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Review

The ecology and evolution of cues and signals in animal interspecies cooperation

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Mutualistic interactions have played a central role in generating biodiversity and are often facilitated by an exchange of information between participating parties. Cues and signals are likely to be particularly crucial in animal interspecies cooperation, a specific form of mutualism that depends on real-time, interactive behavioural coordination to secure mutual benefit. Yet, despite the taxonomic breadth and ecological significance of these interactions, our understanding of the roles of cues and signals in animal interspecies cooperation remains relatively underexplored compared to their well-documented roles in other mutualisms, intraspecies cooperation and interactions involving collective behaviour. Here, we examine the ecology and evolution of cues and signals in animal interspecies cooperation. Drawing on diverse natural history examples, we first assess the ecological functions, benefits and costs of cues and signals, and discuss how the information they convey about partner identity, motivation and reliability informs decisions about whether, when and how to cooperate with heterospecifics. Second, we outline the evolutionary origins, variation and heritability of cues and signals, and discuss the potential for coevolution between signallers and perceivers. Third, we draw on relevant insights from broader mutualisms and cooperation within species to highlight key similarities and differences in the use of cues and signals across interaction types. Overall, our review clarifies how information underpins animal interspecies cooperation, highlights key gaps in the scientific literature, and identifies promising avenues for future research on its ecological and evolutionary significance.

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Animal interspecies cooperation occurs when individuals from different animal species actively coordinate their behaviour in real time, performing complementary actions that yield a mutually beneficial outcome (Axelrod & Hamilton, 1981; Dugatkin, 2002; Noë, 2006). In this review, we adopt the definition of cooperation used in the field of behavioural ecology: a form of mutualism (see Table 1 for definitions) characterized by active, reciprocal behavioural coordination or complementary roles (West et al., 2007a), thus considering both the outcomes and the behaviours that achieve them. This definition captures a wide diversity of interactions across taxa, and often involves distantly related partners (see Table 1), from insects and fishes to birds and mammals, which either coordinate complementary actions to access shared resources (e.g. food; Sampaio et al., 2025) or exchange resources for services such as predator protection (Bronstein & Sridhar, 2024; Bshary & Noë, 2023). Animal interspecies cooperation is thus distinct from other mutualisms and interspecies collective behaviours (e.g. mixed-species mobbing, alarm calling or grouping), which generally provide benefits through parallel action or by-product effects and/or currently lack empirical evidence of reciprocal, partner-dependent coordination (e.g. Carlson et al., 2020; Goodale et al., 2020). Despite its occurrence across diverse taxa, we still have limited understanding of how animal interspecies cooperation functions and evolves, and, in particular, how close coordination can be achieved across species boundaries.

In animal interspecies cooperation, both partners must actively monitor and respond to one another, coordinating in time and space to yield net benefits for both (Duguid & Melis, 2020; Sachs et al., 2004; West et al., 2007a). These benefits can include improved health (e.g. cleaner–client interactions; Soares et al., 2011), enhanced access to resources (e.g. human–honeyguide interactions; Isack & Reyer, 1989), and reduced predation risk (e.g. ant–insect interactions; Ivens & Kronauer, 2022), and at a broader scale, such interactions can contribute to ecosystem stability and functioning (e.g. Lloyd-Jones et al., 2022; Waldie et al., 2011). Achieving these outcomes requires each partner to make informed decisions about whether, when and how to engage with the other. These decisions can be facilitated if individuals are attuned to potential partners' cues (traits that influence the behaviour of perceivers but did not evolve for that purpose) or signals (traits that evolved specifically to influence perceivers; see Table 1). Sensitivity to such cues and signals enables individuals to adjust their responses appropriately, facilitating information exchange across species.

Indeed, cues and signals play well-documented roles in mediating a number of mutualisms (e.g. plant–animal pollination and seed dispersal: Corlett, 2011; Karban, 2008; Karban, 2021; Leonard & Francis, 2017; Lucas-Barbosa, 2016; Schaefer et al., 2004; Schiestl & Dötterl, 2012; Schiestl & Johnson, 2013; plant–microbe: Karban, 2021; Rosier et al., 2016; van't Padje, Whiteside, & Kiers, 2016) and animal intraspecies cooperation (e.g. primates: Duguid & Melis, 2020; canids: Harrington et al.,

Table 1
Definitions of terms used in the article

Term	Definition
Animal interspecies cooperation	A type of mutualism in which individuals of different animal species actively coordinate their behaviour to achieve mutual benefit (Cram et al., 2022)
Aposematism	Conspicuous signals (e.g. bright coloration) that warns potential predators of an individual's unprofitability, toxicity or harmful defences
Coevolution	Reciprocal adaptive evolutionary change in traits that are genetically and/or culturally inherited (Dixit, 2024). Coevolution occurs when two or more traits impose selection pressures on each other, often resulting in rapid evolutionary change in both traits
Collective behaviour	Coordinated actions and patterns that emerge from interactions among multiple individuals, typically governed by local rules or cues rather than centralized control, resulting in group-level organization or function (Sumpter, 2006)
Communication	The transmission of signals from an informer to a perceiver (Owren et al., 2010)
Complementary roles	In cooperative interactions, roles in which each participant provides a benefit that the other cannot achieve on its own
Cooperation	A behaviour that provides a benefit to another individual, and which is selected for because it also provides a benefit to the actor (although multiple definitions exist, see Bshary, 2021; West et al., 2007b)
Coordination	When individuals adjust their behaviour in response to each other to achieve mutual benefits
Cue	An incidental source of information, arising from a trait that influences the behaviour of a perceiver without being specifically produced or having evolved for that purpose (Laidre & Johnstone, 2013)
Deceptive signal	A signal that misleads the perceiver to benefit the signaller
Eavesdropper	An unintended perceiver of a signal who actively and deliberately intercepts it
Exploitation	An interaction in which one partner gains a benefit while providing little to no benefit in return to the other party. In more extreme cases, partners could cause harm
Facultative	A relationship that is not essential for the survival or reproduction of the species
Honest signal	A signal that accurately reflects information about the informer's traits or motivations (Roberts, 2020)
Human–wildlife cooperation	A subset of animal interspecies cooperation where humans and wild nonhuman animals coordinate their behaviour to achieve mutual benefit, with each altering their behaviour in response to the other to reach a common goal (Cram et al., 2022; van der Wal, Spottiswoode, et al., 2022)
Information	Cues and signals that affect a perceiver's behaviour in a way that reduces uncertainty for either the informer, the perceiver or both (Owren et al., 2010)
Information transfer	The process by which signals or cues emanate from one individual and are received by another (Owren et al., 2010)
Informer	An individual whose traits influence another's behaviour, whether through evolved signals or cues. We use this term instead of the more traditional 'sender' to emphasize the informational value of the behaviour rather than the evolved function to communicate (Owren et al., 2010; Ruxton & Schaefer, 2011). We use 'signaller' to refer to informers specifically providing signals
Manipulative signal	A signal that benefits the signaller by altering a signal perceiver's behaviour in a way that serves the signaller's interests, at a cost to the perceiver (Dawkins & Krebs, 1978)
Mutualism	An interaction between individuals of different species in which both experience a net benefit (although multiple definitions exist, see Bshary, 2021; West et al., 2007b)
Obligate	A relationship that is essential for the survival or reproduction of a species
Perceiver	An individual that detects and interprets information from an informer. We use this term instead of the more traditional 'receiver' to emphasize the active, interpretive role of the recipient and to include both cues and signals (Owren et al., 2010; Ruxton & Schaefer, 2011). We use 'signal perceiver' to describe the target individual(s) a signal is directed towards
Punishing signal	A signal that deters exploitation by imposing a cost on a signal perceiver who behaves uncooperatively (Raihani & Bshary, 2015)
Signal	A trait that has evolved specifically to influence the behaviour of a signal perceiver (Laidre & Johnstone, 2013)
Signaller	The individual that produces and transmits a signal. A signaller's traits or behaviours can influence the perception, decisions or actions of a perceiver
Signal content	The information conveyed by a signal, the message that may influence the perceiver's behaviour (e.g. presence of food, level of risk, identity of the signaller; Guilford & Dawkins, 1993)
Signal efficacy	How well the signal is transmitted, detected and discriminated by the perceiver, given the environmental and sensory context (e.g. loudness, clarity or conspicuousness in noise or clutter; Guilford & Dawkins, 1993)
Signal form	The physical or structural properties of the signal itself (e.g. sound frequency, colour pattern, gesture type) that make up its nature
Signal mimicry	When one organism resembles another's signals to gain survival or reproductive advantages (Jamie, 2017)

Terms are defined with respect to the relevance to cooperative interactions and could have additional definitions in other fields. Terms are listed alphabetically.

2003; cetaceans: King et al., 2026). For example, they can help identify and/or attract beneficial partners (e.g. floral colour cues and chemical signals in plant–pollinator and plant–microbe mutualisms: Hempel de Ibarra et al., 2022; van't Padje et al., 2016) and guide coordinated behaviours (e.g. vocalizations and body movements in animal intraspecies foraging and defence: Bailey et al., 2013; King et al., 2019). Information transfer is also well established as playing a central role in a range of other interspecific interactions that can generate mutual benefits via by-product effects but without active, reciprocal coordination (e.g. Goodale et al., 2020), including collective behaviours such as heterospecific predator mobbing (e.g. Carlson et al., 2020; Carlson & Slabbekoorn, 2025; Dutour et al., 2017), alarm calling (e.g. Magrath et al., 2015), and grouping or flocking (e.g. Baigrie et al., 2014; Goodale et al., 2010). Despite extensive work on information transfer across these diverse interaction types, the role of cues and signals in the ecology and evolution of animal interspecies cooperation has received comparatively little systematic attention across taxa and contexts.

