Unsung Songbirds: Advances in the Study of Corvid Communication

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Abstract

Historically, much research in animal communication has focused on the information content and ultimate function of vocalisations. These include defending territories, sounding the alarm, attracting mates, and advertising identity. The proximate mechanisms that shape signal production and perception—including cognitive processes and cultural transmission—have only recently started attracting attention. Corvids are a well-established study system in comparative cognition and social evolution research, yet their vocal communication remains surprisingly understudied compared to other songbirds, which have been central to advancing our understanding of how natural selection shapes communication. With their flexible, context-dependent communication and capacity for vocal learning, corvids represent a particularly promising system for addressing open questions relating to vocal communication. Their diverse ecological and social environments, combined with extensively studied cognitive abilities, make them well-suited for investigating the co-

evolution of communication, sociality, and cognition. To unlock the potential of corvids as a system for studying vocal communication, several methodological opportunities and challenges must be addressed. These include the development of experimental designs suited to both wild and captive settings, and the adoption of advanced technologies for data collection in naturalistic environments. Recent advances in data processing—such as machine learning, acoustic classification, and automated tracking—open up promising new avenues for decoding corvid communication. These tools are promising to reshape the field by enabling more fine-grained, large-scale analyses of vocal behaviour. Ultimately, a deeper understanding of corvid vocal communication can significantly enhance our broader insights into the evolution of animal communication and the origins of human language. Furthermore, it holds applied value for improving animal welfare and conservation, including innovations in welfare monitoring and strategies for addressing human-wildlife conflict.

Key words**:** animal communication, animal linguistics, bioacoustics, cognition, Corvidae, machine learning, meaning, vocal signals

I. Introduction

Communication is the transfer of information from senders to receivers, mediated by one or more sensory channels, or modalities: visual, acoustic, chemical, mechanical or electrical (Bradbury & Vehrencamp, 2011). Signals, in contrast to cues, are generally understood to be adaptive behaviours, or traits, shaped by evolution for effective communication. Receivers' responses to signals offer a window into understanding whether and how information is extracted and used (Smith, 1965; Cherry, 1995), i.e. the 'meaning' of vocalisations (Cheney & Seyfarth, 1990; Rutz *et al.*, 2023; Amphaeris *et al.*, 2023). Key research questions in the study of animal communication concern cognitive processes and social dynamics, such as how individuals use signals for deception or cooperation, or extract information through eavesdropping. In this review, we outline approaches to studying corvid vocal communication, including challenges and future opportunities (Figure 1).

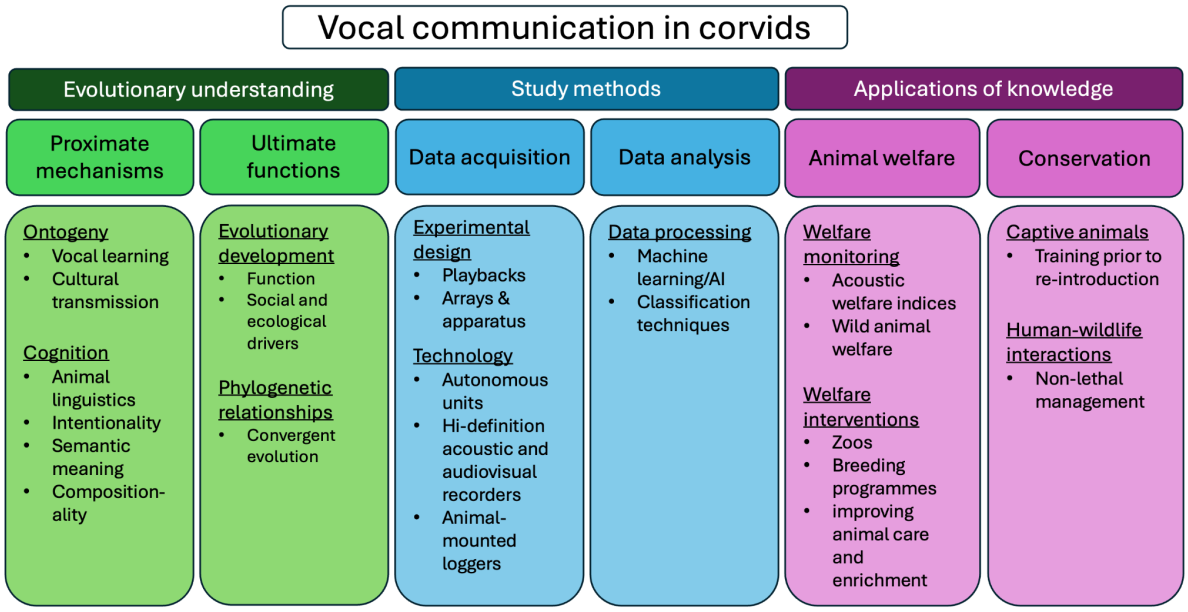

Figure 1: Framework and future directions in the study of corvid vocal communication.

Vocal communication has received particular attention from researchers due to its prominence in humans, its perceptibility to human observers, and its prevalence in a wide range of taxa. *Corvidae* are a large family of birds consisting of more than 120 species (Gill, Donsker & Rasmussen, 2023; Clements *et al.*, 2024) inhabiting most areas of the globe, except Antarctica (Figure 2). The group includes crows, ravens, jays and magpies, which show striking variation in sociality and ecology, enabling powerful comparative analyses addressing the evolution of behaviour, cognition

(Taylor 2014), and vocal communication (Wascher & Reynolds, 2025). They belong to the suborder of oscine passerine birds, commonly known as songbirds. The songbird syrinx, located at the base of the trachea, functions as two independently controlled sound sources within each primary bronchus (medial and lateral labia; Zollinger et al. 2008; Elemans et al. 2015). Specialized syringeal muscles enable complex vocalizations through finely tuned coordination of respiratory and motor patterns, continuously adjusted by somatosensory feedback (Suthers & Zollinger, 2004). As with other songbirds, the structure of corvid vocalisations arises from both the structural configuration of the vocal apparatus and vocal learning (Gaunt & Nowicki, 1998; Goller, 2019, 2022). Corvids are well known for their loud and 'harsh'-sounding broadband vocalisations (Figure 3), caused by unpredictable or irregular ways the sound is produced
(non-linear phenomena). Non-linear phenomena include biphonation, when two independent fundamental frequencies occur in a call spectrum, frequency jumps, defined as an abrupt change in the fundamental frequency, or deterministic chaos, referring to complex, unpredictable sound patterns in vocalisations. While corvid non-linear phenomena in corvid vocalisations are well-known, they have hardly been described in the literature, except deterministic chaos in 'alalā, (Hawaiian crow), *Corvus hawaiiensis* (Tanimoto et al. 2017). Corvids mostly produce calls—short, distinct vocalisations— as opposed to the songs typically associated with oscine passerines, which are heterogeneous, combinatory vocalisations consisting of notes or phrases that are arranged in a specific order and often repeated (Sandoval & Graham, 2025).

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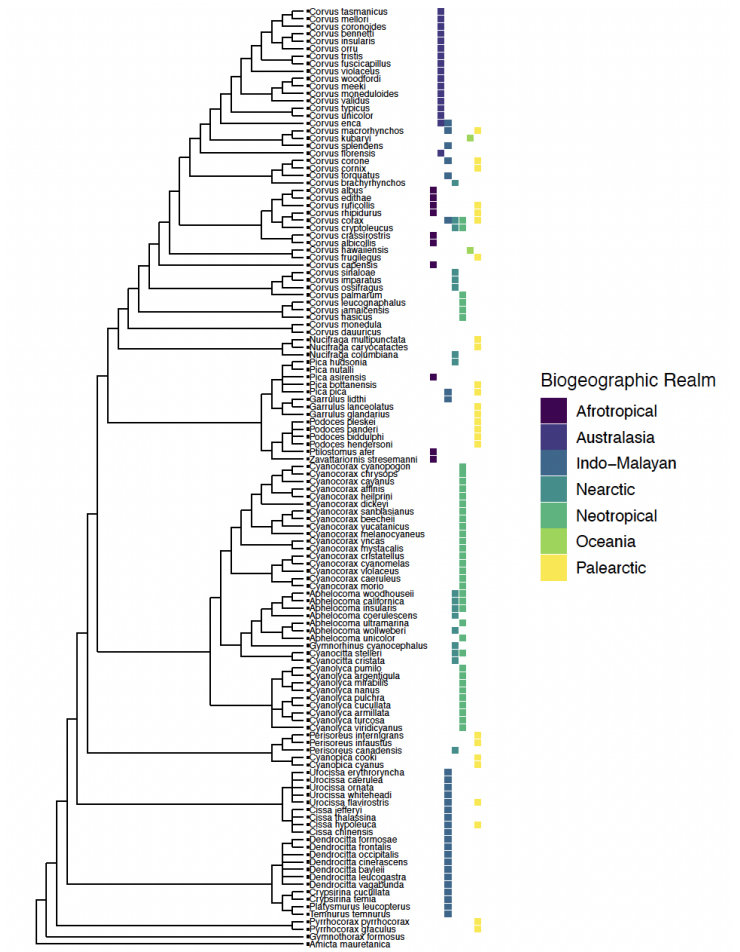

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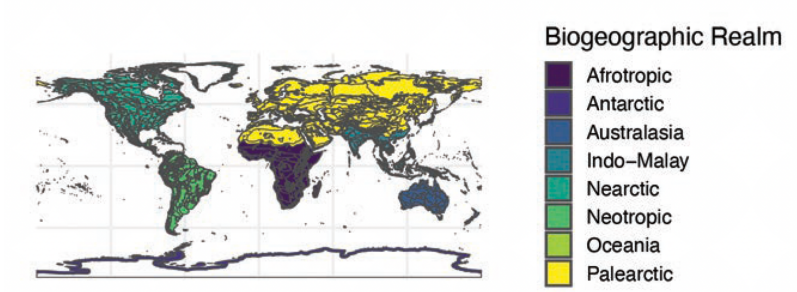

Figure 2: Phylogenetic tree of *Corvidae* and occurrence in biogeographic realms of the world. Corvid phylogeny is from OpenTreeOfLife et al. 2019 and geographical data from Tobias et al. (2022). Map is downloaded from World Wildlife Fund's Terrestrial Ecoregions of the World (Olson *et al.*, 2001).

