure. *Trends in Ecology & Evolution*, *25*(6), 354–361. https://doi.org/10.1016/j.tree.2010.01.002

Goodale, E., & Kotagama, S. W. (2006). Vocal mimicry by a passerine bird attracts other species involved in mixed-species flocks. *Animal Behaviour*, *72*(2), 471–477. https://doi.org/10.1016/j.anbehav.2006.02.004

Goodale, E., & Kotagama, S. W. (2008). Response to conspecific and heterospecific alarm calls in mixed-species bird flocks of a Sri Lankan rainforest. *Behavioral Ecology*, *19*(4), 887–894. https://doi.org/10.1093/beheco/arn045

Goodale, E., Sridhar, H., Sieving, K. E., Bangal, P., Colorado Z., G. J., Farine, D. R., Heymann, E. W., Jones, H. H., Krams, I., Martínez, A. E., Montaño-Centellas, F., Muñoz, J., Srinivasan, U., Theo, A., & Shanker, K. (2020). Mixed company: A framework for understanding the composition and organization of mixed-species animal groups. *Biological Reviews*, *95*(4), 889–910. https://doi.org/10.1111/brv.12591

Gray, L., & Webster, M. M. (2023). Quorum decision making coordinates group departure decisions in Eurasian oystercatchers, *Haematopus ostralegus*. *Animal Behaviour*, *202*, 29–38. https://doi.org/10.1016/j.anbehav.2023.05.012

Griesser, M. (2008). Referential calls signal predator behavior in a group-living bird species. *Current Biology*, *18*(1), 69–73. https://doi.org/10.1016/j.cub.2007.11.069

Griesser, M. (2009). Mobbing calls signal predator category in a kin group-living bird species. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1669), 2887–2892. https://doi.org/10.1098/rspb.2009.0551

Hauser, M. D., Carey, S., & Hauser, L. B. (2000). Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proceedings of the Royal Society B:*

Biological Sciences, *267*(1445), 829–833. https://doi.org/10.1098/rspb.2000.1078

Herbert-Read, J. E., Perna, A., Mann, R. P., Schaerf, T. M., Sumpter, D. J. T., & Ward, A. J. W. (2011). Inferring the rules of interaction of shoaling fish. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(46), 18726–18731. https://doi.org/10.1073/pnas.1109355108

Hillemann, F., Cole, E. F., Keen, S. C., Sheldon, B. C., & Farine, D. R. (2019). Diurnal variation in the production of vocal information about food supports a model of social adjustment in wild songbirds. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1897), 20182740. https://doi.org/10.1098/rspb.2018.2740

Hillemann, F., Cole, E. F., Sheldon, B. C., & Farine, D. R. (2020). Information use in foraging flocks of songbirds: No evidence for social transmission of patch quality. *Animal Behaviour*, *165*, 35–41. https://doi.org/10.1016/j.anbehav.2020.04.024

Hingee, M., & Magrath, R. D. (2009). Flights of fear: A mechanical wing whistle sounds the alarm in a flocking bird. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1676), 4173–4179. https://doi.org/10.1098/rspb.2009.1110

Hollén, L. I., Bell, M. B. V., & Radford, A. N. (2008). Cooperative sentinel calling? Foragers gain increased biomass intake. *Current Biology*, *18*(8), 576–579. https://doi.org/10.1016/j.cub.2008.02.078

Hulse, S. H. (2002). Auditory scene analysis in animal communication. *Advances in the Study of Behavior*, *31*, 163–200. https://doi.org/10.1016/s0065-3454(02)80008-0

Jaakkola, K., Fellner, W., Erb, L., Rodriguez, M., & Guarino, E. (2005). Understanding of the concept of numerically 'less' by bottlenose dolphins (*Tursiops truncatus*). *Journal of Comparative Psychology*, *119*(3), 296–303. https://doi.org/10.1037/0735-7036.119.3.296

Kalan, A. K., & Boesch, C. (2015). Audience effects in chimpanzee food calls and their potential for recruiting others. *Behavioral Ecology and Sociobiology*, *69*(10), 1701–1712. https://doi.org/10.1007/s00265-015-1982-1

Kalan, A. K., Mundry, R., & Boesch, C. (2015). Wild chimpanzees modify food call structure with respect to tree size for a particular fruit species. *Animal Behaviour*, *101*, 1–9. https://doi.org/10.1016/j.anbehav.2014.12.011

King, S. L., & Janik, V. M. (2015). Come dine with me: Food-associated social signalling in wild bottlenose dolphins (*Tursiops truncatus*). *Animal Cognition*, *18*(4), 969–974. https://doi.org/10.1007/s10071-015-0851-7

Kitzmann, C. D., & Caine, N. G. (2009). Marmoset (*Callithrix geoffroyi*) food-associated calls are functionally referential. *Ethology*, *115*(5), 439–448. https://doi.org/10.1111/j.1439-0310.2009.01622.x

LaPergola, J. B., Savagian, A. G., Smith, M. G., Bennett, B. L., Strong, M. J., & Riehl, C. (2023). Referential signaling in a communally breeding bird. *Proceedings of the*

National Academy of Sciences of the United States of America, *120*(19), e2222008120. https://doi.org/10.1073/pnas.2222008120

Leavesley, A. J., & Magrath, R. D. (2005). Communicating about danger: Urgency alarm calling in a bird. *Animal Behaviour*, *70*(2), 365–373. https://doi.org/10.1016/j.anbehav.2004.10.017

Leca, J. B., Gunst, N., Thierry, B., & Petit, O. (2003). Distributed leadership in semifree-ranging white-faced capuchin monkeys. *Animal Behaviour*, *66*(6), 1045–1052. https://doi.org/10.1006/anbe.2003.2276

Lehmann, K. D. S., Jensen, F. H., Gersick, A. S., Strandburg-Peshkin, A., & Holekamp, K. E. (2022). Long-distance vocalizations of spotted hyenas contain individual, but not group, signatures. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1979), 20220548. https://doi.org/10.1098/rspb.2022.0548

Liao, C.-C., Chen, C.-C., & Magrath, R. D. (2024). Asymmetric information in mixed-species mobbing flocks: Why are leader species special? *Animal Behaviour*, *210*, 383–393. https://doi.org/10.1016/j.anbehav.2024.01.014

Lima, S. L. (1994). Collective detection of predatory attack by birds in the absence of alarm signals. *Journal of Avian Biology*, *25*(4), 319–326. https://doi.org/10.2307/3677279

Lima, S. L. (1995). Collective detection of predatory attack by social foragers: Fraught with ambiguity? *Animal Behaviour*, *50*(4), 1097–1108. https://doi.org/10.1016/0003-3472(95)80109-X

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on heterospecific alarm calls: From mechanisms to consequences. *Biological Reviews*, *90*(2), 560–586. https://doi.org/10.1111/brv.12122

Magrath, R. D., Pitcher, B. J., & Gardner, J. L. (2007). A mutual understanding? Interspecific responses by birds to each other's aerial alarm calls. *Behavioral Ecology*, *18*(5), 944–951. https://doi.org/10.1093/beheco/arm063

Mangini, G. G., Rutt, C. L., Sridhar, H., Buitron, G., Muñoz, J., Robinson, S. K., Montaño-Centellas, F., Zarco, A., Fanjul, M. E., Fernández-Arellano, G., Xing, S., & Camerlenghi, E. (2023). A classification scheme for mixed-species bird flocks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *378*(1878), 20220100. https://doi.org/10.1098/rstb.2022.0100

Manser, M. B. (1999). Response of foraging group members to sentinel calls in suricates, *Suricata suricatta*. *Proceedings of the Royal Society B: Biological Sciences*, *266*(1423), 1013–1019. https://doi.org/10.1098/rspb.1999.0737

Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society B: Biological Sciences*, *268*(1483), 2315–2324. https://doi.org/10.1098/rspb.2001.1773

Manser, M. B. (2010). The generation of functionally referential and motivational vocal signals in mammals. In *Handbook of mammalian vocalization: An integrative*

neuroscience approach (Vol. 19). Elsevier B.V. https://doi.org/10.1016/B978-0-12-374593-4.00043-7

Manser, M. B., Seyfarth, R. M., & Cheney, D. L. (2002). Suricate alarm calls signal predator class and urgency. *Trends in Cognitive Sciences*, *6*(2), 55–57. https://doi.org/10.1016/S1364-6613(00)01840-4

Marler, P. (1967). Animal communication signals. *Science*, *157*(3790), 769–774. https://doi.org/10.1126/science.157.3790.769

McComb, K., Moss, C., Durant, S. M., Baker, L., & Sayialel, S. (2001). Matriarchs as repositories of social knowledge in African elephants. *Science*, *292*(5516), 491–494. https://doi.org/10.1126/science.1057895

McComb, K., Packer, C., & Pusey, A. (1994). Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Animal Behaviour*, *47*(2), 379–387. https://doi.org/10.1006/anbe.1994.1052

McLachlan, J. R., Ratnayake, C. P., & Magrath, R. D. (2019). Personal information about danger trumps social information from avian alarm calls. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1899), 20182945. https://doi.org/10.1098/rspb.2018.2945

Montgomery, T. M., Lehmann, K. D. S., Gregg, S., Keyser, K., McTigue, L. E., Beehner, J. C., & Holekamp, K. E. (2023). Determinants of hyena participation in risky collective action. *Proceedings of the Royal Society B: Biological Sciences*, *290*(2011), 20231390. https://doi.org/10.1098/rspb.2023.1390

Murray, T. G., Zeil, J., & Magrath, R. D. (2017). Sounds of modified flight feathers reliably signal danger in a pigeon. *Current Biology*, *27*(22), 3520–3525. https://doi.org/10.1016/j.cub.2017.09.068

Ostreiher, R., & Heifetz, A. (2020). The function of sentinel alarm calls in the Arabian babbler. *Journal of Avian Biology*, *51*(10), e02513. https://doi.org/10.1111/jav.02513

Ouattara, K., Zuberbühler, K., N'Goran, E. K., Gombert, J. E., & Lemasson, A. (2009). The alarm call system of female Campbell's monkeys. *Animal Behaviour*, *78*(1), 35–44. https://doi.org/10.1016/j.anbehav.2009.03.014

Papageorgiou, D., & Farine, D. R. (2020). Shared decision-making allows subordinates to lead when dominants monopolize resources. *Science Advances*, *6*(48), eaba5881. https://doi.org/10.1126/sciadv.aba5881

Pratt, S. C., Mallon, E. B., Sumpter, D. J. T., & Franks, N. R. (2002). Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. *Behavioral Ecology and Sociobiology*, *52*(2), 117–127. https://doi.org/10.1007/s00265-002-0487-x

Quick, N. J., & Janik, V. M. (2008). Whistle rates of wild bottlenose dolphins (*Tursiops truncatus*): Influences of group size and behavior. *Journal of Comparative Psychology*, *122*(3), 305–311. https://doi.org/10.1037/0735-7036.122.3.305

Quinn, J. L., & Cresswell, W. (2005). Escape response delays in wintering redshank, *Tringa totanus*, flocks: Perceptual limits and economic decisions. *Animal Behaviour*, *69*(6), 1285–1292. https://doi.org/10.1016/j.anbehav.2004.10.007

Radford, A. N. (2004). Vocal coordination of group movement by green woodhoopoes (*Phoeniculus purpureus*). *Ethology*, *110*(1), 11–20. https://doi.org/10.1046/j.1439-0310.2003.00943.x

Radford, A. N., Hollén, L. I., & Bell, M. B. V. (2009). The higher the better: Sentinel height influences foraging success in a social bird. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1666), 2437–2442. https://doi.org/10.1098/rspb.2009.0187

Radford, A. N., & Ridley, A. R. (2006). Recruitment calling: A novel form of extended parental care in an altricial species. *Current Biology*, *16*(17), 1700–1704. https://doi.org/10.1016/j.cub.2006.06.053

Radford, A. N., & Ridley, A. R. (2007). Individuals in foraging groups may use vocal cues when assessing their need for anti-predator vigilance. *Biology Letters*, *3*(3), 249–252. https://doi.org/10.1098/rsbl.2007.0110

Radford, A. N., & Ridley, A. R. (2008). Close calling regulates spacing between foraging competitors in the group-living pied babbler. *Animal Behaviour*, *75*(2), 519–527. https://doi.org/10.1016/j.anbehav.2007.05.016

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. *Journal of Animal Ecology*, *79*(1), 44–52. https://doi.org/10.1111/j.1365-2656.2009.01606.x

Rands, S. A. (2011). Approximating optimal behavioural strategies down to rules-of-thumb: Energy reserve changes in pairs of social foragers. *PLoS ONE*, *6*(7), e22104. https://doi.org/10.1371/journal.pone.0022104

Reber, S. A., Townsend, S. W., & Manser, M. B. (2013). Social monitoring via close calls in meerkats. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1765), 20131013. https://doi.org/10.1098/rspb.2013.1013

Reid, C. R., & Latty, T. (2016). Collective behaviour and swarm intelligence in slime moulds. *FEMS Microbiology Reviews*, *40*(6), 798–806. https://doi.org/10.1093/femsre/fuw033

Reid, C. R., MacDonald, H., Mann, R. P., Marshall, J. A. R., Latty, T., & Garnier, S. (2016). Decision-making without a brain: How an amoeboid organism solves the two-armed bandit. *Journal of the Royal Society Interface*, *13*(119), 20160030. https://doi.org/10.1098/rsif.2016.0030

Ręk, P., & Magrath, R. D. (2016). Multimodal duetting in magpie-larks: How do vocal and visual components contribute to a cooperative signal's function? *Animal Behaviour*, *117*, 35–42. https://doi.org/10.1016/j.anbehav.2016.04.024

Ręk, P., & Magrath, R. D. (2022). Reality and illusion: The assessment of angular separation of multi-modal signallers in a duetting bird. *Proceedings of the Royal*

Society B: Biological Sciences, *289*(1978), 20220680. https://doi.org/10.1098/rspb.2022.0680

Roush, R. S., & Snowdon, C. T. (2000). Quality, quantity, distribution and audience effects on food calling in cotton-top tamarins. *Ethology*, *106*, 673–690.

Seeley, T. D., & Buhrman, S. C. (1999). Group decision making in swarms of honey bees. *Behavioral Ecology and Sociobiology*, *45*(1), 19–31. https://doi.org/10.1007/s002650050536

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. *Science*, *210*(4471), 801–803. https://doi.org/10.1126/science.7433999

Shifferman, E., & Eilam, D. (2004). Movement and direction of movement of a simulated prey affect the success rate in barn owl *Tyto alba* attack. *Journal of Avian Biology*, *35*(2), 111–116. https://doi.org/10.1111/j.0908-8857.2004.03257.x

Simpson, S. J., Despland, E., Hägele, B. F., & Dodgson, T. (2001). Gregarious behavior in desert locusts is evoked by touching their back legs. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(7), 3895–3897. https://doi.org/10.1073/pnas.071527998

Slocombe, K. E., & Zuberbühler, K. (2005). Functionally referential communication in a chimpanzee. *Current Biology*, *15*(19), 1779–1784. https://doi.org/10.1016/j.cub.2005.08.068

Smith, C. L., & Evans, C. S. (2008). Multimodal signaling in fowl, *Gallus gallus*. *Journal of Experimental Biology*, *211*(13), 2052–2057. https://doi.org/10.1242/jeb.017194

Soltis, J., King, L. E., Douglas-Hamilton, I., Vollrath, F., & Savage, A. (2014). African elephant alarm calls distinguish between threats from humans and bees. *PLoS ONE*, *9*(2), e89403. https://doi.org/10.1371/journal.pone.0089403

Sperber, A. L., Werner, L. M., Kappeler, P. M., & Fichtel, C. (2017). Grunt to go—Vocal coordination of group movements in redfronted lemurs. *Ethology*, *123*(12), 894–905. https://doi.org/10.1111/eth.12663

Sridhar, H., & Guttal, V. (2018). Friendship across species borders: Factors that facilitate and constrain heterospecific sociality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1746), 20170014. https://doi.org/10.1098/rstb.2017.0014

Stewart, K. J., & Harcourt, A. H. (1994). Gorillas' vocalizations during rest periods: Signals of impending departure? *Behaviour*, *130*, 29–40.

Strandburg-Peshkin, A., Farine, D. R., Couzin, I. D., & Crofoot, M. C. (2015). Shared decision-making drives collective movement in wild baboons. *Science*, *348*(6241), 1358–1361. https://doi.org/10.1126/science.aaa5099

Strandburg-Peshkin, A., Farine, D. R., Crofoot, M. C., & Couzin, I. D. (2017). Habitat and social factors shape individual decisions and emergent group structure during baboon collective movement. *eLife*, *6*, e19505. https://doi.org/10.7554/eLife.19505

Strandburg-Peshkin, A., Twomey, C. R., Bode, N. W. F., Kao, A. B., Katz, Y., Ioannou, C. C., Rosenthal, S. B., Torney, C. J., Wu, H. S., Levin, S. A., & Couzin, I. D. (2013). Visual sensory networks and effective information transfer in animal groups. *Current Biology*, *23*(17), R709–R711. https://doi.org/10.1016/j.cub.2013.07.059

Sumpter, D. J. T., & Pratt, S. C. (2009). Quorum responses and consensus decision making. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1518), 743–753. https://doi.org/10.1098/rstb.2008.0204

Suzuki, T. N. (2011). Parental alarm calls warn nestlings about different predatory threats. *Current Biology*, *21*(1), R15–R16. https://doi.org/10.1016/j.cub.2010.11.027

Suzuki, T. N. (2012a). Calling at a food source: Context-dependent variation in note composition of combinatorial calls in Willow Tits. *Ornithological Science*, *11*(2), 103–107. https://doi.org/10.2326/osj.11.103

Suzuki, T. N. (2012b). Long-distance calling by the willow tit, *Poecile montanus*, facilitates formation of mixed-species foraging flocks. *Ethology*, *118*(1), 10–16. https://doi.org/10.1111/j.1439-0310.2011.01982.x

Suzuki, T. N. (2012c). Referential mobbing calls elicit different predator-searching behaviours in Japanese great tits. *Animal Behaviour*, *84*(1), 53–57. https://doi.org/10.1016/j.anbehav.2012.03.030

Suzuki, T. N. (2014). Communication about predator type by a bird using discrete, graded and combinatorial variation in alarm calls. *Animal Behaviour*, *87*, 59–65. https://doi.org/10.1016/j.anbehav.2013.10.009

Suzuki, T. N. (2016). Referential calls coordinate multi-species mobbing in a forest bird community. *Journal of Ethology*, *34*(1), 79–84. https://doi.org/10.1007/s10164-015-0449-1

Suzuki, T. N., Wheatcroft, D., & Griesser, M. (2016). Experimental evidence for compositional syntax in bird calls. *Nature Communications*, *7*, 10986. https://doi.org/10.1038/ncomms10986

Suzuki, T. N., Wheatcroft, D., & Griesser, M. (2019). The syntax–semantics interface in animal vocal communication. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1789), 20180405. https://doi.org/10.1098/rstb.2018.0405

Templeton, C. N., & Greene, E. (2007). Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(13), 5479–5482. https://doi.org/10.1073/pnas.0605183104

Templeton, C. N., Greene, E., & Davis, K. (2005). Allometry of alarm calls: Black-capped chickadees encode information about predator size. *Science*, *308*(5730), 1934–1937. https://doi.org/10.1126/science.1108841

Toni, P., Gall, G. E. C., Clutton-Brock, T. H., & Manser, M. B. (2020). Signalling adjustments to direct and indirect environmental effects on signal perception in

meerkats. *PLoS ONE*, *15*(8), e0238313. https://doi.org/10.1371/journal.pone.0238313

Townsend, S. W., & Manser, M. B. (2013). Functionally referential communication in mammals: The past, present and the future. *Ethology*, *119*(1), 1–11. https://doi.org/10.1111/eth.12015

von Thienen, W., Metzler, D., Choe, D.-H., & Witte, V. (2014). Pheromone communication in ants: A detailed analysis of concentration-dependent decisions in three species. *Behavioral Ecology and Sociobiology*, *68*(10), 1611–1627. https://doi.org/10.1007/s00265-014-1770-3

Walker, R. H., King, A. J., McNutt, J. W., & Jordan, N. R. (2017). Sneeze to leave: African wild dogs (*Lycaon pictus*) use variable quorum thresholds facilitated by sneezes in collective decisions. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1862), 20170347. https://doi.org/10.1098/rspb.2017.0347

Waters, C. M., & Bassler, B. L. (2005). Quorum sensing: Cell-to-cell communication in bacteria. *Annual Review of Cell and Developmental Biology*, *21*, 319–346. https://doi.org/10.1146/annurev.cellbio.21.012704.131001

Watson, S. K., Townsend, S. W., Schel, A. M., Wilke, C., Wallace, E. K., Cheng, L., West, V., & Slocombe, K. E. (2015). Vocal learning in the functionally referential food grunts of chimpanzees. *Current Biology*, *25*(4), 495–499. https://doi.org/10.1016/j.cub.2014.12.032

Watts, D. P. (2000). Mountain gorilla habitat use strategies and group movements. In S. Boinski & P. A. Garber (Eds.), *On the move: How and why animals travel in groups* (pp. 351–374). University of Chicago Press.

Wheatcroft, D., & Price, T. D. (2018). Collective action promoted by key individuals. *The American Naturalist*, *192*(4), 401–414. https://doi.org/10.1086/698874

Woods, R. D., Kings, M., McIvor, G. E., & Thornton, A. (2018). Caller characteristics influence recruitment to collective anti-predator events in jackdaws. *Scientific Reports*, *8*, 7343. https://doi.org/10.1038/s41598-018-25793-y

Wyman, M. T., Rivers, P. R., Muller, C., Toni, P., & Manser, M. B. (2017). Adult meerkats modify close call rate in the presence of pups. *Current Zoology*, *63*(3), 349–355. https://doi.org/10.1093/cz/zox029

Zhou, L., Peabotuwage, I., Luo, K., Quan, R. C., & Goodale, E. (2021). Using playback to test leadership in mixed-species flocks and compare flocking with mobbing. *Animal Behaviour*, *180*, 151–166. https://doi.org/10.1016/j.anbehav.2021.08.012

Zhou, Y., Radford, A. N., & Magrath, R. D. (2019). Why does noise reduce response to alarm calls? Experimental assessment of masking, distraction and greater vigilance in wild birds. *Functional Ecology*, *33*(7), 1280–1289. https://doi.org/10.1111/1365-2435.13333

Zuberbühler, K. (2000). Referential labelling in Diana monkeys. *Animal Behaviour*, *59*(5), 917–927. https://doi.org/10.1006/anbe.1999.1317

Zuberbühler, K. (2001). Predator-specific alarm calls in Campbell's monkeys, *Cercopithecus campbelli*. *Behavioral Ecology and Sociobiology*, *50*(5), 414–422. https://doi.org/10.1007/s002650100383

Chapter 3

Functionally Referential Communication About Danger in Cooperatively Breeding White-Winged Choughs



An adult white-winged chough raises its head and displays ‘bulging eyes’ as it intently tracks little eagles (*Hieraaetus morphnoides*) circling overhead—a striking response to aerial danger and a potential visual signal explored in this chapter.

This chapter has been published as:

Liao, C.-C., Radford, A. N., Heinsohn, R., & Magrath, R. D. (2025). Functionally referential communication about danger in cooperatively breeding white-winged choughs. *Animal Behaviour*, 229, 123330. https://doi.org/10.1016/j.anbehav.2025.123330

Abstract

Effectively communicating information about danger can enhance the antipredator benefits of group living. Many social mammals use functionally referential alarm calls to convey predator-specific information, such as predator type and threat urgency, enabling appropriate responses. However, relatively few bird species, particularly cooperative breeders, have been subjected to experimental assessment. White-winged choughs, *Corcorax melanorhamphos*, are obligate cooperative breeders living in groups year-round. They have a complex yet barely studied vocal repertoire. We carried out field observations, acoustic analyses and a playback experiment to test whether chough alarm calls are functionally referential. Additionally, we explored the occurrence of a possible visual display when responding to threats. Choughs produced three different alarm calls in response to different threats: terrestrial alarm calls for ground-based predators, aerial whistles for high-flying hawks and flee alarm calls for immediate, high-urgency threats. Blind scoring of video revealed that birds responded appropriately to playbacks of alarm calls alone, typically looking around in response to terrestrial alarms, looking up to aerial whistles and fleeing to flee alarms. Furthermore, birds were much more likely to display 'bulging eyes' in response to aerial whistles compared to terrestrial alarms, suggesting that bulging eyes might be a visual signal associated with aerial threats. Our findings demonstrate that white-winged choughs, a highly social bird species, possess a functionally referential alarm call system that conveys information about the type of threat and urgency. We propose that integrating information from multiple sensory modalities in alarm communication, such as auditory and visual signals/cues, may be common in social animals and warrants further investigation.

Keywords: alarm call, antipredator, functional reference, multimodal signal, visual signal, vocal communication

Introduction

Collective vigilance and coordinated antipredator responses are key benefits of group living, especially when group members can efficiently communicate information about danger (Caro, 2005; Elgar, 1989; Hingee & Magrath, 2009; Liao et al., 2024). Alarm calling, the production of warning vocalizations in response to a threat, is common in many mammal and bird species when a predator is detected (Hollén & Radford, 2009; Klump & Shalter, 1984). Calling is particularly effective as it can quickly alert nearby individuals, even if they are out of sight or not currently vigilant (Devereux et al., 2008; Marler, 1967). This allows receivers to gain information about danger and respond immediately, enhancing their chances of survival.

Functionally referential alarm calls communicate about the type of threat, enabling receivers to respond appropriately even without detecting the threat directly (Evans et al., 1993). Specifically, functionally referential alarm calls are associated with external objects or events and can convey detailed information, such as predator type (Seyfarth et al., 1980a), size (Templeton et al., 2005), behaviour (Griesser, 2008) and level of urgency (Leavesley & Magrath, 2005). The term "functional reference" considers the context and consequences of calls, without making assumptions about underlying mechanisms (Evans, 1997; Evans et al., 1993; Macedonia & Evans, 1993). A classic example is vervet monkeys, *Chlorocebus pygerythrus*, which give different alarm calls to snakes, eagles and leopards, *Panthera pardus* (Seyfarth et al., 1980a). Similarly, chickens, *Gallus gallus*, produce distinct alarm calls for terrestrial and aerial predators (Evans et al., 1993). In addition to signalling predator type, some alarm calls encode information about urgency. For example, white-browed scrubwrens, *Sericornis frontalis*, communicate about urgency, with a greater number of elements in their aerial alarm call indicating a closer predator and therefore higher urgency (Leavesley & Magrath, 2005). Some species even include both types of information in their alarm calls. Meerkats, *Suricata suricatta*, produce alarm calls that convey both the type of predator and the level of urgency, facilitating coordinated group escape (Furrer & Manser, 2009; Manser, 2001). These examples highlight that group-living animals can produce different calls that

convey detailed information about danger (Gill & Bierema, 2013; Townsend & Manser, 2013). Social complexity is thought to drive communicative complexity (Butler et al., 2022; Freeberg et al., 2012; Leighton, 2017) and may favour the evolution of functionally referential alarm communication (Blumstein & Armitage, 1997; Furrer & Manser, 2009; Zuberbühler, 2003; Griesser, 2008). Although such alarm call systems have long attracted interest, few studies have experimentally tested functionally referential alarm communication in birds (Cunningham & Magrath, 2017; Gill & Bierema, 2013; LaPergola et al., 2023; Suzuki, 2016), particularly in cooperative breeders, a complex vertebrate social system.

Predator-specific responses to alarm calls can indirectly reveal the information encoded within them. Gaze direction, for example, is particularly useful for interpreting the meaning of calls because it reflects the receiver's interpretation of the threat (Fichtel, 2004; Seyfarth et al., 1980b). Gaze direction is easy to assess in primates, because of their forward-facing eyes, and has been used to study alarm call meaning in many species (Fichtel, 2004; Fichtel & Kappeler, 2002; Schel et al., 2010; Seyfarth et al., 1980b). For example, vervet monkeys look down in response to snake alarms and look up in response to eagle alarms (Seyfarth et al., 1980a). In birds, despite their lateral vision, gaze direction has also proved to be a valuable indicator (Dawson Pell et al., 2018; Evans et al., 1993; Kaplan & Rogers, 2013; Suzuki, 2012). For instance, chickens increase horizontal scanning in response to both ground and aerial alarm calls but are more likely to look upward, rolling their heads to fixate laterally with one eye, when hearing aerial alarm calls (Evans et al., 1993). Similarly, Japanese tits, *Parus minor*, scan the horizon in response to crow-specific alarm calls and gaze towards the ground in response to snake-specific alarm calls (Suzuki, 2012). Australian magpies, *Gymnorhina tibicen*, respond to eagle alarm calls by looking upward and angling their beaks at least 30 degrees above horizontal (Kaplan & Rogers, 2013). These examples demonstrate that gaze direction in birds serves as a reliable indicator for studying functionally referential alarm calls, reflecting how receivers interpret different alarm calls.

In addition to alarm calls, individuals can obtain information about threats from visual cues or signals from others. Responses to detecting a predator, such as the direction of gaze or the direction of fleeing, could often be cues (Lima, 1995; Seyfarth & Cheney, 1980). For example, Australian magpies face flying hawks and point their beaks towards the threat while giving alarm calls, a behaviour that may help conspecifics locate the predator more quickly (Kaplan, 2008). Young vervet monkeys respond more appropriately to alarm calls if they first look at adults (Seyfarth & Cheney, 1980, 1986), implying that they gain additional information from others' responses. Moreover, some responses may be exaggerated or modified to become signals (Caro, 2005; Holley, 1993). For instance, brown hares, *Lepus europaeus*, exhibit visually distinctive antipredator behaviours, standing bipedally, facing approaching red foxes, *Vulpes vulpes*, with erect ears and turning their white ventral surface towards the predator, which is thought to function as a signal to both predators and conspecifics (Holley, 1993). Taken together, responses to threats can serve as cues or signals that help coordinate antipredator behaviours more effectively and, in some cases, may form part of a multimodal signal. To date, our understanding of how social animals integrate information from multiple sensory modalities, such as auditory and visual signals/cues, remains very limited, despite its likely prevalence in social species (Liao et al., 2024).

White-winged choughs, *Corcorax melanorhamphos*, are obligate cooperative breeders that live in year-round groups with stable membership (Heinsohn, 1992; Rowley, 1978). They forage for invertebrates on the ground, making them vulnerable to both terrestrial and aerial predators such as foxes, feral cats, *Felis catus*, and raptors (Heinsohn, 1987; Rowley, 1978). Additionally, they forage by digging into the substrate, which is likely to reduce their ability to detect predators visually when feeding, thereby increasing the importance of acoustic communication. While their ecology, development and breeding behaviours have been well studied (Beck et al., 2008; Heinsohn, 1987, 1991; Heinsohn & Cockburn, 1994), surprisingly little is known about their vocal communication (Higgins et al., 2006). Choughs are an ideal species for investigating functionally referential alarm communication, given their complex social groups, diverse vocal repertoire and ease of observation, allowing for the quantification of detailed

behavioural responses. Furthermore, choughs appear to use visual displays when interacting with other individuals or when facing threats (Heinsohn, 2009; Rowley, 1978). These potential displays include wing-wave tail-wag motions and 'bulging eyes', when engorging the conjunctiva of their eyes with blood makes them appear more prominent (Rowley, 1978). While the function of these potential visual displays remains unknown, choughs might refine functionally referential communication by using multimodal signals.

We studied alarm calls and communication in choughs through field observations, acoustic analyses and a playback experiment including detailed video analyses of behavioural responses. Demonstrating functionally referential alarm communication in a species requires considering both the production and perception of calls (Evans et al., 1993). We therefore first tested whether choughs produce acoustically different alarm calls to different types of threat. Second, we conducted a playback experiment and used blind-scored video to examine whether different types of alarm calls elicit appropriate antipredator responses. Furthermore, if choughs' alarm calls encode the level of urgency, then we expected that choughs would have a shorter latency to respond and be more likely to flee in response to higher-urgency alarm calls. Finally, we quantified the occurrence of bulging eyes during threatening situations to assess whether they might form part of a multimodal signal.

Methods

(a) Study site and species

White-winged choughs are large passerine birds (350–380 g) endemic to southeastern Australia. Most breeding groups consist of six to eight individuals, including a monogamous breeding pair and nonbreeding helpers, which are usually the offspring from previous years (Beck et al., 2008; Heinsohn et al., 1988). Groups are highly cohesive, with members travelling, foraging and roosting together, and their group membership can remain stable for over a decade (Rowley, 1978). Choughs do not actively defend foraging territories and have overlapping home ranges of up to 1000 ha (Rowley, 1978). However,

during the breeding season (August to January), groups defend their nest, and their home ranges contract to about 20 ha surrounding the nest site (Beck & Heinsohn, 2006; Heinsohn et al., 1988; Rowley, 1978).

We studied choughs between March and December 2022 in nature reserves and on the edges of suburbs in Canberra, Australian Capital Territory, Australia (35°14'46.0"S, 149°06'49.8"E). This population has been studied since the 1980s, with four distinct study periods (Beck & Heinsohn, 2006; Heinsohn, 1987; Heinsohn et al., 2000; Leon et al., 2022). The birds are well habituated to human presence, allowing close-range observation (<3 m) by observers on foot. In the current study, 176 birds were colour-banded for individual identification using a standard metal leg band and either colour leg bands or a white plastic leg band with a unique number (for methods see Beck & Heinsohn, 2006). We collected data on 16 breeding groups in this population.

(b) Production of alarm calls

(i) Natural observations

To examine whether choughs encode specific information about predators in their alarm calls, we opportunistically recorded their vocalizations during natural encounters with predators. During recording, birds were followed at a distance of 3–5 m. Where possible, we noted the number of individuals in the group, the age category (adult, immature and juvenile) of each individual based on its iris colour (Rowley, 1978), the distance between the microphone and the calling bird, the identity of the calling bird and the probable cause of the alarm. All recordings were collected using a Sennheiser ME66 shotgun directional microphone with a K6 power module. Calls were recorded at a sampling rate of 48 kHz as 24-bit WAV files on a Marantz PMD661 recorder.

Based on these natural observations, we identified three call types typically associated with different predator contexts. For ease of reference, we label these call types as follows: ‘terrestrial alarm calls’, given in response to ground-based threats such as dogs and snakes; ‘aerial whistles’, given to high-flying hawks (about 50 m high); and ‘flee alarm

calls', given in response to immediate threats, such as a hawk flying within 15 m. These natural recordings served as preliminary observations to inform our experimental design. They were not used in subsequent acoustic analyses comparing call types, nor were they used to construct playback tracks. We later tested the functional relevance of each call type through a playback experiment using calls prompted in standardized contexts.

(ii) Prompted alarm calls

In addition to gathering recordings of alarm calls under natural conditions, we prompted alarm calls by simulating different types of threat, corresponding to the three natural contexts. We presented 16 breeding groups with (1) a ground-based threat, a rubber model resembling an eastern brown snake, *Pseudonaja textilis*, to prompt terrestrial alarm calls, (2) an aerial threat, playback of a chough aerial whistle chorus, to prompt aerial whistles, and (3) an immediate threat, a life-sized gliding model of a brown goshawk, *Accipiter fasciatus*, to prompt flee alarm calls. We used a matched experimental design where each group received each stimulus, using the specific methods described below. Each group received only one stimulus per day, with a minimum of 3 days before receiving the next stimulus. We audiorecorded choughs during all presentations, using the same equipment as for natural recordings, to allow for the measurement of acoustic structure and the construction of exemplars for playback experiments.

We placed the snake model on the ground and covered it with leaves about 15–20 m from the foraging group's movement path. The head of the snake model was tied to a 5 m long piece of thin fishing line, which an investigator could gently pull to make the model move. A Marantz PMD661 recorder with a Sennheiser ME66 microphone attached to a tripod was positioned 3–5 m away from the model to record the choughs' vocalizations. Having placed the equipment, we used shredded cheese to attract the choughs to the model's location and moved the snake's head as the birds approached.

We were unable to use a physical model to simulate the context of high-flying hawks but, based on our field observations, choughs often gave 'aerial whistles' when they heard similar whistle calls from another group. We therefore constructed a 15 s

playback exemplar recorded from a group of choughs during a natural encounter with a high-flying hawk at the Australian National Botanic Gardens (approximately 3.5 km away from our study sites) in 2020. The exemplar was broadcast about 5 m away from a foraging group using WAV files on an iPhone 13 through a JBL Go 3 Bluetooth loudspeaker. The loudspeaker was attached to the investigator's waist, giving it a height of about 1 m. We then used audio equipment to record vocalizations given by the choughs when the exemplar was played. If choughs did not vocalize, or if their calls could not be isolated from the playback or other sounds, we repeated the trial 3 days later (N=6 groups).

The gliding model was thrown by one person standing 10–15 m from a foraging group, while another investigator stood 3–5 m from the group and used audio equipment to record vocalizations when the gliding model was launched. The model typically glided for 10–20 m and passed the group at a distance of 5–10 m. Failed attempts, where the glider veered off course and hit the ground immediately, were repeated as soon as possible. Similar glider presentations to other local group-living species also prompted flee alarm calls, whereas the act of throwing alone (control "fake throws") never prompted any type of alarm (Cunningham & Magrath, 2017; Magrath et al., 2007). Again, if the vocalizations overlapped and could not be isolated, the trial was repeated 3 days later (N=5 groups).

(c) Acoustic structure

We measured the acoustic structure from spectrograms of the alarm calls given by choughs during natural encounters with predators and during presentation of experimental stimuli. Spectrograms were generated from the recordings using Raven Pro 1.6, a Hann window function with a 512 sample size, a temporal grid resolution of 0.542 ms with an overlap 94.9%, a frequency grid resolution 93.8 Hz, a 5 s duration and a 0–15 kHz frequency bandwidth. The brightness of the greyscale view was set to 55 and the contrast was set to 70. We selected individual call elements manually by placing selection boxes on the spectrogram. All measurements were then calculated automatically by Raven Pro for each selected element. The measurements were (1) low frequency (Hz), the frequency above which 95% of the energy occurs, (2) high frequency

(Hz), the frequency below which 95% of the energy occurs, (3) peak frequency (Hz), the frequency at which amplitude is maximum, (4) bandwidth (Hz), the frequency interval containing 90% of the energy, (5) duration (s), the duration containing 90% of the energy, (6) aggregate entropy (bits), a measure of the disorder in a sound by analysing the energy distribution (pure tone ~0 bits), and (7) peak frequency contour average slope (Hz/ms), the mean of the peak frequency contour slope series of numbers.

To compare differences in the acoustic structure between alarm call types, we restricted our analysis to experimentally prompted calls because (1) the prompted recordings were matched by group, minimizing potential confounding effects of group-level differences, and (2) the exact context was controlled, unlike in natural recordings.

(d) Playback experiment

(i) Overview of experimental design

Playback experiments are essential to demonstrate functionally referential alarm communication, as they isolate the information conveyed by calls from any contextual information, such as the presence of a predator or the behaviour of conspecifics. We therefore broadcast three types of alarm calls to test whether choughs respond appropriately in the absence of direct cues about the type of threat.

The playback experiment was conducted in November 2022, during the choughs' breeding season, at five locations within our study site: O'Connor Ridge, Lyneham Ridge, Bruce Ridge, the suburb of O'Connor and the area around GIO Stadium Canberra. The experiment included four treatments: (1) terrestrial alarm calls; (2) aerial whistles; (3) flee alarm calls; (4) control (Figure 3.1). For the control treatment, we used the 'piping' contact calls of crimson rosellas, *Platycercus elegans*, a parrot species common at the study sites that does not pose a threat to choughs. These control calls were recorded from 16 individuals within the study area. As focal individuals in the experiment, we used one adult chough, which was banded and thus could be individually identified, from each of the 16 breeding groups. Each focal bird received unique playback exemplars of the

three types of alarm calls given by its own group members, as well as unique control calls, so there was complete replication. Although we could not reliably identify the caller when recording alarm calls, we ensured that each focal individual received a unique playback track for each treatment, reducing the likelihood that responses of the recipient were driven by calls from a specific class of individual. To control for potential order effects, we randomly generated treatment orders for each individual using R but rejected those that placed too many specific treatments in the same position, so balancing the order. As a result, each order occurred four times for each treatment across the 16 individuals. To minimize habituation, each bird received only one playback per day, with a minimum of 24 h before the next playback.