This gap in our understanding is noteworthy, because animal interspecies cooperation combines features of multiple interaction types, sharing some challenges with broader mutualisms, such as cross-species communication and increased risk of harm or exploitation (see Table 1; Bronstein, 2001), while also exhibiting features of intraspecific cooperation that help actively promote cooperative outcomes, including interactive, real-time coordination and mutual partner choice (Duguid & Melis, 2020; Noë, 2006). Furthermore, unlike many other mutualisms, in which one or both partners are constrained in their ability to quickly respond to partner actions (e.g. plant–microbe or plant–pollinator mutualisms), animal interspecies cooperation requires interactive, behavioural alignment between partners (e.g. Cram et al., 2022). Although similar rapid coordination is common in animal intraspecies cooperation (e.g. Duguid & Melis, 2020; King et al., 2026), those interactions typically occur among closely related individuals, facilitating kin-selected behaviours and reducing the risk of exploitation. By contrast, animal interspecies cooperation can involve coordination between distantly related species,

creating distinctive demands on the cues and signals mediating these interactions. These information exchange mechanisms might therefore be shaped by both the exploitation–avoidance pressures characteristic of mutualisms and the demands of rapid coordination seen in animal intraspecies cooperation. Recognizing this overlap highlights the value of integrating insights from mutualism and intraspecies cooperation to better understand the ecology and evolution of information exchange in animal interspecies cooperation (Bronstein & Sridhar, 2024).

Here, we review the ecology and evolution of cues and signals in animal interspecies cooperation, focusing on how information transfer (see Table 1) influences the persistence, functioning and outcomes of cooperation. Our review is restricted to animal interspecies cooperative interactions for which empirical evidence demonstrates both cooperation and information transfer. Table 2 summarizes, to our knowledge, all currently documented examples that fit these criteria between nondomesticated, untrained animal species, spanning multiple taxa, including humans. We acknowledge that future studies might document additional qualifying interactions; indeed, we hope our review stimulates such work. Although the literature remains disproportionately focused on a few well-studied systems (e.g. aquatic cleaner–client, ant–insect, human–honeyguide, human–dolphin; Table 2), and our review inevitably reflects this bias, these systems provide ecologically and evolutionarily diverse examples of animal interspecies cooperation. Specifically, we include interactions that vary in the number of species and partners involved, in the degree to which they are repeated or one-off, in the types of benefits accrued (e.g. protection, food), and whether they are facultative or obligate interactions (see Table 1). We also consider both morphological and behavioural cues and signals that vary in stereotypy and modality. These diverse interactions therefore provide valuable insights into the mechanisms, outcomes and broader significance of animal interspecies cooperation.

In Part A, we examine the ecological functions, costs and benefits, and between-system diversity of the informational traits that underpin interspecies cooperation. In Part B, we consider the evolutionary origins, within-system variation, heritability and selection pressures shaping these cues and signals, including the potential for coevolution between signallers and perceivers. Finally, in Part C, we integrate knowledge across interaction types, discussing how the ecology and evolution of cues and signals in animal interspecies cooperation compare with those in other mutualisms and animal intraspecies cooperation, and highlight areas for future research (also see Table 3 for a list of outstanding questions).

PART A: THE ECOLOGY OF CUES AND SIGNALS IN ANIMAL INTERSPECIES COOPERATION

Functions and Benefits

Cues and signals can play key roles at three stages of animal interspecies cooperation: (1) identifying and/or attracting partners; (2) initiating cooperation; and (3) maximizing benefits by coordinating behaviour and preventing exploitation (Fig. 1; Noë, 2001). As detailed in Part C, such functions overlap with mutualisms more broadly (e.g. identifying and/or attracting partners, deterring exploitation) and animal intraspecies cooperation (e.g. identifying partners, coordinating behaviour). Within animal interspecies cooperation, a given cue or signal might contribute to more than one of these functions, as reflected in some of the examples below.

Cooperators often identify potential partners by searching for salient information or by broadcasting signals of their own motivations to cooperate. These signals can help minimize the risks of misaligned motivations and failed cooperation (e.g. preventing interactions with harmful partners instead). In cleaner–client cooperation (Table 2), for example, cleaner fish such as wrasse (*Labroides* spp.) and gobies (*Elacatinus* spp.), as well as cleaner shrimp (e.g. *Lysmata amboinensis*) provide a beneficial service by removing ectoparasites from other animals (termed 'clients'). Some of the cleaner species use morphological signals to communicate their identity as 'cleaners' with stereotyped high-contrast body coloration patterns (shown in Fig. 1; Caves et al., 2024; Cheney et al., 2009; Lettieri & Streelman, 2010; Lettieri et al., 2009; Stummer et al., 2004). Clients can also adopt temporary head-/tail-stand angled body postures next to cleaners (termed 'poses', shown in Fig. 1), to signal their willingness to be cleaned (Côté et al., 1998). Cleaners can then decide whether to engage with clients following an inspection (e.g. Dunkley et al., 2018), illustrating that partner identification and successful interaction can involve multiple sequential decisions.

In addition to indicating partner identity, cooperators can also pay attention to information about partner quality, allowing them to choose those likely to provide the greatest benefits (Roberts, 2020). In human–dolphin cooperation (Table 2), in which humans and dolphins (e.g. *Tursiops truncatus gephyreus* or *Tursiops gephyreus*) share an increased fish catch reward by synchronizing their foraging actions, fishers prefer to interact with individual dolphins known to have a history of successful interaction, whom they identify from cues of identity including body marks and behaviour (Cantor et al., 2023; da Rosa et al., 2020). Signals can also convey general information about partner quality, through their intensity or duration. In cleaner–client systems, client fish with greater parasite loads appear to pose for longer towards Caribbean *Elacatinus* cleaners, perhaps indicating the nutritional value of cooperating (e.g. Sikkel et al., 2004). Likewise, client fish show a preference for interacting with more blue-saturated *Labroides dimidiatus* cleaner wrasse and may associate the relative degree of body colour saturation among individuals with cleaning service quality (Cacela-Rodrigues et al., 2025; Trigo et al., 2020). By revealing partner quality, cues and signals help individuals choose partners that will be most rewarding.

Once suitable partners are located (and within signalling distance), cooperators often also use signals to initiate cooperative interactions. In marine cooperative hunting (Table 2), coral trout, *Plectropomus leopardus*, and groupers, *Plectropomus pessuliferus marisrubri*, use rapid shimmies to recruit eels, *Gymnothorax javanicus*, or octopuses, *Octopus cyanea* (Bshary et al., 2006; Vail et al., 2013), while client fish can signal for cleaning by adopting specific poses and/or, in some species (e.g. *Mulloidichthys* spp.), changing their body colour (Caves et al., 2018; Côté et al., 1998). Signals to initiate cooperation may be particularly crucial where the partner species could cause harm. Indeed, some cleaner shrimp (e.g. *L. amboinensis*) and cleaner fish (e.g. *L. dimidiatus*) both signal more towards potentially predatory clients (using leg rocking behaviour and 'tactile dancing' behaviours, respectively), communicating their value as cooperators and not just as meals (Caves et al., 2019; Grutter, 2004). Similarly, in ant–insect cooperation (Table 2), species-specific cuticular hydrocarbon signals produced by aphids (e.g. *Aphis fabae*) and lycaenid larvae (e.g. *Narathura japonica*) elicit protective behaviour from ants (e.g. *Lasius niger*), which receive a sugar-rich food reward in return (Hayashi et al., 2015; Hojo et al., 2014; Lang & Menzel, 2011). Nonmutualistic species can be killed by ants, illustrating the importance of these signals in maintaining interspecies cooperation.