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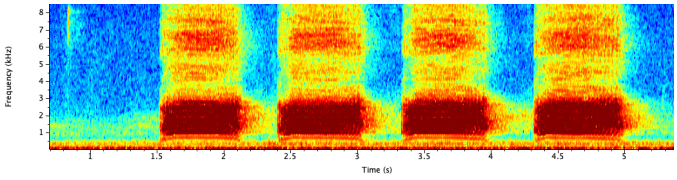

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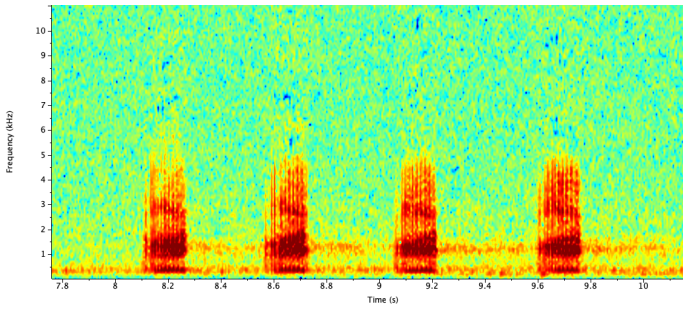

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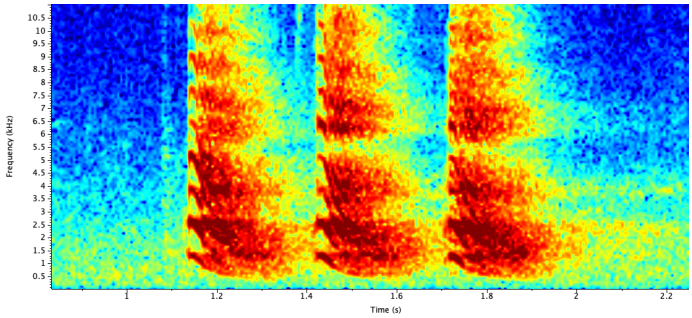

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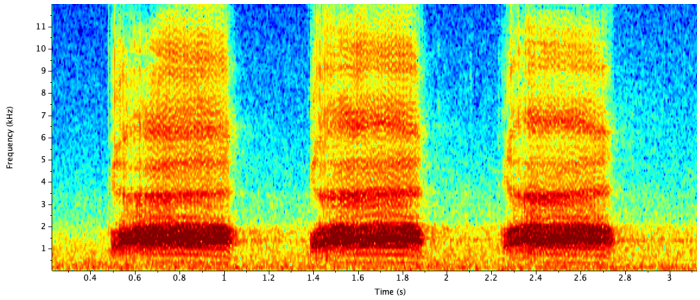


Figure 3: Example spectrograms of different non-harmonic corvid calls of different species. (A) carrion crow (*Corvus corone*), (B) common raven (*Corvus corax*), (C) jackdaw (*Coloeus monedula*) and (D) rook (*Corvus frugilegus*).

Acoustic structure and information encoding

From an evolutionary perspective, understanding the information content in animal vocalisations is crucial because it sheds light on how communication systems evolve to enhance survival and reproduction. Researchers often categorise vocalisations of individuals and species into different types, such as calls, songs, phrases, that have different acoustic structures (Bradbury & Vehrencamp, 2011), as these may correspond to different types of information (Marler, 2004). Different call types can be further attributed to functional contexts, such as maintaining contact between individuals in a social group (Kondo & Watanabe, 2009), indicating the presence of predators (Griesser, 2008, 2009; Suzuki, 2014; Stephan & Zuberbühler, 2014) or a food source (Heinrich & Marzluff, 1991; Pendergraft & Marzluff, 2019), begging for food (Stamps, 1993), aggression (Seyfarth & Cheney, 2017), submission (Fedurek *et al.*, 2021), territory defence (Mennill & Odom, 2010), or searching for a sexual partner (Bradbury & Vehrencamp, 2011; Chen & Wiens, 2020).

In many corvid species, call types are highly graded, with acoustic structures transitioning gradually between categories, making discrete classification challenging (rooks, *Corvus frugilegus*: Martin et al. 2024). This limits the scope for investigating the meaning, or function, of calls by categorising them. Some corvids also produce non-vocal sounds, such as bill-clicking (e.g., carrion crows, *Corvus corone*: Siriwardena 1995), which are known from other taxa (e.g., biphonation in black-capped chickadees, *Poecile atricapillus*: Nowicki and Capranica 1986; graded signals in orangutans, *Pongo pygmaeus*: Erb et al. 2024; non-vocal sound production in chimpanzees, *Pan troglodytes*: Marshall et al. 1999).

In addition to contextual information (see below), acoustic features of vocalisations can provide information about the characteristics of the caller (reviewed in Wascher & Reynolds 2025), such as their sex, breeding status, group membership (Warrington *et al.*, 2014), body mass (Fitch & Hauser, 1995; Ey, Pfefferle & Fischer, 2007; Taylor & Reby, 2010; Garcia & Favaro, 2017) or emotional state. Both emotional arousal (Fitch, Neubauer & Herzel, 2002; Keenan *et al.*, 2020; Corvin *et al.*, 2024; Sibiryakova, Volodin & Volodina, 2024) and valence (Osiecka *et al.*, 2024a; Osiecka, Lefèvre & Briefer, 2024b), can be conveyed, for example, through pitch and degree of harmonicity in calls (Morton, 1977; Briefer, 2012). The acoustic structure of certain calls, such as distress calls, can be sensitive to the composition of the audience and the likelihood to recruit potential support when being attacked (Slocombe & Zuberbühler, 2007; Szipl, Ringler & Bugnyar, 2018). Adult Siberian jays (*Perisoreus*

infaustus) only respond to mobbing calls of group members, while ignoring those of neighbours that use mobbing calls in a deceptive manner to gain access to food (Cunha and Griesser 2021). In common ravens (*Corvus corax*), '*haa*' calls, a call type used to signal the presence of food, acoustically encode the caller's sex, age class, and individual identity (Boeckle, Szipl & Bugnyar, 2018). Moreover, common ravens can attend to this individual information (Boeckle, Szipl & Bugnyar, 2012) and use it in daily life decisions—that is, whether or not to call and respond to calls, respectively (Szipl *et al.*, 2015; Sierro *et al.*, 2020). An interesting feature of raven *haa* calls is the large individual variation in calling probability and calling rate, showing that some birds may be more prone to call at food than others (Szipl & Bugnyar, 2014). Factors influencing this variation include the birds' age, sex and residency status, with adult females calling more than adult males and local birds calling more than vagrants (Szipl & Bugnyar, 2014). These findings suggest that ravens may use individual characteristics in calls to learn about, and identify, specific individuals. They recall this information after years of separation, as captive birds selectively respond to *haa* calls of former group members and even discriminate their former friends from foes (Boeckle & Bugnyar, 2012). Carrion crows are able to differentiate between vocalisations of familiar and unfamiliar humans (Wascher *et al.*, 2012). This ability to infer individual identity from conspecific and heterospecific raises interesting questions around the use of public sensory information and how this is shaped by ecological factors like predation pressure and sociality (Igic *et al.*, 2019).

From vocal production learning to cultural transmission

Corvids have extended developmental periods during which they practice social behaviour and vocalisations (Uomini *et al.*, 2020), and are open-ended vocal learners that acquire new vocalisations throughout their lifetime (Brenowitz, Margoliash & Nordeen, 1997). Vocal learning refers to the ability to modify vocal output in response to social or individual experience (Janik & Slater, 2000; Sewall, Young & Wright, 2016). It can be divided into two distinct processes, namely: (1) vocal production learning, which refers to the ability to produce new vocalisations or modify existing vocalisations using auditory feedback and social experience (Janik & Knörnschild, 2021; Ten Cate, 2021); and (2) usage learning, which refers to learning the contextual use of vocalisation (Hollén & Radford, 2009) or how to combine single calls from a repertoire (Janik & Slater, 2000; Vernes *et al.*, 2021).

Vocal production learning is relatively rare amongst non-human animal species and mostly occurs in singing species, such as oscine songbirds and cetaceans (reviewed

in Wilbrecht and Nottebohm 2003; Sewall et al. 2016), as well as in some non-singing birds (Wright, 1996) and bats (reviewed in Vernes and Wilkinson 2020). It occurs in a so called 'plasticity phase' that is completed by a 'crystallisation phase', after which individuals are no longer able to modify repertoires in the majority of species (Marler 1967; Marler and Peters 1987; Beecher and Brenowitz 2005; Fischer and Hammerschmidt 2020; Ten Cate 2021). Only a few species retain the ability to learn and modify signals into adulthood, which are known as 'open-ended learners' (e.g., galah, *Eolophus roseicapillus*: Scarl and Bradbury 2009, peach-fronted conures, *Eupsittula aurea*: Thomsen et al. 2019; American crows, *Corvus brachyrhynchos*: Brown 1985). Songbirds may also adjust the spectral or temporal arrangement of vocal signals (Veit *et al.*, 2021; Costalunga *et al.*, 2023; Kawaji, Fujibayashi & Abe, 2024) or the rhythmic structures of their songs to differentiate themselves from neighbours (Osiecka *et al.*, 2025), or acquire new vocal combinations through social exposure to adults (Gultekin *et al.*, 2021). Most research investigating usage learning has focused on non-singing species with a fixed vocal repertoire, assessing the ability of individuals to learn the contextual use of specific calls, or to associate species-specific calls to an arbitrary context in experimental settings (reviewed in Hollén and Radford 2009; Seyfarth and Cheney 2010; Janik and Knörnschild 2021). Corvids, as open-ended vocal learners, provide an example of vocal plasticity beyond early development—their social learning, and capacity for both vocal production learning and usage learning into adulthood, make them an interesting model system for understanding vocal learning. In the following section, we explore how they can be used to address key open questions in animal communication.

Vocal learning allows for flexibility and innovation and as such forms the basis for cultural transmission, the spread of vocalisations through social learning. Animals can develop regional dialects (Green, 1975; Jenkins, 1978; Slater, 1986; Deecke, Ford & Spong, 2000), group specific calls (Yurk *et al.*, 2002; Radford, 2005), or individual signatures (McCowan & Reiss, 2001; Charrier, Pitcher & Harcourt, 2009; Kershenbaum, Sayigh & Janik, 2013). These variations are culturally maintained and evolve over time as new individuals learn and possibly modify the sounds. In corvids, regional dialects have been shown in red-billed choughs (*Pyrrhocorax pyrrhocorax*; Laiolo et al. 2001) and rook calls have a clear individual signature (Benti, Curé & Dufour, 2019). Furthermore, New Caledonian crows (*Corvus moneduloides)* exhibit significant large-scale, population-level variation in vocalizations (Bluff, Kacelnik & Rutz, 2010) and call repertoires of common ravens are shared between pair partners

and within the sexes leading to a pronounced sexual dimorphism in vocal behaviour (Enggist-Dueblin & Pfister, 2002).

II. Addressing open questions in animal communication

Do animals vocalise intentionally?

