Unsung Songbirds: Advances in the Study of Corvid Communication

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Abstract

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 understanding of the evolution of animal communication. 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). Studying communicative interactions can inform key questions about cognitive processes and social dynamics, such as how individuals use signals for deception or cooperation, or extract information through eavesdropping. 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. One taxon, the *Corvidae*, has seen a recent increase in studies on vocal communication. *Corvidae* are a large family of birds consisting of more than 130 species (AviList Core Team, 2025) inhabiting most areas of the globe, except Antarctica. 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 and as such, the structure of their vocalisations arises from both the structural configuration of the vocal apparatus and vocal learning (Gaunt & Nowicki, 1998; Goller, 2019, 2022). In this review, we outline approaches to studying corvid vocal communication, including challenges and future opportunities. We propose an integrative framework that advances our evolutionary understanding of vocal communication by combining conceptual innovation with state-of-the-art methodologies, while also identifying concrete applications for animal welfare and conservation (Figure 1). Building an enriched evolutionary understanding of vocal communication requires integrating both proximate and ultimate levels of explanation. At the proximate level, investigating ontogeny, including vocal learning, usage learning, and cultural transmission, reveals how communicative systems emerge, stabilise, and change within and across generations. Examining cognitive mechanisms further clarifies how signals are produced, perceived, and interpreted, including questions of intentional control, semantic representation, combinatorial structure, and insights from animal linguistics into how meaning may be encoded and composed.

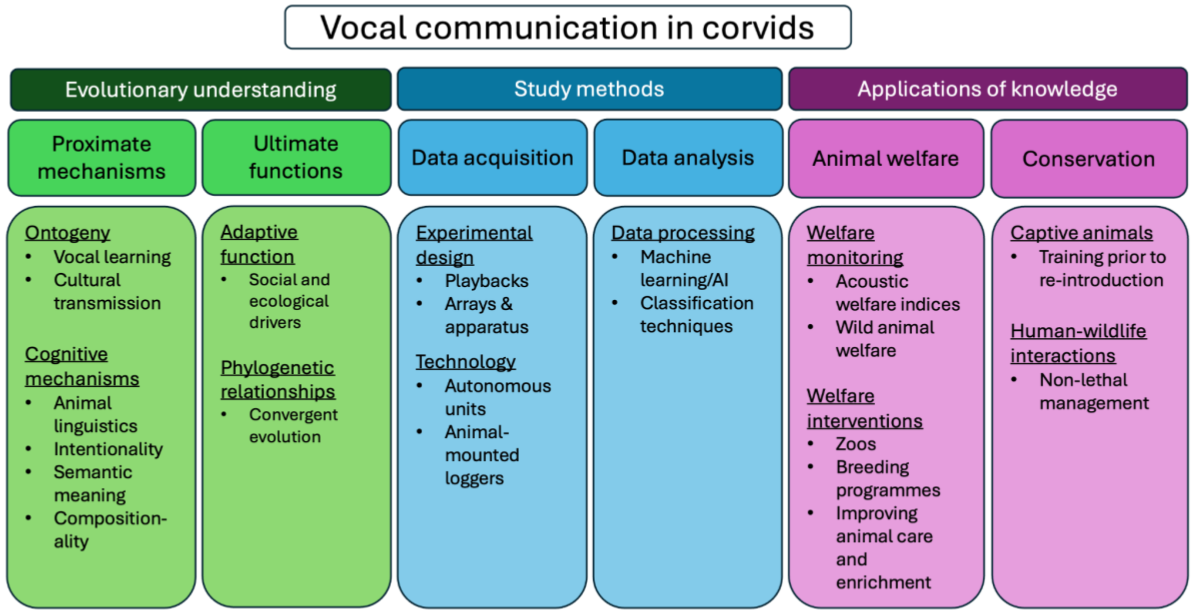

Figure 1: Framework and future directions in the study of corvid vocal communication.