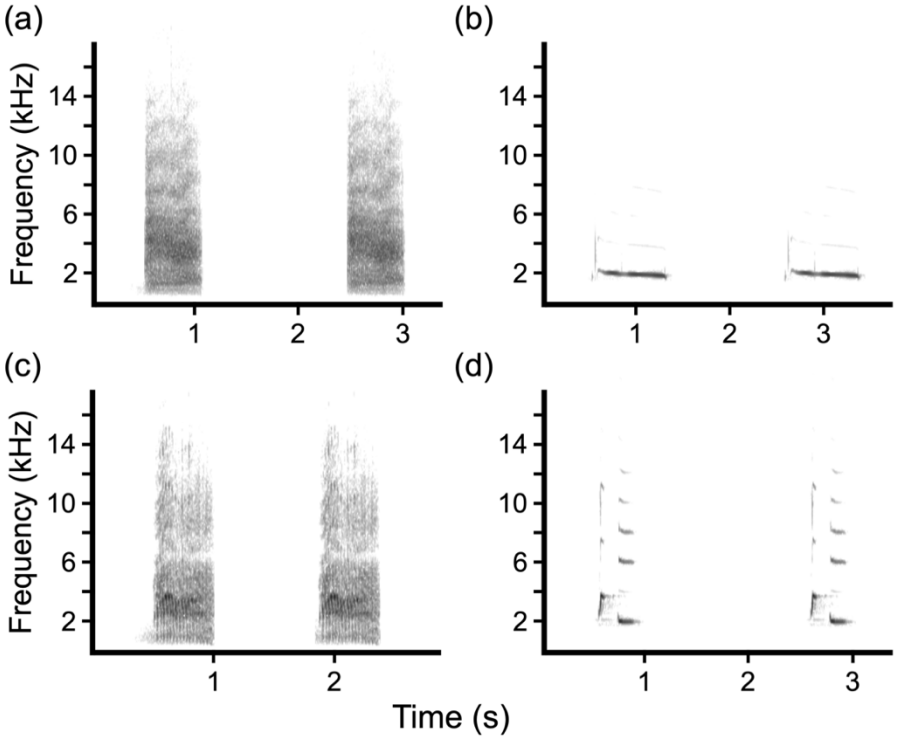


Figure 3.1. Spectrograms of two-element exemplars used in the playback experiment to white-winged choughs: a) terrestrial alarm call, b) aerial whistle, c) flee alarm call, and d) control contact call of the crimson rosella.

(ii) Preparation of playback treatments

For consistency of recording conditions and context, we prepared all alarm playback exemplars from recordings of calls prompted by simulated threats (see Prompted Alarm

Calls above), which were similar in acoustic structure to calls recorded in comparable natural contexts (Appendix Table A1). We selected high-quality recordings without overlapping calls from other individuals or distinct background noise. Each alarm call treatment contained two duplicate call elements, which was within the natural range of element-number for all three alarm call types. We kept the number of call elements constant across treatments to ensure that the number of elements alone could not explain differences in response. The inter-element interval followed each call's mean interval from naturally prompted calls (mean±SD: terrestrial alarms: 1.4±0.8 s, N=5; aerial whistles: 1.2±0.9 s, N=5; flee alarms: 0.8±0.2 s, N=4). Similarly, the control treatment included two call elements with a natural inter-element interval of 1.5 ± 0.8 s (N=5). The total duration of the playback was 2.6–4.5 s, with the first 0.5 s of background sound fading in and the last 0.5 s fading out. We filtered all exemplars at 0.5 kHz to remove sounds below the frequency range of all call types.

We broadcast all playbacks at 65 dB at 5 m, which is within the natural range of all types of alarm calls at that distance (Appendix Table A2). Keeping the same amplitude across treatments excluded the possibility that differences in response could be due to amplitude alone, rather than to differences in call type. We determined the amplitudes by rerecording playbacks at 5 m, along with a calibration 1 kHz tone measured with a Brüel & Kjær 2240 sound level meter. All playback files were adjusted on a computer to achieve the target amplitude when broadcast.

(iii) Field methods

We conducted playback trials in calm, dry weather between 0700 and 1800 hours. On encountering a group, we slowly followed them on foot from a distance of about 5 m for at least 5 min to allow the group to habituate to our presence. During this period, we counted the number of birds and identified banded individuals. We broadcast playbacks to the focal bird from approximately 5 m away, using WAV files on a Roland R-07 via a custom-made amplifier and tweeter loudspeaker (frequency response 2–11 kHz). The loudspeaker was attached to an investigator's waist, giving it a height of about 1 m. We only ran playbacks when (1) the focal bird was the closest to the loudspeaker, (2) the focal

bird was foraging at the edge of the group, (3) there were no signs of potential predators around, and (4) there was no evidence of antipredator behaviours by group members. All playback trials were videorecorded at 50 frames/s on a Panasonic HC-VX1 camcorder, hand-held by an investigator.

(iv) Response measurement

Videos were prepared and scored using Final Cut Pro V10.6.9. We noted the start and end frames of each playback, and exported videos without sound. The video files and their corresponding identities were renamed by someone not involved in the study, ensuring that each focal bird's response was scored blindly with respect to the playback treatment. Video analysis was conducted by the first author 1 month after the final playback to minimize the likelihood of remembering specific playback events.

We defined the bird's immediate antipredator response to playback as the first behaviour after it stopped feeding and initially raised its head (i.e. became alert). We used a protractor template to assist in scoring the head position of the birds. Responses were classified as follows: (1) look around, the bird raised its head with its bill at an angle of less than 30 degrees above horizontal; (2) look up, the bird raised its head with its bill at an angle of more than 30 degrees above horizontal; (3) startle, the bird raised its head, lowered its body and wings, and jumped; or (4) flee, the bird fled from the ground to cover or to a tree without scanning. If the bird continued feeding without raising its head, it was recorded as no response.

We measured three temporal response variables: the latency to respond, the duration of the response and the duration of scanning. Latency to respond (s) was calculated from the onset of the playback to the time when the bird initiated body movement. The duration of the response (s) was calculated as the period between the start of the response and the moment that the bird resumed feeding, including cases where a chough returned to the ground to feed after fleeing. We measured the total time spent scanning before resuming feeding, as well as sub-dividing scanning time into 'looking around' and 'looking up' (as defined above). The choughs' head orientations

were distinct enough to classify their scanning types reliably (see Supplementary video materials). Due to the lateral placement of their eyes, choughs sometimes tilted their heads to one side while looking up, which was also categorized as 'look up' even if the bill angle was estimated at less than 30 degrees. If the focal bird fled, we excluded the scanning data from further analysis as it was difficult to classify the bill angle and the birds were often obstructed by vegetation. All temporal measurements were converted to seconds for analysis by translating video frames to seconds (at 50 frames/s, each frame represents 0.02 s).

Finally, we scored whether choughs engorged their eyes (0/1) during responses to playbacks.

(e) Statistical analysis

We performed all statistical analyses and figure plotting in R 4.0.3 (R Core Team, 2020).

We compared both specific acoustic properties and the overall acoustic structure of natural and prompted alarm calls. We used *t* tests to compare specific acoustic features between alarm calls, using the 't.test()' function. ANOVA was employed to examine the effect of threat type on the acoustic structure of the alarm calls, using the 'aov()' function, with pairwise comparisons using the 'LDuncan()' function. Principal components analysis (PCA) was conducted to visualize overall variation in the acoustic structure of the alarm calls elicited by natural predators and experimental stimuli, using 'prcomp()' function. The PCA included low frequency, high frequency, peak frequency, bandwidth, duration, aggregate entropy and peak frequency contour average slope (see Acoustic Structure above for definitions). We assessed differences among the three alarm call types in multivariate acoustic space using a MANOVA on the first two principal components (PC1 and PC2), followed by ANOVAs and Tukey's HSD tests for pairwise comparisons.

We analysed immediate categorical responses to playback using a cumulative link mixed model (CLMM), which is appropriate for ordinal data as it orders the strength

of response but does not imply quantitatively equal increments between categories. Responses were ranked into four ordered levels: 0 = no response; 1 = scan (including looking around and looking up); 2 = startle; 3 = flee. Playback treatment, group size and playback order were included as fixed effects, with individual identity and location included as random effects. The model was conducted using the 'clmm()' function of the 'ordinal' package, with a probit link function and an equidistant threshold. In addition, we used McNemar tests, appropriate for paired dichotomous data, to compare the probability of looking around versus looking up in response to terrestrial alarm calls versus aerial whistles, using the 'mcnemar.test()' function.

We examined the effects of playbacks on temporal responses, latency to respond, duration of the response, time spent scanning, time spent looking around and time spent looking up, using separate linear mixed effect models (LMMs). Each model included playback treatment, group size and playback order as fixed effects, and individual identity and location as random effects. In each case, LMMs were constructed with normal distributions and identity link functions, using the 'lmer()' function of the 'lme4' package. We carried out pairwise comparisons using 'emmeans()' function of the 'emmeans' package. Conditional R2 values of models were calculated using the 'r.squaredGLMM()' function of the 'MuMIn' package. The full model with all factors of interest was fitted before likelihood ratio tests were used to identify significant fixed effects by removing them individually from the model and assessing the change in deviance. One extreme outlier (319 s) was excluded from the analysis of response duration in the aerial whistle treatment (see Results). It was not possible to measure scanning if individuals fled to playbacks, so we excluded the flee alarm call treatment from any analysis of scanning because 11/16 birds fled immediately. In the aerial whistle treatment, three individuals fled after briefly scanning, leaving 13 birds for analyses of scanning.

We analysed the effects of playbacks on eye engorging (dichotomous response) using a bias-reduced generalized linear model (BRGLM). BRGLM can fit uniform responses of some playback treatments, where the focal individuals all showed the same

response, which cannot be achieved using generalized linear mixed effect models. Playback treatment, group size, playback order, individual identity and location were included as factors in the model. The BRGLM was constructed with a binomial distribution and logit link function, using the 'brglm()' function of the 'brglm2' package. We carried out pairwise comparisons using 'emmeans()' function of the 'emmeans' package. As with the scanning analysis, data from the flee alarm call treatment and from three individuals in the aerial whistle treatment were excluded, as these birds fled and eye engorging could not be measured.

(f) Ethical Note

This study was approved by the Australian National University Ethics Committee (protocol A2022/35) and was designed to minimize any adverse effects on the birds. To reduce disturbance, each playback sound lasted less than 5 s and each focal individual was exposed to only one playback per day, with a minimum interval of 24 h. The birds quickly resumed foraging after the playbacks.

Results

(a) Production of alarm calls

White-winged choughs produced three different alarm calls in response to different types of threats (Table 3.1, Figure 3.1). Based on our field observations, terrestrial alarm calls were given in response to ground-based threats in low-urgency situations, including mammals (e.g. domestic dogs, *Canis familiaris*, feral cats, common brushtail possums, *Trichosurus vulpecula* and red foxes), reptiles (e.g. bearded dragons, *Pogona barbata* and eastern brown snakes) and humans. Aerial whistles were produced in response to high-flying hawks. Common triggers for these calls included brown goshawks, wedge-tailed eagles, *Aquila audax* and little eagles, *Hieraaetus morphnoides*. Unlike the other alarm calls, aerial whistles were often given in a chorus, and sometimes prompted other groups to join in. Both terrestrial alarms and aerial whistles were typically followed by birds stopping feeding and becoming vigilant. In high-urgency situations, regardless of whether the threat was terrestrial or aerial, choughs produced flee alarm calls, such as when a

hawk flew nearby or a dog ran towards them. These alarm calls were typically followed by birds fleeing immediately to cover.

The three alarm call types associated with different threats differed statistically in their acoustic structure (Figure 3.2). Alarm calls elicited by experimental prompts did not differ from those produced to comparable natural prompts (Figure 3.2, Appendix Table A1). PCA analysis revealed that the first two principal components explained over 80% of the variance (Appendix Table A3), and the three alarm call types differed in multivariate acoustic space (MANOVA: $F=42.77$, $P<0.001$; Figure 3.2). Alarm call type also had significant effects on both PC1 and PC2 (ANOVA: PC1: $F=288.3$, $P<0.001$; PC2: $F=9.02$, $P<0.001$). On PC1, aerial whistles differed from both flee and terrestrial alarms, while the difference between flee and terrestrial alarms was marginal (Appendix Table A4). On PC2, flee alarms differed from both aerial whistles and terrestrial alarms, whereas aerial whistles and terrestrial alarms did not differ (Appendix Table A4). More specifically, aerial whistles had higher PC1 values, which were associated with a greater peak frequency contour average slope (component loading 0.31; Appendix Table A5) and longer duration (0.29). Flee alarm calls tended to have higher PC2 values, primarily driven by a lower frequency (0.86).

Analysis of individual acoustic attributes emphasize that the two broad-frequency vocalizations (terrestrial and flee alarm calls) were acoustically similar but distinct from the pure-tone aerial whistles (Figure 3.1, Table 3.1). Despite their similarity, terrestrial and flee alarm calls nonetheless differed in two acoustic features: terrestrial alarm calls had a lower low frequency (mean ± SD: 1699±344 versus 1998±530 Hz) and a steeper decline in peak frequency contour average slop (-4.2±2.5 Hz/ms versus -2.3±2.8 Hz/ms; Duncan's tests: all $P<0.05$; Table 3.1) compared to flee alarm calls. No significant differences were found between terrestrial and flee alarm calls in high frequency, peak frequency, bandwidth, duration or aggregate entropy (Table 3.1). By contrast, aerial whistles differed significantly from both broad-frequency alarm call types (terrestrial and flee) in most acoustic features, including high frequency, peak frequency, bandwidth, duration, aggregate entropy and the peak frequency contour average slope (Table 3.1).

The only exception was low frequency, which showed no significant difference between aerial whistles and either terrestrial alarm calls or flee alarm calls (Table 3.1).

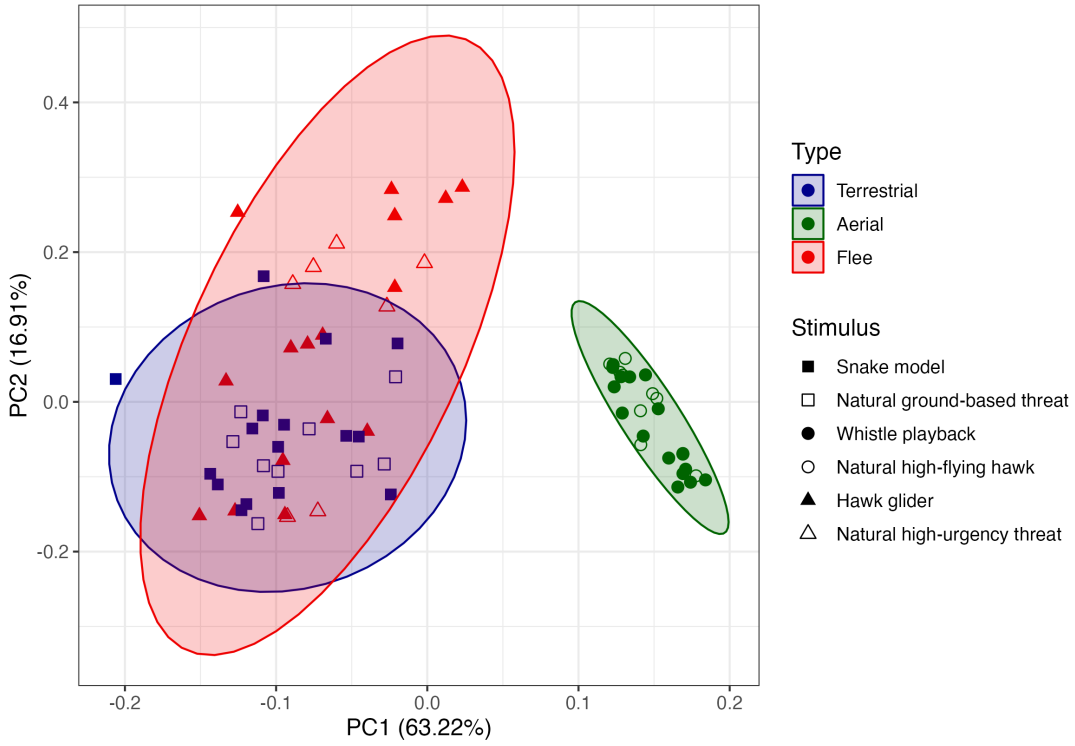


Figure 3.2. Principal components plot of the acoustic properties of experimentally and naturally prompted white-winged chough terrestrial alarm calls, aerial whistles and flee alarm calls. PCA analysis included low frequency, high frequency, peak frequency, bandwidth, duration, aggregate entropy and peak frequency contour average slope (see Methods (c) section for detailed definitions). Statistical analysis details are shown in Appendix Tables A3 and A5.

Table 3.1. Acoustic differences between chough terrestrial alarm calls (given to a snake model), aerial whistles (given to playback of whistle calls) and flee alarm calls (given to a glider hawk model).

Call type	Low frequency (Hz) *	High frequency (Hz) ***	Peak frequency (Hz) ***	Bandwidth (Hz) ***	Duration (s) ***	Aggregate entropy (bits) ***	PFC average slope (Hz/ms) ***
Terrestrial (*N*=16)	1699±344[b]	5988±914[a]	3223±503[a]	4289±919[a]	0.3±0.1[a]	5.4±0.3[a]	-4.2±2.5[a]
Aerial (*N*=16)	1734±123[ab]	2139±120[b]	1904±89[b]	404±45[b]	0.5±0.1[b]	2.5±0.1[b]	-0.3±0.6[b]
Flee (*N*=16)	1998±530[a]	5584±1183[a]	3340±232[a]	3586±1426[a]	0.3±0.1[a]	5.2±0.6[a]	-2.3±2.8[c]

Means ± SD shown. *P=0.055; ***P<0.001 (ANOVA test). Different superscript letters (a, b, c) indicate significant differences among means, as determined by Duncan's post hoc test.

(b) Response to alarm calls

The choughs' immediate categorical responses to playback were appropriate to the type of alarm call (CLMM, likelihood ratio: χ^2=116.99, *df*=3, *P*<0.001; Figure 3.3, Appendix Table A6). Among alarm call types, flee alarms prompted 11/16 birds to flee immediately without scanning, indicating a high-urgency threat, while no bird fled immediately in response to terrestrial alarms or aerial whistles (Figure 3.3, Appendix Table A6). Both terrestrial alarms (15/16) and aerial whistles (16/16) prompted most birds to scan immediately, but there was a difference in gaze direction (McNemar test: χ^2=9.09, *df*=1, *P*=0.003; looking around versus looking up, *N*=15 with scanning behaviour in both; Figure 3.3). Specifically, 15/16 birds looked around after playback of terrestrial alarms, consistent with a ground-based threat, while 12/16 birds looked up after playback of aerial whistles, consistent with an aerial threat. In contrast to alarm calls, only one bird briefly looked around and none fled in response to the control playback (Figure 3.3).

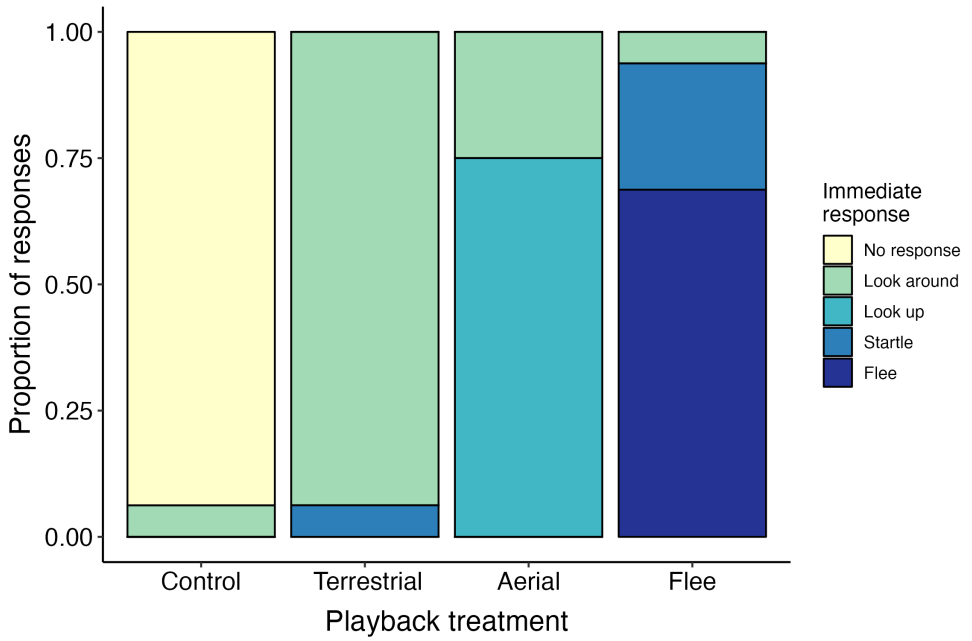


Figure 3.3. White-winged chough responses to playback of conspecific alarm calls and crimson rosella control calls. The *Y* axis shows the proportion of immediate categorical responses to playback. *N*=16 for each playback treatment. Statistical analysis details are given in Appendix Table A6.

Birds took twice as long to react to aerial whistles compared to terrestrial alarms and flee alarms (LMM: χ^2=24.32, P<0.001; Figure 3.4a, Appendix Table A7a), while response times to terrestrial alarms and flee alarms were similar (Appendix Table A8a). Additionally, the duration of the response was affected by treatment (LMM: χ^2=14.27, P<0.001; Figure 3.4b, Appendix Table A7b). Birds took more than three times longer to resume feeding after flee alarms compared to terrestrial alarms and aerial whistles, with no significant difference between terrestrial alarms and aerial whistles (Figure 3.4b, Appendix Table A8b).

Scanning over the course of the response differed according to the type of alarm call (LMM: χ^2=45.97, P<0.001; Figure 3.5a, Appendix Table A9a), with aerial whistles prompting longer scanning durations and an almost unique looking-up response. We focused on terrestrial alarms and aerial whistles because almost all birds fled immediately to flee alarm calls (see above). Birds spent more than twice as long scanning in response to aerial whistles compared to terrestrial alarms and much longer than in the control (Figure 3.5a, Appendix Table A10a). Terrestrial alarms also elicited longer scanning durations than the control (Figure 3.5a, Appendix Table A10a). Notably, birds spent the longest time looking up after aerial whistles, with very few or no instances of looking up observed in response to terrestrial alarms or the control (LMM: χ^2=41.26, P<0.001; Figure 3.5b, Appendix Tables A9b, A10b). Birds showed similar looking-around durations in response to both alarm calls, which were longer than in the control (LMM: χ^2=37.62, P<0.001; Figure 3.5c, Appendix Tables A9c, A10c).

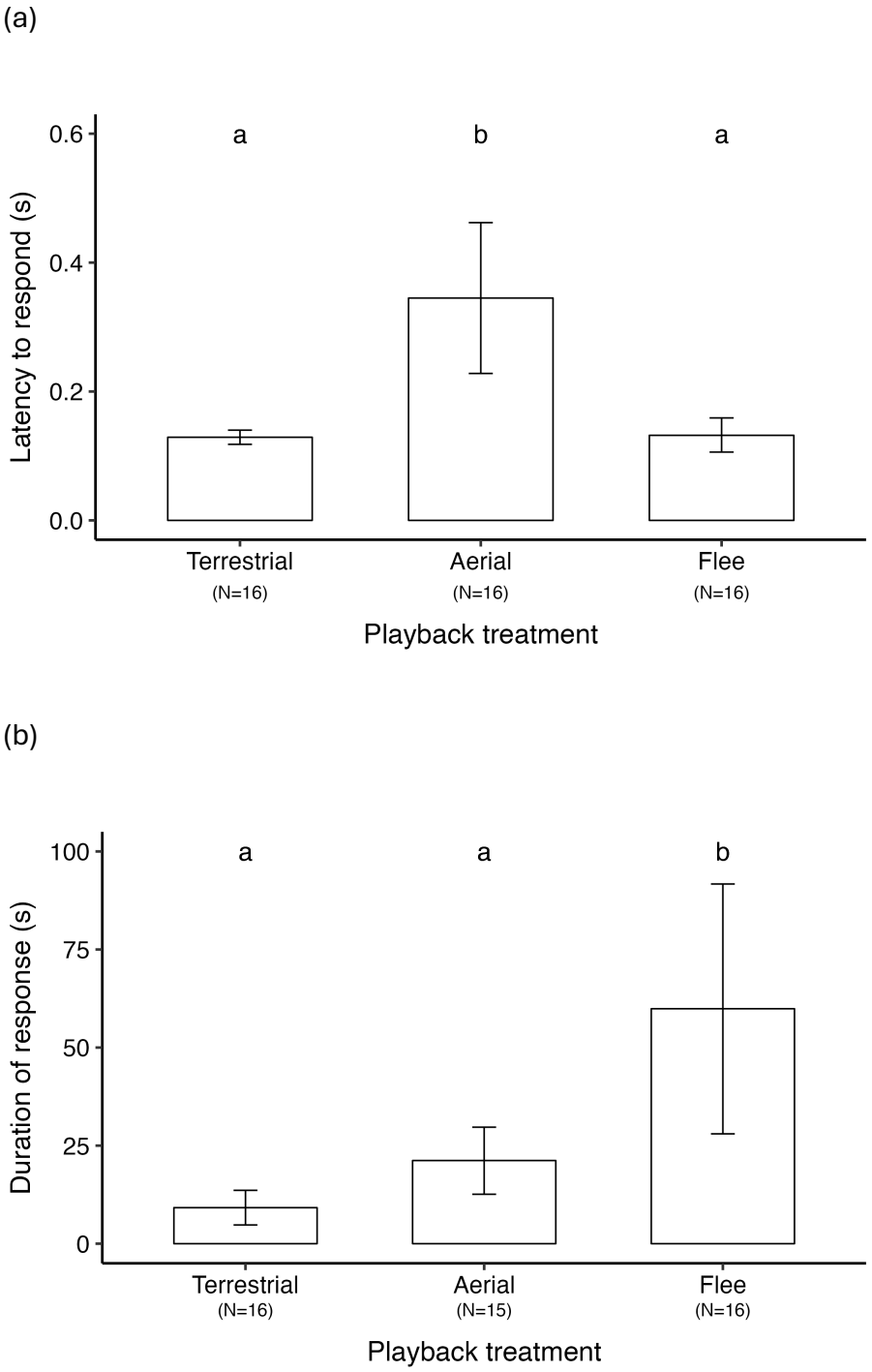


Figure 3.4. White-winged choughs' (a) latency and (b) duration of response to conspecific alarm call playbacks. Predicted means ± SEM shown. Different letters indicate significant differences between means as assessed by post hoc Tukey HSD test ($P<0.05$). Sample sizes are shown for each treatment. Statistical analysis details are given in Appendix Tables A7 and A8.

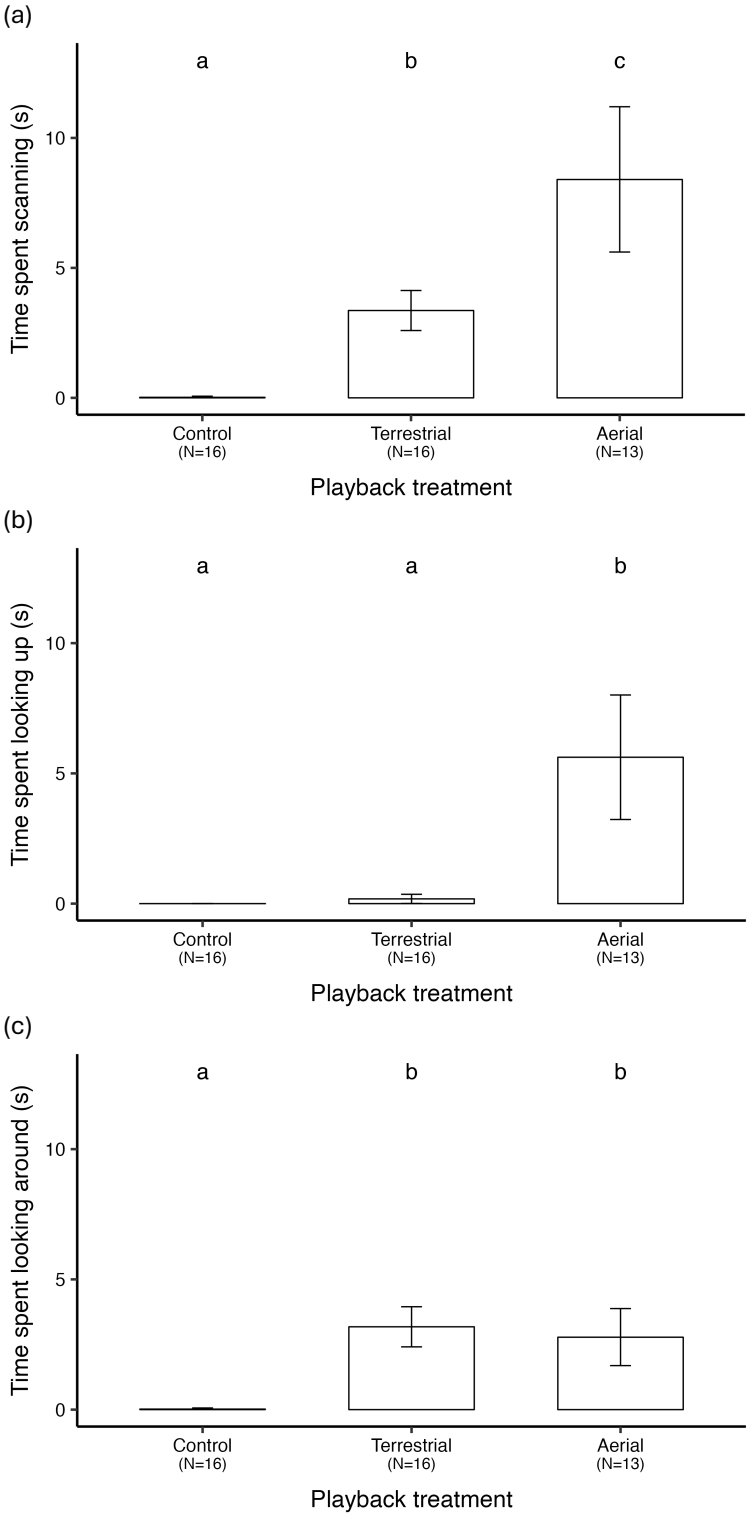


Figure 3.5. Response of white-winged choughs to conspecific alarm call playbacks, showing the time spent (a) scanning, (b) looking up and (c) looking around. Predicted means ± SEM shown. Different letters indicate significant differences between means as assessed by post hoc Tukey HSD test ($P<0.05$). Sample sizes are shown for each treatment. Statistical analysis details are given in Appendix Tables A9 and A10.

Birds were more likely to bulge their eyes in response to aerial whistles than in response to terrestrial alarm calls and the control (BRGLM: aerial versus terrestrial: Z=-2.84, *P*=0.013; aerial versus control: Z=-3.28, *P*=0.003; Figure 3.6, Appendix Table A11). When this response occurred, birds bulged their eyes rapidly, with a latency of 2.0±1.4 s (mean ± SD; range: 0.5–5.4 s; *N*=12 individuals) from playback onset, and the behaviour was typically sustained rather than expressed in short bouts.

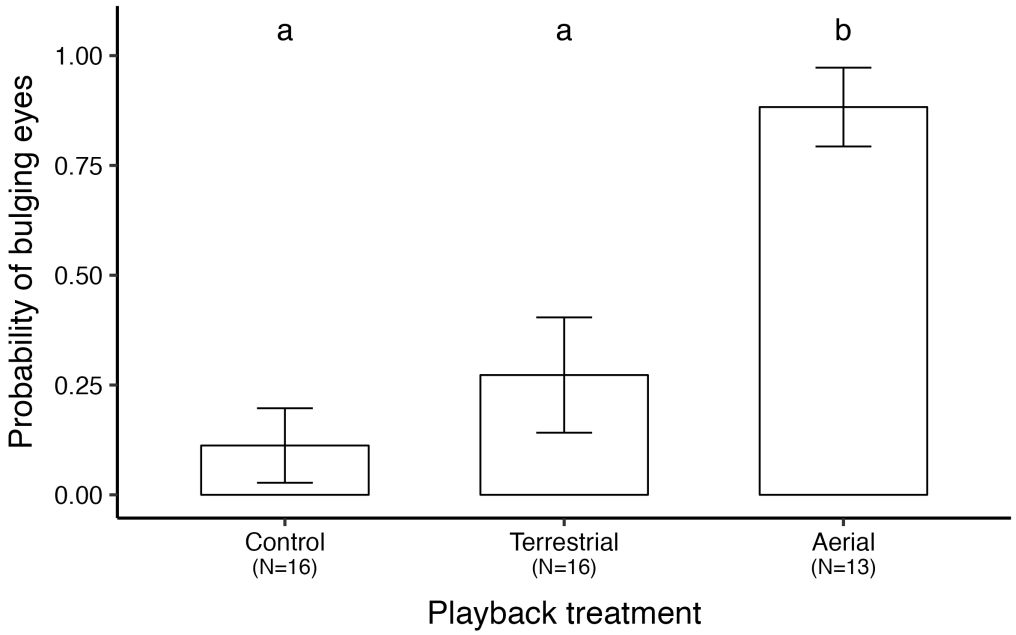


Figure 3.6. Probability of bulging eyes in white-winged choughs responding to conspecific alarm call playbacks. Predicted means ± SEM shown. Different letters indicate significant differences between means as assessed by post hoc Tukey HSD test (P<0.05). Sample sizes are shown for each treatment. Statistical analysis details are given in Appendix Table A11.

Discussion

White-winged choughs exhibit a functionally referential alarm call system that conveys information about threat type and urgency. Choughs produced two low-urgency alarm calls to different types of threats, with terrestrial alarm calls given in response to ground-based threats and aerial whistles given in response to high-flying hawks. By contrast, flee alarm calls were given to nearby, immediate threats regardless of whether they were terrestrial or airborne. The three alarm calls differed acoustically, although with overlap in measured acoustic properties between terrestrial and flee alarm calls. Playback of these alarm calls elicited appropriate responses, even without direct cues from the threat, and regardless of any overlap of measured acoustic features. Birds looked around in response to terrestrial alarms, looked up to aerial whistles while also showing bulging eyes and immediately fled to cover on hearing flee alarms. This communication system enables individuals to respond in context-appropriate ways to various types of threats.

Choughs produced three different alarm calls in response to specific simulated and natural contexts, fulfilling the production criteria for functional reference (Macedonia & Evans, 1993). Although we had only single exemplars of models to prompt alarm calls, the alarm calls given in response to the models were similar to those recorded during multiple natural events, with similar variation among individuals, providing replication of contexts when considering both models and natural prompts. Among chough alarm calls, terrestrial and flee alarms were surprisingly similar, differing significantly in only two measured acoustic features, although some overlap remained. Similarly, a previous study showed that superb fairy-wrens, *Malurus cyaneus*, produce acoustically similar alarm calls with contrasting functions, demonstrating that these birds use multiple acoustic features to discriminate between these calls (Tegtman & Magrath, 2020). We suggest that choughs may similarly rely on multiple acoustic features to distinguish between terrestrial and flee alarms. Alternatively, additional acoustic features not measured in this study may also contribute to their differentiation. For instance, flee alarms tend to exhibit more distinct pulses, rapid sequences of short elements separated by brief intervals, than terrestrial alarms. By

contrast, aerial whistles showed no acoustic overlap with terrestrial alarms or flee alarms in multivariate space, or across most acoustic features. Aerial whistles also differed from the other alarm calls in often being given in a chorus and sometimes being repeated by other groups, likely facilitating the propagation of information about distant aerial threats across groups. Indeed, narrow-frequency calls, such as whistles, can transmit farther with less spectral degradation compared to broad-frequency calls (Naguib et al., 2008). Aerial whistles could therefore function not only as signals to warn of aerial threats within a group but also as long-distance signals for intergroup communication.

Choughs responded appropriately to the playback of each alarm call type, regardless of the partial overlap of measured acoustic features, which fulfils the perception criterion for functional reference (Macedonia & Evans, 1993). Playback of terrestrial alarm calls prompted the birds to become vigilant and look around, aerial whistles prompted them to look upward, and flee alarm calls triggered immediate flight. These responses were similar to their antipredator behaviour during natural encounters. Among these alarm calls, terrestrial alarms and aerial whistles are associated with low-urgency situations and prompted receivers to seek additional information about threats, while providing clues about where to look. This suggests that chough terrestrial alarms and aerial whistles simultaneously convey information about threat type and urgency. By contrast, flee alarm calls function as 'general' high-urgency signals, conveying nonspecific information about the type of threat, as they are given during close encounters with both terrestrial and aerial predators. For choughs, the main response to an immediate threat is to flee to cover. In such urgent situations, conveying urgency alone seems sufficient, especially since there is no time to gather additional details about the threat. Similar mixed alarm call systems have been observed in mongoose species (e.g. meerkats and dwarf mongooses, *Helogale parvula*), which produce functionally referential alarm calls that convey both predator type and urgency, as well as nonspecific alarm calls (Collier et al., 2017; Manser, 2001; Manser et al., 2002). Choughs, like mongooses, may have been driven by similar social (e.g. cooperative breeding) and ecological (e.g. ground foraging) factors to develop such a system, enabling effective coordination of antipredator responses to various threats (Furrer &

Manser, 2009). Our findings are consistent with the suggestion that social species are likely to develop sophisticated alarm call systems to enhance the antipredator benefits of group living (Blumstein & Armitage, 1997; Furrer & Manser, 2009).

Counterintuitively, choughs initiated their response to low-urgency terrestrial alarms as quickly as they did to high-urgency flee alarms, 0.13 s in both cases, although the response was quite different. Choughs never fled in response to terrestrial alarms, whereas most birds fled immediately upon hearing flee alarms and took six times longer to resume feeding. One possible explanation for the comparable response times is that the similar call structure enhances detectability, while subtle acoustic differences then allow discrimination (Tegtman & Magrath, 2020). This similarity may therefore trigger an equally rapid detection and initial motor response before the birds fully process and recognize the specific call type. A similar example has been observed in New Holland honeyeaters, *Phylidonyris novaehollandiae*, which respond extremely quickly to alarm calls (about 0.1 s) (McLachlan & Magrath, 2020). Honeyeaters assess the urgency level based on the acoustic structure of the first element of the alarm calls, which varies with threat level, and adjust their escape strategy depending on the number of subsequent elements (McLachlan & Magrath, 2020). In choughs, terrestrial alarms are highly efficient signals, prompting both a fast initial response but also a rapid resumption of feeding, which balances predator vigilance with foraging efficiency.

When a threat is not immediate, receivers may seek additional information, such as by observing the caller's behaviour, to enhance the effectiveness of their antipredator responses. Functionally referential alarm calls can convey limited information about a threat's location, such as on the ground or in the sky, but there is currently no evidence that such calls provide specific directional details about an approaching threat, such as from the left or right (Liao et al., 2024). Therefore, complementary input from other senses, such as vision, can help receivers refine this information. In choughs, aerial whistles are specifically given in response to high-flying aerial threats, prompting most birds to look upward immediately. However, about 30% of their total scanning time was spent looking around.

While this 'looking around' might appear redundant, it could help receivers gather additional information about the exact direction of an approaching hawk by observing the caller's behaviour, such as their gaze direction. Although no studies have directly tested this possibility, similar behaviour has been observed in other species (Evans et al., 1993; Schel et al., 2010; Seyfarth & Cheney, 1980). For example, chickens were more likely to look up following playback of aerial alarm calls, but the frequency of horizontal scanning did not differ between aerial and terrestrial alarm calls (Evans et al., 1993). As each sensory modality has its own strengths and limitations, this seemingly 'redundant' response may enhance the accuracy of their antipredator behaviour, particularly in low-urgency situations. Therefore, we suggest that it would be valuable, in future studies of functionally referential communication, to integrate information from multiple sensory modalities, such as auditory and visual signals/cues.

Choughs were more likely to display bulging eyes in response to aerial whistles compared to other alarm call types, suggesting that this might be a visual signal associated with aerial threats. Bulging eyes might have various functions that explain association with aerial whistles. First, they might signal to predators that they have been detected (Caro, 2005; Holley, 1993). However, this seems unlikely because high-flying hawks are typically distant (over 50 m high) and, if bulging eyes functioned as an advertisement signal, then it might also be expected in response to terrestrial predators. Second, bulging eyes might not have a signalling function, but perhaps enhance visual acuity when searching for distant predators. This explanation seems improbable, as bulging eyes also occur during close social interactions (Rowley, 1978). Third, we propose bulging eyes are most likely a visual signal to conspecifics (Sherman, 1977; Smith, 1965; Smith & Evans, 2008) either (1) as a redundant component of a multimodal signal, reinforcing the message that the threat is airborne and distant, or (2) as a nonredundant component, conveying directional information about the threat or caller by emphasizing eye orientation. Based on our field observations, choughs often bulge their eyes while producing aerial whistles and looking towards high-flying hawks, which could signal hawk location. However, playback of aerial whistles alone was sufficient to elicit this behaviour, so the eye bulging can occur when the

individual has not itself seen the predator. In this situation, a bird's direction of gaze may signal the location of the alarm caller, from whom others could gain information. Further research is needed to test the possible signalling function of eye bulging, such as whether it affects the gaze direction of listeners.