Intentional communication in animal communication refers to the deliberate production of signals by an individual. This involves active signal production, where the sender tailors their message based on their audience and their response or attention—a crucial feature of human language (Townsend *et al.*, 2017). Intentional communication is difficult to demonstrate in non-human animals, necessitating the formulation of a robust research framework and operational definitions (Ben Mocha & Burkart, 2021). Signal production is expected to stop when a given piece of information has been conveyed to relevant receivers. This has indeed been observed in chimpanzees and bonobos (*Pan paniscus*), where signallers stop emitting alarm calls when nearby individuals appear to have received the information of the presence of a dangerous snake (Crockford *et al.*, 2012; Girard-Buttoz *et al.*, 2020). First-order intentionality refers to signallers acting in a goal-directed manner by producing voluntary recipient-directed signals as a means of reaching a desired outcome, eliciting a change in the recipient's behaviour (Bruner, 1981; Dennett, 1983). This form of intentionality has mainly been studied in the vocal and gestural communication of primates (Hopkins & Leavens, 1998; Crockford *et al.*, 2012; Schel *et al.*, 2013; Girard-Buttoz *et al.*, 2020), but a few studies demonstrated intentionality in the communication of other species (e.g., dogs, Gaunet and Deputte 2011), and gestural communication in common ravens (Pika & Bugnyar, 2011; Ben Mocha, Mundry & Pika, 2019). Moreover, intentional communication requires the ability to volitionally control vocal production, which has been shown in carrion crows (Brecht et al. 2019; Liao et al. 2024). Therefore, we suggest that corvids are an ideal candidate group to study the degree of intentionality involved in vocal communication and the neurophysiological basis of such a control.

Semantic meaning and social cognition

Establishing the 'meaning' of vocal signals, in the sense of semantic information content, has long been a central focus of animal communication research (Schlenker *et al.*, 2022; Rutz *et al.*, 2023). Foundational work on vervet monkeys identified distinct alarm calls for three predator types (Seyfarth, Cheney & Marler, 1980), giving rise to the 'functional referential' framework. Referential signals convey information to conspecifics that can be responded to in a specific way, without contextual

information: in the case of vervet monkeys, the signal is sufficient for all recipients to infer the risk posed by a particular predator, even without the actual presence of a predator. Studies assessing the referential properties of vocalisations focus mainly on predator- (Griesser, 2008; Townsend & Manser, 2013; Gill & Bierema, 2013; Suzuki & Ueda, 2013; Suzuki, 2018) or food-related signals (Slocombe & Zuberbühler, 2005), using playback experiments. For instance, Siberian jays' mobbing calls encode information about the type and behaviour of predators (Griesser 2009; Griesser 2008).

An open question in the study of semantic cognition is whether animals have a mental representation of the meaning of their calls. Playback experiments in Japanese tits have suggested that these birds have a mental image of predators when hearing alarm calls (Suzuki et al, 2018). Operant conditioning experiments in zebra finches (*Taeniopygia castanotis*) have revealed that this songbird has a hierarchical perception of its call types according to the meaning of vocalizations (semantic 'hyper-category'), indicating that it possesses a mental representation of the meaning of all its call types in its repertoire (Elie *et al.*, 2025). Corvids, with their complex vocal repertoires and social interactions provide an ideal model system to further investigate whether corvids have mental representations of the meaning of call types.

Going beyond individual calls, the composition of vocal sequences can also carry meaning (Kershenbaum *et al.*, 2016). In corvids, this remains an understudied but promising aspect of vocal behaviour. Corvids often produce calls in sequences which vary in both the number of calls and their acoustic features such as temporal rhythm, call duration, or sequence length may encode different information (Thompson, 1982). For example, in Siberian jays, the number of mobbing call repetitions is associated with the risk posed by a predator (Griesser, 2009), while in large-billed crows (*Corvus macrorhynchos*), the number of *ka* calls increases when the dominant individual is temporarily removed from a group (Aota, Takano & Izawa, 2025). Across other avian and mammalian species, differences in call number are associated with changes in magnitude, such as severity of a threat, distance from a predator, or competitiveness exhibited by neighbors (Arak, 1983; Blumstein & Armitage, 1997; Templeton, Greene & Davis, 2005; Courter & Ritchison, 2010; Dutour *et al.*, 2021). While the number of calls is traditionally thought to reflect differences in internal states such as arousal, a recent experimental study showed that carrion crows can volitionally control the number of calls in the sequences they produce (Liao *et al.*,

2024a). This opens up the possibility that corvids could use different acoustic features to intentionally signal information, or even to deceive others (Cunha and Griesser 2021). That said, it remains unclear at present whether, and how, composition of a sequence conveys meaning to receivers. Addressing this question will require both careful observations in the full natural context in which communication takes place, as well as controlled playback experiments (Igic *et al.*, 2019; Carlson, Greene & Templeton, 2020).

Cognitive components of vocal communication

The cognitive abilities of non-human animals have always fascinated researchers of animal behaviour (Shettleworth, 2009), and have moral and legal implications for their treatment by humans (Bekoff, 1994). Understanding the cognitive abilities of animals can also aid conservation efforts, such as when training individuals to recognise predators prior to re-introduction into the wild (Greggor *et al.*, 2014, 2021). Different aspects of vocal communication can provide valuable insights into animal cognition. Playback experiments can be used to investigate behavioural responses to specific stimuli, and have shown that different corvid species are able to recognise individuals (Kondo, Izawa & Watanabe, 2012), group membership (Hopp, Jablonski & Brown, 2001), and familiarity of conspecifics (Davídková *et al.*, 2020) and heterospecifics (Wascher *et al.*, 2012). Common ravens and Siberian jays, for instance, memorise affiliated and unaffiliated individuals for multiple years (Boeckle & Bugnyar, 2012; Cunha & Griesser, 2021), and the birds' early social environment may affect their attention to social cues (Gallego-Abenza, Boucherie & Bugnyar, 2022). Scolding calls—loud, harsh vocalisations typically made in response to a perceived threat or disturbance—demonstrated corvids' ability to learn about dangerous humans (Marzluff *et al.*, 2010; Blum, Fitch & Bugnyar, 2020) and revealed how this information socially spread amongst populations (Cornell, Marzluff & Pecoraro, 2012; Lee *et al.*, 2019b).

Compared to the variety of studies examining individual recognition in corvids, there have been surprisingly few attempts to test birds' knowledge about social relationships (Wascher and Reynolds 2025). In most playback studies, individuals show selective responses to pair partners and family or group members, indicating that they are aware of their own social bonds and rank (Wascher & Reynolds, 2025). Yet, when tested with playbacks for the understanding of third-party relationships, results are mixed. On the one hand, female Eurasian jackdaws (*Coloeus monedula*) do not respond to simulated infidelity of their partners: copulation calls with other

females indicate that they may not attend to third-party information in this experimental context (Lee *et al.*, 2019b). On the other hand, ravens respond to simulated rank changes between group members, suggesting that they represent others' relationships and make inferences about dominance ranks from a third-party perspective (Massen *et al.*, 2014). These findings fit with behavioural studies on wild ravens' conflicts, where victims of aggression adjust their calling to audience composition—for example, by suppressing their vocalisation when a bonding partner of the aggressor is present (Szipl *et al.*, 2018). Similarly, Siberian jay breeders suppress the production of hawk attack calls when together with unrelated non-breeding group members, particularly female breeders that are at times socially subdominant to male non-breeders (Griesser & Ekman, 2004).

Because of the breadth of research into corvid cognition, this group presents an ideal model system for investigating further the understanding of third-party relationships, using refined experimental paradigms, such as playback (Szipl *et al.*, 2015; King, 2015) and touch-screen experiments (Brecht *et al.*, 2019; Federspiel *et al.*, 2023; Liao *et al.*, 2024b). Additionally, exploring the neural and cognitive mechanisms underlying social knowledge in corvids could provide deeper comparative insights into the evolution of complex social cognition.

Deciphering vocal communication

Linguistics and socio-ecology have historically developed as separate fields of research. However, recent collaborations between these fields have brought new methods and concepts to explore animal communication that could be particularly specifically useful for studying corvid communication. Specifically, animal linguistics has formulated three objectives, each with specific methodologies (Schlenker *et al.*, 2022; Berthet *et al.*, 2023). The first is integrating evolutionary mechanisms into the study of calls, to their meaning, and to their combinations. For instance, 'boom' calls of some old world monkeys (Cercopithecinae) have been phylogenetically traced back five millions years (Schlenker *et al.*, 2016), and similar analyses suggest call combinations in tits (Paridae) originating around eleven million years ago (Salis, A., under review). A second objective is comparative research, as it can help understand shared coding mechanisms between species occurring either through convergent evolution or shared ancestry as well as patterns of divergence. Recent work has suggested that specific acoustic features can encode meaning (e.g., call rate to signal urgency) in numerous species (Liao *et al.*, 2024a). While primarily developed to explain variation in communication across species (Schlenker *et al.*, 2025), this

feature-based perspective (instead of call-types) may also be useful in corvid research because of their highly gradual and complex call systems. Comparative research can also aid the investigation of 'linguistic laws', such as selection for efficiency and the related 'principle of least effort', which has been supported in several animal groups, such as primates and whales (Semple, Ferrer-i-Cancho & Gustison, 2022; Youngblood, 2025). To our knowledge, similar analyses have not yet been attempted in corvids. Finally, a third objective is to develop formal models to explore the precise semantics of calls, such as the 'compositional syntax' in mobbing calls of the Japanese tit (*Parus minor*, Suzuki et al. 2016). Such application of methods and concepts from linguistics has yet to be explored in the context of corvid communication.

Multimodal communication

One challenge in animal communication research is the bias towards unimodal studies, which focus on a single sensory modality, typically vocalisations (Ratcliffe, Taylor & Reby, 2016; Rutz *et al.*, 2023). This bias is likely due to humans being naturally attuned to auditory information. Additionally, vocalisations are easy to record, analyse, and study experimentally. However, a comprehensive understanding of animal communication requires an integrated, multimodal approach, as signals in different modalities often interact to convey information more effectively.

Multimodal signals can enhance the reliability and effectiveness of communication. Many species combine visual, olfactory, and acoustic signals—for instance, a vocalisation may be reinforced by a specific posture or facial expression, which increases the likelihood that the intended message is successfully transmitted and understood. Redundancy in multi-modal information ('back-up signal hypothesis') can increase the robustness of communication systems as receivers can pick up the information from one modality if another one is missed, for example in situations of increased environmental noise (Akçay & Beecher, 2019). Already in the middle of the twentieth century, researchers observed that many behaviours of corvids are flexible and involve a combination of distinct vocalisations with specific visual features such as body postures, wing formations and feather positions (Gwinner 1964; Coombs 1978; Figure 4). These visual features are used to communicate information and express different degrees of motivation (e.g., threat, begging, mating displays). While some studies have examined non-vocal signals in corvids (Gwinner, 1964; Pika & Bugnyar, 2011), it remains unclear whether their vocalisations are consistently accompanied by specific postures or other types of signals, or if combinations are

context-dependent. For example, in male chickens (*Gallus gallus domesticus*), intense crowing is only possible when the bird adopts an extended and bent neck posture (Claes *et al.*, 2017). A key limitation in studying multimodal communication in corvids, and birds more generally, has been the lack of reliable methods to quantify, amongst other things, body posture, wing displays, feather erection, eye temperature or pupil dilation. Beyond visual signalling, olfactory communication in corvids remains largely unexplored. While birds have traditionally been considered less reliant on olfaction (Grieves *et al.*, 2022), carrion crows have been shown to respond to conspecific scents (Wascher *et al.*, 2015a). Further research is needed to clarify the role of olfactory cues in corvid social interactions.