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These mechanisms provide the developmental and cognitive foundations upon which communicative complexity is built. At the ultimate level, understanding the function of signals and the social and ecological pressures shaping their evolution allows us to test hypotheses such as the social complexity and acoustic adaptation frameworks. Finally, placing corvid vocal systems within a phylogenetic context enables us to disentangle shared ancestry from convergent evolution, clarifying whether similarities in vocal complexity across distant taxa arise from common descent or parallel responses to comparable selective pressures. By linking proximate mechanisms with ultimate explanations, we can move toward a more comprehensive evolutionary account of vocal communication.

II. Open questions to address the evolutionary understanding of animal communication

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). It is a key phenomenon to focus on when investigating how communication systems evolved. 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). 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).

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). To summarize, corvids, as open-ended vocal learners, provide an example of vocal plasticity beyond early development—their social learning, and capacity for both vocal production and usage learning into adulthood, make them an interesting model system for understanding vocal learning.

How do socio-cognitive processes shape vocal communication?

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, Ringler & Bugnyar, 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).

The challenges of deciphering vocal communication

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). 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). They are well known for their loud and ‘harsh’-sounding broadband vocalisations (Figure 2), 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 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).

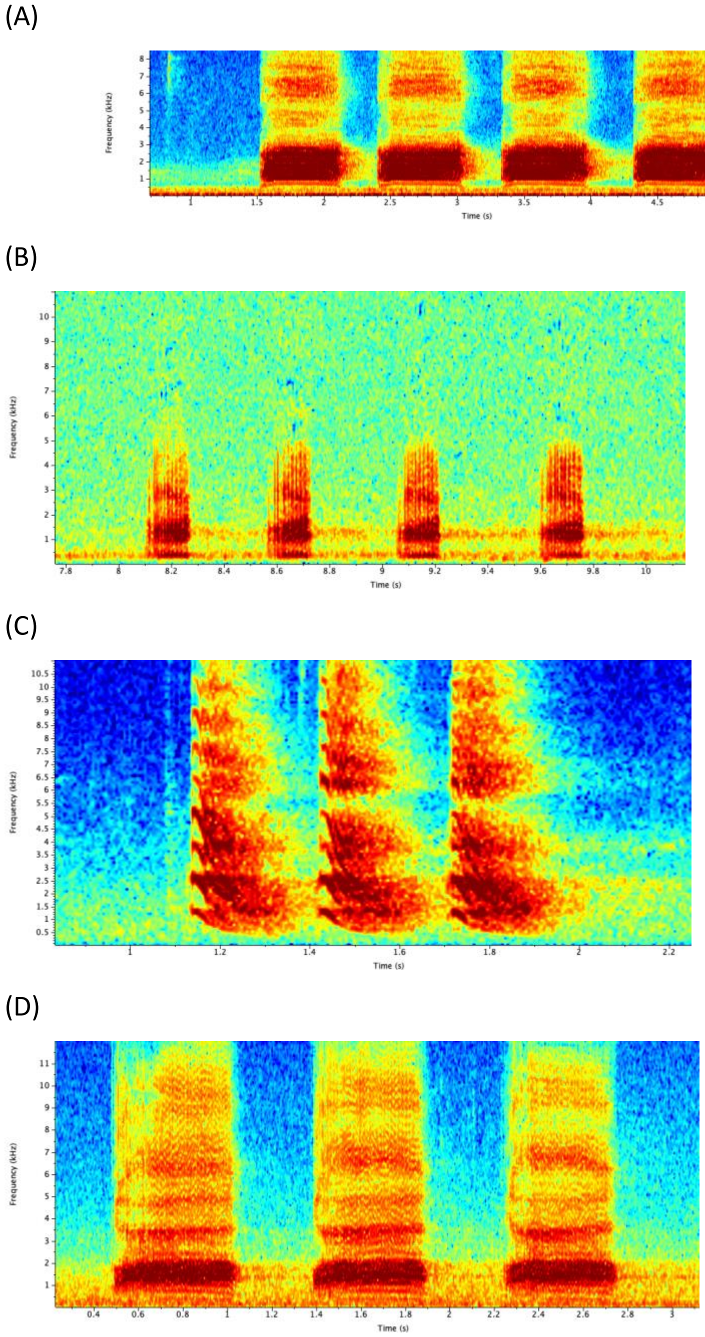

Figure 2: Example spectrograms of different non-harmonic corvid calls of different species. (A) carrion crow (*Corvus corone*), (B) common raven (*Corvus corax*), (C) jackdaw (*Coloeus monedula*) and (D) rook (*Corvus frugilegus*).