After cooperation begins, cues and signals can help enhance beneficial outcomes by coordinating the behaviours of one or both partners. In human–honeyguide cooperation (Table 2), where greater honeyguides, *Indicator indicator*, and human 'honey-hunters' work together to locate, access and feed upon the content

Table 2
Summary of the examples of animal interspecies cooperation in which information transfer has been studied and/or observed

Type	Partner 1	Partner 2	Source
Cooperative foraging/hunting	Partners hunt/forage together to increase their own hunting success. Involves one partner finding/leading another to food resources, and the other helping to successfully obtain the food reward		
	Grouper, *Plectropomus pessuliferus marisrubri*, or coral trout, *Plectropomus leopardus* High-frequency shimmy of body to initiate and vertical head-down posture with head shakes to indicate prey location (S)	Eel, *Gymnothorax javanicus*, wrasse, *Chelinus undulatus*, or octopus, *Octopus cyanea* No cues/signals currently documented	Bshary et al., 2006; Vail et al., 2013
	Octopus, *Octopus cyanea* Can 'punch' to displace partner fish during hunts that do not seek out prey: potential policing signal to reduce exploitation but function unknown (U)	Multiple reef fish species (e.g. *Parupeneus cyclostomus*, *Epinephelus fasciatus* No cues/signals currently documented	Sampaio et al., 2021, 2024
	Northern resident killer whales, *Orcinus orca ater* No cues/signals currently documented	Pacific white-sided dolphins, *Lagenorhynchus obliquidens* Foraging echolocation calls can be used as cues by killer whales to more efficiently find adult Chinook salmon, *Oncorhynchus tshawytscha* (C)	Fortune et al. (2025)
	Human 'fishers' Fishers use acoustic signals (e.g. striking water surface/boat or vocal calls) to initiate cooperative fishing with Irrawaddy dolphins (S), but fishers interacting with bottlenose dolphins do not	Irrawaddy, *Orcaella brevirostris*, or Lahille's bottlenose dolphins, *Tursiops truncatus gephyreus* or *Tursiops gephyreus* Aerial displays (e.g. sudden back-arching dives, partial immersions, tail-slaps and head-slaps) to herd a fish school towards fishers and inform net casting (C)	Cantor et al., 2023; Serpa et al., 2024; Simões-Lopes et al., 1998; Tun, 2004, 2008
	Human 'honey-hunters' Often use acoustic signals (e.g. vocal calls, banging trees, whistling tools) to recruit a partner, and the same or different acoustic signals to continue interaction until a bees' nest is found (S)	Greater honeyguide, *Indicator indicator* Produce stereotyped chattering call to recruit partner and continue interaction until a bees' nest is found (S)	Isack & Reyer, 1989; Spottiswoode et al., 2016; Spottiswoode & Wood, 2023; van der Wal, Gedi, & Spottiswoode, 2022; Nhlabatsi et al., 2025; Kamboe et al., 2025; Wood et al., 2014
Food-for-cleaning services	Food resources (e.g. parasites) are exchanged for a health-enhancing parasite removal cleaning service		
	Multiple cleaner fish species† (e.g. *Labroides dimidiatus, Elacatinus evelynae*, *Pomacanthus paru*) Obligate cleaners have distinctive body coloration (S) and can 'dance' to attract clients (S). Some cleaners can make specific body contacts with potential clients (tactile stimulation) (U)	Multiple 'client' species (e.g. fishes and turtles) Client fish can adopt a stationary stereotyped tail-stand or head-stand posture ('pose') before and during interactions (S). They may jolt if exploited by cleaners (U), and often chase cleaners once exploited (S). Client fish species can also produce vocalizations (e.g. *Myripristis* spp.) following exploitation to terminate interactions (U). Turtle clients can cease swimming and fully extend their flippers downwards (U)	Banse et al., 2024; Bshary & Grutter, 2002; Cheney et al., 2009; Côté et al., 1998; Grossman et al., 2006; Grutter, 2004; Skead, 1951; Stummer et al., 2004; Whittaker et al., 2021
	Multiple cleaner shrimp species† (e.g. *Lysmata amboinensis*, *Stenopus hispidus*) Can display distinctive body coloration and extend their antennae to signal availability for cleaning (S). Can use rocking dances to signal presence (S)	Multiple 'client' species (e.g. fishes) Same posing behaviours observed as for cleaner fishes (S). Client species can change colour (e.g. *Mulloidichthys martinicus*) to increase their likelihood of receiving a cleaning service from shrimp (S)	Becker et al., 2005; Caves, 2021; Caves et al., 2018; Caves et al., 2019; Jonasson, 1987
	Multiple cleaner bird species (e.g. *Jacana jacana*, *Geospiza fuliginosa*, *Daptrius ater*, *Pica pica*, *Corvus corone cornix*) Can use body movements (e.g. wing fluttering, head bowing) upon landing on potential clients (U). Anecdotal evidence that some (e.g. *D. ater*) engage in vocal exchanges (e.g. rasping calls) with potential clients to help locate them (U)	Multiple 'client' species (e.g. mammals, reptiles and fishes) Can adopt stationary body postures with outstretched body parts (e.g. necks, lying on side) (U), but rare. Anecdotal evidence of Brazilian tapir, *Tapirus terrestris*, using whistling calls which could be used to locate their cleaners in forest habitats (U)	Abe et al., 2012; Kilham, 1982; Macdonald, 1981; MacFarland & Reeder, 1974; Massei & Genov, 1995; Peres, 1996; Sazima & Sazima, 2010; Yosef & Yosef, 1991
	Banded mongoose, *Mungos mungo* No cues/signals currently documented	Warthog, *Phacochoerus africanus* Warthog may kneel or lie on its side in apparent solicitation of cleaning ticks from the body. Can also stand still (U)	Sazima, 2010; Channer, n.d.
Food-for-protection services	Food resources (e.g. honeydew) are exchanged for predator protection services		
	Lycaenid butterfly larvae† (e.g. *Lycaeides argyrognomon*, *Arhopala japonica*) Chemical, acoustic, and tactile signals to attract, trick, alarm, or pacify ant partners Chemical: cuticular hydrocarbons are secreted, which ants use to recognize mutualistic	Multiple ant species (e.g. *Pristomyrmex punctatus*) Ants can use their antennae to 'inspect' the larvae, touching and grooming them. This tactile behaviour reinforces cooperation between ants and larvae (S). Ants may also	Axén et al., 1996; Casacci et al., 2019; Fiedler & Maschwitz, 1989; Hojo et al., 2014; Pierce & Dankowicz, 2022; Riva et al., 2017; Travassos & Pierce, 2000

(*continued on next page*)

Table 2 (*continued*)

Type	Partner 1	Partner 2	Source
	partners, facilitating interactions and fostering cooperation (S). Honeydew also contains alarm signals to excite ant bodyguards (S) Acoustic: Larvae produce vibroacoustic signals (e.g. grunts, drums or hisses) to engage with ants and reinforce mutualistic behaviours (S) Tactile: Larvae wave or stroke their tentacles as tactile and/or visual cues to attract ant partners. Tentacle movements may also be paired with alarm pheromone release, although the exact function is debated (U)	release recruitment pheromones to signal other colony members to assist in tending to the larvae (S)	
	Hemiptera† (e.g. treehoppers and aphids) Treehoppers produce substrate-borne vibrational alarm signals in response to predator presence to solicit ant protection (S). Ants use species-specific cuticular hydrocarbons of aphids to identify mutualistic partners (S)	Multiple ant species Some ants limit aphid dispersal from them through chemicals (S): this benefits ants by increasing their access to honeydew rewards. Some ants gently tap aphid partners to 'milk' their honeydew and wave their antennae to solicit honeydew (S).	Hayashi et al., 2015; Ivens & Kronauer, 2022; Morales et al., 2008; Oliver et al., 2007; Salazar et al., 2015
Shelter-for-protection services	Shelter use (e.g. burrows) is exchanged for predator protection services (e.g. warning alert system)		
	Shrimps† (e.g. *Alpheus rapax, A. purpurilenticularis* and *A. rapacida*) Shrimps communicate their presence outside the burrow by touching their goby partner with their antennae (S)	Goby fish† (e.g. *Psilogobius mainlandi, Cryptocentrus steinitzi*) Tactile tail flicks and headfirst entries act as warning signals for shrimp to return to their burrow when danger approaches (S). Shrimp can use chemical cues to find specific goby partner species (C)	Karplus et al., 1972; Karplus, 1979; Karplus & Thompson, 2011; Preston, 1978

C = cue, S = signal, U = unknown whether cue or signal (i.e. not formally tested/discussed) produced by the informer partner. Not all cues/signals listed in the interspecies cooperation examples in the table always occur within each interaction. While most examples are facultative, some systems illustrated here include partner species that engage obligately in the interaction (†).

of bees' nests, honeyguides use a stereotypical chattering call to facilitate coordination of movement towards the bees' nest, and humans reply with their own coordination signals (illustrated in Fig. 1; Isack & Reyer, 1989; Spottiswoode et al., 2016). Additionally, in human–dolphin cooperation, humans respond to dolphins' body movements when casting fishing nets (illustrated in Fig. 1; Serpa et al., 2024; Simões-Lopes et al., 1998), and dolphins adjust their foraging behaviour to match fishing actions, increasing prey capture for both (Cantor et al., 2023). It remains unclear whether this information reflects signalling by dolphins or movement cues opportunistically interpreted by humans (see Origins section). Regardless, fishers consider these dolphin behaviours to be directed to them, and responding to them improves real-time coordination and mutual success (Cantor et al., 2023).