Individuals in social groups rely heavily on communication to coordinate diverse activities, particularly antipredator behaviours (Freeberg, 2006; Freeberg et al., 2012; Liao et al., 2024). White-winged choughs, as obligate cooperative breeders, encode information about threat type and urgency in their alarm calls, similar to social mongoose species (Collier et al., 2017; Manser, 2001). Their distinctive eye-bulging occurred specifically in response to aerial whistles, and so may represent a visual signal associated with high-flying threats and potentially serve to enhance the alarm signal. We therefore propose that the integration of multiple sensory modalities to convey complementary information may be common in alarm communication and warrants further investigation.

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Appendix

Table A1. Acoustic differences in chough alarm calls produced in response to experimental stimuli and in natural contexts

Call type	Low frequency (Hz)	High frequency (Hz)	Peak frequency (Hz)	Bandwidth (Hz)	Duration (s)	Aggregate entropy (bits)	PFC average slope (Hz/ms)
Terrestrial alarm call							
Snake model (*N*=16)	1699±344	5988±914	3223±503	4289±919	0.3±0.1	5.4±0.3	-4.2±2.5
Natural predator (*N*=9)	1510±190	5427±1057	3146±452	3917±1070	0.3±0.1	5.4±0.4	-3.4±1.5
t value	1.77	1.34	0.39	0.88	1.40	0.42	-0.96
P value	0.09	0.20	0.70	0.39	0.18	0.68	0.35
Aerial whistle							
Whistle playback (*N*=16)	1734±123	2139±120	1904±89	404±45	0.4±0.1	2.5±0.1	-0.3±0.6
Natural predator (*N*=10)	1811±111	2201±108	1969±109	391±42	0.4±0.1	2.5±0.1	-0.3±0.6
t value	-1.63	-1.38	-1.59	0.78	0.44	-0.60	-0.06
P value	0.12	0.18	0.13	0.44	0.67	0.56	0.95
Flee alarm call							
Hawk glider (*N*=16)	1998±530	5584±1183	3340±232	3586±1426	0.3±0.1	5.2±0.6	-2.3±2.8
Natural predator (*N*=7)	1862±470	5290±703	3429±222	3429±716	0.3±0.1	5.1±0.3	-0.6±2.6
t value	0.62	0.74	-0.87	0.35	1.35	0.53	-1.45
P value	0.55	0.47	0.40	0.73	0.21	0.60	0.17

Means ± SD shown. *P* value from independent *t* test.

Table A2. The amplitude (dB at 5 m) of white-winged chough naturally prompted alarm calls

Call type	*N*	No. of elements	Amplitude (dB; mean±SD)	Range (dB; min–max)
Terrestrial alarm call	5	46	63.8±4.2	53.6–70.6
Aerial whistle	5	26	59.0±3.0	53.6–65.0
Flee alarm call	5	11	62.4±2.9	57.5–68.0

N refers to the number of different individuals recorded.

Table A3. Eigenvalues and proportion of variance explained from the principal component analysis (PCA) of acoustic properties of alarm calls

PC axis	Eigenvalue	Proportion of variance explained	Cumulative proportion of variance explained
1	2.10	0.63	0.63
2	1.09	0.17	0.80
3	0.80	0.09	0.89
4	0.73	0.08	0.97
5	0.41	0.02	0.99
6	0.20	0.01	1.00

Table A4. Pairwise comparisons of alarm call types along the first two principal components (PC1 and PC2), showing the mean difference between group centroids and *P* values from Tukey's HSD tests

PC Axis	Alarm call types	Mean difference between groups	*P*
PC1	Aerial vs Flee	-3.86	<0.001
	Aerial vs Terrestrial	4.34	<0.001
	Flee vs Terrestrial	0.48	0.057
PC2	Aerial vs Flee	0.90	0.006
	Aerial vs Terrestrial	0.25	0.64
	Flee vs Terrestrial	1.15	<0.001

Table A5. Loadings of the seven measured acoustic variables on each principal component axis

Variable	PC1	PC2	PC3	PC4	PC5	PC6
Low frequency (Hz)	0.04	0.86	-0.19	-0.41	-0.19	-0.06
High frequency (Hz)	-0.46	0.05	-0.25	0.09	-0.38	0.30
Peak frequency (Hz)	-0.43	0.19	-0.15	0.01	0.84	0.23
Bandwidth (Hz)	-0.46	-0.11	-0.21	0.17	-0.33	0.31
Duration (s)	0.29	-0.31	-0.86	-0.26	0.08	-0.05
Aggregate entropy (bits)	-0.46	-0.02	-0.13	0.12	-0.02	-0.87
PFC average slope (Hz/ms)	0.31	0.33	-0.27	0.85	0.03	-0.02

Rows represent acoustic properties, and columns correspond to the principal components derived from the PCA.

Table A6. CLMM output testing the effect of playback treatment on the immediate response of white-winged choughs (also see Figure 3.3)

Fixed effects	Estimate±SE	Likelihood ratio	*df*	*Z*	*P*
Treatment		116.99	3		<0.001
Treatment (Control vs Terrestrial)	-0.33±0.03			-12.20	<0.001
Treatment (Control vs Aerial)	-0.32±0.03			-11.24	<0.001
Treatment (Control vs Flee)	-0.86±0.05			-17.08	<0.001
Treatment (Terrestrial vs Aerial)	0.01±0.03			0.45	0.97
Treatment (Terrestrial vs Flee)	-0.52±0.05			-10.11	<0.001
Treatment (Aerial vs Flee)	-0.54±0.05			-10.74	<0.001
Group size	-0.04±0.07	0.33	1	-0.57	0.57
Playback order	-0.18±0.20	0.88	1	-0.91	0.35

Responses are categorized as follows: 0 = no response; 1= scan (including looking around and looking up); 2 = startle; 3 = flee. Significant outcomes are shown in bold ($P<0.05$).

Table A7. Results of linear mixed effects models (LMMs) examining how different playback treatments affect white-winged chough: a) latency to respond (s) and b) duration of response (s) (also see Figure 3.4)

Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests			$R^{2\,b}$
		Factor levels	Effect ± SE	*df*	χ^2	*P* [a]	
(a) Latency to respond							0.41
	(Intercept)		0.08±0.06				
	Treatment (Terrestrial)	Aerial	0.22±0.05	2	24.32	<0.001	
		Flee	0.00±0.05				
	Group size		0.00±0.00	1	0.00	0.99	
	Playback order		0.02±0.02	1	1.29	0.26	
Random factor	Individual ID		0.00				
	Location ID		0.00				
(b) Duration of response							0.29
	(Intercept)		-8.77±17.70				
	Treatment (Terrestrial)	Aerial	10.90±13.06	2	14.27	<0.001	
		Flee	47.93±12.99				
	Group size		2.21±1.63	1	2.04	0.15	
	Playback order		1.80±4.78	1	0.16	0.69	
Random factor	Individual ID		0.00				
	Location ID		0.00				

Significant outcomes ($P<0.05$) are shown in bold.

[a] *P* value for each factor is derived from a likelihood ratio test for changes in deviance when models with and without that factor are compared.

[b] Conditional R^2 values.

Table A8. Results of post hoc Tukey HSD tests comparing playback treatments for a) latency to respond and b) duration of response (also see Figure 3.4)

Variable	Treatment	Mean ± SE (s)	*t* value	*P*
(a) Latency to respond (s)	Terrestrial vs Aerial	0.13±0.02 vs 0.35±0.22	4.73	<0.001
	Terrestrial vs Flee	0.13±0.02 vs 0.13±0.05	-0.01	1
	Aerial vs Flee	0.35±0.22 vs 0.13±0.05	4.66	<0.001
(b) Duration of response (s)	Terrestrial vs Aerial	9.2±8.3 vs 21.2±15.5	-0.83	0.69
	Terrestrial vs Flee	9.2±8.3 vs 59.9±59.8	3.66	0.003
	Aerial vs Flee	21.2±15.5 vs 59.9±59.8	2.80	0.02

Table A9. Results of linear mixed effects models (LMMs) examining how different playback treatments affect white-winged chough time (s) spent: a) scanning, b) looking up and c) looking around (also see Figure 3.5)

Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests			$R^{2\,b}$
		Factor levels	Effect ± SE	*df*	χ^2	P^{a}	
(a) Time spent scanning							0.64
	(Intercept)		-0.35±1.43				
	Treatment (Control)	Terrestrial	3.32±0.93	2	45.97	<0.001	
		Aerial	8.35±0.97				
	Group size		-0.02±0.13	1	0.03	0.87	
	Playback order		0.21±0.36	1	0.38	0.54	
Random factor	Individual ID		0.00				
	Location ID		0.48				
(b) Time spent looking up							0.59
	(Intercept)		-0.36±1.14				
	Treatment (Control)	Terrestrial	0.14±0.76	2	41.26	<0.001	
		Aerial	5.58±0.80				
	Group size		-0.03±0.10	1	0.09	0.76	
	Playback order		0.24±0.29	1	0.73	0.39	
Random factor	Individual ID		0.14				
	Location ID		0.00				
(c) Time spent looking around							0.57
	(Intercept)		-0.06±0.71				
	Treatment (Control)	Terrestrial	3.18±0.46	2	37.62	<0.001	
		Aerial	2.77±0.49				
	Group size		0.02±0.06	1	0.07	0.79	
	Playback order		-0.02±0.18	1	0.03	0.87	
Random factor	Individual ID		0.00				
	Location ID		0.11				

Significant outcomes (P<0.05) are shown in bold.

[a] P value for each factor is derived from a likelihood ratio test for changes in deviance when models with and without that factor are compared.

[b] Conditional R^2 values.

Table A10. Results of post hoc Tukey HSD tests comparing playback treatments on the time white-winged choughs spent a) scanning, b) looking up and c) looking around (also see Figure 3.5)

Variable	Treatment	Mean ± SE (s)	*t* value	*P*
(a) Time spent scanning (s)	Control vs Terrestrial	0.02±0.08 vs 3.4±1.5	3.57	0.004
	Control vs Aerial	0.02±0.08 vs 8.4±4.6	8.55	<0.001
	Terrestrial vs Aerial	3.4±1.5 vs 8.4±4.6	5.13	<0.001
(b) Time spent looking up (s)	Control vs Terrestrial	0 vs 0.2±0.3	0.19	0.98
	Control vs Aerial	0 vs 5.6±4.0	6.94	<0.001
	Terrestrial vs Aerial	0.2±0.3 vs 5.6±4.0	6.74	<0.001
(c) Time spent looking around (s)	Control vs Terrestrial	0.02±0.08 vs 3.2±1.5	6.83	<0.001
	Control vs Aerial	0.02±0.08 vs 2.8±1.8	5.67	<0.001
	Terrestrial vs Aerial	3.2±1.5 vs 2.8±1.8	0.83	0.69

Table A11. Results of bias-reduced generalized linear models (BRGLMs) with pairwise comparisons examining how different playback treatments affect the probability that white-winged choughs exhibit engorged eyes (also see Figure 3.6)

Fixed effects	Effect ± SE	*Z*	*P*
Treatment (Control vs. Terrestrial)	-1.09±1.06	-1.02	0.56
Treatment (Control vs. Aerial)	-4.09±1.25	-3.28	<0.01
Treatment (Terrestrial vs. Aerial)	-3.00±1.06	-2.84	<0.05
Group size	0.10±0.22	0.43	0.67
Playback order	-0.27±0.47	-0.58	0.56

Significant outcomes (*P*<0.05) are shown in bold.

References

Beck, N. R., & Heinsohn, R. (2006). Group composition and reproductive success of cooperatively breeding white-winged choughs (*Corcorax melanorhamphos*) in urban and non-urban habitat. *Austral Ecology*, *31*(5), 588–596. https://doi.org/10.1111/j.1442-9993.2006.01589.x

Beck, N. R., Peakall, R., & Heinsohn, R. (2008). Social constraint and an absence of sex-biased dispersal drive fine-scale genetic structure in white-winged choughs. *Molecular Ecology*, *17*(19), 4346–4358. https://doi.org/10.1111/j.1365-294X.2008.03906.x

Blumstein, D. T., & Armitage, K. B. (1997). Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. *American Naturalist*, *150*(2), 179–200.

Butler, N. E., Watson, S. J., & Peters, R. A. (2022). Life history characteristics and alarm calling in Australian arid-zone birds. *Emu - Austral Ornithology*, *122*, 155–166. https://doi.org/10.1080/01584197.2022.2104735

Caro, T. (2005). *Antipredator defenses in birds and mammals*. University of Chicago Press.

Collier, K., Radford, A. N., Townsend, S. W., & Manser, M. B. (2017). Wild dwarf mongooses produce general alert and predator-specific alarm calls. *Behavioral Ecology*, *28*(5), 1293–1301. https://doi.org/10.1093/beheco/arx091

Cunningham, S., & Magrath, R. D. (2017). Functionally referential alarm calls in noisy miners communicate about predator behaviour. *Animal Behaviour*, *129*, 171–179. https://doi.org/10.1016/j.anbehav.2017.05.021

Dawson Pell, F. S. E., Potvin, D. A., Ratnayake, C. P., Fernández-Juricic, E., Magrath, R. D., & Radford, A. N. (2018). Birds orient their heads appropriately in response to functionally referential alarm calls of heterospecifics. *Animal Behaviour*, *140*, 109–118. https://doi.org/10.1016/j.anbehav.2018.04.010

Devereux, C. L., Fernàndez-Juricic, E., Krebs, J. R., & Whittingham, M. J. (2008). Habitat affects escape behaviour and alarm calling in Common Starlings *Sturnus vulgaris*. *Ibis*, *150*, 191–198. https://doi.org/10.1111/j.1474-919X.2008.00835.x

Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews*, *64*(1), 13–33. https://doi.org/10.1111/j.1469-185X.1989.tb00636.x

Evans, C. S. (1997). Referential signals. In D. Owings, M. D. Beecher, & N. S. Thompson (Eds.), *Perspectives in ethology* (Vol. 12), pp. 99–143. Plenum. Communication.

Evans, C. S., Evans, L., & Marler, P. (1993). On the meaning of alarm calls: functional reference in an avian vocal system. *Animal Behaviour*, *46*(1), 23–38. https://doi.org/10.1006/anbe.1993.1158

Fichtel, C. (2004). Reciprocal recognition of sifaka (*Propithecus verreauxi verreauxi*) and redfronted lemur (*Eulemur fulvus rufus*) alarm calls. *Animal Cognition*, *7*(1), 45–52. https://doi.org/10.1007/s10071-003-0180-0

Fichtel, C., & Kappeler, P. M. (2002). Anti-predator behavior of group-living Malagasy primates: Mixed evidence for a referential alarm call system. *Behavioral Ecology and Sociobiology*, *51*(3), 262–275. https://doi.org/10.1007/s00265-001-0436-0

Freeberg, T. M. (2006). Social complexity can drive vocal complexity: group size influences vocal information in Carolina chickadees. *Psychological Science*, *17*(7), 557–561. https://doi.org/10.1111/j.1467-9280.2006.01743.x

Freeberg, T. M., Dunbar, R. I. M., & Ord, T. J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1597), 1785–1801. https://doi.org/10.1098/rstb.2011.0213

Furrer, R. D., & Manser, M. B. (2009). The evolution of urgency-based and functionally referential alarm calls in ground-dwelling species. *American Naturalist*, *173*(3), 400–410. https://doi.org/10.1086/596541

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*(6), 449–461. https://doi.org/10.1111/eth.12097

Griesser, M. (2008). Referential calls signal predator behavior in a group-living bird species. *Current Biology*, *18*(1), 69–73. https://doi.org/10.1016/j.cub.2007.11.069

Heinsohn, R. (1987). Age-dependent vigilance in winter aggregations of cooperatively breeding white-winged choughs (*Corcorax melanorhamphos*). *Behavioral Ecology and Sociobiology*, *20*(4), 303–306. https://doi.org/10.1007/BF00292183

Heinsohn, R. (1991). Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. *American Naturalist*, *137*(6), 864–881.

Heinsohn, R. (1992). Cooperative enhancement of reproductive success in white-winged choughs. *Evolutionary Ecology*, *6*(2), 97–114. https://doi.org/10.1007/BF02270705

Heinsohn, R. (2009). White-winged choughs: the social consequences of Boom and Boost. In L. Robin, R. Heinsohn, & L. Joseph (Eds.), *Boom and bust: Bird stories for a dry country*, pp. 223–239. CSIRO. https://doi.org/10.1071/9780643097094

Heinsohn, R., Cockbu, A., & Cunningham, R. B. (1988). Foraging, delayed maturation, and advantages of cooperative breeding in white-winged choughs, *Corcorax melanorhamphos*. *Ethology*, *77*(3), 177–186. https://doi.org/10.1111/j.1439-0310.1988.tb00202.x

Heinsohn, R., & Cockburn, A. (1994). Helping is costly to young birds in cooperatively breeding white-winged choughs. *Proceedings of the Royal Society B: Biological Sciences*, *256*(1347), 293–298. https://doi.org/10.1098/rspb.1994.0083

Heinsohn, R., Dunn, P., Legge, S., & Double, M. (2000). Coalitions of relatives and reproductive skew in cooperatively breeding white-winged choughs. *Proceedings of the Royal Society B: Biological Sciences*, *267*(1440), 243–249. https://doi.org/10.1098/rspb.2000.0993

Higgins, P., Peter, J., & Cowling, S. (2006). *Handbook of Australian, New Zealand & Antarctic Birds. Vol. 7: Boatbill to starlings*. Oxford University Press.

Hingee, M., & Magrath, R. D. (2009). Flights of fear: A mechanical wing whistle sounds the alarm in a flocking bird. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1676), 4173–4179. https://doi.org/10.1098/rspb.2009.1110

Hollén, L. I., & Radford, A. N. (2009). The development of alarm call behaviour in mammals and birds. *Animal Behaviour*, *78*(4), 791–800. https://doi.org/10.1016/j.anbehav.2009.07.021

Holley, A. J. F. (1993). Do brown hares signal to foxes? *Ethology*, *94*, 21–30. https://doi.org/10.1111/j.1439-0310.1993.tb00544.x

Kaplan, G. (2008). Alarm calls and referentiality in Australian magpies: between midbrain and forebrain, can a case be made for complex cognition? *Brain Research Bulletin*, *76*(3), 253–263. https://doi.org/10.1016/j.brainresbull.2008.02.006

Kaplan, G., & Rogers, L. J. (2013). Stability of referential signalling across time and locations: testing alarm calls of Australian magpies (*Gymnorhina tibicen*) in urban and rural Australia and in Fiji. *PeerJ*, *1*, Article112. https://doi.org/10.7717/peerj.112

Klump, G. M., & Shalter, M. D. (1984). Acoustic behaviour of birds and mammals in the predator context; I. factors affecting the structure of alarm signals. II. the functional significance and evolution of alarm signals. *Zeitschrift für Tierpsychologie*, *66*(3), 189–226. https://doi.org/10.1111/j.1439-0310.1984.tb01365.x

LaPergola, J. B., Savagian, A. G., Smith, M. G., Bennett, B. L., Strong, M. J., & Riehl, C. (2023). Referential signaling in a communally breeding bird. *Proceedings of the National Academy of Sciences of the United States of America*, *120*(19), e2222008120. https://doi.org/10.1073/pnas.2222008120

Leavesley, A. J., & Magrath, R. D. (2005). Communicating about danger: Urgency alarm calling in a bird. *Animal Behaviour*, *70*(2), 365–373. https://doi.org/10.1016/j.anbehav.2004.10.017

Leighton, G. M. (2017). Cooperative breeding influences the number and type of vocalizations in avian lineages. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20171508. https://doi.org/10.1098/rspb.2017.1508

Leon, C., Banks, S., Beck, N., & Heinsohn, R. (2022). Population genetic structure and dispersal patterns of a cooperative breeding bird in variable environmental conditions. *Animal Behaviour*, *183*, 127–137. https://doi.org/10.1016/j.anbehav.2021.11.005

Liao, C. C., Magrath, R. D., Manser, M. B., & Farine, D. R. (2024). The relative contribution of acoustic signals versus movement cues in group coordination and collective decision-making. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *379*, 20230184. https://doi.org/10.1098/rstb.2023.0184

Lima, S. L. (1995). Collective detection of predatory attack by social foragers: fraught with ambiguity? *Animal Behaviour*, *50*(4), 1097–1108. https://doi.org/10.1016/0003-3472(95)80109-X

Macedonia, J. M., & Evans, C. S. (1993). Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*, *93*(3), 177–197. https://doi.org/10.1111/j.1439-0310.1993.tb00988.x

Magrath, R. D., Pitcher, B. J., & Gardner, J. L. (2007). A mutual understanding? Interspecific responses by birds to each other's aerial alarm calls. *Behavioral Ecology*, *18*(5), 944–951. https://doi.org/10.1093/beheco/arm063

Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society B: Biological Sciences*, *268*(1483), 2315–2324. https://doi.org/10.1098/rspb.2001.1773

Manser, M. B., Seyfarth, R. M., & Cheney, D. L. (2002). Suricate alarm calls signal predator class and urgency. *Trends in Cognitive Sciences*, *6*(2), 55–57. https://doi.org/10.1016/S1364-6613(00)01840-4

Marler, P. (1967). Animal communication signals. *Science*, *157*(3790), 769–774. https://doi.org/10.1126/science.157.3790.769

McLachlan, J. R., & Magrath, R. D. (2020). Speedy revelations: How alarm calls can convey rapid, reliable information about urgent danger. *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20192772. https://doi.org/10.1098/rspb.2019.2772

Naguib, M., Schmidt, R., Sprau, P., Roth, T., Flörcke, C., & Amrhein, V. (2008). The ecology of vocal signaling: male spacing and communication distance of different song traits in nightingales. *Behavioral Ecology*, *19*(5), 1034–1040. https://doi.org/10.1093/beheco/arn065

R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Rowley, I. (1978). Communal activities among white-winged choughs *Corcorax melanorhamphus*. *Ibis*, *120*(2), 178–197. https://doi.org/10.1111/j.1474-919X.1978.tb06774.x

Schel, A. M., Candiotti, A., & Zuberbühler, K. (2010). Predator-deterring alarm call sequences in Guereza colobus monkeys are meaningful to conspecifics. *Animal Behaviour*, *80*(5), 799–808. https://doi.org/10.1016/j.anbehav.2010.07.012

Seyfarth, R. M., & Cheney, D. L. (1980). The ontogeny of vervet monkey alarm calling behavior: a preliminary report. *Zeitschrift für Tierpsychologie*, *54*(1), 37–56. https://doi.org/10.1111/j.1439-0310.1980.tb01062.x

Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal Behaviour*, *34*, 1640–1658.

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980a). Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. *Science*, *210*(4471), 801–803. https://doi.org/10.1126/science.7433999

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980b). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behaviour*, *28*(4), 1070–1094. https://doi.org/10.1016/S0003-3472(80)80097-2

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

Smith, J. M. (1965). The evolution of alarm calls. *American Naturalist*, *99*(904), 59–63. http://www.journals.uchicago.edu/t-and-c

Smith, C. L., & Evans, C. S. (2008). Multimodal signaling in fowl, *Gallus gallus*. *Journal of Experimental Biology*, *211*, 2052–2057. https://doi.org/10.1242/jeb.017194

Suzuki, T. N. (2012). Referential mobbing calls elicit different predator-searching behaviours in Japanese great tits. *Animal Behaviour*, *84*(1), 53–57. https://doi.org/10.1016/j.anbehav.2012.03.030

Suzuki, T. N. (2016). Semantic communication in birds: evidence from field research over the past two decades. *Ecological Research*, *31*, 307–319. https://doi.org/10.1007/s11284-016-1339-x

Tegtman, N. T., & Magrath, R. D. (2020). Discriminating between similar alarm calls of contrasting function. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*, 20190447. https://doi.org/10.1038/176006a0

Templeton, C. N., Greene, E., & Davis, K. (2005). Allometry of alarm calls: Black-capped chickadees encode information about predator size. *Science*, *308*(5730), 1934–1937. https://doi.org/10.1126/science.1108841

Townsend, S. W., & Manser, M. B. (2013). Functionally referential communication in mammals: The past, present and the future. *Ethology*, *119*(1), 1–11. https://doi.org/10.1111/eth.12015

Zuberbühler, K. (2003). Referential signaling in non-human primates: cognitive precursors and limitations for the evolution of language. *Advances in the Study of Behavior*, *33*, 265–307.

Chapter 4

Slow Development of Alarm-Call Responses in a Highly Social Bird Species



A brown-eyed juvenile chough moves alongside older members of its highly cohesive group. Juveniles remain dependent on their group long after fledging, receiving food for up to eight months and benefiting from the protection of others.

Abstract

Young animals face high predation risk, yet the pace at which effective antipredator behaviour develops varies widely among species. Most birds studied to date acquire appropriate responses soon after fledging, but alarm-call responses often develop slowly in social mammals, a pattern that may be linked to juveniles benefit from extended social protection. We tested whether a highly social bird with prolonged juvenile dependence shows a similarly delayed developmental trajectory. We conducted playback experiments on wild, cooperatively breeding white-winged choughs (*Corcorax melanorhamphos*), which produce functionally referential alarm calls signalling low-urgency terrestrial and aerial threats, and high-urgency flee alarms signalling immediate threats. We compared responses of juveniles (6 – 12 months old) and adults (≥5 years old). Adults showed context-specific responses—looking around to terrestrial alarms, looking up to aerial whistles and fleeing to flee alarms—whereas juveniles responded largely in a generalised manner, typically looking around regardless of alarm-call type. Juveniles also responded more slowly and resumed feeding sooner than adults, suggesting greater reliance on group vigilance. Alarm-call responses therefore developed slowly in juvenile choughs, resembling patterns reported for social mammals. Our results suggest that sociality and broader life-history traits, including prolonged development, may jointly shape the ontogeny of antipredator behaviour and potentially relax selection for early behavioural competence in birds.

Keywords: alarm call, antipredator, sociality, ontogeny, vocal communication

Introduction

Young animals often face high predation risk, yet the pace at which effective antipredator behaviour develops varies markedly across species. Juveniles of some species respond appropriately to danger within days after birth, whereas those in other species require years to develop adult-like responses (Hollén & Radford, 2009). Such variation may reflect age-specific behaviours shaped by natural selection, or gradual refinement of responses through experience and learning (Hollén & Manser, 2006; Hollén & Radford, 2009). Because juveniles typically lack experience in recognising and interpreting threats (Seyfarth & Cheney, 1980), learning through direct encounters with predators can be costly, making social information about danger particularly important during development (Griffin, 2004).

Alarm calls are a widespread form of social information used by birds and mammals to communicate about threats, yet we know relatively little about how young animals respond to these calls (Hollén & Radford, 2009). In some species, alarm calls are functionally referential, conveying specific information about predator type (Seyfarth et al., 1980), urgency (Leavesley & Magrath, 2005) or both (Manser, 2001). Such calls allow receivers to respond appropriately to danger without directly detecting predators (Evans et al., 1993). For example, great tits (*Parus major*) in Japan produce acoustically distinct alarm calls to their two main nest predators, jungle crows (*Corvus macrorhynchos*) and Japanese rat snakes (*Elaphe climacophora*) (Suzuki, 2011). Nestlings crouch to crow alarms but flee nest cavities to snake alarms, responses that selectively reduce predation risk given the predators' contrasting hunting strategies (Suzuki, 2011). Despite functionally referential alarm calls having attracted interest since the 1980s, surprisingly little is known, particularly in birds, about how juveniles respond to such calls (Gill & Bierema, 2013; Hollén & Radford, 2009).

In group-living mammals, alarm-call responses often develop slowly, potentially because young individuals benefit from protection by parents or group members. Such social buffering may relax selection for early antipredator competence, leading juveniles to respond less specifically than adults and to refine appropriate responses gradually

through social learning (Dezecache et al., 2019; Hollén & Manser, 2006; León et al., 2023; Seyfarth & Cheney, 1980, 1986). For instance, infant vervet monkeys (*Chlorocebus pygerythrus*) initially respond broadly to functionally referential alarm calls but refine their behaviour by attending to experienced adults (Seyfarth & Cheney, 1980, 1986). Similar protracted development occurs in chacma baboons (*Papio ursinus*) (Fischer et al., 2000), meerkats (*Suricata suricatta*) (Hollén & Manser, 2006) and Verreaux's sifakas (*Propithecus verreauxi*) (Fichtel, 2008), with juveniles typically requiring about six months to develop adult-like responses (Table S1). Rapid development of alarm-call responses is rarely found in mammals and tends to occur in species with weaker and short-term social buffering (Table S1). For example, juvenile Belding's ground squirrels (*Urocitellus beldingi*) discriminate alarm calls about five days after natal emergence and show adult-like responses within two to three weeks (Mateo, 1996). Together, these patterns suggest that extended social protection may favour slower developmental trajectories of antipredator behaviour.

In contrast to mammals, most birds studied to date appear to acquire appropriate alarm-call responses relatively rapidly. Although few studies have examined developmental trajectories directly, available evidence suggests that young birds often respond appropriately within days or weeks after hatching (Table S1; Davies et al., 2004; Magrath et al., 2006, 2010; Suzuki, 2011). For instance, older white-browed scrubwren (*Sericornis frontalis*) nestlings (10–11 days old) respond not only to conspecific alarm calls but also to heterospecific alarm calls by suppressing begging (Haff & Magrath, 2012). Similarly, fledglings show appropriate call-suppressing responses to conspecific aerial alarm calls shortly after leaving the nest (Magrath et al., 2006), and develop adult-like responses to heterospecific aerial alarm calls within two weeks (Haff & Magrath, 2013). However, most avian studies, including those on cooperative breeders such as white-browed scrubwrens, have focused on nestlings or recently fledged young (Table S1). Consequently, little is known about the development of alarm-call responses in species with prolonged juvenile dependence within stable social groups. It therefore remains unclear whether such extended social buffering is associated with delayed development

similar to that seen in social mammals, or whether birds generally acquire alarm-call responses rapidly.

White-winged choughs (*Corcorax melanorhamphos*) are obligate cooperative breeders that live year-round in stable social groups (Heinsohn, 1992; Rowley, 1978). They forage primarily on the ground and face both terrestrial and aerial predators (Liao et al., 2025). The species possesses a functionally referential alarm-call system with three call types—terrestrial alarms for ground-based threats, aerial whistles for high-flying raptors and flee alarms for nearby, immediate danger—to which adults show predator-specific responses (Liao et al., 2025). Choughs also have an extended developmental period, with a long adolescence (about four years) and gradually improving foraging skills (Heinsohn, 1991; Rowley, 1978). Juveniles show an unusually prolonged period of dependence, typically requiring around 200 days after fledging to attain foraging independence (Heinsohn, 1991). Together, their extended juvenile dependence and functionally referential alarm-call system make choughs an ideal model for examining the development of alarm-call responses in highly social birds.

Here, we investigated age-related differences in responses to experimental playbacks of alarm calls in white-winged choughs. Given juveniles' prolonged dependence on adult group members, we hypothesised that juveniles would show weaker and less differentiated responses to alarm calls than adults. Specifically, we predicted that juveniles would respond in a more generalised and non-specific manner across different alarm-call types, respond more slowly and resume normal behaviour more quickly than adults, reflecting their greater reliance on group vigilance and protection.

Methods

(a) Study species and site

White-winged choughs are large (350–380 g), long-lived (>15 years) passerines endemic to southeastern Australia (Heinsohn, 1988; Rowley, 1978). They live year-round in groups

with membership that can remain stable for over a decade (Rowley, 1978). Groups typically comprise six to eight individuals, including a single breeding pair and non-breeding helpers, most of which are offspring from previous years (Beck et al., 2008; Heinsohn et al., 1988). Choughs can be aged reliably over the first five years in the wild based on iris colour: juveniles (0 – 1 years) have brown eyes, immature individuals (2 – 4 years) have orange eyes, and adults (≥5 years) have red eyes (Rowley, 1978).

We studied a wild population of white-winged choughs in nature reserves and suburban-edge habitats in Canberra, Australian Capital Territory, Australia (35°14′46.0″S, 149°06′49.8″E), between May and June 2023, during the nonbreeding season. This population has been studied for over 40 years (Heinsohn, 1987; Liao et al., 2025), and many individuals are colour-banded or number-ringed, allowing individual identification (for methods see Beck & Heinsohn, 2006). Birds were habituated to human presence, permitting close-range observations (<3 m; Liao et al., 2025).

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(b) Playback experiment

(i) Overview of experimental design

To test whether alarm-call responses differed between juvenile and adult choughs, we conducted playback experiments across 16 breeding groups. In each group, one adult and one juvenile were tested, assigned by age class rather than individual identity because not all birds, particularly juveniles, were individually marked. Thus, focal

individuals could differ across treatments within a group. However, 11 of the 16 groups contained only a single juvenile, whereas the remaining five groups contained two juveniles. Across the experiment, 11 banded adults and 11 single juveniles each received all playback treatments (22 of 32 individuals in total), reducing potential individual variation on treatment responses.

All focal adults had red eyes, indicating that they were five or more years old (Rowley, 1978). We did not know the exact ages of focal juveniles. However, incubation dates were recorded for 13 of the 16 focal groups, and eye colour, morphology and behaviour suggested that all juveniles were 6–12 months old. Specifically, juveniles had brown eyes, browner plumage than older age classes, frequent loud begging calls and continued receiving food from group members. All juveniles were observed to be capable of foraging by digging into soil and leaf litter for food, a skill typically achieved around 200 days after fledging (Heinsohn, 1991; Rowley, 1978).

Our experiment included four playback treatments: (1) terrestrial alarms, (2) aerial whistles, (3) flee alarms and (4) control calls. The control treatment consisted of 'piping' contact calls of the crimson rosella (*Platycercus elegans*), a common parrot species at the study site that poses no threat to choughs. To control for order effects, across the 16 groups we counterbalanced treatment order so that each treatment occurred equally in each serial position, and also counterbalanced whether the adult or juvenile was tested first. To minimise habituation, individuals of a given age class within a group received no more than two playbacks per day, separated by at least 30 min. Once an individual of one age class had received all treatments, we left at least 72 h before conducting playbacks to the other age class within the same group.

(ii) Preparation of playback treatments

We drew playback exemplars from our previous study (Liao et al., 2025). In brief, each treatment comprised 16 unique exemplars recorded from different individuals, including the control calls. Each exemplar contained two duplicate call elements, which falls within the natural range of element numbers for all call types; inter-element intervals

matched the mean intervals observed in naturally recorded calls for each call type (Liao et al., 2025). Each chough group received a unique set of playback exemplars and a unique treatment order. Within each group, we tested both age classes using the same exemplars and treatment order, to ensure that any differences among exemplars or orders did not confound the effect of age on response. All playback tracks were constructed from calls recorded from individuals belonging to breeding groups other than that of the focal group. We used non-group callers because complete recordings of all three alarm-call types were unavailable for several focal groups. This also reduced potential variation associated with familiarity and past interactions with particular group members.

We calibrated playback tracks to an amplitude of 60 dB SPL at 8 m, within the natural range of alarm-call amplitudes at that distance (Liao et al., 2025). Amplitudes were determined by rerecording playbacks at 8 m with a calibrated 1 kHz tone measured using a Brüel & Kjær 2240 sound level meter. All playback files were adjusted on a computer to achieve the target amplitude when broadcast. We kept amplitudes constant across treatments to exclude the possibility that differences in response were due to amplitude alone rather than to differences in call type.

(iii) Field methods

We conducted playback trials in calm, dry weather between 07:00 and 18:00 h. Upon locating a focal group, we followed the birds on foot at a distance of about 5 m for at least 5 min to allow them to habituate to the investigator's presence. During this period, we counted the number of individuals in the group and identified any colour-banded birds.

We broadcast playbacks to the focal bird from about 8–9 m, using WAV files on a Roland R-07 recorder via a custom-made amplifier and tweeter loudspeaker. The loudspeaker was attached to an investigator's waist, giving it a height of about 1 m. We conducted playbacks only when the following conditions were met: (1) the focal individual was foraging by digging into the substrate; (2) the focal individual was the closest bird to the loudspeaker, with no other group member positioned between it and

the loudspeaker; (3) no potential predators were visible in the surrounding area; and (4) no group member was showing antipredator behaviour. All playback trials were video-recorded at 50 frames per second using a Panasonic HC-VX1 camcorder, handheld by an investigator, to allow subsequent blind scoring and measurement of responses.

(iv) Response measurement

We prepared and scored videos using Final Cut Pro v10.6.9. The video frame of playback onset and offset were identified, and videos were exported without sound. Video files and their corresponding IDs were renamed by a person not involved in the study, ensuring that responses were scored blind to playback treatment. All videos were analysed by the first author at least one month after the final playback to minimise recall of specific trials.

We quantified both categorical and temporal response variables from the videos, following the definitions and procedures described in our previous study (Chapter 3; Liao et al., 2025), but define them here for clarity. The immediate antipredator response to playback was defined as the first behaviour shown after the focal bird stopped feeding and initially raised its head (i.e. became alert). Responses were classified into one of five categories: no response, if the bird continued feeding without raising its head; look around, if the bird raised its head with its bill at an angle of less than 30° above horizontal; look up, if the bird raised its head with its bill at an angle of more than 30° above horizontal; startle, if the bird raised its head, lowered its body and wings, and jumped; or flee, if the bird moved rapidly from the ground to cover or to a tree without scanning. By scoring the initial response and positioning the focal bird closest to the loudspeaker, we aimed to minimise the influence of other group members' responses, although indirect social effects cannot be excluded.

We also measured three temporal response variables: latency to respond, response duration and total time spent scanning before resuming feeding (Liao et al. 2025). Latency to respond was calculated from the onset of playback to the moment when the bird initiated body movement. Response duration was calculated as the period between the start of the response and the moment when the bird resumed feeding.

Scanning time was measured as the total time spent visually scanning before resuming feeding, and was further subdivided into time spent looking around and looking up, using the same head-angle definitions as above. We converted all temporal measurements to seconds for analysis by translating video frames to seconds (at 50 frames/s, each frame represents 0.02 s).

(c) Statistical analysis

We performed all statistical analyses and figure plotting in R 4.0.3 (R Core Team, 2020). We analysed age-related differences in immediate categorical responses to playbacks using a cumulative link mixed model (CLMM). Responses were ranked into five ordered levels: 0 = no response; 1 = look around; 2 = look up; 3 = startle; and 4 = flee. We treated "look around" and "look up" as separate categories because they differ functionally in gaze direction and threat assessment; in white-winged choughs, looking up is a distinctive response to aerial threats and is typically associated with longer vigilance durations (Liao et al., 2025). We included age class, playback treatment, their interaction and group size as fixed effects, with playback order and group identity included as random effects. Models were fitted using the clmm() function in the ordinal package with a logit link function and equidistant thresholds. We assessed the interaction between age class and playback treatment using likelihood ratio tests comparing models with and without the interaction term. This tests whether juveniles differed from adults not only in overall response strength but also in their discrimination among alarm-call types. Pairwise post hoc comparisons were conducted using the emmeans() function in the emmeans package.

We examined the effects of age class and playback treatment on temporal responses—time spent looking around, time spent looking up, latency to respond and response duration—using separate linear mixed-effects models (LMMs). All temporal response variables were log-transformed prior to analysis. Each model included age class, playback treatment, their interaction and group size as fixed effects, with playback order and group identity included as random effects. If the interaction was non-significant, we removed it from the model to estimate the main effects of age class and

playback treatment. We fitted LMMs with a Gaussian error distribution and identity link function using the lmer() function in the lme4 package. Pairwise comparisons were conducted using the emmeans() function in the emmeans package. Conditional R^2 values were calculated using the r.squaredGLMM() function in the MuMIn package. We fitted the full model first, and then used likelihood ratio tests to assess the significance of fixed effects by removing each effect in turn and comparing changes in deviance.

Results

Juvenile responses differed between non-threatening control calls and alarm calls but did not differ among the three alarm-call types, typically looking around immediately to all three (Figure 4.1, Table A1a). By contrast, adults showed context-specific responses to the three alarm-call types: all adults looked around to terrestrial alarms, 11 of 16 looked up to aerial whistles and 10 of 16 fled following flee-alarm playback (Figure 4.1, Table A1b). Consistent with these patterns, immediate responses depended on the interaction between the age class and playback treatment (CLMM, likelihood ratio test: $\chi^2 = 27.93$, $df = 3$, $P < 0.001$). There were no significant age differences in responses to control calls ($Z = 0.00$, $P = 1.00$) or terrestrial alarms ($Z = 0.33$, $P = 0.74$), but there were differences for aerial whistles ($Z = -2.74$, $P = 0.006$) and flee alarms ($Z = -5.63$, $P < 0.001$), with juveniles showing less differentiated responses than adults (Figure 4.1, Table A1c).