(A) (B)

(C) (D)

Figure 4: Examples of body postures associated with vocalisations in (A) common ravens, (B) carrion crows, (C) red-billed choughs (*Pyrrhocorax pyrrhocorax*), and (D) a jackdaw.

Complexity in animal communication: diversity, flexibility, and signal combination

'Vocal complexity' is a key concept in the study of communication, which generally assumes that more complex signals allow for more complex information transmission (Peckre, Kappeler & Fichtel, 2019). Rebout et al. (2021) introduced a framework for analysing the complexity of communicative systems through three dimensions: (1) diversity—the number of different signals in a repertoire, their distinctiveness, and how individuals distribute their vocal production across signal types; (2) flexibility—an individual's ability to modify its repertoire via changes in call structure and function or composition, such as the number of different call types; and (3) combinability—how multiple vocalisations are arranged into sequences (see above).

In terms of diversity, some corvid species, such as Siberian jays (Griesser 2008) or common ravens (Enggist-Dueblin & Pfister, 2002) produce easily distinguishable call types, while others use both stereotyped calls and calls with significant graded variations (e.g., carrion crows: Siriwardena 1995; rooks: Martin et al. 2024). Similar inter-individual variation has been noted in some species, such as American crows (Mates *et al.*, 2015) and rooks (Benti *et al.*, 2019). Further investigation into these differences could provide insights into vocal diversity and complexity in corvids (Martin *et al.*, 2024).

Corvid vocal flexibility is characterised by high levels of vocal learning and imitation. Corvids mimic vocalisations of other species and environmental sounds (Wascher, Waterhouse & Beheim, 2025), but also of conspecifics (Brown, 1985; Kondo, 2021), in particular social partners (Luef et al. 2017). They also show high levels of functional flexibility; for example, male rooks produce their most frequent call in as many as seven different contexts (Roskaft and Espmark 1982). It should be noted that in this early study, structural nuances and combinations of calls with other modalities, might have been missed, which highlights the need of further research with standardised analyses methods. Carrion crows can even be trained to produce vocalisations in response to arbitrary stimuli in a laboratory setting (Brecht *et al.*, 2019; Liao *et al.*, 2024b). Very few studies have systematically assessed functional vocal flexibility in birds, indicating rich opportunities for further research.

Vocal combinability refers to how information is encoded in vocal sequences, either by combining the meaning of calls (Suzuki et al. 2016; Engesser and Townsend

2019; Suzuki 2021) or by generating new meanings not directly related to the individual components (Arnold and Zuberbühler 2006). Understanding the extent of vocal combinability in different species is key to tracing the evolutionary pathways that have shaped complex communication systems, including (but not limited to) human language, which is an open-ended combinatorial system capable of generating an infinite number of signals to communicate new meanings indefinitely (Nowak, Plotkin & Jansen, 2000; Nowak & Komarova, 2001). Extensive combinability has recently been shown in bonobos (Berthet, Surbeck & Townsend, 2025). Great apes and marmosets produce a wide range of vocal sequences in diverse social and environmental contexts (Girard-Buttoz *et al.*, 2022; Bortolato *et al.*, 2023; Bosshard *et al.*, 2024), and corvids provide a powerful contrast for comparative studies, to test potential evolutionary drivers of combinatory capacities in two distantly related lineages.

Vocal sequences are also of interest to the emerging field of rhythm studies (Suzuki *et al.*, 2016; Hersh, Ravignani & Burchardt, 2023). Advances in analytical methods, such as rhythm or cluster analysis (e.g., Burchardt and Knörnschild 2020; Burchardt et al. 2021) have revealed that rhythmic patterns can both carry important phylogenetic (Garcia *et al.*, 2020) and social (Mathevon *et al.*, 2017; Osiecka *et al.*, 2024a, 2025) information, and interact with the caller's emotional state (Maldarelli *et al.*, 2024). Studying how rhythm is used, produced and perceived is crucial for understanding the role of rhythm in the evolution of both language and music (Patel, 2014, 2021; Hersh *et al.*, 2023). Similarly, linguistic analyses of animal vocal structures can reveal broader evolutionary patterns of communication, such as the widespread adherence to brevity laws (Youngblood, 2025; Wascher & Youngblood, 2025).

Whether within species variation in vocal complexity provides adaptive benefits to individuals is a longstanding evolutionary question. In songbirds, for example, greater song complexity in males is often linked to mate attraction, signalling individual quality to potential mates (Darolová *et al.*, 2012). Similarly, vocal complexity may play a role in social dynamics and mate choice in primates, as exemplified by female geladas, which tend to pay more attention to more complex male vocalisations (Gustison & Bergman, 2016).

Exploring the influence of social and ecological factors on vocal behaviour

Corvids provide an ideal model for evaluating how social and ecological factors can shape vocal behaviour. Sociality is highly variable, both at inter- and intraspecific levels, from pair-breeding species, such as blue jays (*Cyanocitta cristata*) or pied crows (*Corvus albus)* which become territorial as adults and breed in pairs; to colonial species like rooks or Eurasian jackdaws, which live and breed in large communities; to family-living species like Siberian jays, or cooperatively-breeding species like Florida scrub-jays (*Aphelocoma coerulescens;* for an overview on corvid sociality please see Billerman et al. 2022). However, classifying the social system of corvids is difficult because within-species sociality of some species varies depending on environmental, seasonal, and life-history factors (Kubitza, Bugnyar & Schwab, 2015; Uhl *et al.*, 2019). For example, although carrion crows breed in monogamous pairs in most areas, facultative cooperative breeding occurs in 75% of territories in Northern Spain, depending on environmental factors (Baglione *et al.*, 2005).

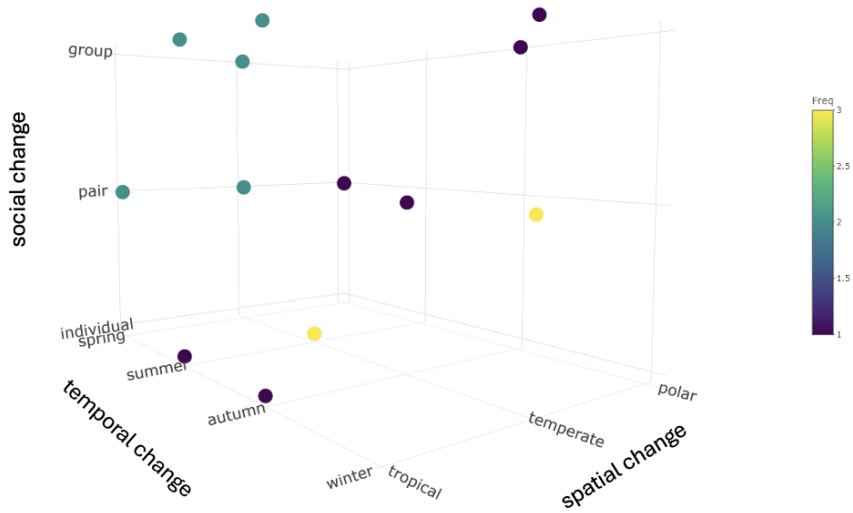
Adult ravens may establish a territorial breeding pair or join non-breeder flocks that mainly consist of juveniles, while individuals in other species gather in large communal roosts (Wascher 2018). Jackdaws and rooks, two communal breeders, even form large mixed-species flocks and roost together in winter (Jolles *et al.*, 2013). Some species, like American crows, are migratory in northern parts of their range and seasonally forage, roost and interact vocally in flocks with birds from distant populations (Verbeek *et al.*, 2024). These specific social situations can provide unique opportunities for information exchange between individuals of the same or of different species, opportunities that may not occur at other times of the year.

Some corvid species are highly specialised in terms of the habitat they occupy, such as Florida scrub-jays and pinyon jays (*Gymnorhinus cyanocephalus*), which only occur in shrubland and open shrub woodlands, respectively, whereas many other species, including Eurasian magpies (*Pica pica)*, Eurasian jackdaws, and several species of crows (including large-billed crows (*Corvus macrorhynchos*), carrion crows, and American crows) can be considered generalists, occupying many different habitats, including forest, grassland, agricultural landscapes, and urbanised areas (Billerman *et al.*, 2022). Corvids significantly contribute to ecosystem functioning, by providing seed dispersal (Pesendorfer *et al.*, 2016; Mendes *et al.*, 2024) and sanitary services, by scavenging on carrion (Inger *et al.*, 2016; Mariyappan *et al.*, 2023). Species conservation status ranges from ‘extinct in the wild’ ('alalā; U.S. Fish and Wildlife Service (USFWS) 2009; although note that

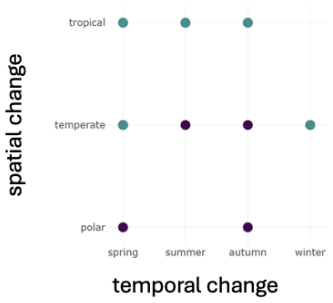
reintroductions are underway), to ‘least concern’, with some species being considered pests by local human populations, becoming the target of (legal and illegal) persecution (Billerman *et al.*, 2022).

This rich variation creates a valuable opportunity to investigate if aspects of vocal communication, such repertoire size, vary with the degree of sociality or environmental context, both within and between species. Yet, this contextual variability can also present research challenges, especially when using a comparative approach, if detailed information about social, temporal, and spatial contexts are not provided. In Figure 5, we provide a framework illustrating what kind of information should ideally be reported by studies on corvid communication, to enable well-informed comparative analyses.