Cooperators can also use signals to manipulate partners (see Table 1), and in interactions vulnerable to exploitation (see Table 1), such as cleaning or protection cooperation, behavioural signals can help deter exploitation and reinforce cooperative behaviour. Punishing signals (see Table 1), for example, can inform exploiting partners that harmful behaviour will not be tolerated, as seen in client fish that chase cleaners that exploit (i.e. bite) them (illustrated in Fig. 1; Bshary & Grutter, 2002; Eckes et al., 2015). Perhaps similarly, individual octopus appear to 'punch' suspected exploiters during cooperative foraging interactions with fishes (Table 2; Sampaio et al., 2021, 2024). Vulnerable partners could also use signals to reduce their risk of exploitation before it occurs. Indeed, in cleaner–client cooperation, the observation that *L. dimidiatus* cleaning interactions become more exploitative in the absence of client behaviours (Bshary & Grutter, 2002) suggests that clients' initiation signals may have evolved (at least in part) to protect them against exploitation or to coerce cleaners into behaving cooperatively. Further, in ant–insect cooperation (Table 2), lycaenid larvae

Table 3
Outstanding questions on the ecology and evolution of cues and signals in animal interspecies cooperation

	Question
(1)	How do cues evolve into signals in animal interspecies cooperation, and does coevolution between signallers and signal perceivers play a role?
(2)	How do naturally occurring cues and signals in animal interspecies cooperation compare to those in trained cooperative interactions (e.g. between humans and captive cormorants, otters, eagles, dogs, etc.)?
(3)	What factors (e.g. number of partner species, risk of exploitation, facultative versus obligate) constrain or promote the diversification of signals in animal interspecies cooperation?
(4)	Are sensory modalities that are difficult for human observers to detect (e.g. electric, olfactory) more widespread in animal interspecies cooperation than previously thought, and could they play important roles in ensuring signal honesty?
(5)	To what degree are signals genetically inherited versus learnt in animal interspecies cooperation? And what conditions make them appear, stay or disappear?
(6)	To what extent have signals that originally evolved to resolve intraspecies conflicts been co-opted to facilitate cooperation between animal species?
(7)	How does the coevolution of communication systems differ within and between species?
(8)	How might anthropogenic change alter the ability to produce or perceive signals or cues, and what would this mean for cases of animal interspecies cooperation?
(9)	To what extent is cognitive and social ability of one or more cooperative partners important in the transition from cues to signals in interspecies cooperation?
(10)	Can experimentally induced changes in information exchange push collective or exploitative interspecific interactions, where benefits are incidental or asymmetrically distributed, towards coordinated animal interspecies cooperation? For example, could increased signalling or responsiveness promote active cooperative coordination in systems such as mixed-species predator mobbing, alarm calling or more exploitative foraging associations?

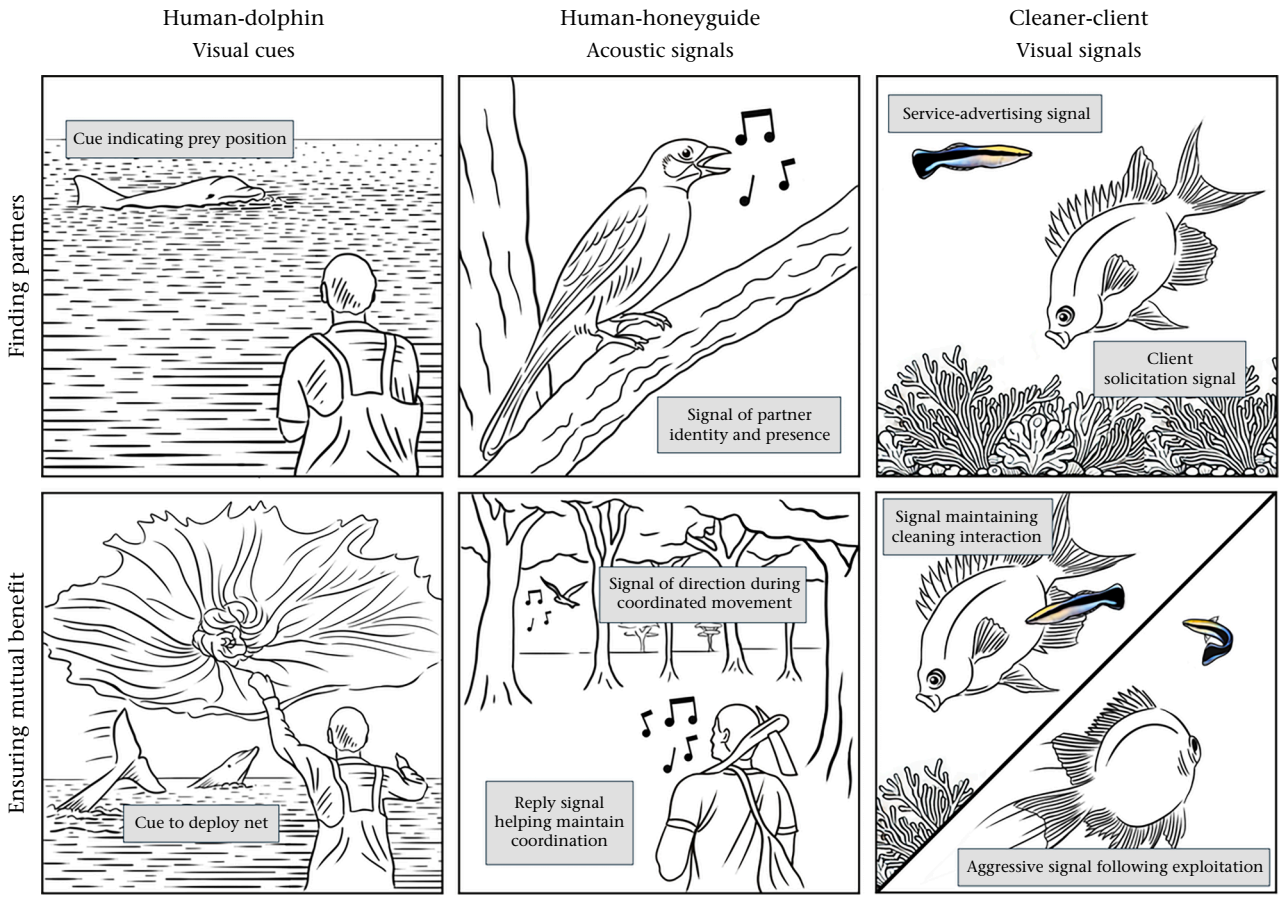

Figure 1. Visual representation of cues and signals in three examples of animal interspecies cooperation, illustrating different sensory modalities of information exchange. In human–dolphin cooperation, human fishers interpret visual cues produced by foraging dolphins to determine the timing and location of net deployment over fish schools. In human–honeyguide cooperation, birds and humans exchange acoustic signals throughout the interaction, supporting partner detection, directional movement and coordinated travel to bees' nests. In cleaner fish–client cooperation, some cleaner fish species are conspicuously coloured to advertise their identity as a cleaner (specifically illustrated with colour on the figure), while many client species adopt oriented poses that function as client solicitation signals, but can also aggressively punish exploitative cleaners. Credit: Alex Boys and Katie Dunkley.

and treehoppers (e.g. *Publilia concava*) use vibratory and/or chemical signals to modify their ant partners' aggressiveness and locomotion to their benefit, enforcing the ants' beneficial defensive behaviour (DeVries, 1990; Hojo et al., 2015; Jackson, 2008; Morales et al., 2008; Travassos & Pierce, 2000). At the same time, ants can use either chemical or tactile signals to manipulate their insect partners into producing greater food rewards (Fiedler & Maschwitz, 1989; Ivens & Kronauer, 2022; Oliver et al., 2007) and limit their dispersal away from them (Oliver et al., 2007; Xu et al., 2021). While manipulative and punishing behavioural signals are also common in noncooperative heterospecific interactions, where they function to facilitate exploitation (e.g. targeted alarm calling of fork-tailed drongos, *Dicrurus adsimilis,* for kleptoparasitic benefits; see Baigrie et al., 2014; Flower, 2011; Magrath et al., 2015), in animal interspecies cooperation such signals instead appear to function to help maintain cooperation as a net positive outcome, preventing its breakdown into exploitation in the long term.

Costs

Like most signals (Johnstone, 1997), those used in animal interspecies cooperation can inflict direct costs that can constrain their use, meaning that only individuals that are genuinely motivated/able to cooperate can afford to produce them. Producing signals can incur energetic costs and can also require investment of other resources (e.g. insect calls: Prestwich, 1994; vibrational signals: Virant-Doberlet & Cokl, 2004, Steiger et al., 2012). Additionally, signal production can reduce time for other activities, such as in client fish that cannot forage or quickly respond to predators while posing to cleaners (Côté et al., 1998; Krause & Godin, 1996). Such investments should help an individual communicate that it is an honest, cooperative partner, increasing the likelihood that potential partners will interact with them: legitimate partners should only use behavioural signals, for example, when the benefits of doing so outweigh the costs. As in other mutualisms, it is important to identify and quantify these costs and to consider the net returns of engaging in the interaction, rather than assessing benefits alone (Bronstein, 2001).

A major cost of signalling arises when signals are eavesdropped upon, i.e. when unintended perceivers intercept information and exploit it for their own benefit (see Table 1; Zuberbühler, 2008). In human–honeyguide cooperation, for example, the honeyguide's conspicuous guiding call appears to attract noncooperative honeyguides or other species that feed on beeswax, thereby reducing wax available for the cooperating bird (Cram et al., 2023; Lloyd-Jones et al., 2022). Similarly, in ant–insect cooperation, predators can exploit chemical cues of cooperation to attack the insect partners (Elgar et al., 2016; Outreman et al., 2010) or the ants themselves (Adams et al., 2020). Such increased predation risk on insects could reinforce the need for ant protection, creating a feedback loop in which the costs of signalling deepen the partners' reliance on cooperation. Alternatively, these cases might reflect a

trade-off, with the benefits of soliciting or securing protection outweighing the risks of drawing in additional enemies. However, potential partners can also use eavesdropping to their own advantage. For example, potential client fish can eavesdrop on one another's punishing signals to avoid cooperating with harmful, exploiting cleaners (Bshary & Grutter, 2006). Similarly, during cooperative foraging, northern resident killer whales, *Orcinus orca ater*, can opportunistically eavesdrop on the echolocation of Pacific white-sided dolphins, *Lagenorhynchus obliquidens*, to locate adult Chinook salmon, *Oncorhynchus tshawytscha*, a prey item too large for dolphins to swallow but a valuable scavenged resource once broken apart by whales (Table 2; Fortune et al., 2025).