In addition to contextual information, 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, Lemasson & Zuberbühler, 2013; 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 *et al.*, 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.*, 2015).

Multimodal communication

Another 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. 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.

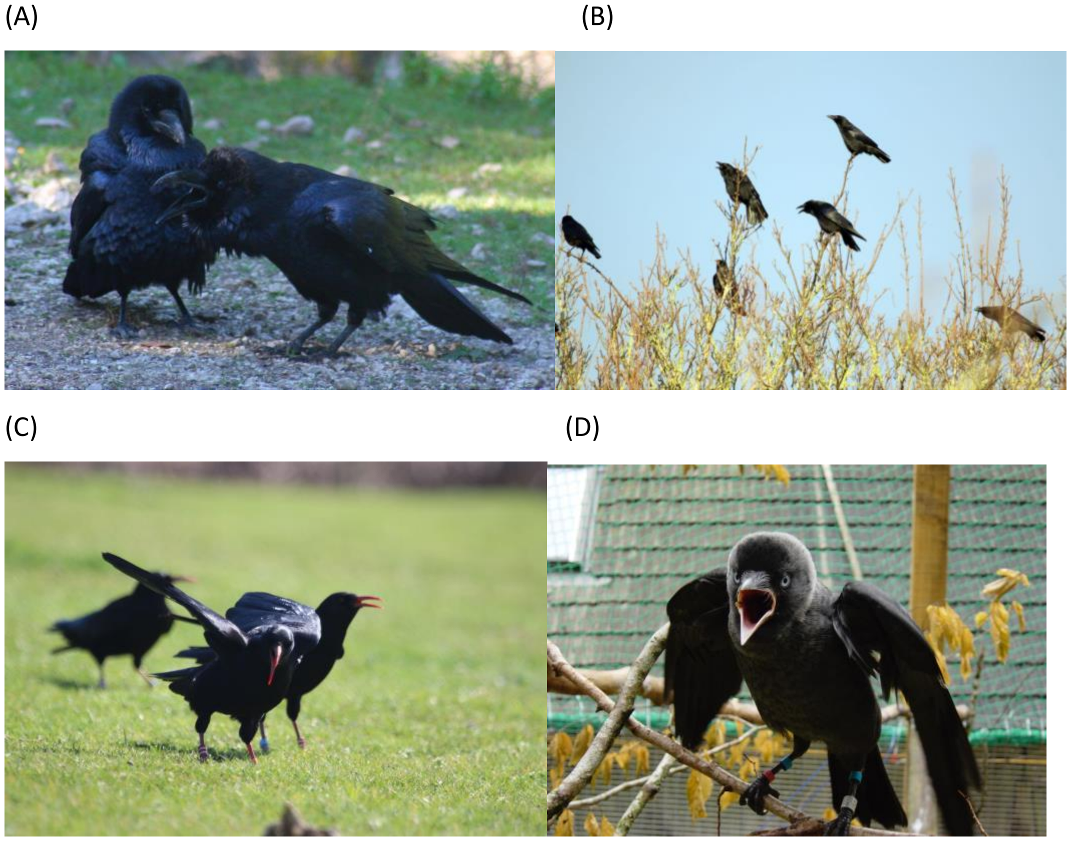

Figure 4: Examples of body postures associated with vocalisations in (A) common ravens, (B) carrion crows, (C) red-billed choughs (*Pyrrhocorax pyrrhocorax*), and (D) a jackdaw.

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

'Vocal complexity' is a recent 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 (Yorzinski *et al.*, 2006; 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). 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.

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 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). A recent experimental study showed that carrion crows can volitionally control the number of calls in the sequences they produce (Liao *et al.*, 2024). 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).

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).

The ultimate functions: 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).

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 as repertoire size, vary with the degree of sociality or environmental context, both within and between species. 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. Methodological challenges and approaches

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.