Age class and playback treatment also shaped quantitative measures of scanning behaviour. The age-by-treatment interaction affected time spent looking up (LMM, interaction: $F = 20.34$, $P < 0.001$; Figure 4.2, Table A2). When treatments were examined separately, adults spent more time looking up than juveniles in response to aerial whistles ($t = -8.54$, $P < 0.001$), but there was no significant difference between age classes in the other treatments (Figure 4.2, Table A3). The effect of the age-by-treatment interaction on time spent looking around was marginally non-significant (LMM, interaction: $F = 2.50$, $P = 0.06$; Figure 4.2, Table A2). When treatments were examined separately, juveniles spent more time looking around than adults following flee alarm playback ($t = 2.89$, $P = 0.005$), consistent with them being less likely to flee, but there were no significant age differences for the remaining treatments (Figure 4.2, Table A3).

Neither response latency (LMM: $F = 1.17$, $P = 0.32$) nor response duration ($F = 1.81$, $P = 0.17$) was significantly affected by the interaction between age class and playback treatment (Table A4). Overall, juveniles responded with slightly longer latencies ($\chi^2 = 3.93$, $P = 0.048$) but shorter response durations ($\chi^2 = 4.08$, $P = 0.043$) than adults (Figure 4.3, Table A4). Across age classes, responses differed among playback treatments: birds responded more slowly to aerial whistles than to terrestrial alarms ($t = -5.28$, $P < 0.001$) or flee alarms ($t = 7.70$, $P < 0.001$), and slightly faster to flee than to terrestrial alarms ($t = 2.43$, $P = 0.046$; Figure 4.3, Table A5). Response durations were shorter to terrestrial alarms than either aerial whistles ($t = -3.02$, $P = 0.01$) or flee alarms ($t = -5.15$, $P < 0.001$) but did not differ significantly between the latter two ($t = -2.13$, $P = 0.09$; Figure 4.3, Table A5).

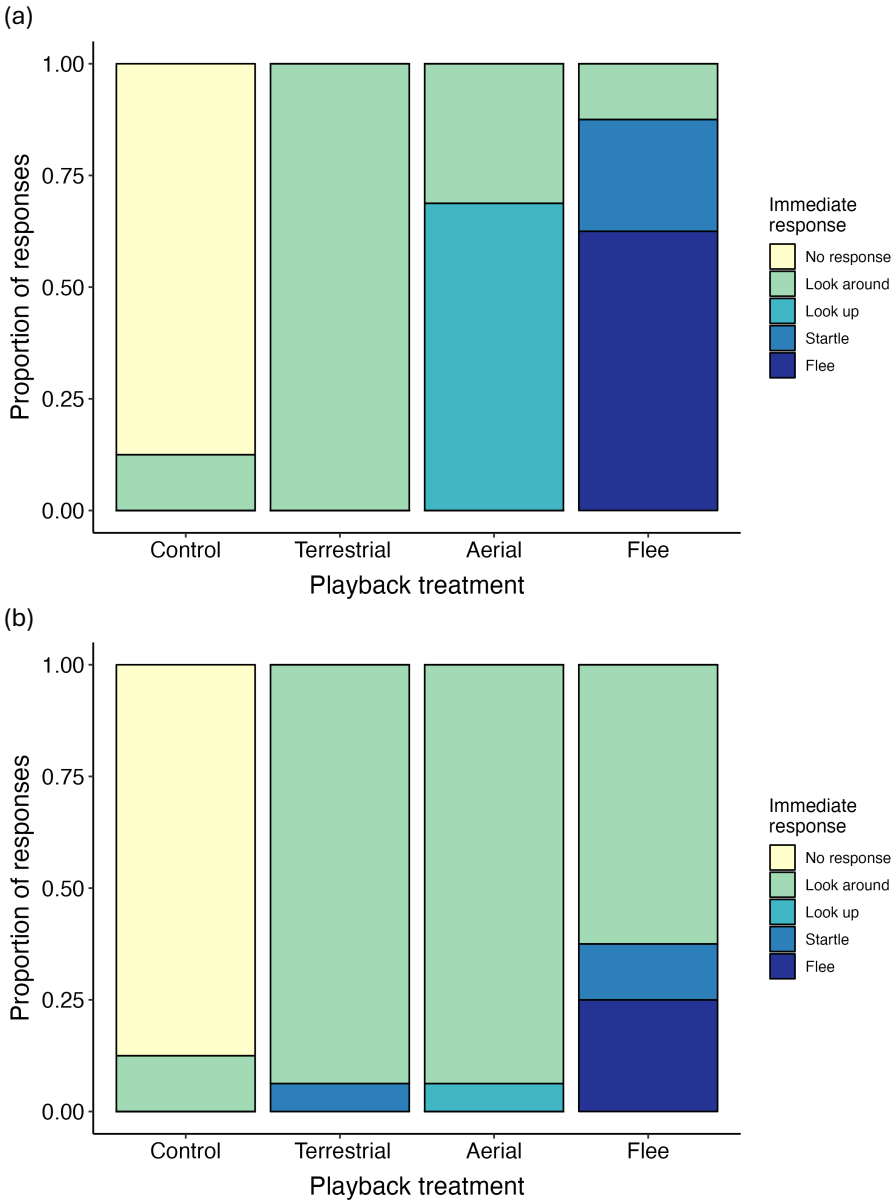


Figure 4.1. Immediate categorical responses of (a) adult and (b) juvenile white-winged choughs to playback of conspecific alarm calls and a non-threatening control call (crimson rosella contact calls). Bars show the proportion of trials in which birds exhibited each response category (no response, look around, look up, startle, flee) immediately following playback onset. N = 16 trials per playback treatment for each age class. Statistical analyses are reported in Appendix Table A1.

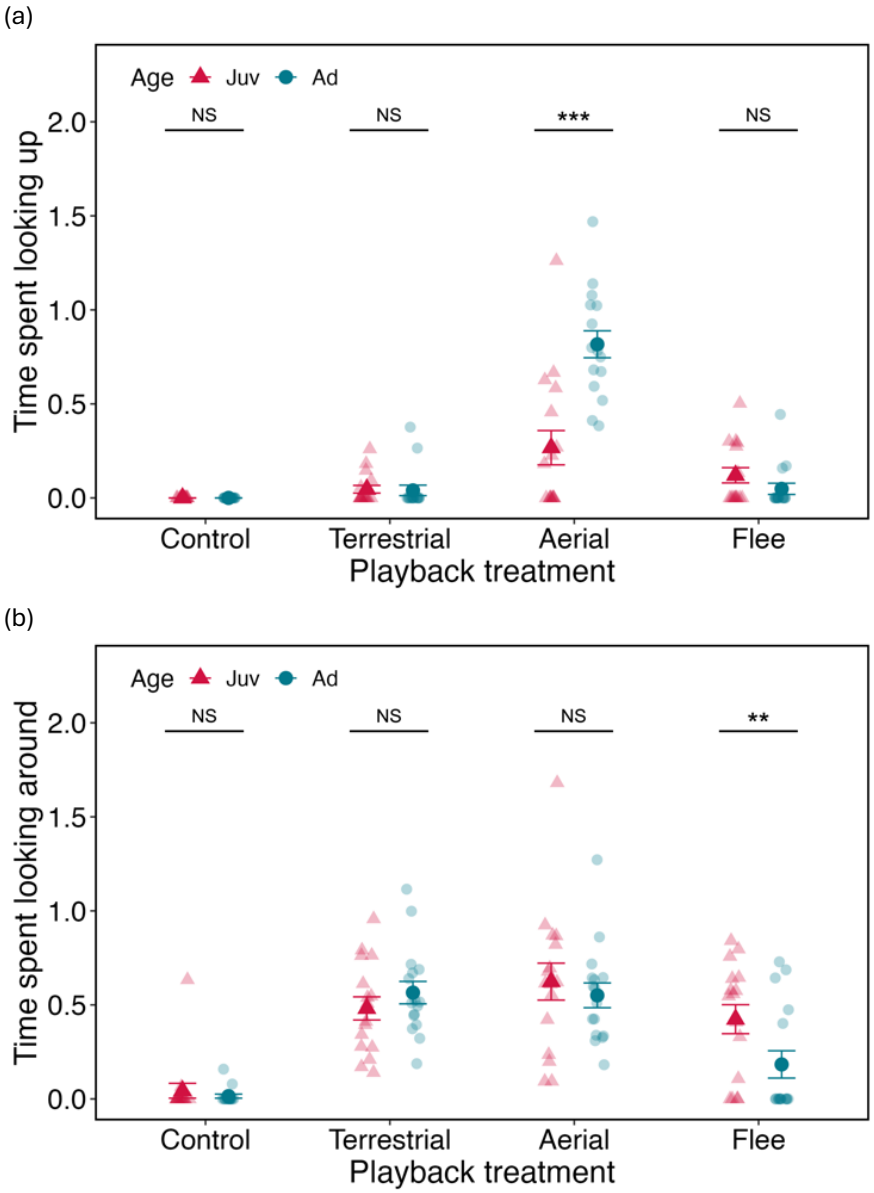


Figure 4.2. Scanning responses of adult and juvenile white-winged choughs to playback of conspecific alarm calls and a non-threatening control call (crimson rosella contact calls), showing time spent (a) looking up and (b) looking around before resuming feeding. All response variables are log-transformed. Main symbols and bars are means ± SE; faded symbols are individual data points jittered for ease of viewing. N = 16 trials per playback treatment for each age class. Significance levels above bars indicate age differences within each playback treatment (NS = not significant; **P < 0.01; ***P < 0.001). Statistical analysis details are provided in Appendix Table A2 and Table A3.

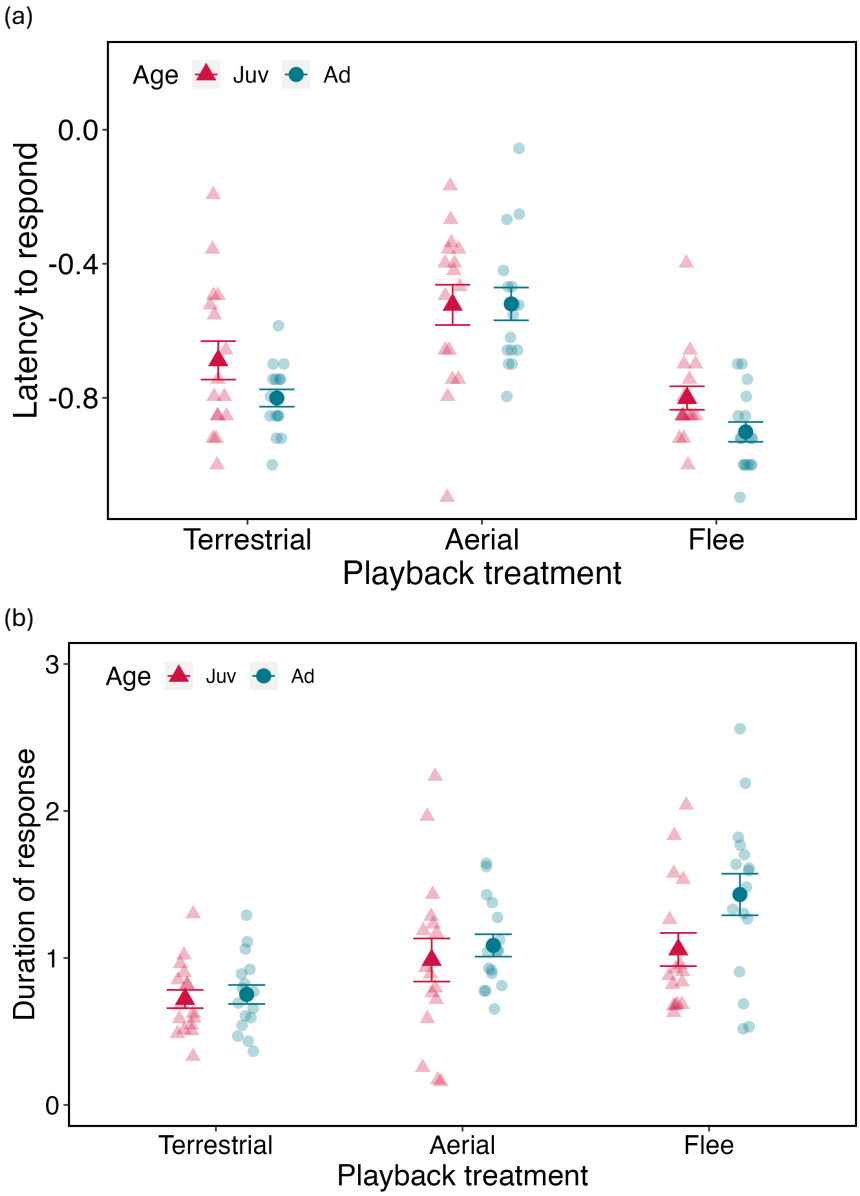


Figure 4.3. Temporal responses of adult and juvenile white-winged choughs to conspecific alarm-call playbacks. (a) Latency to respond, defined as the time from playback onset to initiation of body movement. (b) Duration of response, defined as the time from initiation of the response until resumption of feeding. Both measures are log-transformed. Main symbols and bars are means ± SE; faded symbols are individual data points jittered for ease of viewing. N = 16 trials per playback treatment for each age class. Statistical results are reported in Appendix Table A4 and Table A5.

Discussion

Juvenile white-winged choughs showed a much slower development of alarm-call responses compared with all birds studied to date. Adults showed clear context-specific responses that matched the referent of each alarm call, with the results almost identical to our previous study on adult birds (Liao et al., 2025). By contrast, even more than six months after fledging, juveniles failed to produce context-specific responses to different alarm-call types. Instead, they responded in a largely generalised manner regardless of whether calls signalled terrestrial threats, aerial predators or immediate danger. Juveniles also responded more slowly and resumed feeding sooner than adults. These findings demonstrate that delayed development of alarm-call responses can occur in birds, a pattern commonly documented in non-human primates and other social mammals, but not previously in birds (Hollén & Manser, 2006; Hollén & Radford, 2009; Lea & Blumstein, 2011).

Juvenile choughs recognised conspecific alarm calls as signals of danger but made limited use of the call-specific information that they encode, with development potentially differing among alarm-call types. Both age classes typically looked around following terrestrial alarms—the appropriate response to ground threats—but juveniles also responded to aerial whistles and flee alarms largely by looking around. This pattern suggests that responses to terrestrial alarms may develop earlier than responses to other alarm-call types. However, similar scanning behaviours need not serve identical functions. For example, in patas monkeys (*Erythrocebus patas*), males and females both engaged in visual monitoring but for different purposes (Hanzawa et al., 2026). Thus, the looking-around behaviour of juveniles may also reflect general vigilance or monitoring of group members rather than targeted predator assessment. By contrast, the clearest difference between age classes occurred for aerial whistles. Adults typically looked up immediately to these calls, which signal aerial predators (Liao et al., 2025), whereas almost all juveniles looked around instead, suggesting that they had not yet interpreted the calls correctly. Responses to flee alarms in juveniles suggested the start of differentiation. Although most juveniles also looked around, a few individuals showed

adult-like fleeing or startle responses. Because flee alarms signal immediate danger regardless of predator type (Liao et al., 2025), their higher urgency may promote earlier acquisition of appropriate responses than lower-urgency alarm calls such as aerial whistles. Acoustic stereotypy could also influence these developmental differences: if flee alarms are more consistent across callers than other alarm types, juveniles may find them easier to recognise and generalise. Together, these results suggest that juvenile choughs at this age mainly treat these alarm calls as general danger signals rather than using call-specific information, while showing a gradual development of adult-like responses, a pattern similar to that reported in most social mammals (Hollén & Manser, 2006; Seyfarth & Cheney, 1986).

Social learning is likely to play an important role in the development of alarm-call responses in white-winged choughs. In group-living animals, juveniles learning from more experienced individuals is particularly adaptive because it reduces the costs and risks of trial-and-error learning (Hollén & Radford, 2009; León et al., 2023). For example, infant vervet monkeys are more likely to respond appropriately to alarm calls after visually orienting towards nearby adults (Mohr et al., 2023; Seyfarth & Cheney, 1980, 1986). Similarly, young meerkats frequently run towards nearby adults following alarm calls during early development, facilitating observation of adult responses (Hollén & Manser, 2006). Although we did not directly test whether juvenile choughs visually oriented towards nearby group members following alarm-call playback, social learning is nevertheless plausible given the highly cohesive nature of chough social groups, in which individuals typically remain close to each other (Heinsohn, 1987, 1991; Rowley, 1978). Our results showed that seven of 16 juveniles, after initially looking around in response to aerial whistles, also spent some time looking up before resuming feeding (Figure 4.2a). This sequence could reflect monitoring of group members followed by adjustment of responses (Dezecache et al., 2019; Hollén & Manser, 2006; León et al., 2023; Seyfarth & Cheney, 1980, 1986), although looking around could also reflect general vigilance. Such scanning may represent a cautious information-gathering strategy rather than simply an incomplete adult response (Magrath et al., 2010). However, our study cannot distinguish social learning from maturation or inherited predispositions, which may also contribute

to alarm-call responses (Davies et al., 2004; Magrath et al., 2006, 2010). Longitudinal studies of known-age juveniles, tracking exposure to adult alarm responses alongside visual orientation and neighbour behaviour, could help clarify how social experience contributes to the development of call-specific responses.

We suggest that the slow development of alarm-call responses in white-winged choughs reflects the combined effects of several factors. First, choughs live in highly cohesive cooperative groups in which adults devote a greater proportion of time to vigilance during foraging than juveniles (Beck et al., 2008; Heinsohn, 1987; Rowley, 1978). Such social buffering may reduce the need for juveniles to detect threats on their own, potentially reducing selection for early antipredator responses. Consistent with this, juveniles in our study responded more slowly to alarm calls and resumed feeding sooner than adults, suggesting a greater reliance on group vigilance. Second, juveniles may face strong developmental trade-offs. Choughs have an unusually extended period of foraging dependence, with juveniles provisioned for up to eight months after fledging and taking up to five years to achieve maximal foraging success (Heinsohn, 1991; Heinsohn et al., 1988). Because food limitation is thought to be a major driver of juvenile mortality in this species (Rowley, 1978), juveniles may prioritise the acquisition of foraging skills over the refinement of antipredator responses during early development. Finally, communication complexity may also contribute to the time juveniles require to learn and interpret call meaning (Hollén & Radford, 2009; Macedonia, 1990; Seyfarth & Cheney, 1986). Choughs use a diverse range of vocalisations to coordinate group activities, including functionally referential alarm calls (Liao et al., 2025), food-associated calls (von Kietzell et al. under review) and long-distance contact calls (unpublished data). Moreover, terrestrial and flee alarms are acoustically similar despite differing in meaning (Liao et al., 2025), which may further prolong the learning needed to associate specific calls with appropriate contexts. Together, these factors suggest that prolonged social buffering, competing developmental demands and communicative complexity could shape the development of alarm-call responses in this highly social bird species.

Young individuals in social groups can rely on protection from group members, potentially relaxing selection for the early development of adult-like alarm-call responses. Our results provide experimental evidence that such delayed development, previously documented only in social mammals, also occurs in a highly social bird. Further studies examining whether delayed acquisition of adult-like alarm-call responses is a common feature of group-living birds will enhance our understanding of how sociality shapes behavioural development.

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Appendix

Table A1. Results of cumulative link mixed models (CLMMs) examining the effects of age class and playback treatment on immediate categorical responses of white-winged choughs. Table sections show (a) pairwise comparisons among treatments within juveniles, (b) pairwise comparisons among treatments within adults, and (c) age differences within each playback treatment. Significant effects (P < 0.05) are shown in bold.

Treatment	Estimates±SE	*Z*	*P*
(a) Juvenile			
Control vs Terrestrial	-3.61±0.90	-4.00	<0.001
Control vs Aerial	-3.56±0.90	-3.96	<0.001
Control vs Flee	-5.30±1.00	-5.30	<0.001
Terrestrial vs Aerial	0.05±0.65	0.07	1.00
Terrestrial vs Flee	-1.70±0.76	-2.24	0.11
Aerial vs Flee	-1.74±0.75	-2.31	0.10
(b) Adult			
Control vs Terrestrial	-3.40±0.89	-3.81	<0.001
Control vs Aerial	-5.40±0.95	-5.68	<0.001
Control vs Flee	-10.94±1.29	-8.49	<0.001
Terrestrial vs Aerial	-2.00±0.67	-2.97	0.016
Terrestrial vs Flee	-7.54±1.02	-7.38	<0.001
Aerial vs Flee	-5.54±0.89	-6.22	<0.001
(c) Juvenile vs Adult			
Control	0.00±1.07	0.00	1.00
Terrestrial alarm	0.21±0.65	0.33	0.74
Aerial whistle	-1.83±0.67	-2.74	0.006
Flee alarm	-5.63±1.00	-5.63	<0.001

Table A2. Results of linear mixed-effects models (LMMs) testing the effects of age class, playback treatment, their interaction and group size on time spent looking up and looking around in white-winged choughs. Response variables were log-transformed prior to analysis. Conditional R^2 values are reported. Significant effects (P < 0.05) are shown in bold.

Response variable	Fixed effects	df	F-value	P	$R^{2\,a}$
Time spent looking up					0.68
	Age*Treatment	3	20.34	<0.001	
	Age	1	13.24	<0.001	
	Treatment	3	61.77	<0.001	
	Group size	1	0.73	0.41	
Time spent looking around					0.53
	Age*Treatment	3	2.50	0.06	
	Age	1	2.65	0.11	
	Treatment	3	36.13	<0.001	
	Group size	1	3.75	0.07	

[a] Conditional R2 values.

Table A3. Results of post hoc Tukey-adjusted pairwise comparisons testing age differences (juveniles vs adults) in time spent looking up and looking around within each playback treatment. Estimates represent juvenile minus adult values. Significant effects (P < 0.05) are shown in bold.

Variable	Treatment	Estimates±SE	*t* value	*P*
Time spent looking up (Juvenile vs Adult)	Control	0.00±0.06	0.00	1.00
	Terrestrial	0.01±0.06	0.13	0.90
	Aerial	-0.55±0.06	-8.54	<0.001
	Flee	0.07±0.06	1.13	0.26
Time spent looking around (Juvenile vs Adult)	Control	0.03±0.08	0.34	0.73
	Terrestrial	-0.08±0.08	-0.90	0.37
	Aerial	0.08±0.08	0.93	0.35
	Flee	0.24±0.08	2.89	0.005

Table A4. Results of linear mixed-effects models (LMMs) examining the effects of age class, alarm-call playback treatment and group size on (a) latency to respond and (b) response duration in white-winged choughs. Both response variables were log-transformed prior to analysis. Fixed effects were assessed using likelihood ratio tests. Conditional R^2 values are reported. Significant effects (P < 0.05) are shown in bold.

Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests			$R^{2\,b}$
		Factor levels	Effect ± SE	*df*	χ^2	*P* [a]	
(a) Latency to respond							0.46
	(Intercept)		-0.79±0.07				
	Age (Juvenile)	Adult	-0.07±0.03	1	3.93	0.048	
	Treatment (Terrestrial)	Aerial	0.22±0.04	2	47.93	<0.001	
		Flee	-0.10±0.04				
	Group size		0.01±0.01	1	2.22	0.136	
Random factor	Playback order		0.0018				
	Group ID		0.0014				
(b) Duration of response							0.36
	(Intercept)		0.88±0.19				
	Age (Juvenile)	Adult	0.16±0.08	1	4.08	0.043	
	Treatment (Terrestrial)	Aerial	0.30±0.10	2	23.91	<0.001	
		Flee	0.51±0.10				
	Group size		-0.03±0.02	1	2.03	0.154	
Random factor	Playback order		0.00				
	Group ID		0.03				

[a] *P*-value for each factor is derived from a likelihood ratio test for changes in deviance when models with and without that factor are compared.
[b] Conditional R^2 values.

Table A5. Results of post hoc Tukey HSD tests comparing alarm-call playback treatments for (a) latency to respond and (b) duration of response; shown in Figure 4.3. Significant effects ($P < 0.05$) are shown in bold.

Variable	Treatment	Mean ± SE (s)	*t* value	*P*
(a) Latency to respond	**Terrestrial vs Aerial**	0.20±0.02 vs 0.34±0.03	-5.28	<0.001
	Terrestrial vs Flee	0.20±0.02 vs 0.15±0.01	2.43	0.046
	Aerial vs Flee	0.34±0.03 vs 0.15±0.01	7.70	<0.001
(b) Duration of response	**Terrestrial vs Aerial**	6.48±0.78 vs 20.30±5.80	-3.02	0.01
	Terrestrial vs Flee	6.48±0.78 vs 39.5±12.0	-5.15	<0.001
	Aerial vs Flee	20.30±5.80 vs 39.5±12.0	-2.13	0.09

Supplementary materials

Table S1. Studies examining the development of alarm-call responses in mammals and birds based on experimental playback approaches.

Species	No. alarm/ playback type[a]	Referential response tested[b]	Caller	Receiver	Time of development[c]	Year-round group living[d]	Cooperative breeder	Note for development	Source
Mammals									
Richardson's ground squirrel, *Spermophilus richardsonii*	1/2	No	Conspecific	Juveniles	42–47 days	No	No	Juveniles responded to calls by increasing vigilance as adults	[1]
Belding's ground squirrel, *Spermophilus beldingi*	3/4	Yes	Conspecific	Juveniles	43–53 days	No	No	By 43 – 55 days, at least 90% of juveniles responded to trill and whistle playbacks similarly to adults	[2]
Chacma baboon, *Papio cynocephalus ursinus*	2/4	No	Conspecific	Infants	6 months	Yes	No	At 6 months, infants responded strongly to alarm barks but not to contact barks	[3]
Verreaux's sifaka, *Propithecus verreauxi*	4/5	Yes	Conspecific, Heterospecific	Infants, Adults	6 months	Yes	No	At 6 months, infants performed adult-like escape responses	[4]
Meerkat, *Suricata suricatta*	6/6	Yes	Conspecific	Juveniles, Adults	6 months	Yes	Yes	At 6 months, juveniles performed adult-like escape responses	[5]
Yellow-bellied marmot, *Marmota flaviventris*	1/1	No	Conspecific	Yearlings, Adults	~ 1 year	No	No	Male yearlings responded more strongly to alarm calls while female yearlings, adult females, adult males responded similarly	[6]
California ground Squirrel, *Spermophilus beecheyi*	2/2	No	Conspecific	Juveniles, Adults	>1 year	No	No	Juveniles exhibited more urgent responses to adult chatters and less urgent responses to adult whistles	[7]
Squirrel monkey, *Saimiri sciureus*	1/3	No	Conspecific	Infants, Juveniles,	>1 year	Yes	No	>70% of juveniles and subadults showed adult-like responses in the first month of study	[8]

Species	No. alarm/ playback type[a]	Referential response tested[b]	Caller	Receiver	Time of development[c]	Year-round group living[d]	Cooperative breeder	Note for development	Source
				Subadults, Adults					
Bonnet macaque, *Macaca radiata*	1/3	No	Conspecific	Juveniles, Subadults, Adults	1–2 years	Yes	No	Juveniles responded similarly to adults to the adult alarm calls	[9]
Ruffed lemur, *Varecia variegata*	2/2	Yes	Conspecific	Immatures, Adults	<3 years	Partially	Some reported	Immatures responded similarly to adults to both alarm calls, neither adults nor immatures looked up to aerial alarm calls	[10]
Ringtailed lemur, *Lemur catta*	2/2	Yes	Conspecific	Immatures, Adults	>3 years	Yes	No	Immatures responded similarly to adults to terrestrial alarms but not respond as appropriate as adults to aerial alarms	[10]
Japanese macaque, *Macaca fuscata*	2/3	No	Conspecific	Infants, Juveniles	3.3–4 years	Yes	No	The response patterns of juveniles were similar to those of adults	[11]
Sooty mangabey, *Cercocebus atys*	6/6	Yes	Conspecific, Heterospecific	Juveniles, Adults	>5 years	Yes	No	The responses varied among different alarm types, old juveniles only showed appropriate response to conspecific leopard alarm as adults, but not for other types of alarm calls	[12]
Vervet monkey, *Cercopithecus aethiops*	3/3	Yes	Conspecific	Infants, Adults	3 years	Yes	No	Individuals over 3 years responded differently to playbacks of different alarm-call types, but infants first observe mothers	[13]
	1/2	Yes	Conspecific	Yearlings, Juveniles, Adults	>4 years	Yes	No	Juveniles (2–4 years) responded differently to adults	[14]
	3/3	Yes	Conspecific	Infants, Juveniles, Adults	NA	Yes	No	Juveniles did not respond appropriately to different types of alarm calls	[15]

Species	No. alarm/ playback type[a]	Referential response tested[b]	Caller	Receiver	Time of development[c]	Year-round group living[d]	Cooperative breeder	Note for development	Source
	4/4	Yes	Conspecific	Infants, Juveniles, Adults	NA	Yes	No	Juveniles sometimes responded incorrectly and needed to watch for others	[16]
Thirteen-lined ground squirrel, *Spermophilus tridecemlineatus*	1/3	No	Conspecific	Juveniles, Adults	NA	No	No	Juveniles responded similarly to adults to the trill alarm calls, but not to other non-threatening calls	[17]
Barbary macaque, *Macaca sylvanus*	2/4	No	Conspecific	Juveniles, Adults	NA	Yes	No	Juveniles could not discriminate disturbance calls from alarm calls	[18]
Birds									
Mallard, *Anas platyrhynchos*	1/1	No	Conspecific	Ducklings	12 hours	Yes	No	12 h ducklings showed strong vocal inhibition and freezing behaviour to alarms	[19]
Laughing gull, *Larus Atricilla*	2/3	No	Conspecific	Nestling	1 day	Yes	No	Day-old nestlings suppressed calling and showed crouching to both alarms, but less to 'Kow' alarms that might also indicate conspecific disturbances	[20]
Yellow warbler, *Dendroica petechia*	2/2	Yes	Conspecific	Nestling	4–8 days	No	No	Nestlings suppressed calls more to general alarms than to cuckoo alarms	[21]
Vinous-throated parrotbill, *Sinosuthora webbianus*	2/3	No	Conspecific, Heterospecific	Nestlings	5 days	Yes	No	Nestlings suppressed begging calls to mobbing alarms from conspecifics and heterospecifics	[22]
White-browed scrubwren, *Sericornis frontalis*	1/2	No	Conspecific	Nestlings	5 days	Yes	Yes	Nestlings suppressed calls to mobbing alarms at day 5, 8 and 11	[23]
	4/4	Yes	Conspecific	Nestlings	>11 days	Yes	Yes	Nestlings at day 5 and 11 suppressed calls to mobbing alarms. Nestling at day 5 did not respond	[24]

Species	No. alarm/ playback type[a]	Referential response tested[b]	Caller	Receiver	Time of development[c]	Year-round group living[d]	Cooperative breeder	Note for development	Source
								to aerial alarms, and at day 11 partly suppressed calls to aerial alarms.	
	1/2	No	Conspecific	Nestlings, Fledglings	17–19 days	Yes	Yes	Fledglings suppressed calls to aerial alarm calls but not nestlings	[25]
	3/4	No	Conspecific, Heterospecific	Fledglings	16–19 days	Yes	Yes	Fledglings 0–4 days after fledging suppressed calls to conspecific aerial alarm calls. They responded to fairy-wren aerial alarms 2 weeks after fledging , and to New Holland honeyeater aerial alarms 5 weeks after fledging	[26]
Oriental reed warbler, *Acrocephalus orientalis*	8/10	Yes	Conspecific, Heterospecific	Nestlings	5–6 days	No	No	Nestlings suppressed calls to all alarm calls (cuckoo alarms, raptor alarm calls from conspecifics and three heterospecifics), but not to control songs or background noise. They responded similarly to cuckoo and raptor alarms	[27]
Reed warbler, *Acrocephalus scirpaceus*	3/4	No	Conspecific, Heterospecific	Nestlings	6 days	No	No	Nestlings only suppressed calls to alarms of their own species	[28]
Dunnock, *Prunella modularis*	3/4	No	Conspecific, Heterospecific	Nestlings	6 days	No	Yes	Nestlings only suppressed calls to alarms of their own species	[28]
Robin, *Erithacus rubecula*	3/4	No	Conspecific, Heterospecific	Nestlings	6 days	No	No	Nestlings only suppressed calls to alarms of their own species	[28]
Common cuckoo, *Cuculus canorus*	2/3	No	Heterospecific	Nestlings	6–8 days	No	No	Nestlings only suppressed calls to alarms of their host species	[29]
Red-winged blackbird, *Agelaius phoeniceus*	2/3	No	Conspecific, Heterospecific	Nestlings	7 days	Yes	No	Nestlings only suppressed calls to alarms of their own species	[30]

Species	No. alarm/ playback type[a]	Referential response tested[b]	Caller	Receiver	Time of development[c]	Year-round group living[d]	Cooperative breeder	Note for development	Source
Brown-headed cowbird, *Molothrus ater*	2/3	No	Heterospecific	Nestlings	7 days	No	No	Nestlings only suppress calls to alarms of their host species, the red-winged blackbird	[31]
Pied flycatcher, *Ficedula hypoleuca*	1/4	No	Conspecific	Nestlings	9 days	No	No	After 9 days, the alarm signal produced more effectively the defensive behavior than the tonal signals	[32]
Grey warbler, *Gerygone igata*	2/5	No	Conspecific, Heterospecific	Nestlings	12 days	No	No	Nestlings altered begging call amplitude, frequency and duration to conspecific and heterospecific alarm calls, but not the calls rate, no age effect	[33]
Noisy minor, *Manorina melanocephala*	3/4	Yes	Conspecific, Heterospecific	Nestlings	14 days	Yes	Yes	Nestlings suppressed calls for longer in response to terrestrial rather than aerial calls, and they ignored the alarms from grey butcherbirds	[34]
Tree Swallow, *Tachycineta bicolor*	1/2	No	Conspecific	Nestlings	15 days	Yes	No	Nestlings suppressed calls to alarm calls and crouched down in day 15, but rarely crouched in day 10	[35]
Great tit, *Parus major*	2/4	No	Conspecific, Heterospecific	Nestlings	16–18 days	No	No	Nestlings responded to conspecific alarms more than blackbird alarms and control sounds	[36]
	2/2	Yes	Conspecific	Nestlings	17 days	No	No	Nestlings showed appropriate responses to different alarm calls	[37]
Willow tit, *Parus montanus*	1/1	No	Conspecific	Juveniles, Adults	NA	No	No	Adults froze more than juveniles to alarms	[38]
Eastern phoebe, *Sayornis phoebe*	2/3	No	Conspecific, Heterospecific	Nestlings	NA	No	No	Nestlings at 7 days responded similarly to alarms of phoebes, contact calls of blackbirds and grosbeak	[30]

[a] Number of alarm-call types used in the playback experiment/Number of playback types used in the playback experiment
[b] Whether the study tested appropriate different responses of receivers to different type of referential alarm calls
[c] The time when receivers show appropriate responses to alarm calls
[d] Group of three or more individuals living together for the whole year

Source

1. Wilson DR, Hare JF. 2006 The adaptive utility of Richardson's ground squirrel (*Spermophilus richardsonii*) short-range ultrasonic alarm signals. *Can. J. Zool.* 84, 1322–1330. (doi:10.1139/z06-120)
2. Mateo JM. 1996 The development of alarm-call response behaviour in free-living juvenile Belding's ground squirrels. *Animal Behaviour* 52, 489–505. (doi:10.1006/anbe.1996.0192)
3. Fischer J, Cheney DL, Seyfarth RM. 2000 Development of infant baboons' responses to graded bark variants. *Proc. R. Soc. Lond. B* 267, 2317–2321. (doi:10.1098/rspb.2000.1285)
4. Fichtel C. 2008 Ontogeny of conspecific and heterospecific alarm call recognition in wild Verreaux's sifakas (*Propithecus verreauxi verreauxi*). *American J Primatol* 70, 127–135. (doi:10.1002/ajp.20464)
5. Hollén LI, Manser MB. 2006 Ontogeny of alarm call responses in meerkats, Suricata suricatta: the roles of age, sex and nearby conspecifics. *Animal Behaviour* 72, 1345–1353. (doi:10.1016/j.anbehav.2006.03.020)
6. Lea AJ, Blumstein DT. 2011 Age and sex influence marmot antipredator behavior during periods of heightened risk. *Behav Ecol Sociobiol* 65, 1525–1533. (doi:10.1007/s00265-011-1162-x)
7. Hanson MT, Coss RG. 2001 Age differences in the response of California ground squirrels (*Spermophilus beecheyi*) to conspecific alarm calls. *Ethology* 107, 259–275. (doi:10.1046/j.1439-0310.2001.00659.x)
8. McCowan B, Franceschini NV, Vicino GA. 2001 Age differences and developmental trends in alarm peep responses by squirrel monkeys (*Saimiri sciureus*). *American J Primatol* 53, 19–31. (doi:10.1002/1098-2345(200101)53:1<19::AID-AJP2>3.0.CO;2-#)
9. Ramakrishnan U, G. Coss R. 2000 Age differences in the responses to adult and juvenile alarm calls by Bonnet macaques (*Macaca radiata*). *Ethology* 106, 131–144. (doi:10.1046/j.1439-0310.2000.00501.x)
10. Macedonia JM. 1990 What is communicated in the antipredator calls of lemurs: evidence from playback experiments with ring-tailed and ruffed lemurs. *Ethology* 86, 177–190. (doi:10.1111/j.1439-0310.1990.tb00428.x)
11. Masataka N. 1983 Psycholinguistic analyses of alarm calls of Japanese monkeys (*Macaca fuscata fuscata*). *American J Primatol* 5, 111–125. (doi:10.1002/ajp.1350050203)

12. León J, Thiriau C, Crockford C, Zuberbühler K. 2023 Comprehension of own and other species' alarm calls in sooty mangabey vocal development. *Behav Ecol Sociobiol* 77, 56. (doi:10.1007/s00265-023-03318-6)

13. Seyfarth RM, Cheney DL. 1986 Vocal development in vervet monkeys. *Animal Behaviour* 34, 1640–1658. (doi:10.1016/S0003-3472(86)80252-4)

14. Dubreuil C, Barrett L, Henzi PS, Notman H, Pavelka MSM. 2023 Age differences in the responses of vervet monkeys, *Chlorocebus pygerythrus*, to terrestrial alarm calls. *Animal Behaviour* 201, 87–100. (doi:10.1016/j.anbehav.2023.04.014)

15. Seyfarth RM, Cheney DL, Marler P. 1980 Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behaviour* 28, 1070–1094. (doi:10.1016/S0003-3472(80)80097-2)

16. Seyfarth RM, Cheney DL. 1980 The ontogeny of vervet monkey alarm calling behavior: A Preliminary Report. *Zeitschrift für Tierpsychologie* 54, 37–56. (doi:10.1111/j.1439-0310.1980.tb01062.x)

17. Schwagmeyer P, Brown CH. 2010 Conspecific reaction to playback of thirteen-lined ground squirrel vocalizations. *Zeitschrift für Tierpsychologie* 56, 25–32. (doi:10.1111/j.1439-0310.1981.tb01281.x)

18. Fischer J, Hammerschmidt K, Todt D. 1995 Factors affecting acoustic variation in barbary-macaque (*Macaca sylvanus*) disturbance calls. *Ethology* 101, 51–66. (doi:10.1111/j.1439-0310.1995.tb00345.x)

19. Miller DB, Blaich CF. 1987 Alarm call responsivity of mallard ducklings: V. Age-related changes in repetition rate specificity and behavioral inhibition. *Developmental Psychobiology* 20, 571–586. (doi:10.1002/dev.420200603)

20. Impekoven M. 1976 Responses of laughing gull chicks (*Larus Atricilla*) to parental attraction- and alarm-calls, and effects of prenatal auditory experience on the responsiveness to such calls. *Behav* 56, 250–277. (doi:10.1163/156853976X00046)

21. Gill SA, Sealy SG. 2003 Tests of two functions of alarm calls given by yellow warblers during nest defence. *Can. J. Zool*. 81, 1685–1690. (doi:10.1139/z03-162)

22. Jiang Y, Han J, Yang C. 2022 Anti-predation responses to conspecific versus heterospecific alarm calls by the nestlings of two sympatric birds. *Animals* 12, 2156. (doi:10.3390/ani12162156)

23. Platzen D, Magrath RD. 2004 Parental alarm calls suppress nestling vocalization. *Proc. R. Soc. B.* 271, 1271–1276. (doi:10.1098/rspb.2004.2716)

24. Platzen D, Magrath RD. 2005 Adaptive differences in response to two types of parental alarm call in altricial nestlings. *Proc. R. Soc. B.* 272, 1101–1106. (doi:10.1098/rspb.2005.3055)

25. Magrath RD, Platzen D, Kondo J. 2006 From nestling calls to fledgling silence: Adaptive timing of change in response to aerial alarm calls. *Proc. R. Soc. B.* 273, 2335–2341. (doi:10.1098/rspb.2006.3610)

26. Haff TM, Magrath RD. 2013 Eavesdropping on the neighbours: Fledglings learn to respond to heterospecific alarm calls. *Animal Behaviour* 85, 411–418. (doi:10.1016/j.anbehav.2012.11.016)