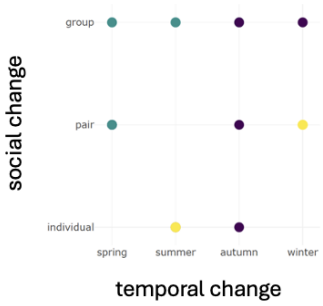
a) spatial-temporal-social (n=21)



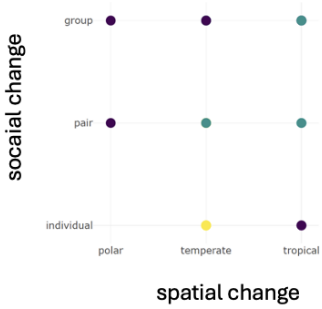
b) spatial-temporal (n=25)



c) social-temporal (n=21)



d) social-spatial (n=25)



e) dimensions of change

i) spatial change

	examples
climate zones	polar, temperate, tropical
habitats	open, close

ii) temporal change

	examples
annual seasons	spring, summer, autumn, winter
breeding seasons	breeding season, non-breeding season
age	juvenile, subadult, adult

iii) social change

	examples
social status	individual, pair, group
dominance	dominant, subordinate

Figure 5: Framework of spatial-temporal-social information that should be reported by studies on corvid vocal communication. Data from Wascher and Reynolds 2025, selecting publications reporting the vocal repertoire of a corvid species. Colours in (a-d) code by number of studies. (a) Studies providing information on all three axes (spatial, temporal, social); studies providing information on at least two axes: (b) spatial-temporal, (c) social-temporal, (d) social-spatial. (e) Change can happen in many dimensions. Clear provisioning of contextual information in studies on vocal repertoire allows to systematically investigate how dimensions of change can affect outcomes of studies.

The evolution of vocal complexity is often explained by two non-mutually exclusive hypotheses: the 'social complexity hypothesis' and the 'acoustic adaptation hypothesis.' The social complexity hypothesis for communication postulates that social complexity has been the main driver of vocal complexity (Freeberg, 2006; Peckre *et al.*, 2019). In species with complex social systems, individuals interact with a wide range of conspecifics across different contexts, potentially requiring a more diverse and flexible vocal repertoire to facilitate coordination, competition, and bonding.

In contrast, the acoustic adaptation hypothesis posits that vocal signals are shaped by environmental factors to optimise information transmission (Morton 1975). Habitat structure, including ground surface and vegetation type, wind direction, microclimatic conditions, ambient noise from both biotic and abiotic sources, can all influence the physical properties of acoustic signals (Forrest, 1994; Mullet, Farina & Gage, 2017). According to this hypothesis, vocalisations with high-frequency modulations (e.g., trills) and short elements should be favoured in open habitats, whereas vocalisations with low-frequency modulations (e.g., whistles) and long elements should be favoured in habitats with complex vegetation structure (Morton, 1975; Tubaro & Lijtmaer, 2006; Hao *et al.*, 2021; Netoskie *et al.*, 2023). While supported by many theoretical studies, there is a paucity of empirical evidence (Boncoraglio & Saino, 2007; Ey & Fischer, 2009; García-Navas, Feliu & Blumstein, 2023), except in the context of urbanisation and habitat fragmentation (Briefer et al. 2010; Deoniziak and Osiejuk 2019; Rhodes et al. 2023). Corvids offer an ideal test case for exploring these hypotheses.

III. Challenges and approaches

Technological and methodological advances

In the following sections, we argue that the increased accessibility of study species to test hypotheses, combined with major technological (e.g., recording equipment, computer hardware, and software), methodological (e.g., new analytical techniques), and research culture advances (e.g., data sharing, research coordination), will enable a step-change in our understanding of corvid communication and cognition.

A number of corvid species have become model species in the study of animal behaviour as they can be studied in the wild as well as in captivity, facilitating detailed behavioural observations and repeated experimental testing, including on

tasks that require training (Brecht *et al.*, 2019; Liao *et al.*, 2024b). Some corvid species can be habituated to human observers or hides, enabling controlled experiments in wild populations (Baglione *et al.*, 2006; Davidson, Clayton & Thornton, 2015; Horn *et al.*, 2020). This allows researchers to study communication at different levels. For example, studies of wild common ravens visiting feeding sessions at a rural game park, scavenging on food provided to wolves and wild boar, investigated the function of vocalisations, such as food calls, in a meaningful socio-ecological context (Bugnyar & Kotrschal, 2001). This was complemented with studies on captive ravens, which afforded more detailed and controlled analysis, for example, of vocal similarity in long-term pair-bonded individuals (Luef *et al.*, 2017), long-term memory for calls (Boeckle & Bugnyar, 2012), and third-party understanding (Massen *et al.*, 2014). Some species, like New Caledonian crows, should not be held in permanent captivity, but tolerate brief periods in field aviaries well (Rutz & Hunt, 2020), where they can be tested before being released into the wild again (e.g., St Clair and Rutz 2013; Klump et al. 2021). Whatever the chosen methodological approach, the samples of subjects researchers draw for their studies are susceptible to sampling biases, limiting generalisation of findings to the source population and beyond (Webster & Rutz, 2020).

Recording of corvid vocalisations in the field

Like most field data collection of wild animals, research on corvid vocal communication presents challenges. It can be difficult to detect their location, and often observations will be disturbed when focal individuals move out of sight or start interacting with fieldworkers. Commonly, the collected audio data will be noisy—masked by wind noise, voices of humans, or other species. Some of these issues can be partially addressed by using wind shields, appropriate recording equipment, and hides. In other contexts, manual or automated post-processing will be required; for example, audio fragments saturated with wind noise can be automatically detected and removed prior to analysis (Terranova *et al.*, 2024), and recorders can be built to detect the acoustic presence of the focal species in audio fragments (Bergler et al. 2022).

Active and passive recordings

In captive settings, or with birds that are trained to approach an experimental set-up, it is possible to place a high-quality recording device close to the target signaller to increase the quality of sound recordings. This is especially useful for capturing soft

calls, such as social vocalisations that may be otherwise hard to record with high enough signal-to-noise ratios (SNR) at a distance. In an ongoing long-term study of Siberian jays, individuals are trained to come down to a feeding device to allow for observation of social interactions at a limited food source, or approach experimental apparatus designed for cognitive experiments (Figure 6). Placement of an autonomous recording unit nearby allowed for capturing clear recordings of the soft social calls that are given in that foraging context. Such high SNR recordings enable the implementation of machine-learning analyses (Lü *et al.*, 2024), achieving fast processing of data-rich material (audio recordings, videos), which would be much more laborious to process manually (Williams *et al.*, 2020; Nieto-Mora *et al.*, 2023).

Figure 6: Siberian jays can be trained to use a feeding device (left; as part of a standardised protocol to observe social interactions), or will approach experimental apparatus (right; designed for a social learning experiment). Images taken by Liam Paulson in a long-term study population near Arvidsjaur, Sweden (Ekman & Griesser, 2016).

Bio-loggers

Sound-recording 'bio-loggers' (Rutz & Hays, 2009) can also be placed directly on focal individuals. This technique has the advantage that vocalisations can be recorded simultaneously with other data, using additional sensors, such as GPS loggers for movement tracking and 3D accelerometers for mapping behaviours of interest (e.g., flight, foraging, or resting), providing important contextual information for functional decoding (Rutz et al. 2023). Such audio-loggers offer a valuable tool for recording

both animal and environmental sounds with minimal human interference (Lynch *et al.*, 2013; Wilson *et al.*, 2020). When used with corvids, they are particularly useful for capturing soft, short-range vocalisations, which are routinely missed in studies employing more traditional methods. In jackdaws, audio-loggers have provided insights into extra-pair copulations by recording copulation calls (Gill *et al.*, 2020).

But, the use of bio-loggers is not without challenges. One concern is the potential impact on the animals themselves (see section on animal welfare), especially with larger devices. Studies in birds have revealed sub-lethal effects of the increased masses or handling-induced stress associated with tags (Chivers, Hatch & Elliott, 2016; Evans *et al.*, 2020; Puehringer-Sturmayr *et al.*, 2020). Kittiwakes reduced the amount of time they spent flying by thirty percent when tagged with bio-loggers that were five percent of their body mass, whilst tags that were one percent of their body mass had no recorded effects on a variety of behavioural measures (Gillies et al. 2020). There has been an increase in the use of bio-loggers on animals as technology becomes more miniaturised, and this has allowed for using the loggers on smaller species (Portugal & White, 2018). Smaller corvids, such as Siberian jays (adult mass: approximately 80 grams), offer insights in corvid behaviour and communication, but we caution against the blind use of the five percent rule (Portugal & White, 2018). A study on pigeons showed that effects on locomotion were measured below six percent of body mass (Tian *et al.*, 2020), which is consistent with a study that found tagging impacts to be stronger in smaller species (Brlík *et al.*, 2020). Thus, tagging mass limitations will limit the data that can be collected via attached loggers. Instead, in smaller corvids, bio-loggers can be used in conjunction with other off-body technologies such as passive acoustic monitoring devices (PAM), or video data to answer in-depth questions about corvid acoustic communication and behaviours. In addition to evidence showing that five percent rule has often been broken (Portugal & White, 2018), hazards against well-being such as associated ringing protocols (Griesser *et al.*, 2012) for individual identification of birds, and the use of harnesses that may pose different risks. It is important to note that there are different harnesses used to attach tags to birds (e.g., backpack harnesses, leg loops), as well as material used in harnessing, and selection of the harness type will depend on the physical attributes and flight requirements, with species-specific impacts to animal welfare (Blackburn *et al.*, 2016; Longarini *et al.*, 2023).

In order to avoid the need to re-capture individuals to retrieve equipment, a tag self-release mechanism can be pivotal, as demonstrated by Rutz and Troscianko (2013), who describe a simple and effective release technique. It is important to thoroughly investigate the impacts of all aspects of the capture, tagging and deployment protocols before using acoustic tagging technologies (Blackburn *et al.*, 2016; Tian *et al.*, 2020). As the computer chips that underlie data capture are light, the total tag weights are often limited by the capacity to store the data and/or the battery size (Williams *et al.*, 2020). The necessity of decreasing tag weights often requires using a smaller battery, which can result in an increased number of times animals are captured to get sufficient data, and/or decreased time between subsequent captures (to mount and then remove tags), which can increase handling stress in handled birds. Additionally, harness materials and mounting strategy can affect well-being. In whinchats (*Saxicola rubetra)* tied harnesses significantly decreased resighting rates compared to elastic harnesses (Blackburn *et al.*, 2016), and in five soaring raptor species, tags attached by leg loops had less impacts on ascent speed and time spent in active flights, suggesting fewer impacts associated with drag (Longarini *et al.*, 2023). In addition to these ethical considerations, it is important to remember that loggers may fail under harsh meteorological conditions or get lost, a common occurrence in field studies. Pilot projects designed to estimate failure rates can help researchers plan the number of deployments needed to ensure sufficient data collection. Thus, it is important to consider the effects of attaching biologging acoustic devices when designing studies.

Finally, audio-loggers often produce large volumes of data, in which vocalisations of interest may be infrequent and challenging to locate. Duty-cycling can address this issue by scheduling recording times to coincide with periods of peak vocal activity. Nevertheless, manually detecting and classifying calls within such recordings still remains time-consuming, highlighting the need for automated methods. Machine-learning techniques are increasingly addressing this challenge (Stowell, Benetos & Gill, 2017; Bergler *et al.*, 2022), although the required expertise and computational power present challenges in terms of inclusivity and sustainability (Kershenbaum *et al.*, 2024).