Recording of corvid vocalisations

Like most field data collection, research on corvid vocal communication presents challenges. Recording corvid vocalisations presents several methodological challenges that have limited systematic study of their communication. Corvids often vocalise unpredictably, making it difficult to obtain balanced and representative samples across call types. Corvids frequently vocalise in noisy, open environments, such as forests or urban areas, where wind, anthropogenic noise, and overlapping calls from conspecifics or heterospecifics can obscure fine acoustic features. Their high mobility and tendency to vocalise while flying or moving through the canopy further reduce recording quality and limit control over recording distance and angle. Finally, corvids are behaviourally flexible and sensitive to human presence; observer effects can alter calling behaviour or suppress vocalisations altogether, posing additional challenges for obtaining naturalistic recordings suitable for quantitative acoustic analyses.

Active and passive recordings

Recent technological advances in both active and passive recording methods are increasingly overcoming many of the challenges associated with documenting corvid vocalisations and, importantly, are enabling new classes of research questions to be addressed. Active recording approaches in captive settings or in wild populations habituated or trained to approach experimental set-ups (Figure 6) allow microphones to be positioned in close proximity to the focal signaller, resulting in high signal-to-noise ratio (SNR) recordings. Such high-quality recordings are essential for analysing fine-scale acoustic features, including subtle temporal and spectral cues that may underpin individual recognition (Hopp *et al.*, 2001; Kondo *et al.*, 2012; Martin *et al.*, 2022), social status (Kondo & Hiraiwa-Hasegawa, 2015), or contextual information (Griesser, 2009; Mates *et al.*, 2015; Gallego-Abenza *et al.*, 2022). They are also critical for capturing low-amplitude social calls that are otherwise difficult to record at a distance. In parallel, advances in passive recording technologies, such as autonomous recording units and microphone arrays, enable continuous, long-term monitoring across spatial scales without the need for constant human presence, thereby reducing observer effects. Passive recording technology in corvids has previously been applied to investigate for example collective behaviour (Dibnah *et al.*, 2022). When combined with automated detection, classification, and machine learning pipelines (Lü *et al.*, 2024), these approaches allow researchers to process large, data-rich datasets efficiently (Williams *et al.*, 2020; Nieto-Mora *et al.*, 2023), facilitating quantitative analyses of graded call systems and feature-based encoding of meaning. Together, active and passive recording technologies thus make it possible to link high-resolution acoustic structure to behavioural context, individual identity, and semantic function, substantially expanding the scope of questions that can be addressed in corvid vocal communication research.

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 (Baglione *et al.*, 2025). 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. Studies in birds have revealed sub-lethal effects of the increased weight or handling-induced stress associated with tags (Chivers, Hatch & Elliott, 2016; Evans *et al.*, 2020; Puehringer-Sturmayr *et al.*, 2020). 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). 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.

Analysing corvid calls

Commonly, the collected audio data from corvids will be noisy—masked by wind noise, overlapping calls, or vocalisations of 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).

Processing data before analyses

Modern 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).

When recording audio outside of a controlled environment, noise will be present. Audio detection and classification methods can be made reasonably resilient to environmental (wind, rain), biological (vocalisations from non-focal individuals), or mechanical (body movements against microphone) 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. 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 (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.

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 (Bugnyar, 2013; Taylor, 2014; Cunha & Griesser, 2021). 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.

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 and speech (Wascher *et al.*, 2012; Schalz & Izawa, 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).

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.*, 2024), 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. Opportunities and 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). 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).

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.

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.

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 have 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 (Bergman & Östlund, 2022; Joy, Armstrand & Helander, 2024). Generally, corvids evoke strong and polarized emotions in human societies (Jürgens *et al.*, 2022), which presents an interesting area of research. Several corvid species have been shown to be sensitive to differences in human voices and speech, for example depending on familiarity, gender, or language (Wascher *et al.*, 2012; Schalz & Izawa, 2020; McIvor *et al.*, 2022; Schalz, 2023). This may provide fitness benefits by avoiding unfamiliar, potentially dangerous humans. 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.

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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