27. Wang J, Feng Y, Ma L, Wang L, Yang C, Hou J. 2025 How nestlings of oriental reed warbler respond to adult alarm calls. *Avian Research* 16, 100270. (doi:10.1016/j.avrs.2025.100270)

28. Davies NB, Madden JR, Butchart SHM. 2004 Learning fine-tunes a specific response of nestlings to the parental alarm calls of their own species. *Proc. R. Soc. B.* 271, 2297–2304. (doi:10.1098/rspb.2004.2835)

29. Davies NB, Madden JR, Butchart SHM, Rutila J. 2006 A host-race of the cuckoo *Cuculus canorus* with nestlings attuned to the parental alarm calls of the host species. *Proc. R. Soc. B.* 273, 693–699. (doi:10.1098/rspb.2005.3324)

30. Madden JR, Kilner RM, Davies NB. 2005 Nestling responses to adult food and alarm calls: 1. Species-specific responses in two cowbird hosts. *Animal Behaviour* 70, 619–627. (doi:10.1016/j.anbehav.2004.11.019)

31. Madden JR, Kilner RM, Davies NB. 2005 Nestling responses to adult food and alarm calls: 2. Cowbirds and red-winged blackbirds reared by eastern phoebe hosts. *Animal Behaviour* 70, 629–637. (doi:10.1016/j.anbehav.2004.11.020)

32. Korneeva EV, Aleksandrov LI, Golubeva TB, Raevskii VV. 2006 Development of the auditory sensitivity and formation of the acoustically guided defensive behavior in nestlings of the pied flycatcher *Ficedula hypoleuca*. *J Evol Biochem Phys* 42, 691–698. (doi:10.1134/S0022093006060056)

33. Anderson MG, Brunton DH, Hauber ME. 2010 Species specificity of grey warbler begging solicitation and alarm calls revealed by nestling responses to playbacks. *Animal Behaviour* 79, 401–409. (doi:10.1016/j.anbehav.2009.11.017)

34. Barati A, McDonald PG. 2017 Nestlings reduce their predation risk by attending to predator-information encoded within conspecific alarm calls. *Sci Rep* 7, 11736. (doi:10.1038/s41598-017-11528-y)

35. McIntyre E, Leonard ML, Horn AG. 2014 Ambient noise and parental communication of predation risk in tree swallows, *Tachycineta bicolor*. *Animal Behaviour* 87, 85–89. (doi:10.1016/j.anbehav.2013.10.013)

36. Rydén O. 1978 Differential responsiveness of great tit nestlings, *Parus major*, to natural auditory stimuli: response-strength as related to stimulus significance and previous individual exposure. *Zeitschrift für Tierpsychologie* 47, 236–253. (doi:10.1111/j.1439-0310.1978.tb01834.x)

37. Suzuki TN. 2011 Parental alarm calls warn nestlings about different predatory threats. *Current Biology* 21, R15–R16. (doi:10.1016/j.cub.2010.11.027)

38. Rajala M, Rätti O, Suhonen J. 2003 Age differences in the response of willow tits (*Parus montanus*) to conspecific alarm calls. *Ethology* 109, 501–509. (doi:10.1046/j.1439-0310.2003.00890.x)

References

Beck, N. R., & Heinsohn, R. (2006). Group composition and reproductive success of cooperatively breeding white-winged choughs (*Corcorax melanorhamphos*) in urban and non-urban habitat. *Austral Ecology*, *31*(5), 588–596. https://doi.org/10.1111/j.1442-9993.2006.01589.x

Beck, N. R., Peakall, R., & Heinsohn, R. (2008). Social constraint and an absence of sex-biased dispersal drive fine-scale genetic structure in white-winged choughs. *Molecular Ecology*, *17*(19), 4346–4358. https://doi.org/10.1111/j.1365-294X.2008.03906.x

Davies, N. B., Madden, J. R., & Butchart, S. H. M. (2004). Learning fine-tunes a specific response of nestlings to the parental alarm calls of their own species. *Proceedings of the Royal Society B: Biological Sciences*, *271*(1554), 2297–2304. https://doi.org/10.1098/rspb.2004.2835

Dezecache, G., Crockford, C., & Zuberbühler, K. (2019). The development of communication in alarm contexts in wild chimpanzees. *Behavioral Ecology and Sociobiology*, *73*, 104. https://doi.org/10.1007/s00265-019-2716-6

Evans, C. S., Evans, L., & Marler, P. (1993). On the meaning of alarm calls: functional reference in an avian vocal system. *Animal Behaviour*, *46*(1), 23–38. https://doi.org/10.1006/anbe.1993.1158

Fichtel, C. (2008). Ontogeny of conspecific and heterospecific alarm call recognition in wild Verreaux's sifakas (*Propithecus verreauxi verreauxi*). *American Journal of Primatology*, *70*, 127–135. https://doi.org/10.1002/ajp

Fischer, J., Cheney, D. L., & Seyfarth, R. M. (2000). Development of infant baboons' responses to graded bark variants. *Proceedings of the Royal Society B: Biological Sciences*, *267*(1459), 2317–2321. https://doi.org/10.1098/rspb.2000.1285

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*(6), 449–461. https://doi.org/10.1111/eth.12097

Griffin, A. S. (2004). Social learning about predators: A review and prospectus. *Learning and Behavior*, *32*(1), 131–140. https://doi.org/10.3758/BF03193188

Haff, T. M., & Magrath, R. D. (2012). Learning to listen? Nestling response to heterospecific alarm calls. *Animal Behaviour*, *84*(6), 1401–1410. https://doi.org/10.1016/j.anbehav.2012.09.005

Haff, T. M., & Magrath, R. D. (2013). Eavesdropping on the neighbours: Fledglings learn to respond to heterospecific alarm calls. *Animal Behaviour*, *85*(2), 411–418. https://doi.org/10.1016/j.anbehav.2012.11.016

Hanzawa, M., Morimitsu, Y., Owusu, E. H., Suu-Ire, R. D., & Nakagawa, N. (2026). How do individual behaviors based on visual and auditory cues facilitate spatiotemporal coordination in collective movement of patas monkeys

(*Erythrocebus patas*)? *Behavioral Ecology and Sociobiology*, *80*, 9. https://doi.org/10.1007/s00265-025-03684-3

Heinsohn, R. (1987). Age-dependent vigilance in winter aggregations of cooperatively breeding white-winged choughs (*Corcorax melanorhamphos*). *Behavioral Ecology and Sociobiology*, *20*(4), 303–306. https://doi.org/10.1007/BF00292183

Heinsohn, R. (1988). Inter-group ovicide and nest destruction in cooperatively breeding white-winged choughs. *Animal Behaviour*, *36*(6), 1856–1858. https://doi.org/10.1016/S0003-3472(88)80134-9

Heinsohn, R. (1991). Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. *American Naturalist*, *137*(6), 864–881. https://doi.org/10.1086/285198

Heinsohn, R. (1992). Cooperative enhancement of reproductive success in white-winged choughs. *Evolutionary Ecology*, *6*(2), 97–114. https://doi.org/10.1007/BF02270705

Heinsohn, R., Cockburn, A., & Cunningham, R. B. (1988). Foraging, delayed maturation, and advantages of cooperative breeding in white-winged choughs, *Corcorax melanorhamphos*. *Ethology*, *77*(3), 177–186. https://doi.org/10.1111/j.1439-0310.1988.tb00202.x

Hollén, L. I., & Manser, M. B. (2006). Ontogeny of alarm call responses in meerkats, *Suricata suricatta*: the roles of age, sex and nearby conspecifics. *Animal Behaviour*, *72*(6), 1345–1353. https://doi.org/10.1016/j.anbehav.2006.03.020

Hollén, L. I., & Radford, A. N. (2009). The development of alarm call behaviour in mammals and birds. *Animal Behaviour*, *78*(4), 791–800. https://doi.org/10.1016/j.anbehav.2009.07.021

Klump, G. M., & Shalter, M. D. (1984). Acoustic behaviour of birds and mammals in the predator context; I. factors affecting the structure of alarm signals. II. the functional significance and evolution of alarm signals. *Zeitschrift Für Tierpsychologie*, *66*(3), 189–226. https://doi.org/10.1111/j.1439-0310.1984.tb01365.x

Lea, A. J., & Blumstein, D. T. (2011). Ontogenetic and sex differences influence alarm call responses in mammals: A meta-analysis. *Ethology*, 117(10), 839–851. https://doi.org/10.1111/j.1439-0310.2011.01947.x

Leavesley, A. J., & Magrath, R. D. (2005). Communicating about danger: Urgency alarm calling in a bird. *Animal Behaviour*, *70*(2), 365–373. https://doi.org/10.1016/j.anbehav.2004.10.017

León, J., Quintero, F., & Zuberbühler, K. (2023). Acquisition of predator knowledge in sooty mangabeys. *Animal Behaviour*, *205*, 1–14. https://doi.org/10.1016/j.anbehav.2023.08.012

Liao, C.-C., Radford, A. N., Heinsohn, R., & Magrath, R. D. (2025). Functionally referential communication about danger in cooperatively breeding white-winged

choughs. *Animal Behaviour*, *229*, 123330. https://doi.org/10.1016/j.anbehav.2025.123330

Macedonia, J. M. (1990). What is communicated in the antipredator calls of lemurs: Evidence from playback experiments with ring-tailed and ruffed lemurs. *Ethology*, *86*(3), 177–190. https://doi.org/10.1111/j.1439-0310.1990.tb00428.x

Magrath, R. D., Haff, T. M., Horn, A. G., & Leonard, M. L. (2010). Calling in the face of danger: Predation risk and acoustic communication by parent birds and their offspring. *Advances in the Study of Behavior*, *41*, 187–253. https://doi.org/10.1016/S0065-3454(10)41006-2

Magrath, R. D., Platzen, D., & Kondo, J. (2006). From nestling calls to fledgling silence: Adaptive timing of change in response to aerial alarm calls. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1599), 2335–2341. https://doi.org/10.1098/rspb.2006.3610

Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society B: Biological Sciences*, *268*(1483), 2315–2324. https://doi.org/10.1098/rspb.2001.1773

Mateo, M. J. (1996). The development of alarm-call response behaviour in free-living juvenile Belding's ground squirrels. *Animal Behaviour*, *52*(3), 489–505. https://doi.org/10.1006/anbe.1996.0192

Mohr, T., van de Waal, E., Zuberbühler, K., & Mercier, S. (2023). Juvenile vervet monkeys rely on others when responding to danger. *Animal Cognition*, *26*(4), 1443–1447. https://doi.org/10.1007/s10071-023-01765-2

R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Rowley, I. (1978). Communal activities among white-winged choughs *Corcorax Melanorhamphus*. *Ibis*, *120*(2), 178–197. https://doi.org/10.1111/j.1474-919X.1978.tb06774.x

Seyfarth, R. M., & Cheney, D. L. (1980). The ontogeny of vervet monkey alarm calling behavior: a preliminary report. *Zeitschrift Für Tierpsychologie*, *54*(1), 37–56. https://doi.org/10.1111/j.1439-0310.1980.tb01062.x

Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal Behaviour*, *34*, 1640–1658. https://doi.org/10.1016/S0003-3472(86)80252-4

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. *Science*, *210*(4471), 801–803. https://doi.org/10.1126/science.7433999

Suzuki, T. N. (2011). Parental alarm calls warn nestlings about different predatory threats. *Current Biology*, *21*(1), R15–R16. https://doi.org/10.1016/j.cub.2010.11.027

Chapter 5

Reliability and Urgency Shape Alarm Propagation and Collective Antipredator Decisions in a Social Bird



A group of choughs scans its surroundings after detecting a potential threat. This chapter shows how the number of callers and the urgency of their alarm calls shape whether danger information spreads and how the group responds collectively.

Abstract

Animals often rely on social information about danger, but responding to inaccurate or dishonest signals can be costly. Many species appear to assess information reliability using numerical cues such as the number of callers, yet how these cues interact with the urgency encoded in alarm signals remains unclear. We conducted playback experiments on highly social white-winged choughs (*Corcorax melanorhamphos*) to test how individuals integrate information reliability (one versus three callers) and urgency (low-urgency aerial whistles versus high-urgency flee alarms) when making collective antipredator decisions. Alarm-call type determined the form of the response: aerial whistles typically triggered vigilance, whereas flee alarms elicited immediate flight. Caller number shaped response intensity and the propagation of alarm information. Three-caller flee alarms more often triggered collective fleeing than one-caller flee alarms, whereas three-caller aerial whistles prolonged vigilance compared with single-caller whistles. Vocal alarm propagation depended strongly on caller number rather than call type, with individuals rarely relaying information from a single caller but more often doing so after hearing three callers. These findings suggest that choughs apply simple decision rules that allow groups to maximise the benefits of social information while minimising the potential costs of responding to unreliable signals.

Keywords: alarm call, collective behaviour, decision-making, social information, vocal communication

Introduction

Animals often rely on information provided by others to guide behaviour, which can have both benefits and costs (Dall et al., 2005; Giraldeau et al., 2002; Ward & Webster, 2016). Using social information can enhance foraging efficiency (Thiebault et al., 2014), reduce predation risk (Liao, Chen, et al., 2024; Sosna et al., 2019), facilitate group coordination (Conradt & Roper, 2005; Walker et al., 2017), and facilitate social learning (Aplin et al., 2025; Griffin, 2004; Whiten, 2000), representing key benefits of group living. The same information can spread rapidly through groups, amplifying collective benefits but also propagating costly errors when signals are inaccurate or dishonest (Gray & Webster, 2023; Lima, 1995; McCormick et al., 2024). Balancing the advantages of social information against the risks of false signals therefore represents a central challenge for decision-making in animal societies.

Alarm-call communication provides a powerful system for examining this trade-off. Alarm calls are widely used by birds and mammals to signal danger, enabling receivers to respond to threats without direct detection (Caro, 2005; Gill & Bierema, 2013; Townsend & Manser, 2013). Upon hearing alarm calls, individuals can rapidly spread information through the group via behavioural cues or signals that coordinate antipredator responses (Beauchamp & Ruxton, 2007; Lima, 1995; Murray et al., 2017). For example, individuals may flee immediately, providing passive cues to companions that a threat may be imminent (Beauchamp & Ruxton, 2007; Lima, 1995). Receivers may also produce alarm calls themselves—alarm-call propagation—thereby becoming new sources of information for others (Carlson et al., 2020). Such propagation is common in mobbing contexts, where calls recruit additional individuals to harass predators that do not pose immediate danger and can spread within and between species (Carlson et al., 2020; Dutour et al., 2017; Liao, Chen, et al., 2024; Nolen & Lucas, 2009). However, alarm calls are not always reliable, and false alarms appear surprisingly frequent in animal societies (Beauchamp & Ruxton, 2007; Blumstein et al., 2004; Giraldeau et al., 2002; Gray & Webster, 2023; Searcy & Nowicki, 2005). Responding to or propagating false alarms can therefore be costly, leading to unnecessary energy expenditure, lost foraging

opportunities and information cascades (Beauchamp, 2010; Beauchamp & Ruxton, 2007; McCormick et al., 2024; Ridley & Raihani, 2007). These opposing pressures suggest that animals should use decision rules that minimise the costs of unreliable social information while still enabling rapid responses to genuine threats. To date, collective antipredator decision-making remains poorly understood, particularly how individuals decide whether to propagate alarm information. This issue may be especially important for high-urgency alarms that trigger escape responses, as propagating false signals could impose particularly high costs.

One way animals can reduce unnecessary responses to false alarms is by assessing the reliability of social information. A simple strategy is to use numerical rules, responding only or more strongly when multiple individuals signal the same information, because an increasing number of callers typically enhances reliability (Blumstein et al., 2004; Coomes et al., 2019; Igic et al., 2019). For example, jackdaws (*Coloeus monedula*) decide whether to participate in mobbing events by evaluating the number of callers producing recruitment calls, with playbacks of three or five callers attracting more participants than a single caller (Coomes et al., 2019); similar patterns have also been found in great tits (*Parus major*) (Dutour et al., 2021). These studies suggest that animals may reduce uncertainty by collating information from several individuals, because concordant signals from multiple callers are less likely to be erroneous (Coomes et al., 2019; Dutour et al., 2021). Therefore, numerical reliability cues, such as caller number, likely play an important role in shaping how animals use social information about danger and minimise costly responses to false alarms.

In addition to reliability, the level of urgency conveyed by alarm calls can also shape antipredator responses. In some species, alarm calls encode not only the presence of danger but also more specific information about threat urgency (Blumstein, 1995; Blumstein & Armitage, 1997; Furrer & Manser, 2009; Leavesley & Magrath, 2005). Urgency can be signalled by variation within or among alarm-call types (Leavesley & Magrath, 2005; Manser, 2001; McLachlan & Magrath, 2020). For example, white-browed scrubwrens (*Sericornis frontalis*) produce aerial alarm calls with more elements when

predators are closer, indicating greater danger (Leavesley & Magrath, 2005). In addition, different alarm call types can signal different categories of threat, which may vary in both the urgency of the response required and the magnitude of danger (Cunningham & Magrath, 2017; Fichtel & Kappeler, 2002; Liao et al., 2025; Manser et al., 2002). For instance, in common with many other species, noisy miners (*Manorina melanocephala*) produce aerial alarms to flying predators and 'chur' alarms to terrestrial or perched bird predators, typically fleeing in response to aerial alarms but remaining vigilant in response to chur calls (Cunningham & Magrath, 2017; Farrow et al., 2017, 2020). Recent frameworks suggest that urgency may influence how individuals apply numerical decision rules when responding to social information (Liao, Magrath, et al., 2024). High-urgency signals may trigger immediate collective escape even when produced by a single caller, whereas responses to less urgent signals may depend more strongly on reliability and require multiple callers (Liao, Magrath, et al., 2024). Despite growing interest in numerical decision-making (Conradt & Roper, 2005; Dibnah et al., 2022; Strandburg-Peshkin et al., 2015; Walker et al., 2017), how these decision rules are shaped by additional factors such as urgency remains largely unexplored in group-living animals.

White-winged choughs (*Corcorax melanorhamphos*) are obligate cooperative breeders that live in stable, year-round social groups (Heinsohn, 1992; Rowley, 1978). Groups are highly cohesive: members travel, forage and roost together, and membership can remain stable for over a decade (Rowley, 1978). Choughs forage by digging into the substrate, a behaviour that likely reduces visual predator detection and increases reliance on vocal alarm communication (Heinsohn, 1987, 1991). They possess a functionally referential alarm-call system that encodes information about threat type and urgency (Liao et al., 2025). High-urgency flee alarms, typically given when a hawk flies nearby, often trigger immediate flight, whereas aerial whistles signal lower-urgency aerial threats, such as high-flying hawks (>50 m high), and elicit upward scanning (Liao et al., 2025). Together, their cohesive social structure and referential signalling system make white-winged choughs an ideal model for examining how social information shapes collective antipredator decisions.

In this study, we conducted playback experiments to test how caller number (one versus three callers) and alarm-call type (low versus high urgency) influence collective antipredator responses in white-winged choughs. We predicted that increasing caller number would strengthen responses overall because multiple callers provide more reliable social information, whereas alarm-call type would determine the form of the response. For low-urgency aerial whistles, we predicted that more callers would increase vocal propagation, the likelihood of collective vigilance and the duration of vigilance. By contrast, for high-urgency flee alarms, we predicted that even a single caller would usually trigger immediate collective escape (Liao, Magrath, et al., 2024), although multiple callers might further strengthen this response. We also predicted that vocal propagation would be rare in high-urgency situations, because immediate escape is typically the most appropriate response and may limit the opportunity to produce alarm calls and perhaps the value of propagating the calls.

Methods

(a) Study species and sites

White-winged choughs are large passerines (350–380 g) endemic to southeastern Australia (Rowley, 1978). They are cooperative breeders that live in stable social groups of closely related individuals, with most groups comprising six to eight birds (Beck et al., 2008; Heinsohn et al., 1988). Choughs do not defend foraging territories and have overlapping home ranges (Rowley, 1978). During winter, they often form foraging aggregations of up to 40 individuals, while maintaining distinct group identities (Heinsohn, 1987; Rowley, 1978).

We studied choughs in nature reserves and suburban-edge habitats in Canberra, Australian Capital Territory, Australia (35°14′28.7″S, 149°06′51.3″E). This population has been studied since the 1980s, and many individuals are colour-banded or number-ringed, allowing individual identification (Heinsohn, 1987; Liao et al., 2025). Birds were habituated to human presence, permitting close-range observations (<3 m) (Liao et al., 2025). We collected data from 16 breeding groups: 13 groups in which more than 40% of

individuals were banded and three groups without banded individuals. Although no birds in these three groups were marked, groups were reliably identified based on home range, group size, and age-class structure.

(b) Playback experiment

(i) Overview of experimental design

To test how white-winged choughs integrate reliability and alarm-call urgency when making collective antipredator decisions, we conducted a playback experiment between July and August 2025. This period spanned the non-breeding season and the onset of the breeding season, when choughs begin nest building.

The experiment followed a 2×2 factorial design manipulating numerical reliability (one caller vs. three callers) and alarm-call urgency (low-urgency aerial whistles vs. high-urgency flee alarms). This resulted in four playback treatments: (1) one-caller aerial whistles, (2) three-caller aerial whistles, (3) one-caller flee alarms, and (4) three-caller flee alarms. Each focal group received all four treatments, using unique playback exemplars drawn from unfamiliar individuals belonging to other breeding groups. Treatment order was counterbalanced across the 16 focal groups such that each order occurred four times. To minimise habituation, each group received only one playback per day, with a minimum interval of about 24 hours between trials.

(ii) Preparation of playback treatments

Playback exemplars were constructed from alarm calls recorded in our previous study and processed using Audacity (Liao et al., 2025). Briefly, flee alarms were elicited using a life-sized gliding model of a brown goshawk (*Accipiter fasciatus*), whereas aerial whistles were elicited by playback of a chough aerial-whistle chorus recorded during a natural encounter with a high-flying hawk. A total of 16 high-quality alarm calls (both flee alarms and aerial whistles) from 16 different breeding groups were used to construct playback exemplars. Calls were randomly or pseudorandomly assigned to treatments to ensure balanced representation and to avoid repeated call combinations. In the single-caller

treatments, each of the 16 calls was used once across the 16 focal groups. In the three-caller treatments, triplets were formed pseudorandomly from the same pool so that all calls were used approximately equally across trials.

Each one-caller exemplar consisted of one call of two elements, constructed from a signal element repeated after a 1 s interval. Each three-caller exemplar consisted of one two-element call per individual (six call elements in total), overlapping by 0.1 s to simulate a natural chorus; each call was constructed in the same way as in the single-caller treatment, with the inter-element interval again being 1 s. For each focal group, the same source group provided recordings of both flee alarms and aerial whistles. All playback exemplars were constructed from calls recorded from individuals belonging to breeding groups other than that of the focal group. Using unfamiliar callers reduced potential variation arising from differences in familiarity and past interactions with particular individuals. Calls from different individuals also provided potential acoustic cues to multiple callers. Playback exemplars were calibrated to 55.5 dB SPL at 10 m, corresponding to the natural amplitude of calls from approximately 15 m away (Liao et al., 2025). This lower amplitude than in previous experiments was chosen to simulate alarms from a neighbouring group, motivated by field observations of alarm propagation between groups.

(iii) Field methods

Playback trials were conducted during calm, dry weather between 07:00 and 17:30 h. On encountering a focal group, we followed the group on foot from a distance of about 5 m for at least 5 min to allow habituation to our presence. During this period, we counted the number of individuals, identified any banded birds, and noted whether any other groups were nearby.

Playbacks were broadcast to focal groups from a distance of 9–10 m using stereo WAV files played on an iPhone 13 through two JBL Go 4 Bluetooth speakers controlled via the JBL Portable app. In the one-caller treatments, calls from one individual were broadcast from one speaker. In the three-caller treatments, calls from three different

individuals were broadcast from the two speakers, with calls from one individual played from one speaker and calls from the other two individuals played from the second speaker. Two speakers were mounted on tripods positioned 1 m above the ground and separated by 3–5 m. Using two rather than three speakers provided spatial separation while keeping setup time manageable, reducing the risk that mobile chough groups would move away before trials could begin. Together, calls from different individuals, greater call-element number and spatially separated sound sources were intended to simulate an ecologically realistic multiple-caller event. The same speaker configuration was used in all treatments, ensuring that the number and placement of objects around focal groups were identical regardless of the number of callers simulated.

For each playback trial, we directed the playback toward three focal individuals within the group (hereafter referred to as the subgroup), defined as the three individuals closest to the speakers at playback onset. We used this subgroup as a standardized local response unit for three reasons. First, these individuals were most directly exposed to the playback, experienced similar acoustic conditions, and could be reliably filmed. Second, measuring responses of the entire group was less feasible because group members often differed in their distance from the speakers and were not always all visible under field conditions. Third, using three individuals provided the smallest practical unit for quantifying local collective antipredator responses in a standardized way across trials. Responses of this subgroup therefore provide a standardised measure of initial local collective responses that may influence wider group behaviour.

Playbacks were conducted only when the following criteria were met: (1) the focal subgroup was the closest to the speakers; (2) the focal subgroup was foraging cohesively at the edge of the group, with inter-individual distances <1 m and including at least one adult (>5 years old); (3) there was no evidence of ongoing antipredator behaviour, with most individuals engaged in foraging; and (4) there were no signs of potential threats around. Restricting focal subgroups to three adults was impractical under field conditions, so younger birds were also included, provided that at least one adult was present. All playback trials were recorded using both audio and video equipment to allow

quantification of responses. Audio was recorded with a Zoom F3 recorder and a Sennheiser ME66 directional microphone aimed at the focal group, allowing calls from that group to be distinguished from those of other groups. Video was recorded using a Panasonic HC-VX1 camcorder (recording at 50 frames/s) and an Insta360 small camera. Responses of focal subgroups were filmed with the camcorder handheld by an investigator, while the small camera was mounted on a Wizmount CU2 shoulder rig to provide a wider field of view and a backup recording.

(iv) Response measurement

Audio recordings were analysed using Raven Pro 1.6 to quantify alarm calling by group members. Vocal responses were identified from spectrograms of the original audio recordings, independently of the silent videos used for behavioural scoring, and were attributed to the focal group as a whole because callers could not be reliably distinguished within the group, including whether they belonged to the three-bird focal subgroup. Specifically, we measured: (1) whether any individual in the focal group produced alarm calls (yes/no); (2) latency to alarm calling, defined as the time from playback onset to the first alarm call; and (3) the number of alarm-call elements of each call type (flee alarms and/or aerial whistles) produced in response to the playback.

Videos were prepared and blind scored using Final Cut Pro v10.6.9. The video frame of playback onset and offset were identified, and videos were exported without sound. Video files and their corresponding IDs were renamed by a person not involved in the study, ensuring that responses were scored blind to playback treatment. All videos were analysed by the first author at least one month after the final playback to minimise recall of specific trials.

From the video recordings, we quantified both categorical and temporal response variables at the subgroup level. Scanning was defined as stopping feeding and looking around or upwards, whereas fleeing was defined as flying directly from the ground into cover or a tree without first scanning. Birds that continued feeding were recorded as showing no response. First, we recorded the number of individuals in the focal subgroup

that fled or scanned in response to the playback (0–3 individuals). Second, we measured two temporal response variables: (1) latency to respond, defined as the time from playback onset to the moment when the first individual in the subgroup initiated movement; and (2) response duration, defined as the time from the first individual initiating movement to the moment when all subgroup members resumed feeding. Temporal measurements were converted to seconds by translating video frames to time (at 50 frames/s, each frame represents 0.02 s).

(c) Statistical analysis

We performed all statistical analyses and figure plotting in R 4.0.3 (R Core Team, 2020).

We analysed the effects of playbacks on vocal propagation, collective fleeing and collective scanning (all dichotomous responses) using bias-reduced generalized linear models (BRGLMs). Collective responses were scored as 1 when all three individuals in the focal subgroup showed the behaviour and 0 otherwise (collective fleeing = all three individuals fled; collective scanning = all three individuals scanned). These scores identify shared behavioural outcomes but do not distinguish coordination among group members from independent responses to the same playback. Bias reduction was used because some playback treatments produced uniform responses across focal groups. Models for vocal propagation and collective fleeing included alarm-call type, number of callers, their interaction, group size, group identity and playback order as predictors. If the interaction was non-significant, it was removed to estimate the main effects of alarm-call type and caller number. Collective scanning could not be measured when individuals fled immediately after playbacks. Because at least one bird fled in most flee-alarm trials (7/16 in the one-caller treatment and 13/16 in the three-caller treatment), flee-alarm treatments were excluded from this analysis. The collective scanning model included only aerial whistle treatments and tested the effect of caller number, with group size, group identity and playback order included as additional predictors. All models were fitted with binomial errors and a logit link using the brglm() function in the brglm2 package. Pairwise comparisons were conducted using the emmeans() function in the emmeans package.

To examine whether alarm-call type influenced vocal propagation behaviour, we compared latency to call and the number of propagated call elements between the aerial whistle and flee-alarm three-caller treatments using Wilcoxon rank-sum tests. Non-parametric tests were used because of the small sample sizes and non-normal distributions of the response variables. Analyses were conducted using the wilcox.test() function.

We examined the effects of playbacks on response duration using a linear mixed-effects model (LMM). Because response duration could not be measured when individuals fled immediately following playbacks, we restricted this analysis to aerial whistle treatments. Flee-alarm treatments were therefore excluded, and we also excluded trials in which at least one bird fled or did not resume feeding (three groups in the one-caller aerial whistle treatment and two groups in the three-caller treatment). The model included caller number and group size as fixed effects, with group identity and playback order fitted as random effects. The LMM was fitted with Gaussian errors and an identity link using the lmer() function in the lme4 package. Conditional R^2 values of models were calculated using the r.squaredGLMM() function of the MuMIn package.

Results

Vocal propagation depended on the number of callers but not on alarm-call type. Birds were more likely to propagate alarm calls in response to playbacks from three callers than from a single caller, whereas the type of alarm call had no effect (BRGLM: one vs. three callers: Z=-2.91, P=0.004; aerial whistle vs. flee alarm: Z=0.47, P=0.64; Figure 5.1, Table A1).

Subsequent analyses of call propagation focused on the three-caller treatments, as vocal propagation occurred only rarely following one-caller playbacks (Table 5.1). The latency to the first propagated call was significantly longer following aerial whistle three-caller playbacks than flee alarm three-caller playbacks (6.0±4.9 s versus 1.5±1.1 s; Wilcoxon rank-sum test: W=34, P=0.005; Table 5.1). The number of call elements propagated did not differ between alarm call types (Wilcoxon rank-sum test: W=24,

P=0.31; Table 5.1). When birds propagated alarms, they always matched the call type of the playback treatment (Table 5.1).

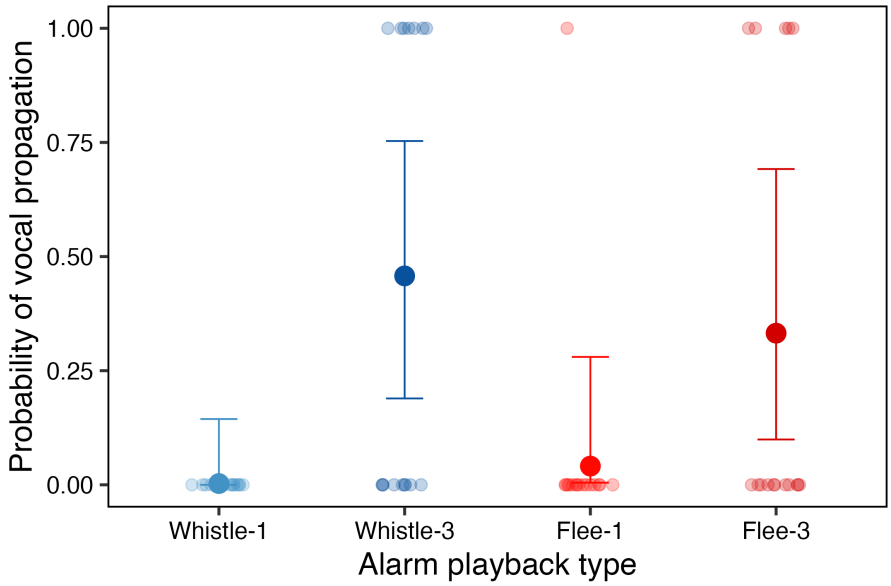


Figure 5.1. Probability of vocal propagation in white-winged choughs responding to playback of aerial whistles and flee alarms given by one or three callers. *N*=16 groups per treatment. Predicted means±95% CI shown. Statistical details are provided in Appendix Table A1.

Table 5.1. Vocal propagation responses of white-winged choughs to playback treatments simulating aerial whistles or flee alarms from one or three callers. N = 16 groups per treatment.

Playback treatment	Groups showing vocal propagation	Latency to call (s) [a]	Call elements propagated [b]		First propagated call type	
			Mean±SD	Range	Whistle	Flee
Whistle-1	0	-	-	-	-	-
Whistle-3	7	**6.0±4.9**	9.3±14.2	1–41	7	0
Flee-1	1	0.39	4	-	0	1
Flee-3	5	**1.5±1.1**	2.0±1.7	1–5	0	5

[a] Wilcoxon rank-sum test comparing whistle-3 and flee-3 treatments; significant effects (P=0.005) are shown in bold.
[b] Call elements counted matched the alarm-call type of the playback; one group propagated both alarm-call types (flee alarms and aerial whistles) in response to the flee-3 treatment.

Collective fleeing was rare following aerial whistle playbacks but increased in response to flee alarms, particularly when three callers were simulated (Figure 5.2). Overall, birds were more likely to flee collectively in response to flee alarms than aerial

whistles (BRGLM, Z=2.77, P=0.006). Birds were also more likely to flee when playbacks simulated three callers rather than a single caller (BRGLM, Z=2.56, P=0.01; Figure 5.2, Table A2). There was no significant interaction between alarm-call type and caller number (BRGLM, interaction: Z=-0.31, P=0.76).

In aerial whistle treatments, caller number did not affect the probability of collective scanning but did influence response duration. Collective scanning did not differ between aerial whistle playbacks produced by one caller and those produced by three callers (BRGLM, Z=0.65, P=0.52; Figure 5.3, Table A3). However, birds took significantly longer to resume feeding after three-caller whistle playbacks than after one-caller whistle playbacks (LMM, χ^2=11.03, P<0.001; Figure 5.4, Table A4).

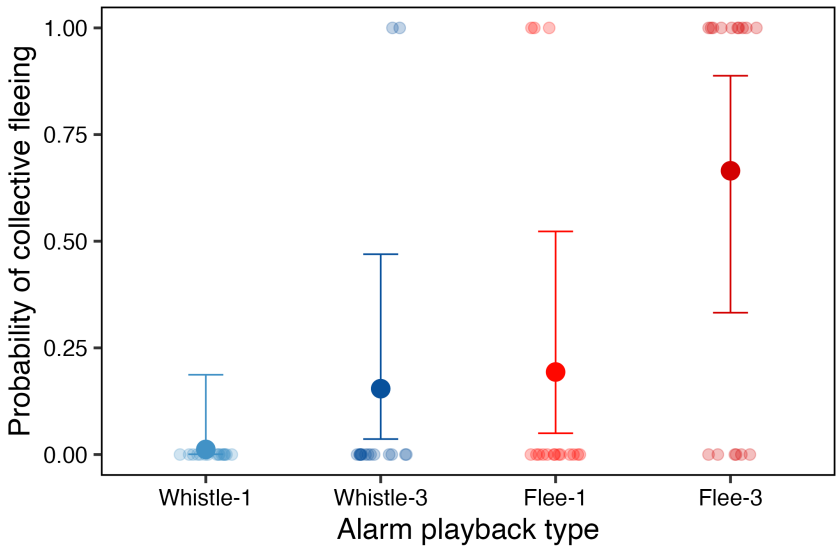


Figure 5.2. Probability of collective fleeing in white-winged chough in response to playback of aerial whistles and flee alarms given by one or three callers. *N*=16 groups per treatment. Predicted means±95% CI shown. Statistical details are provided in Appendix Tables A2.

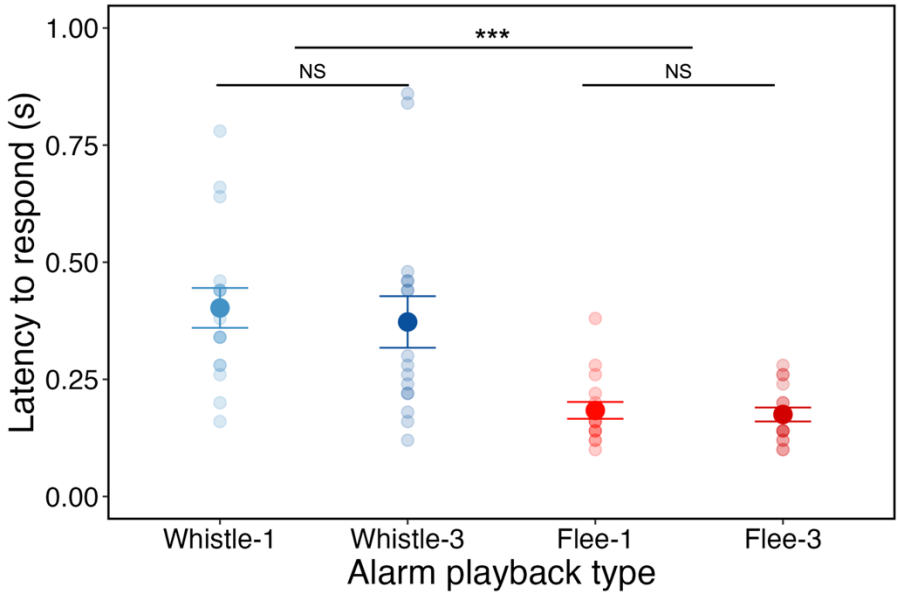


Figure 5.3. Probability of collective scanning in white-winged choughs following playbacks of aerial whistles given by one or three callers. Flee-alarm treatments were excluded because at least one bird in the subgroup immediately fled in most trials, making scanning behaviour impossible to measure. *N*=16 groups per treatment. Predicted means±95% CI shown. Statistical details are provided in Appendix Tables A3.

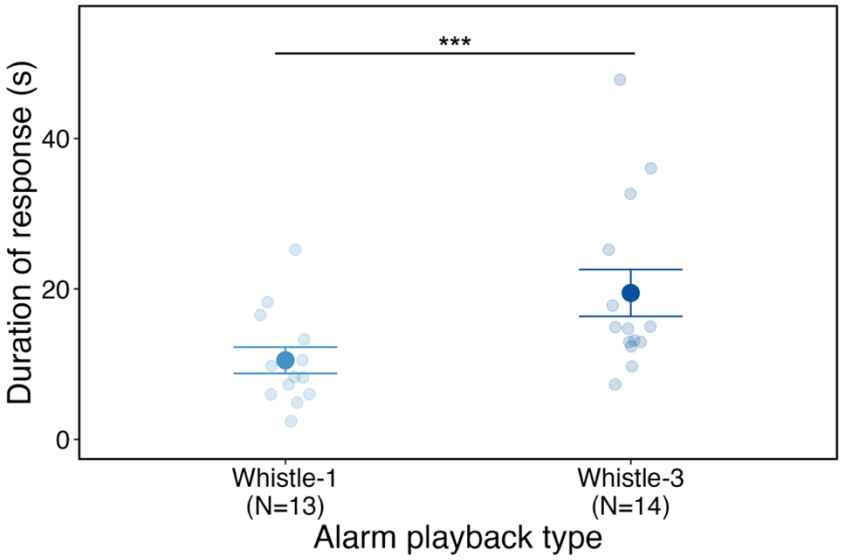


Figure 5.4. Duration of response (s) in white-winged choughs following playbacks of aerial whistles given by one or three callers. Flee-alarm treatments and aerial-whistle trials where at least one bird fled or did not resume feeding were excluded. Sample sizes are shown for each treatment. Means±SE shown. Statistical details are provided in Appendix Table A4.

Discussion

White-winged choughs adjusted alarm propagation and collective antipredator responses according to simulated caller number and alarm-call type. Caller number, a potential cue to information reliability, increased alarm propagation and strengthened collective responses, whereas alarm-call type determined the form of those responses. Birds were more likely to propagate alarms after hearing three callers than one, regardless of call type. Collective fleeing was most common following three-caller flee alarms, whereas aerial whistles primarily elicited collective vigilance. Increasing the number of callers strengthened collective flight responses to flee alarms, but did not increase the likelihood of collective scanning after aerial whistles; instead, three-caller aerial whistles prolonged vigilance duration. These collective responses do not, by themselves, establish whether individuals influenced one another or responded independently to the same playback. Nevertheless, these findings suggest that choughs apply simple decision rules that allow groups to maximise the benefits of social information while minimising the potential costs of responding to unreliable signals.