Third-party species and nonmutualistic partners may also mimic signals to exploit interactions, inflicting costs on those that cooperate. Some aphid morphs, for example, copy the hydrocarbon cues of other, cooperative morphs, allowing them to enter ant nests and receive care without actively excreting honeydew for the ants in return (cooperative aphids can direct their anus to ants to facilitate their honeydew consumption, Salazar et al., 2015). Such deceptive signalling (see Table 1) is commonplace in other mutualisms (e.g. over 7500 plant species feature rewardless flowers; Renner, 2006) and likely persists because of its relatively low costs of signal production and the difficulty of discrimination by cooperative partners (e.g. Lichtenberg et al., 2020). However, the costs imposed by third-party mimics might be great enough to alter or even jeopardise animal interspecies cooperation. For example, the morphological identity signals of *L. dimidiatus* to attract clients, are visually mimicked by some blenny fish species (e.g. *Aspidontus taeniatus*), which bite (i.e. exploit) clients instead of cleaning them (Côté & Cheney, 2004; Fujisawa et al., 2020). Following such deception, nearby true cleaner fish receive fewer client interactions (Côté & Cheney, 2004), highlighting that cues and signals can expose both partner species to exploitation costs imposed by deceptive third parties.

Broadly, the persistence of cues and signals depends on the balance of benefits and costs, including those from production, interception and deception (Webster et al., 2018). Selection is expected to favour signals that maintain function while minimizing unnecessary risks and energetic costs (see Part B).

Between-system Diversity

Information is transmitted through diverse sensory channels in animal interspecies cooperative interactions, yet visual and acoustic modalities dominate our current understanding (Table 2), possibly because they are more easily detected by human observers (Keeley, 2002; Wozny et al., 2008). Nevertheless, these channels may offer distinct functional advantages (e.g. Marler, 1967). Acoustic (including vibrational) signals, like for example those used (reciprocally) in human–honeyguide cooperation (e.g. Spottiswoode et al., 2016), are particularly effective for transferring information across larger distances (Demartsev et al., 2023; Virant-Doberlet & Cokl, 2004). Visual signals can aid coordination at closer distances by helping partners locate one another (Marler, 1967), provided the information can be adequately perceived. Cleaner fish coloration signals appear to be shaped by the same selective pressures that apply to aposematic (see Table 1) and sexually selected signals in aquatic contexts (Arenas et al., 2014; Seehausen et al., 1997; Tuttle et al., 2021). Specifically, *Labroides* and *Elacatinus* cleaner fishes feature body colour patterns that must effectively signal their identity, despite the challenges of their colourful coral reef environments, using stable, bright and high-contrast elements to remain conspicuous underwater and over long distances (Cheney et al., 2009; Lettieri et al., 2009).

Despite the functional advantages of visual and acoustic channels, olfactory, tactile and chemical signals also play key roles in animal interspecies cooperation. For example, in shrimp–goby cooperation (Table 2), *Alpheus* shrimps share their burrows with *Cryptocentrus* goby fish in return for predator protection, and tactile and chemical cues help partners maintain contact and assess threats (Karplus, 1979; Karplus et al., 1972). Numerous cases of ant–insect cooperation are underpinned by sensing of specific cuticular hydrocarbons, as outlined above. Even where visual and auditory channels are prevalent, these modalities often function alongside other channels. For example, ant–insect cooperation can rely on visual, tactile, chemical and acoustic signals (Axén et al., 1996; Casacci et al., 2019; Jackson, 2008; Morales et al., 2008; Pierce & Dankowicz, 2022) and lycaenid larvae encourage ant cooperative behaviour using flexible signals that combine several sensory modalities (Casacci et al., 2019).

Such multimodal signals (i.e. those using multiple sensory modalities) likely offer distinct advantages in specific contexts. They could, for example, improve the efficacy of communication across varying environments (as in other animal inter- and intraspecies interactions; Higham & Hebets, 2013), and amplify salience, such as the visual-acoustic punishing signals of Holocentridae clients following negative interactions with cleaner wrasses (*Labroides* spp.; Banse et al., 2024). In other cases, multimodal signals may make eavesdropping or mimicry (see Table 1) more difficult to achieve, thus protecting both parties in the cooperative interaction. As is the case in the evolution of any signals, the perceivers' perceptual system shapes the form of the signal in animal interspecies cooperation. For example, lycaenid larvae likely evolved complex multichannel signals to match their ant partners' own multimodal communication and sensory systems (Casacci et al., 2019; Hölldobler, 1999).

In most of the examples listed in Table 2, unimodal signals appear to be sufficient for a particular function (e.g. partner identification), and result in communication that is simple to produce and interpret across species boundaries. Nevertheless, considering only morphological and behavioural signals that are acoustic, visual and/or simple for humans to decrypt risks overlooking key communication components in animal interspecies cooperation. By investigating less obvious and/or less human-accessible modalities, future research might uncover neglected signalling mechanisms that underpin animal interspecies cooperative interactions across ecological contexts.

PART B: THE EVOLUTION OF CUES AND SIGNALS IN ANIMAL INTERSPECIES COOPERATION

In this section we discuss how cue responsiveness and signalling may have evolved in animal interspecies cooperation. Despite the wide taxonomic breadth and ecological significance of these interactions, this area of the literature is particularly underexplored, and where it has been studied, it is biased towards certain systems (e.g. cleaner–client, ant–insect). We discuss the potential origins of information transfer and consider its development through the three key conditions for evolution by natural selection: within-system variation, heritability and selective pressure. We also consider the potential for coevolution between signallers and perceivers (see Table 1) in these systems.

Origins

Signals often evolve from cues through repeated use and feedback mechanisms (Bradbury & Vehrencamp, 1998; Laidre & Johnstone, 2013). Distinguishing between signals that originated from cues and those that did not, however, can be challenging. In human–honeyguide cooperation, tree-chopping sounds may have initially served as incidental cues that a human may be accessing a bees' nest, but many honey-hunters now actively use these sounds to attract honeyguides (Kilawi, 2023; M'manga, 2024). In

human–dolphin cooperation, it remains unclear the extent to which dolphins' behaviours are signals. Although these behaviours can be part of their general foraging repertoire, they are performed distinctively in this cooperation context (e.g. abruptly and in close proximity to fishers) and fishers therefore interpret them as targeted signals (Catão & Barbosa, 2018; Tun, 2008; Zappes et al., 2011). Most researchers, however, currently interpret them more conservatively as cues (Cantor et al., 2023; Serpa et al., 2024; Simões-Lopes et al., 1998), since it has not yet been empirically demonstrated that these behaviours are actively directed towards fishers. Interactions like this, in which distinctions between cues versus signals are blurred, thus present an interesting yet challenging opportunity to study how signals originate and evolve within the context of cooperation (see Table 3). Such systems are consistent with early stages of interspecific communication, in which one or both species assess the other without yet producing signals specifically evolved to manage the partner's behaviour (Kostan, 2002).

Alternatively, in some systems, signals appear to originate from those used in other interaction contexts. For example, some fish adopt temporary head- or tail-stand body postures when mediating potential conflicts with conspecifics (Rodgers et al., 2007; Ruberto et al., 2020), and similar relatively short body poses are used by client fish when attempting to interact with a cleaner fish (shown in Fig. 1), perhaps also to resolve conflict by signalling their nonthreatening (and indeed beneficial) status to cleaners. This potential consistency of function across contexts suggests that signals that originally evolved to resolve animal intraspecies conflicts may have later been co-opted for animal interspecies cooperation (see Table 3). Similarly, the honeyguide's guiding call (used to cooperate with humans) shares notes with its nestling begging call (used to solicit food from host parents; Skead, 1951; Blair et al., n.d.). Because this species has been brood-parasitic far longer than it has cooperated with humans, young honeyguides may have already been predisposed to produce strident food-searching calls towards heterospecifics (Isack, 1987; Skead, 1951), which humans could then exploit, and which then reinforced their production towards humans, effectively turning cues into cooperative signals.

A challenge in tracing the origins of signals is to determine their role in the emergence of cooperation: was a specific signal required from the outset, or did it evolve later to enhance benefits? Phylogenetic methods may help by testing for correlations between the evolution of signalling traits and cooperative behaviour. For example, in ant–lycaenid larvae cooperation, Schönrogge et al. (2017) hypothesized that the ancestral ability of lycaenids to produce vibrational sounds may have served as a preadaptation for forming associations with ants, with their specific acoustic profiles later shaped by the ants' own intraspecific communication repertoires. Conversely, the bright blue-yellow body coloration of some obligate (see Table 1) cleaner fishes and dark lateral stripe (both highlighted in colour in Fig. 1) appears to have evolved after the initial emergence of cleaning behaviours, perhaps because they further increase attractiveness to clients, thus helping to facilitate the obligate nature of the interaction (Arnal et al., 2006; Cheney et al., 2009). Exploring when and how signals emerge, particularly in systems that differ in their reliance on cooperation (e.g. facultative versus obligate; see Table 1), and/or where closely related species adopt contrasting strategies such as cooperation or parasitism with the same partners (e.g. lycaenid larvae with ants; Riva et al., 2017), may help illuminate the evolutionary foundations of interspecies communication (see Table 3).