Analysing corvid calls

Processing data before analyses

Bio-loggers and automated recording units have the ability to record large volumes of data, which requires automated methods for efficient processing prior to subsequent analyses. A frequently applied method, commonly adapted from speech and image recognition, are supervised machine-learning models, which are trained with data that have been manually annotated (Smith & Pinter-Wollman, 2021; Naik *et al.*, 2023). While automated methods allow for high-volume data processing, it is necessary that study designs incorporate protocols that ensure data are usable for automated analysis pipelines.

There are automated methods for identifying vocal activity available, for example classification models (Stowell, 2022). Pre-trained models, such as BirdNET (Kahl *et al.*, 2021), may generally provide good performance in corvids, however for more specific problems, researchers may choose to train their own model (Bergler *et al.*, 2022; Ghani *et al.*, 2023). In studies where it is necessary to know the start- and end-time of each vocalisation, more advanced sound event detection methods may be required (Martin *et al.*, 2022). One regular problem in acoustic recordings are multiple conspecifics vocalising simultaneously, which can be dealt with by adopting object detection methods (Mahon *et al.*, 2025).

Beyond detection, it is often important to identify the sender of a vocalisation. When there exists some ground-truth data about which vocalisation belongs to which individual, supervised machine learning methods may be adapted to predict the origin of each vocalisation (Martin *et al.*, 2022). When this data does not exist, but the recordings come from bio-loggers, the relative amplitude of vocalisations in synchronized recordings may be used to infer the identity of the sender (Zeh *et al.*, 2024). If multiple synchronized bio-loggers are not available, cues available within a single recording such as relative amplitude, presence of environmental filtering, and changes in these features over time may be a last resort (Baglione *et al.*, under review).

When recording audio outside of a controlled environment, noise will be present. Sources of noise may be environmental (wind, rain), biological (vocalisations from non-focal individuals), or mechanical (body movements against microphone; Grinfeder et al. 2022). Audio detection and classification methods can be made reasonably resilient to these types of noises through data augmentation, which can

expose an algorithm to artificially degraded sounds during training (Zhang *et al.*, 2018). When analyses rely on the specific acoustic properties of recorded vocalisations, removing noise may be necessary. In vocal repertoire studies relying on the construction of a latent representation, the representation obtained can inadvertently reflect the background noise profile of recorded vocalisations (Thomas *et al.*, 2022). Stationary noise, such as rain or cicadas can be mitigated through signal processing methods (Sainburg, Thielk & Gentner, 2020). Non-stationary noise, such as wind, wing flapping or vocalisations of non-focal species presents a greater challenge, however recent machine learning efforts in denoising (Miron *et al.*, 2025) and source separation (Denton, Wisdom & Hershey, 2022) may provide tools for this challenge.

Identifying meaningful acoustic features and classifying vocalisations

Characterising corvid vocalisations can present analytical and conceptual challenges, due to their diversity, gradedness and complexity as discussed above (for fuller discussions of vocalisation analysis, see Kershenbaum et al. 2016; Odom et al. 2021). The features important for traditional analysis such as fundamental frequency measures are often not detectable. Corvid calls tend to contain many non-linear phenomena which makes automatic extractions of parameters like fundamental frequency or amplitude modulations challenging and requires manual annotations (Massenet *et al.*, 2022). Semi-automated feature extraction, e.g., existing Praat codes that allow for point-by-point corrections can maximise accuracy while speeding up the process (Reby & McComb, 2003). Going beyond ‘simple feature extraction’ or frequency contours can be particularly important for vocalisations with significant non-linear contributions. One method still rarely used but of high importance to such calls are modulation spectra (Singh & Theunissen, 2003), providing detailed time average envelope statistics of the entire sound structure rather than specific values such as maximum or minimum frequencies (see application on Egyptian fruit bat (*Rousettus aegyptiacus*) vocalisations in (Elie *et al.*, 2024).

Representations of vocalisations range from the measurement of expert-chosen features that may be tailored to the vocalisations under study such as the ‘caws’ of 28 corvid species (Laiolo & Rolando, 2003), to general-purpose choices such as spectrograms (Sainburg *et al.*, 2020; Martin *et al.*, 2024) or embeddings derived from the intermediate layers of a neural network (Sethi *et al.*, 2020; McGinn *et al.*,

2023; Best *et al.*, 2023). Expert-chosen acoustic features are interpretable but can be difficult to choose, design and measure robustly. This can apply to commonly used features such as fundamental frequency, as well as more complex or subtle features. Currently, non-linear phenomena are typically manually annotated. Anikin and Herbst (2024) provide a set of current best practices for annotating and measuring non-linear phenomena as well as a suite of visualization tools for aiding in their detection and classification. General-purpose analyses can be relatively easily applied to audio waveforms, but they may not adequately reflect perceptible features and may also be sensitive to extraneous information (e.g., due to recording conditions). Furthermore, especially if involving neural networks, they are not immediately interpretable. Here, best practice includes visualization and validation (see Thomas et al. 2022). One option is to utilize these general-purpose features as an aid to manual annotation (Merino Recalde, 2023; Poupard *et al.*, 2024). Validation may also be based on whether the features can correctly predict perceptual judgments of the species themselves, as collected in discrimination tasks (Zandberg *et al.*, 2024; Elie *et al.*, 2025), although this may not currently be feasible for all species or comparative studies (Odom *et al.*, 2021). Finally, graded variation can complicate the notion of a repertoire of call types (Kershenbaum *et al.*, 2016; Fischer, Wadewitz & Hammerschmidt, 2017; Cusano, Noad & Dunlop, 2021). Representing vocal complexity which consists of a combination of graded variation and stereotyped call types remains an ongoing area of research.

Preliminary data on cooperatively breeding carrion crows equipped with bio-loggers that allow continuous sound recording for up to six days suggest that a substantial proportion of their vocalisations consist of ‘soft calls’, which are characterised by low amplitude (Baglione et al. under review). These vocalisations are detectable only through animal-borne recording devices, as conventional directional microphones lack the sensitivity required to capture them at a distance. Furthermore, the ambiguous acoustic structure and highly variable duration of these soft calls present significant challenges for classification, whether based on human perception or current machine learning algorithms.

Linking vocalisations to behaviour and context

To assess the functions and semantic meaning of vocalisations, they must be linked to contextual factors such as environmental variables, caller and receiver identities, life histories, behaviours and past interactions. Such long term factors may be

especially relevant to understanding vocalisations in corvids with long term memory for social interactions (Bugnyar, 2013; Taylor, 2014; Cunha & Griesser, 2021). For some corvids, vocalisations have been difficult to exclusively identify with a particular context (Siriwardena 1995), suggesting the potential in developing additional methods of observation and of associating vocalisations with context. For a brief review of methodologies used to study corvid behaviour and associated ethical considerations, see Rutz (2018).

Studying vocalisations and behaviour of corvids synchronously can be challenging, especially in wild animals, who are freely moving over large areas and often difficult to follow. Technological advances like animal-borne loggers (e.g., proximity and video loggers in New Caledonian crows, St Clair et al. 2015; Troscianko and Rutz 2015; accelerometers and audio loggers in carrion crows, Baglione et al. under review) and camera-based systems (e.g., flight tracking in jackdaws and rooks, Ling et al. 2018; nest cameras to document cooperative behaviours in carrion crows, Trapote et al. 2024) increasingly allow to analyse behaviour associated with vocalisations. Importantly, the mitigation of ethical risks, such as disturbance of focal animals need to be taken into account when applying technology such as camera setups. Although several studies report neutral effects of camera use for remotely observing bird behaviour, even when cameras are placed near or within nests (López-López, 2022), it is important to acknowledge that the installation of electronic devices may still influence avian behaviour (Harrison *et al.*, 2019). This concern is particularly relevant for corvid species, which are highly neophobic. Additionally, disturbances may arise when video cameras require frequent maintenance, such as battery recharging or troubleshooting technical issues, potentially exacerbating behavioural disruptions.

Improved recording technology increasingly results in large datasets and machine learning can aid in extending manual annotations of behaviour (Tuia *et al.*, 2022). Once contextual factors are measured, machine learning has the potential to play a key role in discovering their associations with vocalisations (Rutz *et al.*, 2023). In marmosets, supervised machine learning has been used to demonstrate that vocalisations contain sufficient information to identify the receiver of a vocalisation (Oren *et al.*, 2024). Such analyses require accounting for confounds in observational data (Demartsev *et al.*, 2023) and must be complemented with playbacks and other field experiments.

While environmental noise presents a challenge when working with vocal data, it may present opportunities for identifying behavioural conditions salient to communication. Hoffman et al. (2024) uses wing flapping recorded in bio-loggers to identify periods of flight in carrion crows. In jackdaws, Stowell et al. (2017) characterize a broad array of behavioural contexts using audio recorded by bio-loggers. In cetaceans, flow noise has been used to identify feeding lunges in humpback whales (Friedlaender *et al.*, 2013).

What is a segment?

In terms of understanding animal vocalisations, it is not only relevant to categorize calls into different call types, but also understand vocal sequences. As such, it is fundamentally important to be able to distinguish between biologically meaningful sequences, which at times can be challenging as these are not necessarily the same units, which seems intuitive to a human eye and ear. Some new methods segment animal vocal sequences automatically (Mann *et al.*, 2021). Similarly, vocalisations within sequences can be grouped to types using unsupervised machine learning techniques rather than subjective grouping by an investigator based on spectral shapes (Xie et al. 2024). In all such cases, the question remains open whether the extent to which segmentation corresponds to the structure of communication.

Experimental approaches

Experiments provide valuable opportunities for testing hypotheses related to the evolution of communication and the cognitive mechanisms underlying vocal behaviour. However, the neophobic nature of many corvid species (Miller *et al.*, 2022) along with their fear of human observers, can make field experiments challenging. On the other hand, some corvids habituate well to human presence (Ekman, Sklepkovych & Tegelstrom, 1994) and individuals in urban areas are generally less neophobic compared to their rural counterparts (Matsyura, Jankowski & Zimaroyeva, 2015). Thus, the scope of field experiments in corvids varies widely, from experiments that do not require observers to be close to test subjects, such as automated camera and recording systems (Trapote *et al.*, 2024), to those that involve direct interactions between individuals and human experimenters (e.g., Horn et al. 2020).