Alarm propagation in choughs depended strongly on caller number rather than alarm-call type, suggesting that information reliability mattered more than urgency in determining whether alarms were propagated. This pattern indicates that choughs may apply a simple decision rule in which multiple callers are required before individuals propagate alarm signals, potentially reducing costly information cascades caused by inaccurate signals within social groups. Indeed, false alarms occasionally occur in choughs. For example, aerial whistles are sometimes directed at non-threatening species, including Australian white ibis (*Threskiornis molucca*) and yellow-tailed black cockatoos (*Zanda funerea*) (C.-C. Liao, personal observation). Requiring multiple callers before relaying an alarm may therefore function as a social filter that increases the likelihood that the signal reflects a genuine threat. The value of multiple callers depends on the assumption that they provide independent information rather than simply copying one another (Igic et al., 2019; Sloan & Hare, 2008; Wolf et al., 2013). However, simulated caller number covaried with call-element number and the spatial distribution of sound

sources, so the treatment effect cannot be attributed solely to caller number. Experiments manipulating these cues independently could clarify which information receivers use when deciding whether to propagate alarms. Alarm reliability can also vary with caller identity (Blumstein et al., 2004; Hare & Atkins, 2001; Kern et al., 2016; Ramakrishnan & Richard, 2000) and species identity in heterospecific communication networks (Magrath et al., 2009; Palmer & Gross, 2018). Examining how caller characteristics, such as social dominance, sex, age or species identity, influence responses could further clarify the mechanisms underlying information propagation in animal societies.

Contrary to our prediction, choughs sometimes propagated high-urgency flee alarms despite the apparent priority of immediate escape. This pattern suggests that alarm propagation can still occur under acute threat, but is likely constrained by the rapidly declining value of social information. When danger is imminent, individuals must respond quickly, leaving only a narrow window in which information can be propagated before it becomes outdated. By contrast, in lower-urgency contexts such as mobbing, predators often remain present for longer, allowing alarm information to retain value even when transmitted with some delay. Our results support this temporal constraint: propagated calls following high-urgency flee-alarm playbacks occurred much more rapidly (mean latency 1.47 s) than those following low-urgency aerial whistle playbacks (mean latency 6.0 s; Table 5.1). This difference suggests that the opportunity for effective information propagation is strongly shaped by urgency. When choughs did propagate alarms, they consistently produced the same call type as the playback stimulus, indicating that propagation preserves information about threat urgency rather than simply signalling general danger. Such matched propagation is well documented in mobbing systems (Carlson et al., 2020; Liao, Chen, et al., 2024; Nolen & Lucas, 2009). For example, red-breasted nuthatches (*Sitta canadensis*) adjust their mobbing calls based on information source and reliability, and can selectively propagate this information (Carlson et al., 2020; Templeton & Greene, 2007). To our knowledge, alarm-call propagation has been documented mainly in mobbing contexts, with other alarm types rarely tested experimentally. Our findings suggest that such propagation may be

more widespread, particularly in highly social species, and warrant further study of its mechanisms and constraints.

Why do choughs propagate alarm information within groups? One possibility is that propagation, particularly of high-urgency flee alarms, amplifies critical information and promotes synchronised antipredator responses, such as collective fleeing, thereby facilitating rapid coordination. Such coordination may benefit caller indirectly by enhancing survival at the group level (Hingee & Magrath, 2009; Liao, Magrath, et al., 2024; Lima, 1995), especially in cooperative species like choughs, where group members are often closely related (Beck et al., 2008). Propagation may also provide direct benefits to callers. When multiple individuals flee simultaneously, predators may become confused or less able to single out a target (Sherman, 1985). By triggering coordinated escape, individuals may reduce the risk of standing out as a conspicuous moving target, thereby increasing their chances of escape. Finally, alarm propagation may facilitate social learning. Social learning about danger is widespread across taxa (Dezecache et al., 2019; León et al., 2023; Potvin et al., 2018; Szymkowiak, 2021), and juvenile choughs show slow development of appropriate alarm-call responses, even six months after fledging (Chapter 4). Repeated exposure to propagation events may therefore help young individuals associate specific alarm-call types with appropriate responses. Together, these possibilities suggest that alarm propagation may play an important role in shaping collective behaviour, individual risk, and information use, highlighting the need for future work to disentangle its benefits and underlying decision rules.

The weak response to one-caller flee alarms suggests that choughs consider additional information when making antipredator decisions. Conceptual frameworks predict that high-urgency signals such as flee alarms should trigger collective escape even when produced by a single caller (Liao et al., 2024), yet in our study one-caller flee alarms rarely elicited collective flight. One possible explanation is that choughs also assess the spatial relevance of alarm information when evaluating danger. In our previous study, louder flee alarm playbacks with the same call elements, broadcast at closer range, elicited immediate flight in 11 of 16 adults (65 dB at 5 m) (Liao et al., 2025).

In the present study, playbacks were softer and simulated alarms from neighbouring groups about 15 m away (55 dB at 10 m), prompting collective fleeing in only three of 16 groups. The relevant distance here is the perceived distance of the alarm caller, rather than the predator's attack distance: softer calls from more distant callers may be perceived as less relevant to the focal group. Consistent with this possibility, pilot playbacks simulating callers more than 30 m away were often ignored, suggesting that call amplitude may influence whether birds respond. Under this interpretation, flee alarms convey high urgency but relatively restricted spatial risk for the focal group. By contrast, although aerial whistles signal lower urgency, they may have greater spatial relevance to nearby groups because they indicate high-flying predators (about 50 m high). This difference in spatial relevance may explain why caller number did not influence collective vigilance responses to aerial whistles. Future studies explicitly testing how animals assess spatial relevance, for example by manipulating playback amplitude to vary the apparent distance of the caller, will help clarify the mechanisms underlying collective decision-making in social species.

Our findings provide experimental evidence that wild animals integrate multiple dimensions of social information, reliability and urgency, when making collective antipredator decisions. In white-winged choughs, alarm-call type determines the form of the response, whereas caller number acts as a reliability filter that shapes whether alarm information spreads through the group. Such simple decision rules may allow animals to respond rapidly to genuine threats while limiting costly information cascades. Future studies could investigate how animals assess additional components of social information, such as the reliability of callers differing in identity or age class and the spatial relevance of alarm information. Such work would help reveal the perceptual and cognitive mechanisms underlying collective decision-making in social animals.

Appendix

Table A1. Results of bias-reduced generalized linear models (BRGLMs) examining how (a) alarm-call types and (b) number of callers affect the probability that white-winged choughs vocally propagate the alarm calls (shown in Figure 5.1). Significant effects (P<0.05) are shown in bold.

Fixed effects	Estimates± SE	Z	P
(a) Alarm-call types			
Aerial whistle vs. Flee alarm	-0.30±0.64	-0.47	0.64
Group size	0.20±0.31	0.65	0.51
Playback order	-0.36±0.30	-1.20	0.23
(b) Number of callers			
1 caller vs. 3 callers	4.52±1.55	2.91	0.004
Group size	-0.33±0.40	-0.84	0.40
Playback order	-0.98±0.48	-2.03	0.04

Table A2. Results of bias-reduced generalized linear models (BRGLMs) examining how (a) alarm-call types and (b) number of callers affect the probability that white-winged choughs collective flee (shown in Figure 5.2). Significant effects (P<0.05) are shown in bold.

Fixed effects	Estimates± SE	Z	P
(a) Alarm-call types			
Aerial whistle vs. Flee alarm	2.58±0.93	2.77	0.006
Group size	0.46±0.42	1.11	0.27
Playback order	-0.29±0.37	-0.76	0.45
(b) Number of callers			
1 caller vs. 3 callers	2.24±0.87	2.56	0.01
Group size	0.56±0.41	1.37	0.17
Playback order	-0.34±0.37	-0.92	0.36

Table A3. Results of bias-reduced generalized linear models (BRGLMs) examining how different number of callers (1 vs. 3) given aerial whistles affect the probability that white-winged choughs collective scanning (shown in Figure 5.3).

Fixed effects	Estimates± SE	Z	P
Number of callers (1 vs. 3)	0.96±0.94	0.65	0.52
Group size	-0.16±0.63	-0.26	0.80
Playback order	-0.32±0.54	-0.59	0.56

Table A4. Results of linear mixed-effects models (LMMs) examining how caller number affects response duration (s) to aerial whistles in white-winged chough subgroups (shown in Figure 5.4). Significant effects ($P < 0.05$) are shown in bold.

Response variable	Fixed effects	*df*	χ^2	*P*	$R^{2\,a}$
Duration of response (s)					0.75
	Number of callers	1	11.03	<0.001	
	Group size	1	1.10	0.29	

[a] Conditional R^2 values.

Supplementary materials

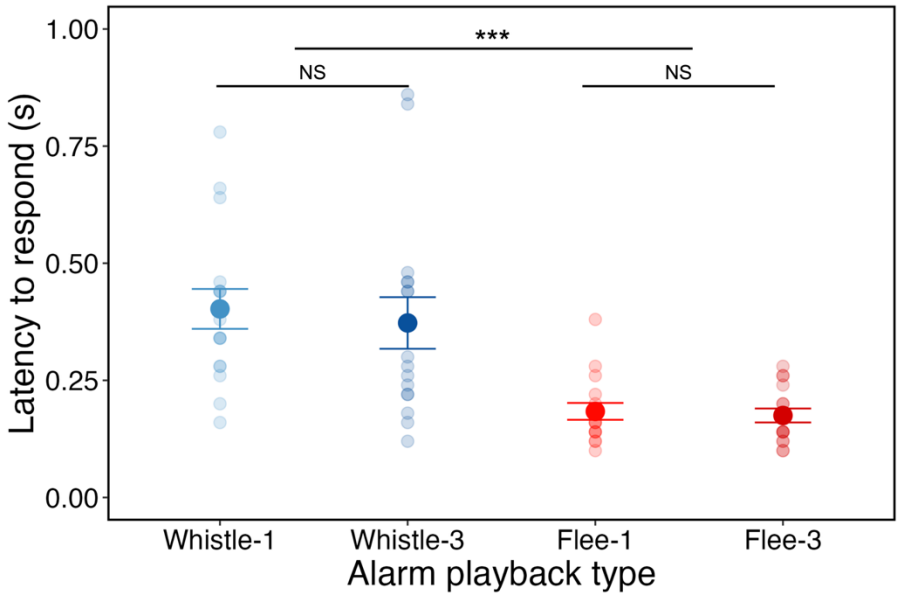


Figure S1. Latency to respond (s) in white-winged choughs following playbacks of aerial whistles and flee alarms given by one or three callers. *N*= 6 groups per treatment. Means ± SE shown. Statistical details are provided in Table S1.

Table S1. Results of linear mixed-effects models (LMMs) examining how alarm-call type and caller number affect latency to respond (s) in white-winged chough subgroups (shown in Figure S1). Significant effects (*P*<0.05) are shown in bold.

Response variable	Fixed effects	*df*	*F*	*P*	$R^{2\,a}$
Latency to respond (s)					0.34
	Alarm call types	1	32.37	<0.001	
	Group size	1	0.01	0.94	
Latency to respond (s)					0.004
	Number of callers	1	0.18	0.67	
	Group size	1	0.06	0.81	

[a] Conditional R^2 values.

References

Aplin, L., Crates, R., Flack, A., & McGregor, P. (2025). Social learning and culture in birds: emerging patterns and relevance to conservation. *Philosophical Transactions of the Royal Society B: Biological Sciences, 380*(1925), 20240128. https://doi.org/10.1098/rstb.2024.0128

Beauchamp, G. (2010). Determinants of false alarms in staging flocks of semipalmated sandpipers. *Behavioral Ecology*, *21*(3), 584–587. https://doi.org/10.1093/beheco/arq032

Beauchamp, G., & Ruxton, G. D. (2007). False alarms and the evolution of antipredator vigilance. *Animal Behaviour*, *74*(5), 1199–1206. https://doi.org/10.1016/j.anbehav.2007.02.014

Beck, N. R., Peakall, R., & Heinsohn, R. (2008). Social constraint and an absence of sex-biased dispersal drive fine-scale genetic structure in white-winged choughs. *Molecular Ecology*, *17*(19), 4346–4358. https://doi.org/10.1111/j.1365-294X.2008.03906.x

Blumstein, D. T. (1995). Golden-marmot alarm calls. I. The production of situationally specific vocalizations. *Ethology*, *100*, 113–125.

Blumstein, D. T., & Armitage, K. B. (1997). Alarm calling in yellow-bellied marmots: I. The meaning of situationally variable alarm calls. *Animal Behaviour*, *53*(1), 143–171. https://doi.org/10.1006/anbe.1996.0285

Blumstein, D. T., Verneyre, L., & Daniel, J. C. (2004). Reliability and the adaptive utility of discrimination among alarm callers. *Proceedings of the Royal Society B: Biological Sciences*, *271*(1550), 1851–1857. https://doi.org/10.1098/rspb.2004.2808

Carlson, N. V., Greene, E., & Templeton, C. N. (2020). Nuthatches vary their alarm calls based upon the source of the eavesdropped signals. *Nature Communications*, *11*(526), 1–7. https://doi.org/10.1038/s41467-020-14414-w

Caro, T. (2005). *Antipredator defenses in birds and mammals*. University of Chicago Press.

Conradt, L., & Roper, T. J. (2005). Consensus decision making in animals. *Trends in Ecology and Evolution*, *20*(8), 449–456. https://doi.org/10.1016/j.tree.2005.05.008

Coomes, J. R., McIvor, G. E., & Thornton, A. (2019). Evidence for individual discrimination and numerical assessment in collective antipredator behaviour in wild jackdaws (*Corvus monedula*). *Biology Letters*, *15*, 20190380. https://doi.org/10.1098/rsbl.2019.0380

Cunningham, S., & Magrath, R. D. (2017). Functionally referential alarm calls in noisy miners communicate about predator behaviour. *Animal Behaviour*, *129*, 171–179. https://doi.org/10.1016/j.anbehav.2017.05.021

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. *Trends in Ecology and Evolution*, *20*, 187–193. https://doi.org/10.1016/j.tree.2005.01.010

Dezecache, G., Crockford, C., & Zuberbühler, K. (2019). The development of communication in alarm contexts in wild chimpanzees. *Behavioral Ecology and Sociobiology*, *73*(8), 1–9. https://doi.org/10.1007/s00265-019-2716-6

Dibnah, A. J., Herbert-Read, J. E., Boogert, N. J., McIvor, G. E., Jolles, J. W., & Thornton, A. (2022). Vocally mediated consensus decisions govern mass departures from jackdaw roosts. *Current Biology*, *32*(10), R455–R456. https://doi.org/10.1016/j.cub.2022.04.032

Dutour, M., Kalb, N., Salis, A., & Randler, C. (2021). Number of callers may affect the response to conspecific mobbing calls in great tits (*Parus major*). *Behavioral Ecology and Sociobiology*, *75*, 29. https://doi.org/10.1007/s00265-021-02969-7

Dutour, M., Léna, J. P., & Lengagne, T. (2017). Mobbing calls: a signal transcending species boundaries. *Animal Behaviour*, *131*, 3–11. https://doi.org/10.1016/j.anbehav.2017.07.004

Farrow, L. F., Doohan, S. J., & McDonald, P. G. (2017). Alarm calls of a cooperative bird are referential and elicit context-specific antipredator behavior. *Behavioral Ecology*, *28*(3), 724–731. https://doi.org/10.1093/beheco/arx020

Farrow, L. F., Barati, A., & McDonald, P. G. (2020). Cooperative bird discriminates between individuals based purely on their aerial alarm calls. *Behavioral Ecology*, *31*(2), 440–447. https://doi.org/10.1093/beheco/arz182

Fichtel, C., & Kappeler, P. M. (2002). Anti-predator behavior of group-living Malagasy primates: Mixed evidence for a referential alarm call system. *Behavioral Ecology and Sociobiology*, *51*(3), 262–275. https://doi.org/10.1007/s00265-001-0436-0

Furrer, R. D., & Manser, M. B. (2009). The evolution of urgency-based and functionally referential alarm calls in ground-dwelling species. *American Naturalist*, *173*(3), 400–410. https://doi.org/10.1086/596541

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*(6), 449–461. https://doi.org/10.1111/eth.12097

Giraldeau, L. A., Valone, T. J., & Templeton, J. J. (2002). Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *357*(1427), 1559–1566. https://doi.org/10.1098/rstb.2002.1065

Gray, L., & Webster, M. M. (2023). False alarms and information transmission in grouping animals. *Biological Reviews*, *98*(3), 833–848. https://doi.org/10.1111/brv.12932

Griffin, A. S. (2004). Social learning about predators: A review and prospectus. *Learning and Behavior*, *32*(1), 131–140. https://doi.org/10.3758/BF03193188

Hare, J. F., & Atkins, B. A. (2001). The squirrel that cried wolf: Reliability detection by juvenile Richardson's ground squirrels (*Spermophilus richardsonii*). *Behavioral Ecology and Sociobiology*, *51*(1), 108–112. https://doi.org/10.1007/s002650100414

Heinsohn, R. (1987). Age-dependent vigilance in winter aggregations of cooperatively breeding white-winged choughs (*Corcorax melanorhamphos*). *Behavioral Ecology and Sociobiology*, *20*(4), 303–306. https://doi.org/10.1007/BF00292183

Heinsohn, R. (1991). Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. *American Naturalist*, *137*(6), 864–881.

Heinsohn, R. (1992). Cooperative enhancement of reproductive success in white-winged choughs. *Evolutionary Ecology*, *6*(2), 97–114. https://doi.org/10.1007/BF02270705

Heinsohn, R., Cockburn, A., & Cunningham, R. B. (1988). Foraging, delayed maturation, and advantages of cooperative breeding in white-winged choughs, *Corcorax melanorhamphos*. *Ethology*, *77*(3), 177–186. https://doi.org/10.1111/j.1439-0310.1988.tb00202.x

Hingee, M., & Magrath, R. D. (2009). Flights of fear: A mechanical wing whistle sounds the alarm in a flocking bird. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1676), 4173–4179. https://doi.org/10.1098/rspb.2009.1110

Igic, B., Ratnayake, C. P., Radford, A. N., & Magrath, R. D. (2019). Eavesdropping magpies respond to the number of heterospecifics giving alarm calls but not the number of species calling. *Animal Behaviour*, *148*, 133–143. https://doi.org/10.1016/j.anbehav.2018.12.012

Kern, J. M., Sumner, S., & Radford, A. N. (2016). Sentinel dominance status influences forager use of social information. *Behavioral Ecology*, *27*(4), 1053–1060. https://doi.org/10.1093/beheco/arv240

Leavesley, A. J., & Magrath, R. D. (2005). Communicating about danger: Urgency alarm calling in a bird. *Animal Behaviour*, *70*(2), 365–373. https://doi.org/10.1016/j.anbehav.2004.10.017

León, J., Quintero, F., & Zuberbühler, K. (2023). Acquisition of predator knowledge in sooty mangabeys. *Animal Behaviour*, *205*, 1–14. https://doi.org/10.1016/j.anbehav.2023.08.012

Liao, C.-C., Chen, C.-C., & Magrath, R. D. (2024). Asymmetric information in mixed-species mobbing flocks: why are leader species special? *Animal Behaviour*, *210*, 383–393. https://doi.org/10.1016/j.anbehav.2024.01.014

Liao, C.-C., Magrath, R. D., Manser, M. B., & Farine, D. R. (2024). The relative contribution of acoustic signals versus movement cues in group coordination and collective decision-making. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *379*(1905), 20230184. https://doi.org/10.1098/rstb.2023.0184

Liao, C.-C., Radford, A. N., Heinsohn, R., & Magrath, R. D. (2025). Functionally referential communication about danger in cooperatively breeding white-winged choughs. *Animal Behaviour*, *229*, 123330. https://doi.org/10.1016/j.anbehav.2025.123330

Lima, S. L. (1995). Collective detection of predatory attack by social foragers: fraught with ambiguity? *Animal Behaviour*, *50*(4), 1097–1108. https://doi.org/10.1016/0003-3472(95)80109-X

Magrath, R. D., Pitcher, B. J., & Gardner, J. L. (2009). An avian eavesdropping network: Alarm signal reliability and heterospecific response. *Behavioral Ecology*, *20*(4), 745–752. https://doi.org/10.1093/beheco/arp055

Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society B: Biological Sciences*, *268*(1483), 2315–2324. https://doi.org/10.1098/rspb.2001.1773

Manser, M. B., Seyfarth, R. M., & Cheney, D. L. (2002). Suricate alarm calls signal predator class and urgency. *Trends in Cognitive Sciences*, *6*(2), 55–57. https://doi.org/10.1016/S1364-6613(00)01840-4

McCormick, J. S., White, T. E., Middleton, E. J. T., & Latty, T. (2024). Information cascades spread adaptive and maladaptive behaviours in group-living animals. *Animal Behaviour*, 209, 53–62. https://doi.org/10.1016/j.anbehav.2023.12.007

McLachlan, J. R., & Magrath, R. D. (2020). Speedy revelations: How alarm calls can convey rapid, reliable information about urgent danger. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1921), 20192772. https://doi.org/10.1098/rspb.2019.2772

Murray, T. G., Zeil, J., & Magrath, R. D. (2017). Sounds of modified flight feathers reliably signal danger in a pigeon. *Current Biology*, *27*(22), 3520-3525.e4. https://doi.org/10.1016/j.cub.2017.09.068

Nolen, M. T., & Lucas, J. R. (2009). Asymmetries in mobbing behaviour and correlated intensity during predator mobbing by nuthatches, chickadees and titmice. *Animal Behaviour*, *77*(5), 1137–1146. https://doi.org/10.1016/j.anbehav.2009.01.023

Palmer, M. S., & Gross, A. (2018). Eavesdropping in an African large mammal community: antipredator responses vary according to signaller reliability. *Animal Behaviour*, *137*, 1–9. https://doi.org/10.1016/j.anbehav.2017.12.018

Potvin, D. A., Ratnayake, C. P., Radford, A. N., & Magrath, R. D. (2018). Birds learn socially to recognize heterospecific alarm calls by acoustic association. *Current Biology*, *28*(16), 2632-2637.e4. https://doi.org/10.1016/j.cub.2018.06.013

R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Ramakrishnan, U., & Richard, G. C. (2000). Age differences in the responses to adult and juvenile alarm calls by Bonnet Macaques (*Macaca radiata*). *Ethology*, (106), 131–144.

Ridley, A. R., & Raihani, N. J. (2007). Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. *Behavioral Ecology*, *18*(2), 324–330. https://doi.org/10.1093/beheco/arl092

Rowley, I. (1978). Communal activities among white-winged choughs *Corcorax Melanorhamphus*. *Ibis*, *120*(2), 178–197. https://doi.org/10.1111/j.1474-919X.1978.tb06774.x

Searcy, W. A., & Nowicki, S. (2005). *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton University Press.

Sherman, P. W. (1985). Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation? *Behavioral Ecology and Sociobiology*, 17, 313–323.

Sloan, J. L., & Hare, J. F. (2008). The more the scarier: Adult Richardson's ground squirrels (*Spermophilus richardsonii*) assess response urgency via the number of alarm signallers. *Ethology*, *114*(5), 436–443. https://doi.org/10.1111/j.1439-0310.2008.01479.x

Sosna, M. M. G., Twomey, C. R., Bak-Coleman, J., Poel, W., Daniels, B. C., Romanczuk, P., & Couzin, I. D. (2019). Individual and collective encoding of risk in animal groups. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(41), 20556–20561. https://doi.org/10.1073/pnas.1905585116

Strandburg-Peshkin, A., Farine, D. R., Couzin, I. D., & Crofoot, M. C. (2015). Shared decision-making drives collective movement in wild baboons. *Science*, *348*(6241), 1358–1361. https://doi.org/10.1126/science.aaa5099

Szymkowiak, J. (2021). Wood warblers learn to recognize mobbing calls of an unfamiliar species from heterospecific tutors. *Animal Behaviour*, *171*, 1–11. https://doi.org/10.1016/j.anbehav.2020.11.004

Templeton, C. N., & Greene, E. (2007). Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *Proceedings of the National Academy of Sciences*, *104*(13), 5479–5482. https://doi.org/10.1073/pnas.0605183104

Thiebault, A., Mullers, R. H. E., Pistorius, P. A., & Tremblay, Y. (2014). Local enhancement in a seabird: Reaction distances and foraging consequence of predator aggregations. *Behavioral Ecology*, *25*(6), 1302–1310. https://doi.org/10.1093/beheco/aru132

Townsend, S. W., & Manser, M. B. (2013). Functionally referential communication in mammals: The past, present and the future. *Ethology*, *119*(1), 1–11. https://doi.org/10.1111/eth.12015

Walker, R. H., King, A. J., McNutt, J. W., & Jordan, N. R. (2017). Sneeze to leave: African wild dogs (*Lycaon pictus*) use variable quorum thresholds facilitated by sneezes

in collective decisions. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1862), 20170347. https://doi.org/10.1098/rspb.2017.0347

Ward, A., & Webster, M. (2016). *Sociality: The Behaviour of Group-Living Animals*. Springer International Publishing.

Whiten, A. (2000). Primate culture and social learning. *Cognitive Science*, *24*(3), 477–508. https://doi.org/10.1207/s15516709cog2403_6

Wolf, M., Kurvers, R. H. J. M., Ward, A. J. W., Krause, S., & Krause, J. (2013). Accurate decisions in an uncertain world: Collective cognition increases true positives while decreasing false positives. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1756), 20122777. https://doi.org/10.1098/rspb.2012.2777

Chapter 6

Asymmetric Information in Mixed-Species Mobbing Flocks:

Why Are Leader Species Special?



A black-throated tit (*Aegithalos concinnus*) calls from the forest canopy. These gregarious birds are common leaders of mixed-species bird flocks in Taiwan's montane forests, giving soft contact calls while foraging but becoming highly vocal when danger threatens.

This chapter has been published as:

Liao, C.-C., Chen, C.-C., & Magrath, R. D. (2024). Asymmetric information in mixed-species mobbing flocks: why are leader species special? *Animal Behaviour*, 210, 383–393. https://doi.org/10.1016/j.anbehav.2024.01.014

Abstract

Asymmetric information transfer can shape the social structure of animal groups. Birds in mixed-species flocks can gain anti-predation benefits by relying on both personal and social information, ultimately increasing their survival. However, not all species in a flock contribute danger-related information equally, leading to complex patterns of information flow between species. Understanding these differences in information flow and usage among species is key to exploring the mechanisms underlying the formation of such social assemblages. In this study, we combined mixed-species flock surveys with playback experiments to investigate the asymmetric information transfer about danger between leader and follower species in the montane forests of Taiwan. The playback experiments included four treatments: predator calls (personal information), leader and follower mobbing calls (social information), and control. We predicted that leader species would be better at detecting threats than follower species, and that the mobbing calls of leader species would elicit stronger anti-predator responses in mixed-species flocks than those of follower species. As predicted, and more striking than anticipated, leader species were always the first to initiate mobbing calls in response to predator calls, suggesting strong asymmetry in predator detection and/or danger communication between the two species roles. Moreover, our results showed that birds responded much more strongly to the playback of predator calls than to playback of mobbing calls. Contrary to our prediction, there was not a greater anti-predator response to mobbing calls given by leader compared to follower species. Here, we propose that larger conspecific group sizes and associated kin-selected behaviour could drive leader species to develop superior anti-predator signalling systems, potentially leading to asymmetric information transfer about predation risk between species. We also suggest that mutual anti-predator benefits may be common in mixed mobbing flocks, promoting positive interactions among bird species, and ultimately strengthening the cohesion and formation of mixed flocks.

Keywords: acoustic communication; alarm call; anti-predator; bird; eavesdropping networks

Introduction

Interspecific information flow is a critical factor shaping the social structure of animal communities (Goodale et al., 2010; Martínez et al., 2018). Mixed-species bird flocks (hereafter referred to as "mixed flocks"), consisting of multiple species that forage and move together in a coordinated manner, provide a typical example of a social assemblage that is influenced by interspecific communication and eavesdropping (Carlson, Healy, et al., 2020; Goodale et al., 2010; Jiang et al., 2020). Information about predators may be a key driver selecting for mixed flocks (Goodale et al., 2010). By gathering both personal and social information about danger, flock members can gain anti-predation benefits, including increased foraging efficiency and ultimately survival (Goodale et al., 2010, 2020; Sullivan, 1984a).

Birds in mixed flocks can acquire information about predators either directly from a predator's cues (personal information) or through eavesdropping on social signals (social information) from other flock members' alarm calls (Goodale et al., 2010; Magrath et al., 2007, 2015; Martínez & Zenil, 2012). However, social information may not always be reliable (Magrath et al., 2009, 2015; Satischandra et al., 2010), which means that individuals must be selective in using different types of information. This decision to act on various sources of information is mainly influenced by the quality of the information, such as its reliability and relevance (Barrera et al., 2011; Hämäläinen et al., 2023; Magrath et al., 2009; McLachlan et al., 2019; Turner et al., 2023). For instance, foliage-gleaning and bark-foraging species in mixed flocks rely more on heterospecific alarm calls to detect predators than aerially foraging species (Goodale & Kotagama, 2008; Jones & Sieving, 2019; Martínez & Zenil, 2012). This may be because substrate-gleaning species encounter more visual obstructions that impede their ability to detect predators, making social information more valuable to them (Jones & Sieving, 2019; Martínez & Zenil, 2012). Although social information is important for many reasons, it may not be as reliable as personal information. For example, greater racket-tailed drongos *Dicrurus paradiseus*, which are important sentinel species in mixed flocks (Goodale & Kotagama, 2005, 2008), sometimes use "false" alarm calls to startle other birds and gain foraging benefits

through kleptoparasitism (Satischandra et al., 2010). Thus, personal information may be a better indicator of risk (Barrera et al., 2011), as direct predator cues can provide more information about risk, such as accurate spatial information about a predator, compared to social information from either conspecific or heterospecific alarm calls.

Information transfer about predation risk is often asymmetrical among species in mixed flocks, as flock members can differ in ecological, morphological, and behavioral traits which could affect information transfer (Goodale et al., 2010; Jones & Sieving, 2019; Nolen & Lucas, 2009). For instance, aerial insectivores like flycatchers are better at detecting predators than other species (Jones & Sieving, 2019), as their perch-based scanning for prey provides a wider visual field that enhances their ability to spot predators (Goodale & Kotagama, 2008; Jones & Sieving, 2019). Similarly, gregarious bird species like orange-billed babblers *Argya rufescens* are more likely to communicate potential dangers in mixed flocks (Goodale & Kotagama, 2005, 2008), due to their superior anti-predator signaling systems facilitated by kin-selected behaviour (Goodale & Beauchamp, 2010; Sridhar et al., 2009). Additionally, species such as greater racket-tailed drongo and New Holland honeyeater *Phylidonyris novaehollandiae* elicit especially strong anti-predator responses to their alarm calls because of their usually higher reliability in conveying information about dangers (Goodale & Kotagama, 2008; Magrath et al., 2009, 2015). These examples suggest that species differ in their capacity for information transfer and do not contribute information equally to mixed flocks. Understanding differences in information flow and usage between species is fundamental for exploring the mechanisms behind the formation of social assemblages.

In mixed flocks, species often have distinct roles that can be categorized based on features such as frequency of participation, conspecific group size, specific behaviours, and spatial positions in the flock (Greenberg, 2000; Hutto, 1994; Mangini et al., 2023; Sridhar et al., 2009). Generally, “leader” species are the first species to move in a particular direction, “follower” species are those that follow the leaders, and “occasional” species may only temporarily join the flock when it passes through their territories (Goodale et al., 2020; Greenberg, 2000; Hutto, 1994; Mangini et al., 2023;

Sridhar et al., 2009). Of these roles, leader species are considered crucial for the formation and maintenance of flock cohesion (Goodale et al., 2020; Greenberg, 2000; Sridhar et al., 2009). Information commonly flows from leaders to other species in the flock, providing foraging and/or anti-predation benefits to the other flock members (Goodale et al., 2010; Goodale & Kotagama, 2008; Munn & Terborgh, 1979; Pagani-Núñez et al., 2018). For example, woodpecker species, which are typical followers, show significantly lower vigilance rates inside mixed flocks, suggesting that they receive anti-predator benefits by joining flocks and making use of heterospecific alarm calls (Limparungpatthanakij et al., 2019; Sullivan, 1984b, 1984a). However, in some cases, the flow of information during mobbing can be from followers to leaders. For example, the white-breasted nuthatch Sitta carolinensis, a common follower in tit flocks, often responded first to the playback of screech-owl *Megascops asio* calls than the leader species (Nolen & Lucas, 2009). It appears that the flow of information in mixed flocks is more complex than often thought and may vary depending on specific conditions.

Mobbing calls are an important source of social information about dangers in avian communities, produced in response to predators that do not pose an immediate threat (Curio, 1978; Dutour et al., 2017). Previous studies have indicated that mobbing behaviour is also a vital anti-predator behaviour in mixed flocks, with participants often provoked by the mobbing calls of other members (Carlson, Greene, et al., 2020; Coppinger et al., 2020; Jiang et al., 2020; Zhou et al., 2021). For example, red-breasted nuthatches *Sitta canadensis*, a typical follower species, eavesdrop on subtle variations in heterospecific chickadee mobbing calls and are able to respond appropriately in mixed winter flocks (Templeton & Greene, 2007). They even vary their own mobbing calls in response to personal or social information, which suggests that nuthatches are sensitive to the source and reliability of information (Carlson, Greene, et al., 2020). Although both mobbing behaviour and mixed-species flocking are generally regarded as adaptations to reduce predation risk, their connections have rarely been experimentally investigated (Zhou et al., 2021). In particular, the potential consequences of interspecific asymmetries in information transfer in mixed mobbing flocks are not well understood (Carlson, Greene, et al., 2020; Carlson, Healy, et al., 2020; Nolen & Lucas, 2009).

Here, we combine mixed flock surveys with playback experiments in the montane forests of Taiwan to investigate asymmetric information transfer about danger between leader and follower species in mixed mobbing flocks. The specific objectives of this study were to: (1) investigate whether leaders are more likely to be the first to respond to danger; (2) test whether personal information (from hearing a predator calling) provokes a greater response than social information (from hearing other species giving mobbing calls); and (3) examine whether the leaders' mobbing calls elicit stronger anti-predator responses than those of followers. We predicted that leaders would be faster to communicate about predator cues than followers, based on the highly gregarious nature of the leader species in our flocking system and their potentially better anti-predator systems (Chen & Hsieh, 2002; Liao et al., 2022). We predicted that flocking birds would be more responsive to direct predator cues than indirect mobbing calls, as direct cues from predators may provide more information about risk than indirect signals from conspecifics or heterospecifics. Finally, we predicted that leaders' mobbing calls would elicit stronger anti-predator responses than followers' mobbing calls, as followers commonly depend more on information from leaders in mixed flocks.

Methods

(a) Study sites and the flocking systems

Fieldwork was carried out in two locations in central Taiwan, from October 2021 to January 2022. One was in the Alishan area (23.51° N, 120.79° E; elevation 1300–2000 m), and the other was in the Zhushan area (23.68° N, 120.74° E; elevation 950–1700 m). Both study sites were dominated by conifer-broadleaf mixed forests and bamboo forests. Extensive trails within each study site were used to search for mixed flocks on foot. There were four (total length: 12.54 km; range: 1.37–4.5 km) and three (total length: 6.36 km; range: 1.31–3.35 km) main trails in the Alishan and the Zhushan areas, respectively. The trails were each located in a large patch of forest and at least 500 m apart from one another to avoid repeated encounters with the same flock in a day.

Mixed flocks regularly form during the non-breeding season when cold weather prevails in Taiwan. Most of these mixed flocks are led by one or two numerically dominant bird species that account for a major portion of the overall flock size (Chen & Hsieh, 2002; Liao et al., 2022). For example, in our study sites, black-throated tit *Aegithalos concinnus* and Morrison's fulvetta *Alcippe morrisonia* are the most common leader species in canopy and understory flocks, respectively, often comprising up to two-thirds of the individuals in a mixed flock (Chen et al., 2022; Chen & Hsieh, 2002). On the other hand, most follower species are found in smaller numbers within mixed flocks, typically 1 to 3 individuals. Due to the evenly distributed vegetation layers in the forests at our study sites, particularly in bamboo forests, canopy and understory flocks frequently meet and form larger "mega-flocks" (Liao et al., 2022). Sometimes, such combined flocks can consist of more than 100 individuals and include more than 10 bird species.

In this study, a mixed-species flock was defined as a roving group of three or more individuals, consisting of at least two species, which moved together in the same direction for at least 5 minutes while foraging (Morse, 1970). We defined "leader" species as those found at the forefront of flocks, initiating movement and being followed by other species as the group travels from one area to another; "follower" species as those that consistently follow leader species in a mixed flock; and "occasional" species as those that temporarily join a mixed flock when it passes through their territories but remain in the mixed flock during a playback trial. Before initiating a playback, we classified each bird species' role within a mixed flock based on these definitions. Due to the diverse composition and structure of each mixed flock, the same species could potentially assume any of the three roles depending on the particular mixed flock (see Table A6). Sometimes, a mixed flock may include more than one leader species, such as when canopy and understory mixed flocks converge to form a single mixed flock (Greenberg, 2000; Liao et al., 2022; Munn, 1985; Poulsen, 1996). In such cases, species roles are generally maintained within each sub-unit of the mixed flock (Liao et al., 2022; Munn, 1985). Thus, in this study, we considered bird species that initially led their respective types of mixed flocks to be leader species, allowing for the possibility of two leader species within a single mixed flock.

(b) Study species

We chose three focal bird species for our playback experiments that are commonly found in mixed flocks in the mid-elevation mountains of Taiwan. The black-throated tit is a cooperative breeding bird (Li et al., 2012) that commonly forms large conspecific flocks of a dozen or more birds in the forest canopy (Severinghaus et al., 2010). During the non-breeding season, black-throated tit is also a dominant leader species in mixed flocks (Chen et al., 2022; Liao et al., 2022). They usually emit soft contact calls while foraging but become highly vocal when threatened. Green-backed tits *Parus monticolus* are often active in mixed flocks with black-throated tits and can be considered as an obligate follower species (Liao, 2015). They usually produce loud, clear vocalizations, particularly alarm calls. Steere's liocichla *Liocichla steerii*, a typical understory bird, temporarily participates in mixed flocks when they pass through its territory (Liao et al., 2022). This species produces common, loud, and non-threatening vocalizations throughout the year, making their calls ideal for use as a control playback treatment.

The three species used in playback experiments are vulnerable to similar predators, including the collared owlet *Glaucidium brodiei* and the besra *Accipiter virgatus* (Severinghaus et al., 2010). For our experiment, we chose the collared owlet to simulate predator presence. This is a diurnal owl that preys on small passerines and is commonly found in forests (Severinghaus et al., 2010). With a body length of 15-17 cm and extended foraging time, the owlet poses a significant threat to small birds. The owlet's distinct 4-note whistled call can be heard during both day and night, eliciting strong mobbing responses in forest birds (Severinghaus et al., 2010).

In this study, we played back the vocalizations of three treatment species (i.e., black-throated tit, green-backed tit, and Steere's liocichla) and one predator species (i.e., collared owlet) to the mixed flocks. However, our focus extended beyond merely observing the behavioural responses of the three treatment species. Instead, we quantified the behavioural responses to the playbacks from all species present in each mixed flock. In total, we found 29 bird species participating in the mixed flocks (n=64; Table A6). Among these species, four were classified as leader species in at least one

flock according to our definitions: the black-throated tit, Morrison's fulvetta, Taiwan yuhina *Yuhina brunneiceps*, and rusty laughingthrush *Pterorhinus poecilorhynchus* (Table A6). Some commonly found follower species included the rufous-faced warbler *Abroscopus albogularis*, green-backed tit, and rufous-capped babbler *Cyanoderma ruficeps* (Table A6).

(c) Playback experiment and recordings

We used a playback experiment to test our hypotheses about information flow in these mixed-species flocks. The experiment included four playback treatments: (1) leader mobbing calls, from black-throated tits; (2) follower mobbing calls, from green-backed tits; (3) predator calls, from collared owlets; and (4) control songs, from Steere's liocichlas (Figure 6.1). Previous studies have demonstrated that mobbing behaviour can be elicited by using the playback of a predator's calls in mixed flocks (Jiang et al., 2020; Zhou et al., 2021). Using playback rather than predator models also ensured that all individuals had the opportunity to simultaneously detect the predator's cues. Each playback treatment lasted 30 s, and was made with Raven Pro 1.6 software (Cornell Laboratory of Ornithology, Ithaca, NY, U.S.A.).