Within-system Variation

While cues and signals serve consistent functions in animal interspecies cooperation, their expression can vary widely, providing the raw material on which selection operates. In some contexts, certain signals have not evolved: facultative cleaners, which do not feed solely by cleaning, typically lack the convergent, stereotyped and conspicuous body colours and dark lateral stripe that obligate cleaner fish use to signal their identity (Caves et al., 2024). In other cases, signals are not produced even though partners are able to produce them (e.g. for many behavioural signals). For example, client fish do not always need to adopt angled body poses to receive a cleaning service, and a client's likelihood of adopting body poses for cleaner fish (and their duration if adopted) varies within and between species (Côté et al., 1998), possibly because of different food reward values to cleaners (e.g. Sikkel et al., 2004; Soares et al., 2007). Likewise, while many honey-hunting cultures direct specialized acoustic signals to honeyguides (e.g. Spottiswoode et al., 2016), some cultures do not (always) employ signals to initiate cooperation, possibly because of variation in the practice's subsistence and economic value (Kamboe et al., 2025; Nhlabatsi et al., 2025). Similarly, fisher communities interacting with dolphins vary in whether (Tun, 2004, 2008) they emit acoustic signals to initiate cooperative fishing (Serpa et al., 2024; Simões-Lopes et al., 1998). This variation in the presence or absence of signals may be influenced by partner need, signalling ability, type of signal (e.g. morphological versus behavioural) and whether communication is essential for successful cooperation.

In addition to whether signals are expressed, signal form (see Table 1) can vary in some examples of animal interspecies cooperation yet show remarkable consistency in others (even for behavioural signals). Behavioural signals, for example, are sometimes highly stereotyped, with minimal variation in how they are produced between individuals or contexts. Remarkably, client fish across hundreds of fish species and aquatic environments (e.g. both marine and freshwater) can often adopt one of only two body postures (head- or tail-stands, albeit varying in angle degree) when soliciting cleaning from obligate or facultative cleaners (e.g. Côté et al., 1998; Sikkel et al., 2004), and coral trout and grouper use consistent shimmying head-stands to initiate and carry out marine hunting partnerships (Bshary et al., 2006; Vail et al., 2013). In contrast, other cooperative signals appear more variable in form across similar systems. Although observations of behavioural signalling in terrestrial cleaning interactions are much more limited (see Table 2), terrestrial clients such as Galápagos tortoises, *Chelonoidis niger*, wild boars, *Sus scrofa*, capybaras, *Hydrochoerus hydrochaeris*, and common warthogs, *Phacochoerus africanus*, may offer a range of different relaxed postures presenting certain body areas to invite cleaning from crows, *Corvus corone cornix*, magpies, *Pica pica*, or banded mongooses, *Mungos mungo* (Kilham, 1982; MacFarland & Reeder, 1974; Massei & Genov, 1995; Sazima, 2010; Channer, n.d.). While these posturing behaviours share some loose similarities with cleaner fish and cleaner shrimp cooperation systems, their forms are much more diverse compared to the highly stereotyped nature of client fish body poses. The fact that some behavioural signals are highly stereotyped while others are not suggests that specific signal forms may be critical for achieving specific outcomes in certain cases (see Coevolution section), yet this possibility has received little attention.

The behavioural signals used by both human and nonhuman partners in human–wildlife cooperation (see Table 1) show even greater geographical variation. Honey-hunter cultures across Africa produce diverse acoustic signals to attract honeyguides, using instruments, voices or tools, differing in form, repetition and duration (e.g. Isack & Reyer, 1989; Nhlabatsi et al., 2025; Spottiswoode & Wood, 2023; van der Wal, Gedi, & Spottiswoode, 2022). Similarly, different fisher communities engaging with different populations of dolphins vary in how they interpret

dolphin behaviours (such as 'tail slaps', 'head slaps' and 'sudden back-arching dives') as triggers to net casting (Serpa et al., 2024; Simões-Lopes et al., 1998). Despite this variability, outcomes remain mutually beneficial, suggesting that interspecies communication can be flexible enough to confer net benefits across different cultural and environmental contexts (see Coevolution section).

Ultimately, the potential for variation in behavioural signal form depends on its function, mode of production, the risks of misinterpretation (see Selection section) and how it is acquired (e.g. innate versus learnt, see Heritability section). Comparative studies within cooperative systems (e.g. facultative versus obligate), in which the prevalence and form of cues and signals differ, can offer valuable insights into the evolutionary mechanisms and selective pressures driving these variations (see Table 3 and also ant–lycaenid larvae interactions: Riva et al., 2017; Schönrogge et al., 2017).

Heritability

The ability to produce signals and interpret partner information in animal interspecies cooperation is often innate, but learning nonetheless shapes the use of information transfer for behaviour-based signals. Client fish can adopt cleaning solicitation poses without prior experience (Losey et al., 1995), and juvenile honeyguides appear to instinctively approach humans and call (Short & Horne, 2001), even where they have had no previous opportunities to learn to do so. Learning, either through individual trial-and-error or by observing others, can subsequently help refine when and how such behavioural signals are appropriately used, and how information is interpreted. Similar learnt refinement is observed in other types of positive interspecies interactions (Magrath et al., 2015). Juvenile honeyguides likely learn to recognize acoustic human signals associated with cooperation, while cooperating fishers and honey-hunters learn to interpret their wildlife partners' cues and signals by observing others (Cantor et al., 2023; Cantor et al., 2024; Simões-Lopes et al., 2016; Spottiswoode et al., 2016; Spottiswoode & Wood, 2023; van der Wal, Gedi, & Spottiswoode, 2022). Similarly, ants can learn to associate the hydrocarbon signals of mutualistic lycaenid larvae and aphids with food rewards, increasing their likelihood of tending to them (Hayashi et al., 2015; Hojo et al., 2014). As for other behavioural signals (Bradbury & Vehrencamp, 1998), these examples suggest that while genetic predispositions underlie the ability to produce certain signals, learning refines their use to adaptively suit ecological and social contexts.

Whether signals and their responses are innate or learnt has implications for both the nature of information transfer and the evolution of animal interspecies cooperation. Innate signals are often highly stereotyped and conserved, enabling cooperation to persist across generations despite contextual change. For example, stereotypical head- or tail-stand body poses by client fish occur in both freshwater and marine cleaning systems, across taxonomically diverse client and cleaner species (Côté et al., 1998; Narvaez et al., 2015; Sulak, 1975), suggesting an adaptive function that consistently elicits cooperation. By contrast, learnt signals and responses are more variable, shaped by environmental or cultural factors, such as the regional differences in honey-hunter acoustic signals (van der Wal et al., 2026). In this system, such culturally specific signals can vanish locally when social learning breaks down (Spottiswoode & Wood, 2023; van der Wal, Spottiswoode, et al., 2022). Therefore, while this flexibility of learning allows partners to adapt to changing conditions, it also makes communication systems vulnerable to extinction if knowledge transmission is disrupted for any reason (Cantor et al., 2024; Thornton & Malapert, 2009; van der Wal, Spottiswoode, et al., 2022). For example, the collapse of human–orca cooperation in southeastern Australia, where orcas, *Orcinus orca*, herded baleen whales into Twofold Bay and reportedly signalled to hunters in exchange for shared carcasses, followed the displacement of the Indigenous Thaua people, the killing of a key orca and reduction in prey: all these factors contributed to the disruption of knowledge transmission, to ending the cooperative hunt and to the local extinction of the orca group (Clode, 2002; Neil, 2002; Reeves et al., 2023).

Selection

In general, signal characteristics are shaped by selection to optimize information transfer ('signal content', see Table 1) and ensure detection by intended perceivers ('signal efficacy'; see Table 1; Guilford & Dawkins, 1993). As such, signals are under selection arising from the sensory capabilities of the intended perceiver (also see Coevolution section), to ensure the signal faithfully transmits the relevant information. Of the ca. 6000 lycaenid butterfly species, around 75% engage in cooperative or exploitative associations with ants (DeVries, 1990), and many produce substrate-borne vibrations (DeVries, 1990; Riva et al., 2017; Travassos & Pierce, 2000). This trait is uncommon in other butterfly families, and in lycaenids it is likely shaped by the sensory abilities of their ant partners, which commonly communicate intraspecifically via stridulation and drumming (Schönrogge et al., 2017; Travassos & Pierce, 2000). When perceivers span multiple species with different constraints, selection may instead favour generalized more stable signals, such as the blue hues and black stripes of obligate cleaner fishes, which fall within the visual range of many fish species to attract a diverse range of client partners (Cheney et al., 2009).

Environmental conditions also shape signal evolution by influencing detectability (Endler, 1993). In human–dolphin cooperation, for example, water impedance and sound refraction at the water–air boundary restrict acoustic communication, resulting in either no human acoustic signals (Serpa et al., 2024; Simões-Lopes et al., 1998) or methods such as striking the water or boats (Tun, 2004, 2008). In human–honeyguide cooperation, by contrast, savannah habitats select for acoustic signalling to honeyguides, with one reported exception in which smoke was used to attract them (Isack, 1987).