Playback experiments lend themselves to test different aspects of vocal

communication in corvids and can be conducted in captivity (Boeckle & Bugnyar, 2012; Wascher *et al.*, 2012; Massen *et al.*, 2014) as well as in the field (Griesser 2008, Szipl et al. 2015; Lee et al. 2019; Davídková et al. 2020). A wide range of stimuli can be used, e.g., conspecific calls (Boeckle & Bugnyar, 2012; Kondo *et al.*, 2012; Zandberg *et al.*, 2014; Szipl *et al.*, 2015; Wascher *et al.*, 2015b), non-human heterospecifics calls (Wascher *et al.*, 2012), human voices (Wascher *et al.*, 2012; Schalz & Ei-Ichi, 2020; McIvor, Lee & Thornton, 2022), or anthropogenic sounds (Federspiel *et al.*, 2023). Playbacks can be used to test different behavioural and cognitive aspects related to vocal communication, e.g., individual recognition (Boeckle & Bugnyar, 2012; Kondo *et al.*, 2012; Cunha & Griesser, 2021), recognition of relationships (Massen *et al.*, 2014; Lee *et al.*, 2019a), function of vocalisations (McCaig, Brown & Jones, 2015; Davídková *et al.*, 2020), theory of mind (Bugnyar, Reber & Buckner, 2016). A wide range of setups are available, from fully automated remote systems (Suraci *et al.*, 2017; Palmer *et al.*, 2022) to more interactive approaches, which require the presence of a human observer (King, 2015). Playback experiments can make use of audio- and video-recordings to analyse the behavioural responses of focal individuals (Palmer et al. 2022; Mennill and Vehrencamp 2008). Importantly, experimental equipment should be placed out of sight of focal individuals or carefully camouflaged to minimise potentially negative effects of visible loudspeakers. In addition to minimising potential interference and disturbance to the animals, it also avoids habituation to the playback setup and individuals recognising the artificial setup, e.g. calls being emitted from playback speakers. Besides consideration of potential disturbance playback experiments can cause when studying animals, other ethical risks need to be carefully considered and mitigated, for example simulated territory intrusion can cause territory abandonment or increased risk of predation (Watson, Znidersic & Craig, 2019). Another key challenge in playback experiments is stimulus preparation and setup, e.g., sound volume, in order to ensure stimuli are perceived as realistically as possible by focal individuals.

Training corvids in laboratory settings allows researchers to set and control a variety of conditions and complement field studies and playback experiments. With tools like touchscreens and automated feeders, researchers can precisely control the set-up and present a variety of stimuli (Rust & Movshon, 2005; Hauber *et al.*, 2015). These setups can help separate factors like arousal and vocal control (Brecht *et al.*, 2019;

Liao *et al.*, 2024a), or explore how different acoustic features or call types relate to individual recognition (Elie & Theunissen, 2018). Complex training paradigms can further reveal cognitive mechanisms that shape evolutionary processes. However, behaviours, brains, and bodies are inseparable (Gomez-Marin & Ghazanfar, 2019), and training paradigms should integrate with ecological knowledge from field observations or experiments. Moreover, experimental paradigms that involve training typically require many more trials, which are crucial for establishing quantitative links between vocal behaviour and neural activity. Understanding whether the results from these controlled experiments are consistent or vary in more naturalistic contexts is essential (Lanzarini *et al.*, 2025). Exciting methodological improvements in behavioural tracking and recording technologies hold great promise to deepen our understanding of the physiology behind corvid communication.

IV. Future directions

A deeper understanding of animal vocal communication is not only crucial for fundamental research on the evolution of communication, but has practical applications in animal welfare and conservation. In particular, studying corvid vocal communication can help address societal challenges such as reducing human-wildlife conflict, improving animal care and enrichment in captivity, and enhancing conservation efforts by informing strategies for reintroducing species or managing populations. Understanding how corvids communicate in both wild and human-modified environments can also contribute to mitigating the negative impacts of urbanisation.

Advancing animal welfare

Vocalisations provide an opportunity for non-invasive assessment of emotional and psychological states, and improving ethical and animal care standards.

Animal welfare assessments have evolved to include both negative-focused and positive-focussed assessments, such as the 'five freedoms' framework (freedom from hunger and thirst, freedom from discomfort, freedom from pain, injury, or disease, freedom to express normal behaviour, and freedom from fear and distress), and the 'opportunities to thrive' model (Woods, Eyer & Miller, 2022). Bioacoustic methods are increasingly used to assess welfare in captive animals (Coutant, Villain & Briefer, 2024). For example, emotional arousal is expressed in call typical non-linear phenomena (Marx *et al.*, 2021), or call frequency (Gosselin *et al.*, 2025).

Avian welfare research has lagged behind work on mammals, accounting for less than ten percent of welfare research in zoos in the last decade (Woods *et al.*, 2022), despite many species, including corvids being kept in captivity, including for research (Miller et al. 2024; see Appendix Table 1 and Table 2). In these settings, forced social groupings, overcrowding, or solitary living can alter vocal patterns and other behaviours in social birds such as corvids, often revealing distress (Harvey et al. 2002; Munteanu et al. 2017; Wolff and Stevens 2024). Interactions with human visitors and carers can further disrupt captive birds' lives and compromise their welfare, especially in species with pronounced neophobia (Wascher *et al.*, 2021). Captive environments and social grouping also shape individuals' development, as shown in a captive breeding programme of the critically endangered 'alalā, where autonomous audio and video recordings revealed that captive birds had a smaller vocal repertoire, compared to wild birds, notably losing crucial alarm and broadcast calls essential for survival in the wild (Tanimoto *et al.*, 2017).

Altered and reduced vocal repertoire in captive birds highlights how stressors, limited learning opportunities, and unnatural social environments can have lasting impacts on welfare–or, in the case of 'alalā, compromise reintroduction success. Given the central role of vocal communication in corvids' social lives, this raises the question of how enriching environments can stimulate natural vocal behaviours. Enrichment may include 'unnatural' stimuli; for example, music was found to encourage vocal activity and reduce stress-related behaviours in temporarily captive hooded crows during rehabilitation (Jablonska, Golik & Burnat, 2023). However, while responses to both auditory enrichment and acoustic stressors likely vary across individuals and species, excessive noise, including vocalisations from nearby species, create welfare concerns (Bílá *et al.*, 2017; Broad, 2024; Miller *et al.*, 2024). Understanding how corvids perceive and respond to different sounds can inform facilities to design cognitively stimulating environments that engage these birds meaningfully and minimise welfare concerns.

Keeping wild birds in captivity is strongly regulated, with a focus on research, conservation, and education. Zoos, wildlife parks, and research institutes housing corvids not only facilitate research that informs evidence-based conservation programmes (Sabol *et al.*, 2022), but also help raise public awareness of these birds' natural behaviours, ecological roles, as well as welfare concerns and conservation threats they face, both globally and locally (Keulartz, 2015).

Studying corvid vocal communication within zoos also has broader implications for impacting the zoos missions of research, conservation, and education. Housing local corvid species allows for a strong educational message related to these species and the problems they face, which can encourage local involvement and action. Zoo research findings can be used to inform public awareness about the complexity and intelligence of these birds, fostering a greater understanding of their ecological roles locally. This can be demonstrated to visitors within the corvid's enclosure by utilising forms of enrichment such as intellectually stimulating feeding enrichment e.g., solving puzzles or finding hidden food (Hawkins, 2010). Furthermore, corvids are well-suited for training, as they can habituate to human presence and environmental pressures (Deventer *et al.*, 2016). This makes corvids potentially useful for educational demonstrations within zoos, whilst also allowing for greater research potential in the form of cognitive testing as demonstrated by Dufour et al (2012), and the facilitation of multi-institutional studies as shown by Miller et al (2022). Additionally, zoos can use vocalisation research to improve reintroduction programs for endangered corvid species, by maintaining their calls needed for survival and reproduction in the wild as demonstrated by the work on 'alalā (Greggor *et al.*, 2021). Ultimately, by researching, educating visitors on, and preserving the vocal repertoire of corvids, zoos can play a critical role in advancing avian welfare, conservation, and the public understanding of these remarkable birds.

Corvids are not only a useful group for educating the public about nature but throughout history and across cultures, corvids have also held profound symbolic and cultural significance, appearing in myths, folklore, and traditions around the world (Marzluff & Angell, 2007). To Hawaiian's, the 'alalā are sacred 'aumakua (Banko, Ball & Banko, 2002), family messengers and protectors that originate from deified ancestors (Barrow, 1999). These birds were included in meetings between ali'i (royalty and chiefs) and, during battles, it is said that warriors would imitate the 'alala's haunting caws that were able to reach long distances (Walters, 2012). Similarly, the Siberian jay holds cultural significance, particularly among the indigenous Sámi people and other communities in northern Europe and Siberia. They are often regarded as a protective spirit, a harbinger of good luck, and a messenger between the living and deceased ancestors or spirits. Thus, their presence is often seen as a positive omen (Bergman & Östlund, 2022; Joy, Armstrand & Helander, 2024).

Human-wildlife interactions

Vocal monitoring offers valuable insights beyond captivity. Wild animal welfare is an emerging field in need of effective methods (Browning & Veit, 2023), and shifts in vocal activity may indicate environmental disturbance, with potentially cascading effects on population resilience. Broad et al (2024) found that noise pollution disrupted jackdaws' vocal communication at winter roosts, delaying settlement and increasing nocturnal calling, highlighting how anthropogenic disturbance may disrupt sleep and cognition, elevate stress, and impair vocal consensus during group coordination and collective behaviours.

Many corvid species, such as carrion crows or large-billed crows, are highly adapted to human environments and therefore present an ideal model system to study the effects of urbanisation on wildlife (Benmazouz *et al.*, 2021). Urbanisation is a major driver of biodiversity loss and a better understanding of how animals adapt to human modified environments can help inform conservation strategies, mitigate negative impacts, and promote coexistence between wildlife and urban populations.

In the context of vocal communication, urbanisation represents a rapid and drastic change in the environment, often associated with a higher cover in impervious structures that prevent sound propagation, but also with increased light pollution and noise levels (Swaddle *et al.*, 2015; Moll *et al.*, 2019; Halfwerk & Jerem, 2021). Recent studies have pointed out how urban habitats can influence, and even shape animal communication (Patricelli & Blickley, 2006; Singh *et al.*, 2023). For instance, urban birds shift their vocal activity to an earlier time (Bergen & Abs, 1997; Warren *et al.*, 2006) or use a higher-frequency signal (Wood and Yezerinac, 2006). Anthropogenic disturbance on communication could potentially have fitness consequences, e.g., by reducing coordination between group members (Broad, 2024). As many corvid species have successfully established themselves within cities, comparing the vocal behaviour between urban and rural corvid populations could be an interesting approach to understand the acoustic adaptations of urban individuals (Slabbekoorn, 2013). Understanding how habitat structure can be linked to vocal behaviour is of prime importance, especially as the earth becomes increasingly urbanized.