Mobbing and control playbacks were prepared from recordings of species at the study sites during the non-breeding season. We prompted mobbing calls from the two tit species by playing back a 10-second recording of collared owlet calls. Recordings were made from a distance of 3–5 m using a Sennheiser ME67 directional microphone and a Marantz PMD660 digital recorder, sampling wave files at 48 kHz and 16 bits. Specifically, we placed a camouflaged JBL Go 3 Bluetooth speaker 1.5–2 m above the ground, within 10 m of a focal individual or single-species flock. We then stood about 5 m from the speaker, broadcast the owlet calls, recorded any calls and noted the behavioural responses from the target birds. The birds all exhibited typical mobbing responses, including: 1) stopping foraging and looking around, 2) emitting calls, and 3) approaching the speaker. Additionally, we recorded the Steere's liocichla songs at a distance of 3–5 m from a singing individual. Playback exemplars for these three species were prepared from high-quality recordings without calls from other bird species or distinct background noise.

Using these recordings, we made five different 30s exemplars for each species by trimming or repeating them as needed. We filtered out sounds below the frequency of the calls: below 2 kHz for leader mobbing calls, and 1 kHz for both follower mobbing calls and control calls.

We were unable to record collared owlets calling, so had to use recordings from the Macaulay Library (https://www.macaulaylibrary.org/). We selected five high-quality wave files of owlet recordings, which included recordings from Taiwan (2 tracks: 24.9s, and 19.1s), Malaysia (1 track: 14.4s), Thailand (1 track: 9.5s), and India (1 track: 9.7s). These recordings were characterized by prominent owlet calls with little or no background noise and were ranked as having the best signal-to-noise ratio (5 or 4-star). Despite the calls being selected from different locations, they were acoustically similar, each consisting of a series of 3 to 4-note 1 kHz tones (peak frequency range: 937.5–1033.6 kHz; n = 5). At present, there is no evidence to suggest that these owlets have geographic variation in call structure. We made five different exemplars from these recordings by repeating tracks from the beginning to achieve a total duration of 30s each. We filtered these exemplars at 0.3 kHz to remove sounds below the frequency of the owlet calls.

All playback treatments were played at 60 dB at 5 m, which is within the natural range of all three focal species, as measured at that distance using a TES-1350A sound level meter, with A-weighting and fast setting (Table A1). The same level meter and settings were used to measure playback amplitude. We kept playback amplitude constant to control for the possibility that amplitude alone might account for differences in response among playback treatments. For that reason, we also broadcast owlet calls at the same amplitude, even though we could not confirm natural levels.

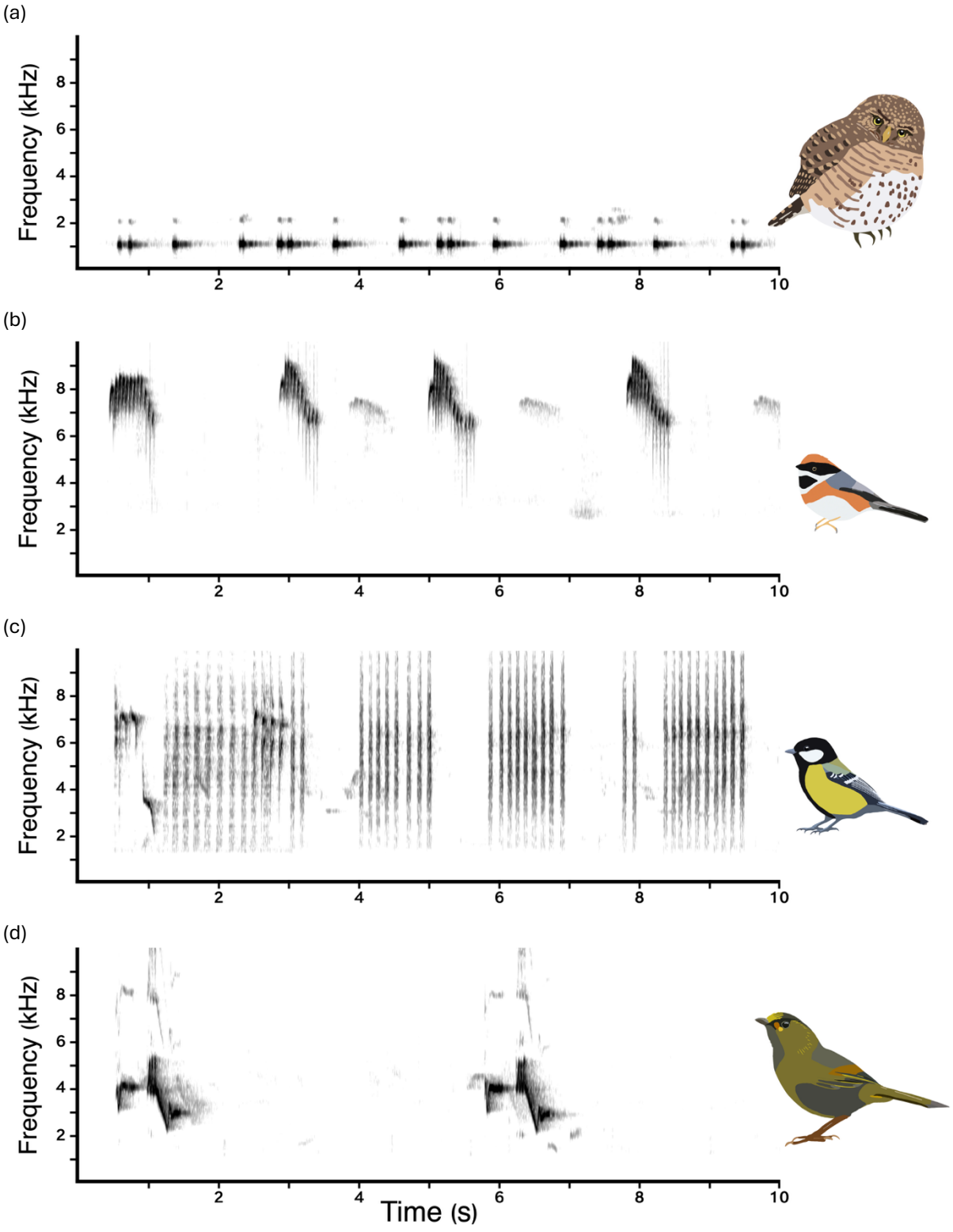


Figure 6.1. Spectrograms of selections from call types used for playback. Examples of a) collared owlet (predator) calls, b) black-throated tit (leader) mobbing calls, c) green-backed tit (follower) mobbing calls, and d) Steere's liocichla (control) songs. Bird illustrations provided by Ying-Hsuan Lu.

(d) Playback experiment and response measures

Two investigators searched for mixed flocks at each study site between 7:00 and 17:00 hours, averaging three days per week. We avoided using the same trail twice within a 24-hour period to minimize the possibility of encountering the same flock more than once. When we encountered a flock, we identified all species, determined their species roles (e.g., leader, follower, or occasional species), and counted with binoculars the number of individuals of each species. Before starting a playback experiment, we followed the flock from a distance of about 5 meters for at least 5 minutes to let the flock habituate to our presence. After a single playback, we continued walking along the trail, looking for a new flock to receive playback. The average distance between two playbacks was 492.93 ± 280.07 m (mean ± SD; range: 75.09 m - 1,610 m; n = 47). Furthermore, we were able to distinguish between flocks based on their unique composition and structure.

Playbacks were broadcast from wave files on an iPhone 13 through a JBL Go 3 Bluetooth speaker positioned on a branch at a height of about 1.5–2 meters. Two investigators positioned themselves about 5 meters away from the speaker, each at a different angle, and stood in a direction away from the movement of the mixed flocks. One investigator (C-C Liao) initiated playback when the flock was 5–8 m from the speaker. Throughout the playback trial, the investigators positioned themselves at different angles relative to the mixed flock. This allowed for a broader view when scoring the behavioural responses of the birds and minimized the potential for visual obstructions that could arise from viewing from a single angle. Playbacks were initiated when: 1) the flocking birds were foraging; 2) there was no sign of predators; and 3) there was no evidence of anti-predator behaviour by the flocking birds. The playback exemplar and order were randomized for each flock to control for potential effects of specific exemplars and order effects. We recorded 30 s of background sounds before playback and then audio-recorded the vocal responses of birds during playback and afterwards until all birds had moved more than 10 m from the speaker. The following behavioural responses were also noted by both investigators: 1) responding species (those giving mobbing alarm calls and/or approaching the speaker); and 2) how closely each bird species came to the speaker (<1m, 1-5m, 5-10m, and >10m).

Audio recordings were analysed to create an index of mobbing call intensity within the 30 second period after playback. For each 1 second interval, we noted the presence or absence (0/1) of alarm calls for each bird species in the flock. Since mobbing events often involve multiple species emitting intense and loud alarm calls simultaneously, calls from different species may overlap, making it difficult to distinguish bird species based solely on their alarm calls. However, to improve the accuracy of our data, two researchers (C-C Liao and J-C Wu) with over 20 years of birding experience in Taiwan independently scored the audio recordings. Out of a total of 10,470 one-second samples, there was a 1.19% difference in the two datasets. The discrepancy mainly occurred in the predator treatment due to: 1) some species' calls being masked by louder calls from other species; 2) the difficulty in detecting high-frequency and soft alarm calls, such as those from rufous-faced warblers and flamecrests *Regulus goodfellowi*; and 3) some alarm calls slightly crossing two 1-second sample periods, resulting in different interpretations between the two researchers. After cross-checking, our final dataset included a total of 2,143 seconds with alarm calls across 64 mixed flocks. These data were then used to calculate "calling intensity", as the proportion of one-second intervals that contained mobbing calls.

The behavioural and audio data were used to create five response variables for quantifying the effects of the playbacks. From the behavioural data, we identified 1) the species that responded by giving mobbing calls, and 2) the species that responded by approaching the speaker during each playback trial in the mixed flocks. We defined 'approaching' as birds moving within 10 meters of the speaker. This distance range was chosen because accurately identifying species and measuring distances beyond 10 meters is challenging, particularly in dense forest environments. By analyzing the audio data, we identified 3) the initiator species, which is the species that first gave an alarm call in response to the playbacks. We also measured 4) the latency to call as the time from the onset of the playback to the time when a bird initiated an alarm call, and 5) the overall calling intensity of each mixed flock.

(e) Statistical analysis

All statistical analyses and figure plotting were performed in R 4.0.3 (R Core Team, 2020).

We used chi-squared tests to examine whether leader species are more likely than follower species to initiate alarm calls upon detecting threat signals. Specifically, we used chi-square goodness-of-fit tests with Monte Carlo simulations with 2000 replicates to calculate the p-value, using the chisq.test() function from the stats package. We used Monte Carlo simulations because of the small expected values in some cells.

We used linear mixed effect models (LMMs) to examine the effects of playbacks on the timing and intensity of responses to playback. In each case, we constructed LMMs with normal distributions and identity link functions, using the lmer() function of the lme4 package. Latency to call (s) and the index of calling intensity were entered separately as response variables into LMMs. The playback type, total flock size, and total flocking species were entered as fixed effects in the model, and the identity of the playback track, trail, and study site were entered as random effects.

We used generalized linear mixed effects models (GLMMs) to examine the effects of playbacks on the dichotomous responses of whether a species gave mobbing calls or approached the speaker within 10m. The playback type, conspecific flock size, and total flocking species were entered as fixed effects, and the identity of the playback track, trial, and study site were entered as random effects in our models. As flocking birds never approached the controls (Steere's liocichla songs) in any playback experiment, these were excluded from the GLMM analysis to avoid issues associated with complete separation of data (Figure 6.4b). The GLMMs were constructed with binomial distributions and logit link functions, using the glmer() function of the lme4 package. We carried out pairwise comparisons using emmeans() function of the emmeans package. Conditional R^2 values of models were calculated using the r.squaredGLMM() function of the MuMIn package. The full model with all factors of interest was fitted before likelihood ratio tests were used to identify significant fixed effects by removing them individually from the model and assessing the change in deviance.

(f) Ethical note

Research approval and permission were granted by the Institutional Animal Care and Use Committee of Kaohsiung Medical University (IACUC-110049), and the Forestry Bureau, Council of Agriculture, Executive Yuan of Taiwan (No. 1105165388). To reduce disturbance to the birds, each playback sound was limited to a duration of 30 seconds. We also avoided visiting each trail more than once per day, thus reducing the likelihood of the same flock receiving two playback stimuli within a single day and minimizing stress to the birds.

Results

Consistent with our predictions, leader species were more likely to respond to playbacks than the follower species and were always the first to respond to the predator's calls. Leader species were proportionally more likely than follower species to be the first to emit alarm calls upon hearing acoustic information about threats (Figure 6.2). In particular, leader species always initiated mobbing calls in the predator treatment (Chi-square test, $\chi^2 = 16.00$, $df = 1$, $p < 0.001$), while their response to the follower ($\chi^2 = 0.29$, $df = 1$, $p = 0.79$) and the leader treatments ($\chi^2 = 4.00$, $df = 1$, $p = 0.08$) did not differ significantly from that of follower species (Figure 6.2; Table A2). Flocking birds responded significantly more quickly to playbacks of the predator compared to the leader or follower mobbing calls (LMM, difference among treatments: $\chi^2 = 9.98$, $df = 2$, $p < 0.01$; Figure 6.3; Table A3).

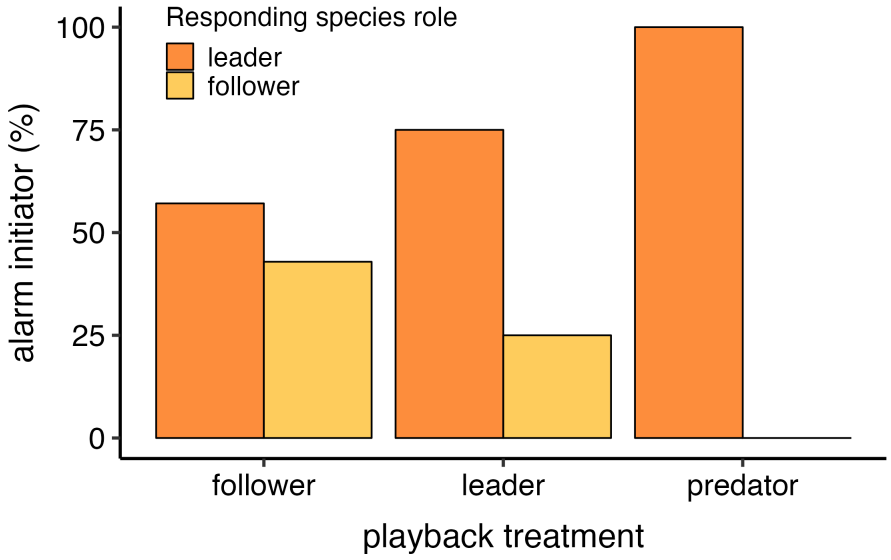


Figure 6.2. The proportion of alarm initiation by species' roles according to playback treatments. For the playbacks, follower = green-backed tit mobbing calls; leader = black-throated tit mobbing calls; predator = collared owlet calls. Specific leader and follower species responding to playbacks are listed in Table A2, and were defined by their roles in flocks, as explained in the text. The results of statistical analyses are presented in the text and Table A2; n = 14 flocks in follower treatment (data from two flocks excluded because no birds gave alarm calls), n = 16 flocks in both leader and predator treatments.

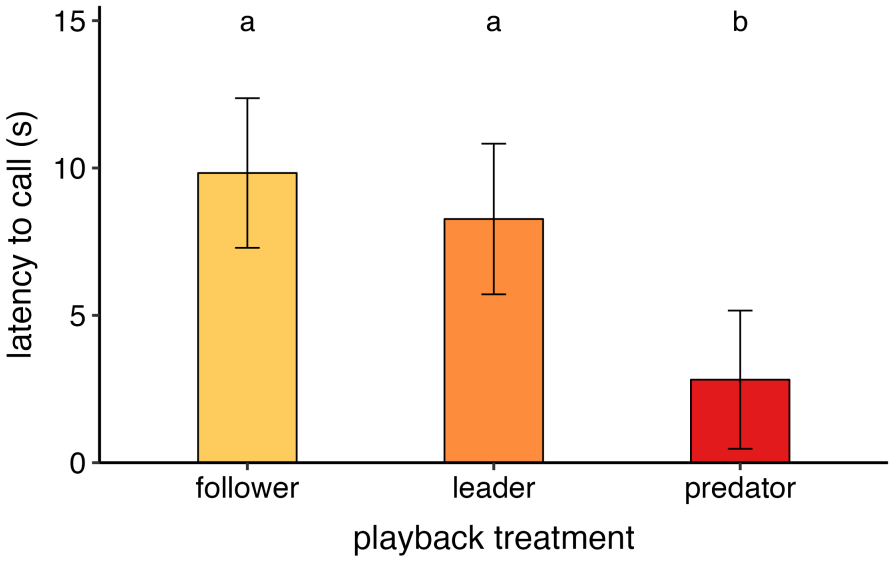


Figure 6.3. Latency to call (s) to playbacks. The latency was the first bird to call, regardless of their role in the flock. For the playbacks, follower = green-backed tit mobbing calls; leader = black-throated tit mobbing calls; predator = collared owlet calls. Predicted means ± s.e.m. shown. Different letters indicated significant differences among means as assessed by post hoc Tukey HSD test ($p < 0.05$). The results of statistical analyses are presented in the text and Table A3; n = 14 flocks in follower treatment (data from two flocks excluded because no birds gave alarm calls), n = 16 flocks in both leader and predator treatments.

As predicted, birds responded more frequently and strongly to playback of the predator's calls than they did to playback of mobbing calls. In the predator treatment, birds were both more likely to give mobbing calls and approach the speaker compared to the other treatments (alarm calling: GLMM, $\chi^2 = 43.73$, $df = 3$, $p < 0.0001$; Figure 6.4a; Table A4a; approaching: GLMM, $\chi^2 = 26.74$, $df = 2$, $p < 0.0001$; Figure 6.4b; Table A4b). Similarly, in the 30-second period after playbacks, alarm call intensity was higher in the predator treatment than in the other treatments (LMM, $\chi^2 = 55.59$, $df = 3$, $p < 0.0001$; Figure 6.4c; Table A5). Our results also demonstrated that conspecific flock sizes influenced birds' alarm calling and approaching behaviour, with larger conspecific groups in mixed flocks showing a higher probability of giving alarm calls and approaching the speaker (Table A4). Additionally, there was a slightly lower likelihood of approach when there was a greater total number of species in the mixed flock (Table A4).

Contrary to our prediction, the leader's mobbing calls did not provoke stronger responses than the follower's mobbing calls. There was no significant difference in the latency to give the first alarm call between the leader (mean ± se: 8.3 ± 2.5 s) and follower treatments (10.1 ± 2.5 s; Figure 6.3). Similarly, the probability of alarm calling (Figure 6.4a), approaching (Figure 6.4b), and even alarm call intensity (Figure 6.4c) showed no significant differences between leader and follower treatments, with the weakest or no response found in the control (Figure 6.4).

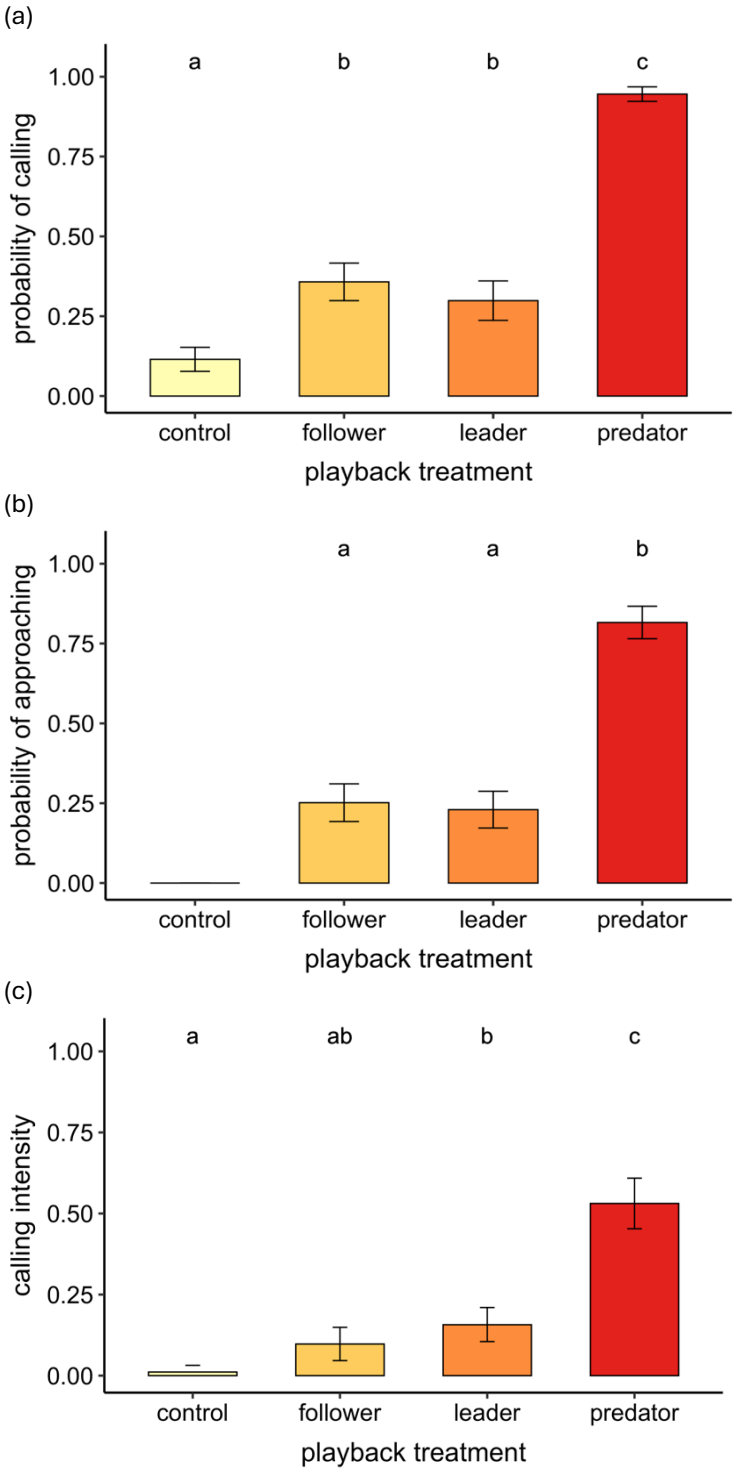


Figure 6.4. Response to playbacks: (a) probability of calling, (b) probability of approaching to the speaker, and (c) calling intensity. For the playbacks, control = Steere's liocichla songs; follower = green-backed tit mobbing calls; leader = black-throated tit mobbing calls; predator = collared owlet calls. Predicted means ± s.e.m. shown. Different letters indicated significant differences among means as assessed by post hoc Tukey HSD test ($p < 0.05$). The results of statistical analyses are presented in the text and Table A4 and A5. n = 16 flocks in each treatment.

Discussion

Our findings reveal asymmetries between leader and follower species in the response to information about danger, yet we found no evidence that a leader's mobbing calls were more evocative than those of followers. Leader species were more responsive to playbacks than follower species, and in particular always reacted first to predator calls, revealing a strong asymmetry in predator detection or communication between the two roles within mixed flocks. Birds were more responsive to direct cues from the predator than mobbing calls from flock members, showing that personal information was important in the response to danger. Social information nevertheless played a crucial role in amplifying anti-predator behaviour, with birds responding equally to mobbing calls from both leader and follower species. Our results highlight a complex dynamic in interspecific information flow about danger that will contribute to maintaining flock cohesion and promoting the formation of mixed flocks.

As predicted, but even more striking than anticipated, leader species were always the first to initiate mobbing calls in response to predator calls. This pattern means that there is a strong asymmetry in information flow, from leader to follower species, in these Taiwanese mixed flocks. We suggest that this pattern arises because the leader species were more gregarious than follower species within these mixed flocks, which is likely to reduce the costs and increase the benefits of mobbing (Goodale et al., 2010; Sridhar et al., 2009). For example, black-throated tits and Morrison's fulvettas, the two most common leader species, had mean conspecific flock sizes of 16.4 and 14.8 individuals, respectively, whereas follower species typically had 1-3 individuals (Table A6). Previous studies suggest that larger groups may dilute an individual's risk of being attacked or reduce predator attack efficiency by confusing the predator (Lima, 1995; Roberts, 1996). Hence, due to their gregarious nature, leader species may bear lower risks and costs than follower species when initiating mobbing calls. Another potential explanation is the greater presence of kin within larger groups, prompting individuals to rapidly emit alarm calls to alert their kin (Goodale & Beauchamp, 2010; Goodale & Kotagama, 2008; Sridhar et al., 2009). Indeed, black-throated tits are cooperative breeders (Li et al., 2012) that

flock with their siblings and offspring in mixed flocks (unpublished data). Previous studies also indicated that Morrison's fulvettas likely flock with their mates and offspring during non-breeding seasons (Chen & Hsieh, 2002; Lin et al., 2003). Therefore, our findings suggest that initiation of mobbing calls in response to predator calls by these leader species may be primarily influenced by their sociality, facilitated by risk dilution effect and kin-selected behaviour.

Another explanation for the faster initiation of mobbing by leader species is that their larger numbers within mixed flocks means that they simply detect predators more quickly, but we consider this less likely because predator cues were auditory. The "many eyes" effect is a prevalent adaptive explanation for enhancing anti-predator benefit in mixed flocks (Morse, 1977). It suggests that collective vigilance in larger groups enables prey to detect predators more quickly, especially via visual cues (Lima, 1995; Olson et al., 2015; Pulliam, 1973). Having more eyes looking for danger is likely to be a benefit, because different individuals can look in different directions and from different angles. However, in our study, we provided only auditory cues of danger, so flock members should have received cues of danger almost simultaneously, so that the number of individuals may make little difference to the ability to detect danger. Therefore, it seems more likely that the faster response by leaders to predator calls in our study related to communication about danger (above), rather than detection of danger. However, if auditory cues became difficult to perceive, for instance due to lower amplitude or degradation, any one individual may have a low chance of detecting danger and group size may make detection quicker, an effect more like visual detection. Future studies could examine the anti-predator benefits of group size according to sensory channel and the ease of detection. That approach could offer valuable insights into the mechanisms underlying asymmetric information transfer in intricate mixed-species animal groups.

Consistent with our second prediction, based on the principle that direct information is more reliable than social information, birds responded much more strongly to the playback of predator calls than to playback of mobbing calls. Specifically, our results showed that birds reacted to predator calls over twice as quickly as they did

to either leader or follower mobbing calls (Figure 6.3). Furthermore, the probability of alarm calling, approaching, and the intensity of calling in response to predator calls were all more than three times greater compared to the responses elicited by mobbing calls (Figure 6.4). The greater response to predator calls may be because they not only directly indicate the predator's presence, but also provide more accurate spatial information about the predator's position compared to mobbing calls (Barrera et al., 2011), which in turn can elicit the most intense mobbing. In addition, mobbing calls appear to represent the caller's perceived threat rather than the actual threat, potentially limiting their reliability or accuracy and so response by others (Carlson, Greene, et al., 2020; Carlson, Healy, et al., 2020). For example, red-breasted nuthatches, a follower species, exhibited stronger mobbing behaviour in response to direct high-threat predator calls than to indirect heterospecific mobbing calls (Carlson, Greene, et al., 2020). Similarly, aerial insectivores, such as flycatchers and drongos, tend to rely more heavily on personal information than social information while foraging in mixed flocks (Goodale & Kotagama, 2008; Jones & Sieving, 2019). To sum up, our results indicated that flocking birds were more likely to rely on personal information (from predator calls) than potentially less-reliable social information (from mobbing calls). This might help flocking birds avoid the costs of mistaking the degree of threat and help prevent error cascades (Carlson, Greene, et al., 2020).

Contrary to our third prediction, there was not a greater response to mobbing calls given by leader compared to follower species. There were no substantial differences in any of the four response variables: latency to call, probability of calling, approaching, and calling intensity, between leader and follower treatments (Figure 6.3, 6.4). In mixed flocks, leader species are often considered important information producers (Goodale et al., 2010; Pagani-Núñez et al., 2018; Zhou et al., 2021), providing foraging and/or anti-predation benefits to the other flock members (Greenberg, 2000; Martínez et al., 2018; Sullivan, 1984b). However, the dynamics of information flow among flocking species are rather complex. For instance, the orange-billed babbler and greater racket-tailed drongo, two leader species, have been documented responding to each other's aerial alarm calls in a Sri Lankan rainforest (Goodale & Kotagama, 2008). Furthermore, vocal information in

mobbing was also observed to flow from nuthatches (a follower species) to chickadees and titmice (leader species) in response to eastern screech-owls (Nolen & Lucas, 2009). Here, our results showed that more than 50% of leader species initiated alarm calls in response to follower species' mobbing calls (Figure 6.2), indicating that information about danger flows not only from leader to follower species but also vice versa (Nolen & Lucas, 2009; Zhou et al., 2021). Thus, mutual anti-predator benefits can occur between the species roles in mixed mobbing flocks, promoting positive interactions among species and thus enhancing the cohesion and formation of mixed flocks (Goodale et al., 2020; Sridhar et al., 2012).

Distinguishing among different types of asymmetries between species within mixed-species social groups is a significant challenge. In mixed flocks, certain species are better at detecting dangers, some are more likely to communicate threats, and some others have alarm calls that prove to be more reliable. These species-specific variations construct a complex dynamic of information flow within mixed flocks (Goodale et al., 2010). Other factors, such as the type of predator, urgency level of information, and kin relationships can also indirectly influence these communication networks (Nolen & Lucas, 2009; Sridhar et al., 2009). Our results highlight a strong asymmetry in responses between leader and follower species under more dangerous conditions (i.e., hearing predator calls). However, in the case of lower-urgency mobbing calls from flock members, birds showed similar anti-predator responses, indicating no asymmetry. This implies that different types of interactions within mixed flocks can lead to different symmetry in information flow. Our results suggest that sensory cues from different predators, and alarm calls of different urgency, might affect the symmetry of interspecific information within mixed flocks. Future studies that delve into these differences in information flow and utilization among species can help unravel the evolutionary mechanisms driving the formation of complex interspecific animal societies.

Appendix

Table A1. The measurements of the amplitude (dB) of the vocalizations of the different species that were simulated.

Species	n [a]	Call type	No. elements	Amplitude [b] (dB; mean ± SD)	Range (dB; Min-Max)
Black-throated tit	5	Mobbing	28	55.6 ± 2.3	51.3 – 60.2
Green-backed tit	5	Mobbing	103	57.5 ± 3.2	50.7 – 63.9
Steere's liocichla	6	Song	75	65.8 ± 3.6	58.0 – 74.1

[a] n refers to the number of different individuals recorded

[b] Measurements were made at 5 m, using a TES-1350A sound level meter, with A-weighting and fast meter settings

Table A2. Proportion as a mobbing initiator (i.e., give the first mobbing call) between follower and leader species of treatments.

	Mobbing initiator			
Treatment [a]	Follower species [b]	Leader species [b]	χ^2	*p*-value [c]
Follower	*n* = 6 (MF: 1; GBT:3; RFW: 1; WES: 1)	*n* = 8 (BTT: 6; MF: 2)	0.29	0.79
Leader	*n* = 4 (BTT: 1; MF: 1; RFW: 1; WES: 1)	*n* = 12 (BTT: 12)	4	0.08
Predator	*n* = 0 (Non)	*n* = 16 (BTT: 7; MF: 9)	16	< 0.001

[a] For the playback treatments, follower = green-backed tit mobbing calls; leader = black-throated tit mobbing calls; predator = collared owlet calls

[b] Species codes: black-throated tit (BTT), Morrison's fulvetta (MF), green-backed tit (GBT), rufus-faced warbler (RFW), white-eared sibia (WES)

[c] Chi-square goodness-of-fit test is used to assess whether the frequencies of mobbing call initiation differed from a random distribution (i.e., 50% for each species role) between the two species roles

Table A3. The first mobbing call given in response to acoustic cues and signals of danger. Table shows results of linear mixed effects model (LMM) to investigate the effects of threat signals on the latency to call (s).

Response variable	Fixed effects [a]	Parameter estimates		Likelihood ratio tests			R^{2} [c]
		Factor levels	Effect ± SE	*df*	χ^2	*p* [b]	
Latency to call (LMM)							0.32
	(Intercept)		9.47±2.62				
	Treatment (Follower)	Leader	-1.55±2.19	2	9.98	<0.01	
		Predator	-7.00±2.26				
	Total flock size		-0.03±0.06	1	0.31	0.58	
	Total flocking species		0.28±0.59	1	0.30	0.59	
Random factor	Track ID		1.62				
	Trail ID		0.00				
	Study site ID		0.00				

[a] Bolded factors represent a significant change in deviance when removed from the model (p<0.05)
[b] P-value for each factor is derived from a likelihood ratio test for changes in deviance when models with and without that factor are compared
[c] Conditional R^2 values

Table A4. Flocking birds' response to playbacks. Table shows results of generalized linear mixed effects model (GLMM) to investigate the effects of different treatments on a) the probability of calling, and b) the probability of approaching the speaker.

Response variable	Fixed effects [a]	Parameter estimates		Likelihood ratio tests			R^{2} [c]
		Factor levels	Effect ± SE	*df*	χ^2	*p* [b]	
(a) Probability of calling (GLMM)							0.56
	(Intercept)		-1.86±0.58				
	Treatment (Control)	Follower	1.45±0.42	3	43.73	<0.0001	
		Leader	1.19±0.42				
		Predator	4.89±0.57				
	Conspecific flock size [d]		0.07±0.02	1	17.37	<0.0001	
	Total flocking species		-0.10±0.07	1	2.43	0.12	
Random factor	Track ID		0.08				
	Trail ID		0.18				
	Study site ID		0.00				
(b) Probability of approaching (GLMM)							0.40
	(Intercept)		-0.71±0.55				
	Treatment (Follower)	Leader	-0.15±0.37	2	26.74	<0.0001	
		Predator	2.63±0.39				
	Conspecific flock size [d]		0.06±0.02	1	12.54	<0.001	
	Total flocking species		-0.12±0.07	1	5.94	<0.05	
Random factor	Track ID		0.00				
	Trail ID		0.40				
	Study site ID		0.00				

[a] Bolded factors represent a significant change in deviance when removed from the model (p<0.05)
[b] P-value for each factor is derived from a likelihood ratio test for changes in deviance when models with and without that factor are compared
[c] Conditional R^2 values
[d] The number of individuals for each species within a mixed flock

Table A5. Alarm calls given by flocking birds during 30 s after playbacks. Table shows the results of linear mixed effects models (LMM) examining the effects of different treatments on the index of calling intensity.

Response variable	Fixed effects [a]	Parameter estimates		Likelihood ratio tests			R^{2} [c]
		Factor levels	Effect ± SE	*df*	χ^2	*p* [b]	
Calling intensity (LMM)							0.80
	(Intercept)		0.05±0.04				
	Treatment (Control)	Follower	0.09±0.04	3	55.59	<0.0001	
		Leader	0.14±0.04				
		Predator	0.51±0.04				
	Total flock size		0.00±0.00	1	1.84	0.18	
	Total flocking species		-0.01±0.01	1	3.17	0.08	
Random factor	Track ID		0.00				
	Trail ID		0.00				
	Study site ID		0.00				

[a] Bolded factors represent a significant change in deviance when removed from the model ($p<0.05$)
[b] P-value for each factor is derived from a likelihood ratio test for changes in deviance when models with and without that factor are compared
[c] Conditional R^2 values

Table A6. Twenty-nine bird species were recorded participating in 64 mixed-species flocks in this study. Flocking frequency (%), mean number (±SD) and percentages of species roles in the mixed flocks of each species are presented.

Bird species	Scientific name [a]	Flocking frequency	Mean number	Species role [b]		
				L	F	O
Black-throated tit	*Aegithalos concinnus*	90.6	16.4±11.6	89.7	10.3	0.0
Morrison's fulvetta	*Alcippe morrisonia*	53.1	14.8±12.2	73.5	23.5	2.9
Taiwan yuhina	*Yuhina brunneiceps*	46.9	12.6±10.4	23.3	26.7	50.0
Rufous-faced warbler	*Abroscopus albogularis*	95.3	3.3±2.0	0.0	96.7	3.3
Green-backed tit	*Parus monticolus*	68.8	1.7±0.7	0.0	97.7	2.3
Rufous-capped babbler	*Cyanoderma ruficeps*	51.6	3.2±2.0	0.0	81.8	18.2
Steere's liocichla	*Liocichla steerii*	29.7	2.6±1.1	0.0	10.5	89.5
White-eared sibia	*Heterophasia auricularis*	14.1	3.7±1.7	0.0	66.7	33.3
Dusky fulvetta	*Schoeniparus brunneus*	10.9	2.0±0.0	0.0	14.3	85.7
White-bellied erpornis	*Erpornis zantholeuca*	9.4	3.0±1.4	0.0	100.0	0.0
Arctic warbler [1]	*Phylloscopus borealis*	9.4	1.2±0.4	0.0	16.7	83.3
Taiwan scimitar-babbler	*Pomatorhinus musicus*	7.8	2.4±0.9	0.0	20.0	80.0
Collared bush-robin	*Tarsiger johnstoniae*	7.8	1.0±0.0	0.0	0.0	100.0
Taiwan yellow tit	*Machlolophus holsti*	6.3	1.0±0.0	0.0	100.0	0.0
Fire-breasted flowerpecker	*Dicaeum ignipectus*	6.3	1.8±0.5	0.0	25.0	75.0
Flamecrest	*Regulus goodfellowi*	4.7	2.0±1.0	0.0	100.0	0.0
Gray-chinned minivet	*Pericrocotus solaris*	4.7	2.0±0.0	0.0	100.0	0.0
Taiwan barwing	*Actinodura morrisoniana*	4.7	3.7±0.6	0.0	66.7	33.3
White-tailed robin	*Myiomela leucura*	4.7	1.3±0.6	0.0	33.3	66.7
Black-naped monarch	*Hypothymis azurea*	3.1	1.5±0.7	0.0	100.0	0.0
Eurasian nuthatch	*Sitta europaea*	3.1	2.5±0.7	0.0	50.0	50.0
Gray-capped woodpecker	*Yungipicus canicapillus*	1.6	1.0	0.0	100.0	0.0
Snowy-browed flycatcher	*Ficedula hyperythra*	1.6	1.0	0.0	100.0	0.0
Taiwan fulvetta	*Fulvetta formosana*	1.6	1.0	0.0	100.0	0.0
Black-necklaced scimitar-babbler	*Erythrogenys erythrocnemis*	1.6	2.0	0.0	0.0	100.0
Rusty laughingthrush	*Pterorhinus poecilorhynchus*	1.6	25.0	100.0	0.0	0.0
Swinhoe's white-eye	*Zosterops simplex*	1.6	5.0	0.0	0.0	100.0
White-rumped munia	*Lonchura striata*	1.6	13.0	0.0	0.0	100.0
Yellowish-bellied bush warbler	*Horornis acanthizoides*	1.6	1.0	0.0	0.0	100.0

[a] Scientific name follows Clements *et al*. (2022)

[b] Percentage of species roles, including leader species (L), follower species (F), and occasional species (O). For definitions of the species roles, please refer to the Methods section

[1] Migratory birds of Taiwan

References

Barrera, J. P., Chong, L., Judy, K. N., & Blumstein, D. T. (2011). Reliability of public information: Predators provide more information about risk than conspecifics. *Animal Behaviour*, *81*(4), 779–787. https://doi.org/10.1016/j.anbehav.2011.01.010

Carlson, N. V., Greene, E., & Templeton, C. N. (2020). Nuthatches vary their alarm calls based upon the source of the eavesdropped signals. *Nature Communications*, *11*, 526. https://doi.org/10.1038/s41467-020-14414-w

Carlson, N. V., Healy, S. D., & Templeton, C. N. (2020). What makes a 'community informant'? Reliability and anti-predator signal eavesdropping across mixed-species flocks of tits. *Animal Behavior and Cognition*, *7*(2), 214–246. https://doi.org/10.26451/abc.07.02.13.2020

Chen, C.-C., & Hsieh, F. (2002). Composition and foraging behaviour of mixed-species flocks led by the Grey-cheeked Fulvetta in Fushan Experimental Forest, Taiwan. *Ibis*, *144*(2), 317–330. https://doi.org/10.1046/j.1474-919X.2002.00020.x

Chen, C.-C., Liao, C.-C., & Walther, B. A. (2022). Interspecific competition and facilitation coexist in mixed-species bird flocks of montane coniferous forests in Taiwan. *Journal of Avian Biology*, 2022, e02947. https://doi.org/10.1111/jav.02947

Clements, J. F., Schulenberg, T. S., Iliff, M. J., Fredericks, T. A., Gerbracht, J. A., Lepage, D., Billerman, S. M., Sullivan, B. L., & Wood, C. L. (2022). The eBird/ Clements checklist of birds of the world (version 2022). Cornell Lab of Ornithology. https://www.birds.cornell.edu/clementschecklist/

Coppinger, B. A., Kania, S. A., Lucas, J. R., Sieving, K. E., & Freeberg, T. M. (2020). Experimental manipulation of mixed-species flocks reveals heterospecific audience effects on calling. *Animal Behaviour*, *167*, 193–207. https://doi.org/10.1016/j.anbehav.2020.07.006

Curio, E. (1978). The adaptive significance of avian mobbing: I. teleonomic hypotheses and predictions. *Zeitschrift Für Tierpsychologie*, *48*(2), 175–183. https://doi.org/10.1111/j.1439-0310.1978.tb00254.x

Dutour, M., Léna, J. P., & Lengagne, T. (2017). Mobbing calls: a signal transcending species boundaries. *Animal Behaviour*, *131*, 3–11. https://doi.org/10.1016/j.anbehav.2017.07.004

Goodale, E., & Beauchamp, G. (2010). The relationship between leadership and gregariousness in mixed-species bird flocks. *Journal of Avian Biology*, *41*(1), 99–103. https://doi.org/10.1111/j.1600-048X.2009.04828.x

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C., & Ruxton, G. D. (2010). Interspecific information transfer influences animal community structure. *Trends in Ecology and Evolution*, *25*(6), 354–361. https://doi.org/10.1016/j.tree.2010.01.002

Goodale, E., & Kotagama, S. W. (2005). Testing the roles of species in mixed-species bird flocks of a Sri Lankan rain forest. *Journal of Tropical Ecology*, *21*(6), 669–676. https://doi.org/10.1017/S0266467405002609

Goodale, E., & Kotagama, S. W. (2008). Response to conspecific and heterospecific alarm calls in mixed-species bird flocks of a Sri Lankan rainforest. *Behavioral Ecology*, *19*(4), 887–894. https://doi.org/10.1093/beheco/arn045

Goodale, E., Sridhar, H., Sieving, K. E., Bangal, P., Colorado Z., G. J., Farine, D. R., Heymann, E. W., Jones, H. H., Krams, I., Martínez, A. E., Montaño-Centellas, F., Muñoz, J., Srinivasan, U., Theo, A., & Shanker, K. (2020). Mixed company: a framework for understanding the composition and organization of mixed-species animal groups. *Biological Reviews*, *95*(4), 889–910. https://doi.org/10.1111/brv.12591

Greenberg, R. (2000). Birds of many feathers: The formation and structure of mixed-flocks of forest birds. In S. B. P. A. Garber (Ed.), *On the Move: How and Why Animals Travel in Groups*, pp. 521–558. University of Chicago Press.