The strength of selection on signals and cue responsiveness depends on partner reliance on one another (Edwards & Yu, 2007). In facultative cooperative examples where rewards (e.g. food) can often still be gained without partners, selection should be more relaxed, favouring behavioural versus morphological signals, and producing fewer or less intricate signals (e.g. cooperative fish hunting: Table 2) or greater variability in form (e.g. human–honeyguide cooperation, cleaner bird–client cooperation; Table 2). Costs of honest signalling (Prestwich, 1994; see Table 1) can also favour minimal, one-sided signals in these opportunistic interactions. By contrast, obligate systems (where survival may depend on the interaction) often feature multiple and/or complex signals (including morphological and behavioural signals as in the specialist obligate cleaner fish). In lycaenid butterfly larvae, for example, larvae less dependent on their association with ants (whether it be cooperative or exploitative in nature) produce short, sporadic acoustic call pulses to recruit ants, whereas highly ant-reliant larvae species can emit long, consistent and/or low-frequency calls that are accessible to a wider range of ant partners (Riva et al., 2017). This contrasts with the simpler ant recruitment calls of treehoppers, perhaps reflecting differences in reliance and the costs of reward production between these partner types (Jackson, 2008).

The strength of this selection will also depend on the number of potential partners involved. In some cases of animal interspecies

cooperation, one individual can engage with many potential partner species, placing greater challenges on information transfer. For example, many cleaner fishes and shrimps (including both facultative and obligate species) can provide cleaning services to a range of client species within a day (Dunkley et al., 2019; Quimbayo et al., 2018), and consequently their communication faces further challenges: signals must be broad enough to be recognized across diverse partners (i.e. tens of client species, Dunkley et al., 2019), yet precise enough to coordinate actions in a specific dyad and context. Such constraints may slow or disrupt (co)evolution (see Coevolution section for detail). The need for signals that are both broadly recognizable and context-specific therefore creates evolutionary challenges for multipartner interspecies communication that are largely absent from animal interspecies cooperation examples involving only two possible partner species.

Vulnerability to exploitation can also exert selective pressure on signal complexity. Partners facing a high risk of being exploited, either by noncooperative partners or third parties, could evolve complex or multimodal signals that help them distinguish between cooperators and exploiters. In ant–lycaenid larvae cooperation, for example, cooperative larvae recruit ants using calls that mimic ant signals, a strategy also exploited by social parasites of the ants (including *Phengaris alcon)*, which mimic both queen ant chemicals and calls to infiltrate colonies and manipulate workers into caring for their parasitic larvae (Hojo et al., 2014; Riva et al., 2017; Schönrogge et al., 2017). If ants relied on responding to only a single signal channel/form (e.g. acoustics), it would be easier for exploiters to saturate the system, leading to interaction breakdown. This has likely favoured the evolution of species-specific calls by lycaenid larvae, while ants, in turn, have developed the ability to discriminate cooperators from exploiters by learning their hydrocarbon chemical profiles (Hojo et al., 2014; Riva et al., 2017; Schönrogge et al., 2017). Vulnerability to exploitation should also drive the occurrence of more selfish/manipulative signals that make partners less vulnerable during interactions. Lycaenid larvae, for example, secrete hydrocarbons that not only attract ants but can also modify the ant's locomotion, aggression and brain dopamine levels, which both prevent exploitation and increase defensive behaviours in the ants (Hojo, 2022; Hojo et al., 2015). Such dual-function signals can both secure cooperator recognition and help protect interactions from exploitation.

Coevolution Between Signallers and Signal Perceivers

Coevolution occurs when traits evolve in response to each other (see Table 1), often driving rapid and dynamic change (Dixit, 2024; Thompson, 2019). This evolutionary process is well studied in both intra- and interspecific signalling contexts, including mate choice and recognition (Ryan, 1988; Woolley & Moore, 2011), individual recognition (Miller et al., 2020), prey aposematism (Lehmann et al., 2014; Sherratt, 2002), and mimicry (Dixit et al., 2023; Hoyal-Cuthill & Charleston, 2015; Spottiswoode & Stevens, 2012). By contrast, coevolution between signallers and perceivers in animal interspecies cooperation has received relatively little attention, despite being theoretically likely to occur. In such animal interspecies cooperation, perceivers are likely to impose selection on signallers to produce signals that effectively coordinate behaviour, while signallers in turn are likely to shape how perceivers attend to and respond to those signals, reflecting a coevolutionary process that may proceed from unidirectional or asymmetric assessment towards fully bidirectional, mutualistic communication (Kostan, 2002). Moreover, because many signals and behaviours in interspecies cooperation involve social learning (see Heritability section), cultural or gene–culture coevolution may also arise (Dixit, 2024), with socially transmitted traits imposing selection pressures on other learnt traits (e.g. Spottiswoode & Wood, 2023).

Unlike signals, cues do not evolve through selection imposed by perceivers, so coevolution between cue emitters and perceivers does not occur. However, when perceivers respond to cues, they can create selection pressures that encourage partners to provide more useful or timely information, which would promote the evolution of signals (see Origins section) and could thus result in coevolutionary dynamics. Such a process could occur in human–dolphin cooperation, for example, where coordination among multiple fishers and dolphins could improve if dolphins produced specific signals that differed from their natural foraging behaviours and were more conspicuous to fishers.

Because animal interspecies cooperative interactions vary widely in form and function, they provide a valuable opportunity to test hypotheses relating to coevolution. In cases involving repeated pairwise interactions between two species, consistent perceiver responses are hypothesized to strongly shape signal evolution, producing stereotyped, stable signals: perceiver species that respond preferentially to certain signals should select for their increased use, further reinforcing stronger preferences. For instance, in ant–lycaenid interactions, larvae that form stronger associations with ants (either cooperatively or as exploiters) produce vibrational patterns that closely match, and in some cases mimic, the acoustic repertoires of their ant partners, compared to larvae with weaker associations (Schönrogge et al., 2017). Surprisingly, the few animal interspecies cooperation signals documented across multiple independent populations (e.g. human–honeyguide, cleaner–client) appear to deviate from this predicted stereotypy. In human–honeyguide cooperation, for example, human acoustic signals to honeyguides show striking geographical and cultural variation despite the interaction being only between two species (see Within-system Variation section). This variation reflects cultural differences between human communities, raising the possibility of cultural coevolution generating a geographical mosaic of culturally varying human vocalizations and honeyguide responsiveness in different parts of Africa (Spottiswoode & Wood, 2023).

By contrast, in cases of animal interspecies cooperation in which partners cooperate with multiple species, we might predict the coevolution of signals that are less stereotyped or specific, owing to weaker selection pressures (Anderson, 2015). This pattern appears to have emerged in terrestrial cleaner bird–client cooperation (see Within-system Variation section). However, aquatic cleaner–client systems display highly stereotyped signals (e.g. near-identical client body poses across freshwater and marine systems, convergent cleaner coloration across independent obligate cleaner examples; see Within-system Variation section), despite cooperative interactions involving many species (e.g. tens of client species, and sometimes both facultative and obligate cleaner fishes even within the same local environment, Dunkley et al., 2019; Quimbayo et al., 2018). Such convergence suggests that, in some cases, only a limited subset of signal forms succeed across diverse partners and contexts, promoting stereotypy even in multispecies examples. Convergence could also be driven by signallers benefiting from employing similar signals because these elicit similar responses from perceivers ('rewarding mimicry', Guimarães et al., 2011; Jamie, 2017), analogous to Mullerian mimicry where defended prey species benefit from mutual resemblance due to predators generalizing across species (Sherratt 2008).

Intriguingly, for cooperative systems involving multiple partner species, perceivers could also simultaneously evaluate and compare multiple signallers, further shaping their signal forms

(i.e. through signal–signal coevolution). For example, in aquatic cleaner–client interactions, individual cleaner fish may sometimes face multiple posing client species simultaneously, while individual clients can choose between visiting and engaging with multiple cleaner individuals (Bshary & Noë, 2023; Caves et al., 2021). Slight signal variations (e.g. pose duration: Sikkel et al., 2004; to pose or not: Côté et al., 1998, saturation of the cleaner fish's blue coloration; Cacela-Rodrigues et al., 2025) could alter which client/cleaner is chosen (e.g. Cacela-Rodrigues et al., 2025) and/or whether a cleaner exploits a client, providing a potential case of comparative evaluation across signallers. However, such effects would be somewhat difficult to disentangle. For example, client species differ in their reward value to cleaners and vulnerability to exploitation (Roche et al., 2021), meaning that the behaviour of perceivers towards different signallers could also shift independently of signal differences. Nevertheless, this system may provide a promising example for comparing perceiver responses (both cleaners and clients) to slight variations in signal forms.

Taken together, these contrasts highlight that signals in animal interspecies cooperation do not always align neatly with theoretical expectations of coevolution. Their diversity (or conversely, their stereotypy) likely reflects a complex interplay between the specific information that must be transferred, genetic and cultural coevolution, partner diversity, the degree to which a signal can vary in form and occurrence and the universal accessibility of certain signal forms. Examining both the diversity and stereotypy of signals within animal interspecies cooperation might help elucidate how tight versus diffuse interactions, alongside cultural traits, shape patterns of convergence and diversification.