Because of their closeness to humans, corvids are also an ideal model system to study human-wildlife conflicts and attitudes of people towards animals. Corvids evoke strong and polarized emotions in human societies, ranging from admiration to aversion (Jürgens *et al.*, 2022). Corvids are widely believed to prey on other bird

species and nests, including threatened species (Strong *et al.*, 2021), however a comprehensive review failed to find evidence for the widespread effect of corvids on prey species (Madden, Arroyo & Amar, 2015). In a survey of London residents, the majority of people (57%) felt positive towards carrion crows (Schalz, 2021). American crows in Seattle showed a longer flight initiation distance in areas where levels of discouragement (e.g. chasing or scaring crows away) were higher compared to areas with lower discouragement levels (Clucas & Marzluff, 2012). Similarly, large-billed crows (*Corvus macrorhynchos*) and carrion crows in Japan show a greater flight initiation distance in areas where crows are shot, rather than captured (Fujioka, 2020). For wild crows, the risk of being chased, captured or killed may be partially reduced by detecting early signs of human presence, such as human voices. Large-billed crows who were wild-caught in Japan showed more behavioural responses to playback of an unfamiliar language (Dutch) compared to a familiar language (Japanese) (Schalz & Ei-Ichi, 2020), while captive carrion crows also responded more often to unfamiliar than familiar human voices (Wascher *et al.*, 2012). Carrion crows in the UK responded more to playback of speech than to avian control sounds, though their response did not differ between the local language and a foreign, presumably unfamiliar language (Schalz, 2023). Note that behavioural responses differed, and ranged from taking flight to approaching and investigating the sound source. Jackdaws are more wary of male compared to female human voices, but do not discriminate between different dialects of a language (McIvor *et al.*, 2022). Future studies on corvid responses to human vocalisations could explore whether corvids' abilities to discriminate aspects of human speech patterns reflects abilities evolved for interspecific communication, and what the wider fitness benefits of this behaviour may be.

Human-wildlife conflict with corvids is particularly prevalent in agricultural landscapes, where corvids are considered to raid crops and cause significant economic losses for farmers (Khan, Javed & Zeeshan, 2015) and airport environments, where groups of corvids pose a risk to aviation safety (Kukhta & Matsyura, 2018). As a consequence over four million corvids are killed annually across Europe (Jiguet, 2020), with local cullings often resulting in little impact, as local turnover is high and larger metapopulations exist (Marchand *et al.*, 2018). Vocal communication can provide non-lethal methods to mitigate these conflicts, particularly through playback, by broadcasting alarm calls or distress calls deterring corvids from specific areas (Baxter & Robinson, 2007; Belant, 2011). While such methods can be temporarily effective, corvids often habituate to repeated playbacks, necessitating ongoing modifications in

acoustic deterrents. Understanding how corvids use vocal communication in response to threats is crucial for developing long-term, non-lethal management strategies that balance human interests with conservation goals.

V. Conclusion

As outlined in this review, we argue that corvids present a key model group to advance our understanding of animal communication. Recent conceptual, technological, and methodological advances are suited to address challenges and new questions in the field. With their complex vocal repertoires, social learning abilities, and cognitive skills, corvids offer a particularly valuable opportunity to study the flexibility and function of vocal signals in both natural and human-modified environments. Future research integrating key evolutionary concepts, field experiments and powerful analytical tools will provide deeper insights into how corvids use vocalisations to navigate their social and ecological landscapes. Additionally, understanding corvid vocal communication has practical applications, from improving animal welfare, and mitigating human-wildlife conflict, to informing conservation strategies. By continuing to explore the intricacies of corvid vocalisation, we can not only refine our knowledge of avian communication but also gain broader insights into the evolution of complex signalling systems across species.

VI. Author contributions

This article arose from an investigative virtual workshop ‘Corvid Vocal Communication’ organised by C.A.F.W. and V.D. in September 2024. The workshop was advertised broadly within personal networks and on social media and participation at the workshop was free. Authorship was offered to everybody making a significant contribution according to the International Committee of Medical Journal Editors recommendations for defining the roles of authors and contributors (https://www.icmje.org/recommendations/browse/roles-and-responsibilities/defining-the-role-of-authors-and-contributors.html).

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1309 Table 1 – Number of Crows, Choughs, Jackdaws, Ravens, and Rooks kept in zoos globally and the number of zoos holding each species

Species	Total Kept Number	Institution Amount	Europe	Institution Amount	North America	Institution Amount	South America	Institution Amount	Asia	Institution Amount	Africa	Institution Amount	Oceania	Institution Amount
Crows														
American crow (*Corvus brachyrhynchos*)	39	31			38	30							1	1
- *C. b. hesperis*	4	2			1	1					3	1		
- *C. b. brachyrhynchos*	1	1			1	1								
Cape crow (*Corvus capensis*)	3	2									3	2		
Carrion crow (*Corvus corone*)	10	6	10	6										
- *C. c. cornix*	15	11	15	11										
Fish crow (*Corvus ossifragus*)	7	5			7	5								
Hawaiian crow (*Corvus hawaiiensis*)	129	2			129	2								
House crow (*Corvus splendens*)	3	2							3	2				
Large-billed crow (*Corvus macrorhynchos*)	2	2	1	1					1	1				
- *C. m. macrorhynchos*	1	1							1	1				
Mariana crow (*Corvus kubaryi*)	29	1			29	1								
New Caledonian crow (*Corvus moneduloides*)	6	1											6	1
Papuan crow (*Corvus orru*)	1	1											1	1
Pied crow (*Corvus albus*)	65	34	30	18	23	11			9	3	3	2		
Piping crow (*Corvus typicus*)	4	1	4	1										
Sinaloa crow (*Corvus sinaloae*)	1	1			1	1								
Sunda crow (*Corvus enca*)	2	1							2	1				
Tasmanian crow (*Corvus tasmanicus*)	3	1											3	1
Choughs														
Alpine chough (*Pyrrhocorax graculus*)	4	2	4	2										
Red-billed chough (*Pyrrhocorax pyrrhocorax*)	178	21	178	21										
Jackdaws														
Daurian jackdaw (*Coloeus dauuricus*)	1	1	1	1										
Western jackdaw (*Coloeus monedula*)	25	13	25	13										
Ravens														
Australian raven (*Corvus coronoides*)	7	1											7	1
Brown-necked raven (*Corvus ruficollis*)	7	3							7	3				
Common Raven (*Corvus Corax*)	236	127	164	83	65	40			6	3			1	1
- *C. c. Corax*	24	14	23	13	1	1								
- *C. c. principalis*	21	17	1	1	20	16								
- *C. c. tingitanus*	5	1			5	1								
Chihuahuan raven (*Corvus cryptoleucus*)	5	3			5	3								
Fan-tailed raven (*Corvus rhipidurus*)	1	1							1	1				
White-necked raven (*Corvus albicollis*)	62	25	23	10	38	14			1	1				
Rooks														
Rook (*Corvus frugilegus*)	15	9	15	9										
- *C. f. frugilegus*	1	1	1	1										

1310 Table 2 – Number of Jays, Jayshrikes, Magpies, Nutcrackers, Piapiac, Scrub-jays, and Treepies kept in zoos globally and the number of
1311 zoos holding each species

Species	Total Kept Number	Institution Amount	Europe	Institution Amount	North America	Institution Amount	South America	Institution Amount	Asia	Institution Amount	Africa	Institution Amount	Oceania	Institution Amount
Jays														
Azure jay (Cyanocorax caeruleus)	6	3					6	3						
Black-chested jay (*Cyanocorax affinis*)	10	6					10	6						
- *C. a. affinis*	1	1					1	1						
Black-throated magpie-jay (Cyanocorax colliei)	61	21	8	3	53	18								
Blue jay (*Cyanocitta cristata*)	13	10			13	10								
- *C. c. cristata*	1	1			1	1								
Eurasian jay (*Garrulus glandarius*)	24	17	20	14					4	3				
- *G. g. glandarius*	1	1	1	1										
Curl-crested jay (*Cyanocorax cristatellus*)	3	3					3	3						
Inca jay (*Cyanocorax yncas*)	56	17	17	7	35	7	4	3						
- *C. y. yncas*	8	6			8	6								
- *C. y. luxuosus*	1	1	1	1										
Lidth's jay (*Garrulus lidthi*)	22	3							22	3				
Plush-crested jay (*Cyanocorax chrysops*)	61	26	5	1	54	23	2	2						
- *C. c. chrysops*)	1	1			1	1								
Purplish-backed jay (*Cyanocorax beecheii*)	4	2	2	1	2	1								
San Blas jay (*Cyanocorax sanblasianus*)	2	1	2	1										
Steller's jay (*Cyanocitta stelleri*)	1	1			1	1								
White-naped jay (*Cyanocorax cyanopogon*)	2	1					2	1						
White-throated magpie-jay (Cyanocorax formosus)	21	6	5	3	16	3								
- *C. f.* azureus	1	1			1	1								
White-tailed jay (*Cyanocorax mystacalis*)	2	2	1	1							1	1		
Yucatan jay (*Cyanocorax yucatanicus*)	4	1	4	1										
Jayshrikes														
Crested jayshrike (*Platylophus galericulatus*)	1	1							1	1				
- *P. g. galericulatus*)	4	1							4	1				
Magpies														
Azure-winged magpie (*Cyanopica cyanus*)	150	43	68	20	73	19			9	4				
- *C. c. cyanus*	54	10	54	10										
American magpie (*Pica hudsonia*)	3	2			3	2								
Common green magpie (*Cissa chinensis*)	15	7	8	4	2	1			5	2				
Eurasian magpie (*Pica pica*)	21	10	21	10										
Iberian magpie (*Cyanopica cooki*)	30	13	29	12					1	1				
Javan green magpie (Cissa thalassina)	112	11	25	7					87	4				
Maghreb magpie (*Pica mauritanica*)	1	1	1	1										
Racket-tailed treepie (*Crypsirina temia*)	12	3	2	1					10	2				
Red-billed blue magpie (*Urocissa erythroryncha*)	243	90	181	71	35	12			27	7				
- *U. e. erythroryncha*	17	10			17	10								
- *U. e. occipitalis*	8	3	2	2					6	1				
Sumatran treepie (*Dendrocitta occipitalis*)	1	1	1	1										
Taiwan blue magpie (*Urocissa caerulea*)	4	1							4	1				
Yellow-billed magpie (*Pica nuttalli*)	1	1							1	1				
Yellow-breasted magpie (*Cissa hypoleuca*)	7	2	2	1					5	1				
Scrub-jays														
California scrub jay (*Aphelocoma californica*)	1	1			1	1								
Woodhouse's scrub jay (*Aphelocoma woodhouseii*)	1	1			1	1								
Others														
Northern nutcracker (*Nucifraga caryocatactes*)	10	6	10	6										
Piapiac (*Ptilostomus afer*)	4	2	2	1					2	1				

Rufous treepie (*Dendrocitta vagabunda*)	9	3	7	2		2	1

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