Hämäläinen, R., Kajanus, M. H., Forsman, J. T., Kivelä, S. M., Seppänen, J. T., & Loukola, O. J. (2023). Ecological and evolutionary consequences of selective interspecific information use. *Ecology Letters*, *26*, 490–503. https://doi.org/10.1111/ele.14184

Hutto, R. L. (1994). The composition and social organization of flocks in a tropical deciduous forest in Western Mexico. *Condor*, *96*(1), 105–118.

Jiang, D., Sieving, K. E., Meaux, E., & Goodale, E. (2020). Seasonal changes in mixed-species bird flocks and antipredator information. *Ecology and Evolution*, *10*(12), 5368–5382. https://doi.org/10.1002/ece3.6280

Jones, H. H., & Sieving, K. E. (2019). Foraging ecology drives social information reliance in an avian eavesdropping community. *Ecology and Evolution*, *9*(20), 11584–11597. https://doi.org/10.1002/ece3.5561

Li, J., Lv, L., Wang, Y., Xi, B., & Zhang, Z. (2012). Breeding biology of two sympatric Aegithalos tits with helpers at the nest. *Journal of Ornithology*, *153*(2), 273–283. https://doi.org/10.1007/s10336-011-0740-z

Liao, C.-C. (2015). *Mixed-species bird flock structure and its relationship with environmental factors in high elevation areas of Taiwan* (M.S. thesis). National Taiwan University. https://doi.org/10.6342/NTU201600360

Liao, C.-C., Ding, T.-S., & Chen, C.-C. (2022). The formation of “mega-flocks” depends on vegetation structure in montane coniferous forests of Taiwan. *Ecology and Evolution*, *12*(2), 1–12. https://doi.org/10.1002/ece3.8608

Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, *49*(1), 11–20. https://doi.org/10.1016/0003-3472(95)80149-9

Limparungpatthanakij, W., Brockelman, W. Y., Gale, G., & Round, P. D. (2019). Woodpeckers benefit from participation in mixed-species flocks in lowland deciduous forest, Huai Kha Khaeng Wildlife Sanctuary, Thailand. *Forktail*, *35*, 57–59.

Lin, S. R., Chou, L., & Lin, Y. (2003). Roosting behavior of the Grey-Cheeked Fulvetta *Alcippe morrisonia Swinhoe* in the non-breeding season. *Taiwan Journal of Biodiversity*, *5*(1), 27–32.

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on heterospecific alarm calls: From mechanisms to consequences. *Biological Reviews*, *90*(2), 560–586. https://doi.org/10.1111/brv.12122

Magrath, R. D., Pitcher, B. J., & Gardner, J. L. (2007). A mutual understanding? Interspecific responses by birds to each other's aerial alarm calls. *Behavioral Ecology*, *18*(5), 944–951. https://doi.org/10.1093/beheco/arm063

Magrath, R. D., Pitcher, B. J., & Gardner, J. L. (2009). An avian eavesdropping network: Alarm signal reliability and heterospecific response. *Behavioral Ecology*, *20*(4), 745–752. https://doi.org/10.1093/beheco/arp055

Mangini, G. G., Rutt, C. L., Sridhar, H., Buitron, G., Muñoz, J., Robinson, S. K., Montaño-centellas, F., Zarco, A., Fanjul, M. E., Fernández-arellano, G., & Mangini, G. G. (2023). A classification scheme for mixed-species bird flocks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *378*, 20220100. https://doi.org/10.1098/rstb.2022.0100

Martínez, A. E., Parra, E., Muellerklein, O., & Vredenburg, V. T. (2018). Fear-based niche shifts in neotropical birds. *Ecology*, *99*(6), 1338–1346. https://doi.org/10.1002/ecy.2217

Martínez, A. E., & Zenil, R. T. (2012). Foraging guild influences dependence on heterospecific alarm calls in Amazonian bird flocks. *Behavioral Ecology*, *23*(3), 544–550. https://doi.org/10.1093/beheco/arr222

McLachlan, J. R., Ratnayake, C. P., & Magrath, R. D. (2019). Personal information about danger trumps social information from avian alarm calls. *Proceedings. Biological Sciences*, *286*(1899), 20182945. https://doi.org/10.1098/rspb.2018.2945

Morse, D. H. (1970). Ecological aspects of some mixed-species foraging flocks of birds. *Ecological Monographs*, *40*(1), 119–168. https://doi.org/10.2307/1942443

Morse, D. H. (1977). Avoidance behavior in heterospecific groups. *BioScience*, *27*(5), 332–339. https://doi.org/10.2307/1297632

Munn, C. A. (1985). Permanet canopy and understory flocks in Amazonia: Species composition and population density. In P. Buckley, M. Foster, E. Morton, R. Ridgely, & F. Buckley (Eds.), *Neotropical ornithology*, pp. 683–712. American Ornithologist' Union.

Munn, C. A., & Terborgh, J. W. (1979). Multi-species territoriality in Neotropical foraging flocks. *Condor*, *81*(4), 338–347. https://doi.org/10.2307/1366956

Nolen, M. T., & Lucas, J. R. (2009). Asymmetries in mobbing behaviour and correlated intensity during predator mobbing by nuthatches, chickadees and titmice. *Animal Behaviour*, *77*(5), 1137–1146. https://doi.org/10.1016/j.anbehav.2009.01.023

Olson, R. S., Haley, P. B., Dyer, F. C., & Adami, C. (2015). Exploring the evolution of a trade-off between vigilance and foraging in group-living organisms. *Royal Society Open Science*, *2*(9), 150135. https://doi.org/10.1098/rsos.150135

Pagani-Núñez, E., Xia, X., Beauchamp, G., He, R., Husson, J. H. D., Liang, D., & Goodale, E. (2018). Are vocal characteristics related to leadership patterns in mixed-species bird flocks? *Journal of Avian Biology*, *49*(5), 1–9. https://doi.org/10.1111/jav.01674

Poulsen, B. O. (1996). Structure, dynamics, home range and activity pattern of mixed-species bird flocks in a montane Alder-dominated secondary forest in Ecuador. *Journal of Tropical Ecology*, *12*(3), 333–343. https://doi.org/10.1017/S0266467400009524

Pulliam, H. R. (1973). On the advantages of flocking. *Journal of Theoretical Biology*, *38*(2), 419–422. https://doi.org/10.1016/0022-5193(73)90184-7

R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Roberts, G. (1996). Why individual vigilance declines as group size increases. *Animal Behaviour*, *51*(5), 1077–1086. https://doi.org/10.1006/anbe.1996.0109

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. *Behavioral Ecology*, *21*(2), 396–403. https://doi.org/10.1093/beheco/arp203

Severinghaus, L.-L., Ding, T.-S., Fang, W.-H., Lin, W.-H., Tsai, M.-C., & Yen, C.-W. (2010). *The avifauna of Taiwan*. Taipei, Taiwan: Forestry Bureau of Council of Agriculture of Executive Yuan.

Sridhar, H., Beauchamp, G., & Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour*, *78*(2), 337–347. https://doi.org/10.1016/j.anbehav.2009.05.008

Sridhar, H., Srinivasan, U., Askins, R. A., Canales-Delgadillo, J. C., Chen, C.-C., Ewert, D. N., Gale, G. A., Goodale, E., Gram, W. K., Hart, P. J., Hobson, K. A., Hutto, R. L., Kotagama, S. W., Knowlton, J. L., Lee, T. M., Munn, C. A., Nimnuan, S., Nizam, B. Z., Péron, G., Robin, V. V., Rodewald, A. D., Rodewald, P. G., Thomson, R. L., Trivedi, P., Van Wilgenburg, S. L., & Shanker, K. (2012). Positive relationships between association strength and phenotypic similarity characterize the assembly of mixed-species bird flocks worldwide. *American Naturalist*, *180*(6), 777–790. https://doi.org/10.1086/668012

Sullivan, K. A. (1984a). Information exploitation by downy woodpeckers in mixed-species flocks. *Behaviour*, *91*(4), 294–311.

Sullivan, K. A. (1984b). The advantages of social foraging in downy woodpeckers. *Animal Behaviour*, *32*, 16–22. https://doi.org/10.1016/S0003-3472(84)80319-X

Templeton, C. N., & Greene, E. (2007). Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *Proceedings of the National*

Academy of Sciences, *104*(13), 5479–5482. https://doi.org/10.1073/pnas.0605183104

Turner, C. R., Spike, M., & Magrath, R. D. (2023). The evolution of eavesdropping on heterospecific alarm calls: Relevance, reliability, and personal information. *Ecology and Evolution*, *13*(7), 1–16. https://doi.org/10.1002/ece3.10272

Zhou, L., Peabotuwage, I., Luo, K., Quan, R. C., & Goodale, E. (2021). Using playback to test leadership in mixed-species flocks and compare flocking with mobbing. *Animal Behaviour*, *180*, 151–166. https://doi.org/10.1016/j.anbehav.2021.08.012

Chapter 7

General Discussion



A family group of choughs rests together after feeding, basking lazily in the autumn sunshine. Studying these remarkable birds has made my PhD journey both fascinating and enjoyable, and I have learned a great deal from them along the way.

Social life depends on effective communication because group-living animals must coordinate their behaviour to maintain cohesion and realise the benefits of sociality. My studies show that acoustic communication plays a central role in how social birds manage predation risk and coordinate collective antipredator behaviour. In white-winged choughs, adults use a functionally referential alarm-call system that conveys information on both threat type and urgency, allowing receivers to respond appropriately to different kinds of danger. However, this ability does not emerge immediately: juveniles remain poor at interpreting alarm calls for months after fledging, suggesting that prolonged social protection may relax selection for early antipredator competence and allow these responses to develop gradually. At the group level, choughs integrate multiple components of social information, using alarm-call type to shape the form of the response and caller number as a cue to reliability, which in turn influences both response intensity and the likelihood that alarm information is propagated further. Beyond single-species societies, my work on mixed-species flocks shows that information about danger can flow asymmetrically between species, with leader species contributing information more rapidly than follower species during mobbing. Together, these findings suggest that sociality not only increases animals' reliance on social information, but also favours communication systems that allow information about danger to be encoded, assessed, and shared in ways that support effective antipredator behaviour.

In this chapter, I summarize the main themes of the thesis and then discuss broader future directions emerging from the empirical chapters.

Group coordination and collective decision-making

In Chapter 2, I review how acoustic signals and movement cues coordinate activities in group-living vertebrates, particularly terrestrial birds and mammals, thereby establishing the conceptual foundation for this thesis. I focus on collective behaviours (see definition in Chapter 2) in foraging, antipredator, and movement contexts, and outline a conceptual framework for predicting when coordination is more likely to rely on acoustic signals versus movement cues. In brief, the framework proposes that behaviours involving the timing of events or the expression of specific actions should rely more heavily on acoustic

signals, whereas decisions involving complex choices with multiple options, such as direction or destination, should more often depend on movement cues, because acoustic communication is more susceptible to informational masking and discrimination limits (e.g. Weber's Law effects). This review also highlights the importance of quorum-like thresholds in collective decision-making and identifies broader future directions, including multimodal communication and coordination in mixed-species animal groups. In this way, it sets the context for my empirical chapters, which examine how different forms of information are used to coordinate behaviour in both single-species and mixed-species systems, with a particular focus on antipredator contexts.

From functional reference to call meaning

In Chapter 3, I show that adult white-winged choughs respond appropriately to different alarm calls, consistent with a system of functionally referential alarm communication. In that chapter, I focus on the production context and behavioural consequences of calls within the framework of functional reference, without making assumptions about the underlying cognitive mechanisms. This framework is valuable in ecological studies because it provides a robust way to identify meaningful relationships between signals, contexts, and receiver responses (Evans et al., 1993; Macedonia & Evans, 1993). Building on this foundation, recent work in animal communication and animal linguistics has opened up further questions about how call meaning is structured and interpreted by receivers (Berthet et al., 2023; Suzuki, 2018, 2024). For example, these approaches explore whether calls that appear functionally referential are also used in other contexts, whether meaning depends partly on social or situational context (Berthet et al., 2023, 2025; Fischer et al., 2015; Rajan et al., 2025; Scarantino & Clay, 2015; Wheeler & Fischer, 2012), and whether receivers form mental representations of external events when they hear calls (Berthet et al., 2026; Suzuki, 2018). These ideas are helpful because they allow us to ask whether meaning resides primarily in a particular call type, or whether it instead depends on a combination of call structure, call rate, production context, caller state, and other information available to receivers.

This broader perspective may be especially valuable for future work on white-winged choughs. Although Chapter 3 focused on alarm contexts, my field observations suggest that some alarm calls, particularly terrestrial alarm calls, may also occur in a wider range of situations, such as inter-group interactions or mobbing events. This raises the possibility that calls associated with predator encounters may have broader or more flexible functions than currently recognised, or that there are more subtle, undescribed variations in call structure. For example, noisy miners (*Manorina melanocephala*) give 'chur' calls to terrestrial or perched predators, but sometimes also in the apparent absence of threats, possibly as contact calls (Kennedy et al., 2009; Cunningham & Magrath, 2017). Similar patterns have been reported in several non-human primates, where alarm calls, especially those associated with terrestrial predators, are also produced in response to non-predatory stimuli, including non-threatening animals and social interactions, such as in putty-nosed monkeys (*Cercopithecus nictitans*) (Arnold & Zuberbühler, 2013), lemurs (Fichtel & Kappeler, 2002), and tufted capuchin monkeys (*Cebus apella*) (Wheeler, 2010). A useful next step would therefore be to examine chough call production and structure across a broader range of ecological and social contexts. Doing so would provide a fuller understanding of how these calls are used and interpreted in this highly social bird species.

Social buffering and the ontogeny of alarm-call responses

In Chapter 4, I show that alarm-call responses develop slowly in juvenile white-winged choughs compared with most birds studied to date, and are more similar to the prolonged developmental patterns reported in social mammals. In this study, I focused on a relatively short developmental window, comparing the responses of juveniles (6–12 months old) with those of adults (≥5 years old). Future work on highly social birds such as white-winged choughs could extend this approach in several important directions.

First, longitudinal studies of known-age individuals would allow a more precise determination of when juveniles begin to exhibit adult-like responses and whether different alarm-call types follow different developmental trajectories. To date, such studies have been conducted mainly in social mammals (Fichtel, 2008; Fischer et al.,

2000; Mateo, 1996; McCowan et al., 2001; Seyfarth & Cheney, 1986), with relatively few comparable examples in birds (Haff & Magrath, 2013; Magrath et al., 2006). Previous work suggests that juveniles often learn to discriminate alarm from non-alarm calls before they show fully specific, adult-like responses (Fichtel, 2008; Fischer et al., 2000; Magrath et al., 2006), and that responses to higher-urgency alarm calls may sometimes emerge earlier than responses to lower-urgency calls (Mateo, 1996), a pattern broadly consistent with that observed in juvenile white-winged choughs. Acoustic stereotypy could also contribute to differences among alarm-call types: if flee alarms are more acoustically consistent across callers, juveniles may find them easier to recognise. In addition to differences among alarm types, future studies could examine how responses generalise across callers. Although adults and juveniles in Chapter 4 received the same unfamiliar exemplars, juveniles might initially learn to respond to familiar group members' calls before generalising more broadly. Comparing familiar and unfamiliar callers and quantifying acoustic variation within and among individuals would help test these possibilities. Understanding how responses develop across alarm types and generalise across callers would help reveal which components of alarm-call responses are acquired first, and how variation in urgency, call structure, and social experience shapes the development of antipredator behaviour.

Second, the social environment is likely to play a key role in shaping juvenile development (Dezecache et al., 2019; Heinsohn, 1991; Hollén & Manser, 2006; Hollén & Radford, 2009). In cooperative breeders such as choughs, juveniles in larger groups may be able to rely more heavily on other group members for protection, potentially delaying the acquisition of appropriate alarm-call responses. This idea is consistent with evidence that juvenile choughs in larger groups receive more provisioning but develop foraging skills more slowly (Heinsohn, 1991). However, larger social groups may not always delay development. In cooperatively breeding Australian magpies (*Gymnorhina tibicen dorsalis*), juveniles in larger groups showed better cognitive performance as they developed, suggesting that increased sociality can also promote some aspects of development (Ashton et al., 2018). Testing whether alarm-call responses develop differently under varying degrees of social buffering would help clarify when sociality

delays development and when it promotes it, and more broadly how social structure shapes the ontogeny of communication.

More broadly, variation in the development of antipredator behaviour across species is likely to be shaped by interacting life-history and socioecological factors, including social complexity, the duration of juvenile dependence, age at sexual maturity, dispersal timing, and local predation risk. Life-history differences among avian lineages may also be relevant, as Australian old-endemic passerines tend to have smaller clutches and longer maximum recorded lifespans than more recently arrived species (Bech et al., 2016). Slow development of alarm-call responses in choughs could therefore reflect their broader developmental schedule as well as social buffering, although the present study cannot distinguish their relative contributions. Comparative and meta-analytic approaches may provide a useful framework for addressing these questions, although progress will depend on the availability of detailed developmental data from a broader range of species (Lea & Blumstein, 2011; Leighton, 2017; Leighton & Birmingham, 2021). Identifying which factors, or combinations of factors, best predict developmental trajectories would contribute to a broader framework for understanding how selection shapes not only the structure of communication systems, but also their ontogeny.

From antipredator decisions to collective movement in choughs

In Chapter 5, I show that white-winged choughs integrate urgency and numerical reliability when making collective antipredator decisions. Alarm-call type determines the form of the response, whereas caller number acts as a cue for reliability, shaping both response intensity and the likelihood that listeners will also call, thereby leading to information propagation. These findings suggest that collective decisions emerge from the integration of multiple dimensions of social information, combined through simple, flexible decision rules. Such rules may allow groups to respond effectively to uncertain threats while minimising the risk of cascades of false information.

Although this study focuses on antipredator contexts, similar decision-making processes are likely to operate in other contexts, such as collective movement. Coordinating the timing of group movements is crucial for maintaining group cohesion, and many group-living animals use vocal signals to indicate readiness to travel or to initiate departures (Bousquet et al., 2011; Dibnah et al., 2022; Fischer & Zinner, 2011; Sperber et al., 2017; Walker et al., 2017). In some species, such decisions operate through quorum-like processes, in which group movement occurs only when signalling activity exceeds a threshold (Bousquet et al., 2011; Dibnah et al., 2022; Walker et al., 2017). For example, meerkats (*Suricata suricatta*) use 'moving' calls to coordinate departures, with speed and departure probability increasing as more individuals join the moving-call chorus (Bousquet et al., 2011). By contrast, in other species, movement decisions may be influenced more strongly by particular individuals. In these cases, individuals attempting to initiate movement use vocalisations to recruit followers and avoid becoming isolated. For instance, green woodhoopoes (*Phoeniculus purpureus*) produce calls when departing a group for a new foraging patch, increasing the likelihood of attracting other group members to join (Radford, 2004).

Based on my field observations, choughs seem to use different decision rules to coordinate group movements. First, they produce 'moving' calls (Figure 7.1a) to initiate departures from one foraging patch to another or from a resting site, possibly reflecting a quorum-like process. When multiple individuals give 'moving' calls, this appears to prompt collective departures over relatively short distances. By contrast, choughs sometimes use 'recruitment' calls (Figure 7.1b) to gather group members for longer-distance movements (typically >100 m). In these cases, one or a few individuals often appear to initiate movement, flying first and then producing 'recruitment' calls while in flight, after which other group members follow. These observations raise the possibility that collective decision-making in choughs is flexible and context-dependent, with different decision rules operating under different ecological conditions and movement scales. This system therefore provides a useful opportunity for future work to examine how animals may switch between alternative decision-making processes when coordinating group behaviour.

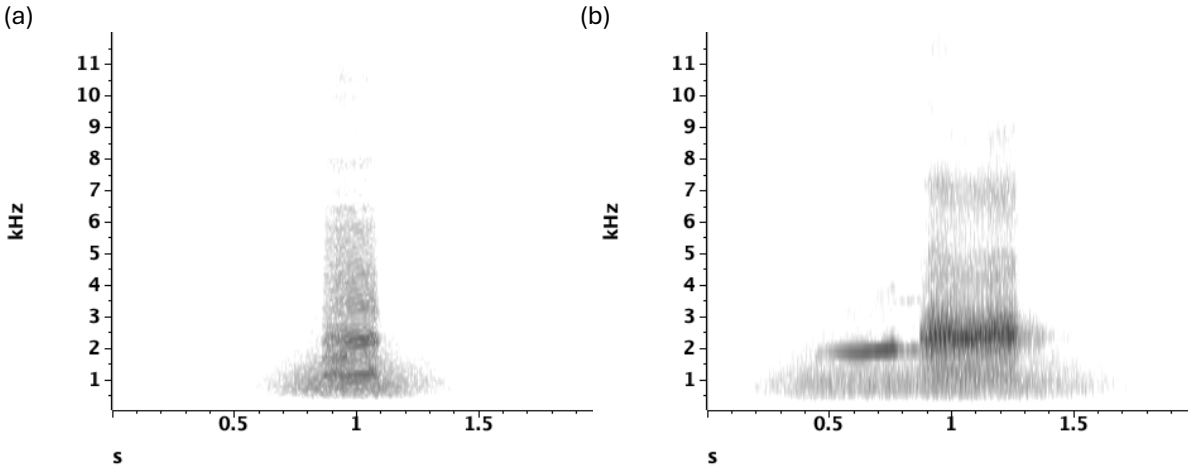


Figure 7.1. Spectrograms of calls used in group movement coordination in white-winged choughs: (a) 'moving' calls, typically associated with short-distance departures, and (b) 'recruitment' calls, typically associated with longer-distance movements.

Information flow and coordination in mixed-species animal groups

In Chapter 6, I show that information flow in mixed-species mobbing flocks is asymmetric, with leader species, typically those with larger conspecific group sizes, always initiating mobbing calls in response to playback of predator calls. However, birds show no difference in their responses to mobbing calls from leader and follower species, indicating a shared use of social information. These findings highlight that while species differ in their contribution to information production, mobbing calls function as a common signal that coordinates antipredator behaviour across species.

Interspecific information flow is known to shape the social structure of animal communities (Goodale et al., 2010, 2020; Goodale & Magrath, 2024; Martínez et al., 2018). In this study, leader species were more gregarious than follower species, typically occurring in groups of more than 10 conspecifics, whereas follower species were usually found in much smaller groups of one to three individuals. This difference in social structure suggests that the disproportionate role of leader species in initiating mobbing may be driven by their higher sociality, with group living potentially reducing the costs of signalling through risk dilution and kin-selected benefits (Goodale & Beauchamp, 2010; Sridhar et al., 2009). Such a system, characterised by numerically dominant leader (or

'nuclear') species, is commonly described in regions such as Taiwan (this study site) and Sri Lanka (Mangini et al., 2023). However, mixed-species flocks can exhibit a wide range of social structure and composition, such as antwren mixed flocks in Neotropical forests and chickadee–tit (Paridae) flocks in northern temperate regions (Mangini et al., 2023). Whether similarly strong asymmetries in information flow occur across these diverse systems remains unclear.

More broadly, mixed-species groups must coordinate their activities despite group members often differing in their ecological niches, morphology, and behavioural traits, potentially making coordination and the maintenance of cohesion more challenging than in single-species groups. Current evidence suggests that the mechanisms underlying coordination in mixed-species groups may parallel those observed in conspecific systems (Liao, Magrath, et al., 2024). In particular, interspecific acoustic communication and eavesdropping appear to play a central role—especially in birds—in coordinating diverse group behaviours (Goodale et al., 2010, 2020; Magrath et al., 2015, 2020), including maintaining group cohesion (Suzuki, 2012b), facilitating foraging (Suzuki, 2012a), and coordinating antipredator responses across species (Goodale & Kotagama, 2008; Magrath et al., 2007; Suzuki, 2016). To date, however, our understanding of how mixed-species groups coordinate movement decisions, such as when to depart, where to move, and how fast to travel, remains limited (Liao, Magrath, et al., 2024). Future work should test whether such coordination emerges through shared rules, such as quorum-like processes, or through asymmetric mechanisms in which particular species, such as 'leader' or 'nuclear' species, contribute disproportionately to information generation and influence group behaviour (Carlson et al., 2023; Coppinger et al., 2023; Goodale et al., 2020; Liao, Chen, et al., 2024). Addressing these questions will be essential for understanding how different species coordinate their activities and function as cohesive groups, and more broadly, how information flow shapes complex social systems in the animal kingdom.

Conclusion

This thesis highlights that communication is central to how social animals remain safe and stay together. In both single-species groups and mixed-species flocks, communication enables individuals to transmit information, coordinate their actions, and maintain cohesion in dynamic environments. My studies further suggest that sophisticated collective outcomes can emerge from relatively simple decision rules, allowing animals to balance the benefits and costs of social living in flexible and adaptive ways. Although this thesis addresses only a small part of these broader questions, it contributes to a better understanding of how communication shapes animal societies. Extending these ideas across a wider range of species, contexts, and developmental stages may help reveal the evolutionary processes through which diverse social systems are formed, maintained, and sustained in a changing world.

References

Arnold, K., & Zuberbühler, K. (2013). Female putty-nosed monkeys use experimentally altered contextual information to disambiguate the cause of male alarm calls. *PLoS ONE*, *8*(6), e65660. https://doi.org/10.1371/journal.pone.0065660

Ashton, B. J., Ridley, A. R., Edwards, E. K., & Thornton, A. (2018). Cognitive performance is linked to group size and affects fitness in Australian magpies. *Nature*, *554*(7692), 364–367. https://doi.org/10.1038/nature25503

Bech, C., Chappell, M. A., Astheimer, L. B., Londoño, G. A., & Buttemer, W. A. (2016). A 'slow pace of life' in Australian old-endemic passerine birds is not accompanied by low basal metabolic rates. *Journal of Comparative Physiology B*, *186*(4), 503–512. https://doi.org/10.1007/s00360-016-0964-6

Berthet, M., Coye, C., Dezecache, G., & Kuhn, J. (2023). Animal linguistics: a primer. *Biological Reviews*, *98*(1), 81–98. https://doi.org/10.1111/brv.12897

Berthet, M., Mesbahi, G., & Leroux, M. (2026). The As and Bs of titi monkey linguistics: why emotional communication is not the enemy. *Biological Reviews*. https://doi.org/10.1002/brv.70131

Berthet, M., Surbeck, M., & Townsend, S. W. (2025). Extensive compositionality in the vocal system of bonobos. *Science*, *388*, 104–108. https://doi.org/10.1126/science.adv1170

Bousquet, C. A. H., Sumpter, D. J. T., & Manser, M. B. (2011). Moving calls: A vocal mechanism underlying quorum decisions in cohesive groups. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1711), 1482–1488. https://doi.org/10.1098/rspb.2010.1739

Carlson, N. V., Freeberg, T. M., Goodale, E., & Theo, A. H. (2023). Mixed-species groups and aggregations: shaping ecological and behavioural patterns and processes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *378*(1878), 20220093. https://doi.org/10.1098/rstb.2022.0093

Coppinger, B. A., Carlson, N. V., Freeberg, T. M., & Sieving, K. E. (2023). Mixed-species groups and the question of dominance in the social ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *378*(1878), 20220097. https://doi.org/10.1098/rstb.2022.0097

Cunningham, S., & Magrath, R. D. (2017). Functionally referential alarm calls in noisy miners communicate about predator behaviour. *Animal Behaviour*, *129*, 171–179. https://doi.org/10.1016/j.anbehav.2017.05.021

Dezecache, G., Crockford, C., & Zuberbühler, K. (2019). The development of communication in alarm contexts in wild chimpanzees. *Behavioral Ecology and Sociobiology*, *73*(8), 104. https://doi.org/10.1007/s00265-019-2716-6

Dibnah, A. J., Herbert-Read, J. E., Boogert, N. J., McIvor, G. E., Jolles, J. W., & Thornton, A. (2022). Vocally mediated consensus decisions govern mass departures from

jackdaw roosts. *Current Biology*, *32*(10), R455–R456. https://doi.org/10.1016/j.cub.2022.04.032

Evans, C. S., Evans, L., & Marler, P. (1993). On the meaning of alarm calls: functional reference in an avian vocal system. *Animal Behaviour*, *46*(1), 23–38. https://doi.org/10.1006/anbe.1993.1158

Fichtel, C. (2008). Ontogeny of conspecific and heterospecific alarm call recognition in wild Verreaux's sifakas (*Propithecus verreauxi verreauxi*). *American Journal of Primatology*, *70*, 127–135. https://doi.org/10.1002/ajp.20464

Fichtel, C., & Kappeler, P. M. (2002). Anti-predator behavior of group-living Malagasy primates: Mixed evidence for a referential alarm call system. *Behavioral Ecology and Sociobiology*, *51*(3), 262–275. https://doi.org/10.1007/s00265-001-0436-0

Fischer, J., Cheney, D. L., & Seyfarth, R. M. (2000). Development of infant baboons' responses to graded bark variants. *Proceedings of the Royal Society B: Biological Sciences*, *267*(1459), 2317–2321. https://doi.org/10.1098/rspb.2000.1285

Fischer, J., Wheeler, B. C., & Higham, J. P. (2015). Is there any evidence for vocal learning in chimpanzee food calls? *Current Biology*, *25*(21), R1028–R1029. https://doi.org/10.1016/j.cub.2015.09.010

Fischer, J., & Zinner, D. (2011). Communication and cognition in primate group movement. *International Journal of Primatology*, *32*(6), 1279–1295. https://doi.org/10.1007/s10764-011-9542-7

Goodale, E., & Beauchamp, G. (2010). The relationship between leadership and gregariousness in mixed-species bird flocks. *Journal of Avian Biology*, *41*(1), 99–103. https://doi.org/10.1111/j.1600-048X.2009.04828.x

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C., & Ruxton, G. D. (2010). Interspecific information transfer influences animal community structure. *Trends in Ecology and Evolution*, *25*(6), 354–361. https://doi.org/10.1016/j.tree.2010.01.002

Goodale, E., & Kotagama, S. W. (2008). Response to conspecific and heterospecific alarm calls in mixed-species bird flocks of a Sri Lankan rainforest. *Behavioral Ecology*, *19*(4), 887–894. https://doi.org/10.1093/beheco/arn045

Goodale, E., & Magrath, R. D. (2024). Species diversity and interspecific information flow. *Biological Reviews*, *99*(3), 999–1014. https://doi.org/10.1111/brv.13055

Goodale, E., Sridhar, H., Sieving, K. E., Bangal, P., Colorado Z., G. J., Farine, D. R., Heymann, E. W., Jones, H. H., Krams, I., Martínez, A. E., Montaño-Centellas, F., Muñoz, J., Srinivasan, U., Theo, A., & Shanker, K. (2020). Mixed company: a framework for understanding the composition and organization of mixed-species animal groups. *Biological Reviews*, *95*(4), 889–910. https://doi.org/10.1111/brv.12591

Haff, T. M., & Magrath, R. D. (2013). Eavesdropping on the neighbours: Fledglings learn to respond to heterospecific alarm calls. *Animal Behaviour*, *85*(2), 411–418. https://doi.org/10.1016/j.anbehav.2012.11.016

Heinsohn, R. (1991). Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. *American Naturalist*, *137*(6), 864–881.

Hollén, L. I., & Manser, M. B. (2006). Ontogeny of alarm call responses in meerkats, *Suricata suricatta*: the roles of age, sex and nearby conspecifics. *Animal Behaviour*, *72*(6), 1345–1353. https://doi.org/10.1016/j.anbehav.2006.03.020

Hollén, L. I., & Radford, A. N. (2009). The development of alarm call behaviour in mammals and birds. *Animal Behaviour*, *78*(4), 791–800. https://doi.org/10.1016/j.anbehav.2009.07.021

Kennedy, R. A. W., Evans, C. S., & McDonald, P. G. (2009). Individual distinctiveness in the mobbing call of a cooperative bird, the noisy miner *Manorina melanocephala*. *Journal of Avian Biology*, *40*(5), 481–490. https://doi.org/10.1111/j.1600-048X.2008.04682.x

Lea, A. J., & Blumstein, D. T. (2011). Ontogenetic and sex differences influence alarm call responses in mammals: A meta-analysis. *Ethology*, *117*(10), 839–851. https://doi.org/10.1111/j.1439-0310.2011.01947.x

Leighton, G. M. (2017). Cooperative breeding influences the number and type of vocalizations in avian lineages. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1868). https://doi.org/10.1098/rspb.2017.1508

Leighton, G. M., & Birmingham, T. (2021). Multiple factors affect the evolution of repertoire size across birds. *Behavioral Ecology*, 32(3), 380–385. https://doi.org/10.1093/beheco/araa139

Liao, C.-C., Chen, C.-C., & Magrath, R. D. (2024). Asymmetric information in mixed-species mobbing flocks: why are leader species special? *Animal Behaviour*, *210*, 383–393. https://doi.org/10.1016/j.anbehav.2024.01.014

Liao, C.-C., Magrath, R. D., Manser, M. B., & Farine, D. R. (2024). The relative contribution of acoustic signals versus movement cues in group coordination and collective decision-making. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *379*(1905), 20230184. https://doi.org/10.1098/rstb.2023.0184

Macedonia, J. M., & Evans, C. S. (1993). Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*, *93*(3), 177–197. https://doi.org/10.1111/j.1439-0310.1993.tb00988.x

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on heterospecific alarm calls: From mechanisms to consequences. *Biological Reviews*, *90*(2), 560–586. https://doi.org/10.1111/brv.12122

Magrath, R. D., Haff, T. M., & Igic, B. (2020). Interspecific Communication: Gaining Information from Heterospecific Alarm Calls. In T. Aubin & N. Mathevon (Eds.), *Animal Signals and Communication* (Vol. 7), pp. 287–314. Springer, Cham. https://doi.org/10.1007/978-3-030-39200-0_12

Magrath, R. D., Pitcher, B. J., & Gardner, J. L. (2007). A mutual understanding? Interspecific responses by birds to each other's aerial alarm calls. *Behavioral Ecology*, *18*(5), 944–951. https://doi.org/10.1093/beheco/arm063

Magrath, R. D., Platzen, D., & Kondo, J. (2006). From nestling calls to fledgling silence: Adaptive timing of change in response to aerial alarm calls. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1599), 2335–2341. https://doi.org/10.1098/rspb.2006.3610

Mangini, G. G., Rutt, C. L., Sridhar, H., Buitron, G., Muñoz, J., Robinson, S. K., Montaño-centellas, F., Zarco, A., Fanjul, M. E., Fernández-arellano, G., Xing, S., & Camerlenghi, E. (2023). A classification scheme for mixed-species bird flocks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *378*(1878), 20220100. https://doi.org/10.1098/rstb.2022.0100

Martínez, A. E., Parra, E., Muellerklein, O., & Vredenburg, V. T. (2018). Fear-based niche shifts in neotropical birds. *Ecology*, *99*(6), 1338–1346. https://doi.org/10.1002/ecy.2217

Mateo, M. J. (1996). The development of alarm-call response behaviour in free-living juvenile Belding's ground squirrels. *Animal Behaviour*, *52*(3), 489–505. https://doi.org/10.1006/anbe.1996.0192

McCowan, B., Franceschini, N. V, & Vicino, G. A. (2001). Age differences and developmental trends in alarm peep responses by squirrel monkeys (*Saimiri sciureus*). *American Journal of Primatology*, *53*, 19–31. https://doi.org/10.1002/1098-2345(200101)53:1<19::AID-AJP2>3.0.CO;2-%23

Radford, A. N. (2004). Vocal coordination of group movement by green woodhoopoes (*Phoeniculus purpureus*). *Ethology*, *110*(1), 11–20. https://doi.org/10.1046/j.1439-0310.2003.00943.x

Rajan, S., Ma, L., Gallego-Abenza, M., Kraft, F. L. H., & Wheatcroft, D. (2025). Geographical variation in parental calls contextually shapes nestling songbird responses. *Animal Behaviour*, *222*, 123114. https://doi.org/10.1016/j.anbehav.2025.123114

Scarantino, A., & Clay, Z. (2015). Contextually variable signals can be functionally referential. *Animal Behaviour*, *100*, 1–8. https://doi.org/10.1016/j.anbehav.2014.08.017

Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal Behaviour*, *34*, 1640–1658.

Sperber, A. L., Werner, L. M., Kappeler, P. M., & Fichtel, C. (2017). Grunt to go—Vocal coordination of group movements in redfronted lemurs. *Ethology*, *123*(12), 894–905. https://doi.org/10.1111/eth.12663

Sridhar, H., Beauchamp, G., & Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour*, *78*(2), 337–347. https://doi.org/10.1016/j.anbehav.2009.05.008

Suzuki, T. N. (2012a). Calling at a food source: Context-dependent variation in note composition of combinatorial calls in Willow Tits. *Ornithological Science*, *11*(2), 103–107. https://doi.org/10.2326/osj.11.103

Suzuki, T. N. (2012b). Long-distance calling by the willow tit, *Poecile montanus*, facilitates formation of mixed-species foraging flocks. *Ethology*, *118*(1), 10–16. https://doi.org/10.1111/j.1439-0310.2011.01982.x

Suzuki, T. N. (2016). Referential calls coordinate multi-species mobbing in a forest bird community. *Journal of Ethology*, *34*(1), 79–84. https://doi.org/10.1007/s10164-015-0449-1

Suzuki, T. N. (2018). Alarm calls evoke a visual search image of a predator in birds. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(7), 1541–1545. https://doi.org/10.1073/pnas.1718884115

Suzuki, T. N. (2024). Animal linguistics. *Annual Review of Evolution, Evolution, and Systematics*, *55*(1), 205–226. https://doi.org/10.1146/annurev-ecolsys-102622-030253

Walker, R. H., King, A. J., McNutt, J. W., & Jordan, N. R. (2017). Sneeze to leave: African wild dogs (Lycaon pictus) use variable quorum thresholds facilitated by sneezes in collective decisions. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1862), 20170347. https://doi.org/10.1098/rspb.2017.0347

Wheeler, B. C. (2010). Production and perception of situationally variable alarm calls in wild tufted capuchin monkeys (*Cebus apella nigritus*). *Behavioral Ecology and Sociobiology*, *64*(6), 989–1000. https://doi.org/10.1007/s00265-010-0914-3

Wheeler, B. C., & Fischer, J. (2012). Functionally referential signals: A promising paradigm whose time has passed. *Evolutionary Anthropology*, *21*(5), 195–205. https://doi.org/10.1002/evan.21319