PART C: COMPARING CUES AND SIGNALS IN ANIMAL INTERSPECIES COOPERATION, OTHER MUTUALISMS AND INTRASPECIES COOPERATION

Cues and signals are central to animal interspecies cooperation, helping to align partner interests across systems that differ in their degree of reliance, complexity and vulnerability to exploitation. Their form, function, and evolution likely reflect a blend of influences common to both mutualisms and animal intraspecies cooperation. In this final section, we highlight these parallels to draw out the key conclusions from this review.

Animal interspecies cooperation requires active coordination for mutual benefit (Cram et al., 2022) and is often mediated by targeted behavioural signals across species that align the actions of heterospecific partners. This necessity for directed information transfer helps distinguish animal interspecies cooperation from other positive interspecies interactions, such as predator mobbing (e.g. Carlson & Slabbekoorn, 2025) or mixed-species grouping (e.g. Goodale et al., 2020), in which heterospecifics typically eavesdrop on signals exchanged between conspecifics to gain incidental benefits, rather than coordinating behaviour with one another (Carlson et al., 2020; Kostan, 2002; Magrath et al., 2015; Martínez et al., 2022; Sampaio et al., 2025). For animal interspecies cooperation, this dependence on targeted behavioural signals parallels animal intraspecies cooperation where signals directed at identified partners, such as honey bee waggle dances or wolf vocalizations, elicit rapid contingent responses (Barker et al., 2017; Hadjitofi & Webb, 2024; Harrington et al., 2003; Sachs et al., 2004; Bronstein & Sridhar, 2024; West et al., 2007a). In contrast to such dynamic communication, many other mutualisms rely on passive or broadcast communication, such as floral scents or colour changes in plant–pollinator systems, whose effects then depend largely on partner behaviour once emitted (Cseke et al., 2007; Lo et al., 2024; Weiss & Lamont, 1997). Even in partner-specific associations including rhizobia–legume and mycorrhizae–plant mutualisms, behaviours tend to be fixed or conditionally triggered rather than negotiated in real time (e.g. Harrison, 2005; Nelson & Sadowsky, 2015). While some animal interspecies cooperative interactions also use broadcast signals to attract partners, including cleaner fish coloration and ant chemical cues, they nonetheless depend on additional targeted signals (such as client fish body posing), to coordinate the interaction itself. Reliance on precise, partner-directed behavioural communication therefore distinguishes animal interspecies cooperation from most other mutualisms and aligns it more closely with animal intraspecies cooperation.

Both inter- and intraspecies cooperation require individuals to adjust their behaviour conditionally in response to their partners. In models of intraspecies cooperation, such conditionality is thought to be achieved through individual, social group or kin level recognition, whereby individuals distinguish cooperative conspecifics from noncooperative ones (Sheehan et al., 2017). These identification processes therefore operate at a fine perceptual scale, supported by shared sensory systems that shape how information is perceived and interpreted (an animal's umwelt; von Uexküll, 1992), helping individuals to detect subtle, meaningful differences between conspecifics' cues or signals. For example, cooperatively nesting paper wasps, *Polistes fuscatus*, use fine-scale visual signals (i.e. detecting individual variability in their yellow facial markings) to recognize and cooperate with individual nestmates (Tumulty et al., 2023). By contrast, animal interspecies cooperation typically occurs between partners that do not share a fully overlapping umwelt, making fine-grained individual recognition across species more challenging. As such, conditional responses should not need to rely on recognition of particular heterospecific individuals. Instead, it is more parsimonious for individuals to categorize cooperative versus noncooperative partners at a coarser level, distinguishing between beneficial and harmful partner species (and, in some systems, between alternative morphs, as in ant–aphid cooperation; Salazar et al., 2015), as seen in other mutualisms such as plant–pollinator interactions (e.g. van der Kooi et al., 2021). Such categorization is less perceptually and cognitively demanding, requiring broadly accessible (e.g. acoustic or visual) and relatively simple species-specific cues or signals sufficient to initiate interspecific cooperation, rather than on finer-scale individual-level recognition that would require precise signal interpretation across mismatched sensory systems. The evolution of aggressive mimics, such as false cleaner fishes exploiting the advertising coloration of *L. dimidiatus* cleaners (Côté & Cheney, 2004; Fujisawa et al., 2020), demonstrates that species-level cues are sufficient to initiate interspecific cooperation. Where such exploitation arises, there will likely be selection for additional cues or signals that mediate partner discrimination and regulate interactions once cooperation is underway (see Functions and Benefits section).

The signals and cues used in animal interspecies cooperation, and how they compare with other mutualisms and animal intraspecies cooperation, can be strongly shaped by whether partners pursue shared or different goals. When rewards are shared (e.g. cooperative hunting), partners benefit directly from working together, and signals tend to be more facilitative in nature, helping to align attention and timing through solicitation gestures and recruitment calls, much like in many forms of animal intraspecies cooperation (e.g. King et al., 2026). When goals differ, as in service-for-resource exchanges (e.g. cleaner–client, ant–insect), partners must coordinate while also negotiating fair exchanges for how services or resources should be traded under a higher risk of exploitation. In these cases, partners should evolve signals that positively encourage cooperation but also help limit their own

vulnerability to exploitation. In other interspecies contexts, individuals reduce their risk of harm through aposematic coloration, behavioural threat displays (e.g. posturing) and/or alarm calls (Arenas et al., 2014; Bergstrom & Lachmann, 2001; Rowe & Halpin, 2013). In animal interspecies cooperation, signals may simultaneously need both defensive and facilitative functions. For example, cleaner fish coloration may function like an aposematic signal, warning potential predators of toxicity while also attracting a diversity of clients (Cheney et al., 2008; Tuttle et al., 2021). Likewise, lycaenid butterflies use chemical, auditory and visual cues to both attract and regulate ant partners (DeVries, 1990; Hojo, 2022; Hojo et al., 2015; Travassos & Pierce, 2000). This dual function also occurs in other mutualisms that are under high risk from exploiters (e.g. plant–pollinator) where some floral displays, for example, recruit pollinators while deterring nectar robbers (e.g. Irwin et al., 2010) but should not occur in intraspecies cooperation where the risk of exploitation is often reduced because these interactions often evolve through kin selection. Across service-for-resource mutualisms, partner signals are often considered as manipulative (e.g. Baigrie et al., 2014; Grutter, 2004; Hojo, 2022) helping individuals to influence their partner's behaviour in their favour to gain greater rewards from the interactions. Animal interspecies cooperation thus parallels both animal intraspecies coordination and mutualistic exchange, requiring communication strategies that balance shared interests with protective negotiation and partner control.

CONCLUSION AND FUTURE DIRECTIONS

Together, the distinctive functions and requirements of cues and signals in animal interspecies cooperation position it between other mutualisms and animal intraspecies cooperation, with the need for, and form of, signals showing both overlapping and unique features with these differing interactions (see also Barker et al., 2017). Further, the requirement to communicate effectively across unaligned sensory systems while coordinating complementary actions in real time may therefore represent a key constraint on the evolution of animal interspecies cooperation, helping to explain why it appears relatively rare. Fully understanding these signalling and coordination constraints will ultimately require further (1) quantification of the costs, benefits and trade-offs of using cues and signals and (2) investigation of the conditions under which cues and signals are maintained and evolve in animal interspecies cooperation. Several gaps remain (see Table 3), and the unavoidable focus of this review on a few relatively well-studied systems further highlights the need to investigate the ecology and evolution of cues and signals across a wider range of animal interspecies cooperation examples. Useful parallels may be found in systems where humans train nonhuman animals by actively teaching associations between signals, behaviours and rewards (e.g. human–otter fishing: Feeroz et al., 2011; human-cormorant fishing: Manzi & Coomes, 2002; human–eagle hunting: Soma, 2012). Experimental manipulations that amplify or suppress specific signals could also reveal how signalling systems evolve, persist and influence the nature of the interaction. Such manipulations could also be particularly fruitful in other mutualisms or interspecies associations, where benefits to one or both partners are incidental or arise as by-products, and information transfer already plays a key role. Interactions such as fork-tailed drongos, *Dicrurus adsimilis*, using alarm calls to manipulate heterospecific foraging behaviour (see Baigrie et al., 2014; Flower, 2011; Magrath et al., 2015), and corvid–raptor carcass mutualistic associations in which corvids gain foraging benefits from raptor presence but do not appear to intentionally recruit them (Orr et al., 2019), may provide ideal opportunities to test how direct, targeted information transfer could facilitate transitions from noncoordinated interactions towards animal interspecies cooperation (see Kostan, 2002).

Ultimately, as we begin to uncover the role of cues and signals in driving and maintaining animal interspecies cooperation, we hope this review highlights an underexplored area and encourages further research across systems and taxa, providing broader insights into the origins, functions and persistence of cooperative behaviours across species. By synthesizing examples across taxa and contexts and comparing these cases with broader mutualisms and animal intraspecies cooperation, we offer a conceptual framework for understanding how information shapes cooperation between species. Broadly, our review emphasizes the ecological and evolutionary implications of communication across species boundaries, and we hope it helps move the field from case-specific accounts towards a more generalized understanding of cues and signals in interspecies cooperation.

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Data Availability

No data were used for this review.

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