

The ecology and evolution of human-wildlife cooperation

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Abstract

1. Human-wildlife cooperation is a type of mutualism in which a human and a wild, free-living animal actively coordinate their behaviour to achieve a common beneficial outcome.
2. While other cooperative human-animal interactions involving captive coercion or artificial selection (including domestication) have received extensive

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attention, we lack integrated insights into the ecology and evolution of human-wildlife cooperative interactions.

3. Here, we review and synthesise the function, mechanism, development, and evolution of human-wildlife cooperation.
4. Active cases involve people cooperating with greater honeyguide birds and with two dolphin species, while historical cases involve wolves and orcas.
5. In all cases, a food source located by the animal is made available to both species by a tool-using human, coordinated with cues or signals.
6. The mechanisms mediating the animal behaviours involved are unclear, but they may resemble those underlying intraspecific cooperation and reduced neophobia.
7. The skills required appear to develop at least partially by social learning in both humans and the animal partners. As a result, distinct behavioural variants have emerged in each type of human-wildlife cooperative interaction in both species, and human-wildlife cooperation is embedded within local human cultures.
8. We propose multiple potential origins for these unique cooperative interactions, and highlight how shifts to other interaction types threaten their persistence.
9. Finally, we identify key questions for future research. We advocate an approach that integrates ecological, evolutionary and anthropological perspectives to advance our understanding of human-wildlife cooperation. In doing so, we will gain new insights into the diversity of our ancestral, current and future interactions with the natural world.

KEYWORDS

animal culture, cooperation, dolphins, honeyguides, human-wildlife interaction, mutualism, orcas, social learning, wolves

1 | INTRODUCTION

Human-wildlife cooperation occurs when a human (*Homo sapiens*) and a wild, free-living, non-human animal actively coordinate their behaviour to achieve a common, mutually beneficial outcome (Box 1: Glossary). While other forms of human-animal cooperation, such as domestication and captive training, have received extensive attention (reviewed in Larson & Fuller, 2014), we lack similar insights into the ecology and evolution of human-wildlife cooperation. Historically, humans may have cooperated with up to 16 species in the wild (Tables S1 and S2), but many of these interactions are either extinct or declining (Clode, 2002; Gruber, 2018; Neil, 2002). There is consequently an urgent need to clarify how these unique interactions function and how they arise. Here, we review active and historical cases of human-wildlife cooperation, then synthesise our understanding of these interactions using a Tinbergian approach to investigate their function, mechanistic basis, development and evolution (Bateson & Laland, 2013; Tinbergen, 1963).

We position human-wildlife cooperation as a specific case within a larger set of mutually beneficial interactions between humans and wild animals, which we term human-wildlife mutualisms. In common

with many of the other diverse mutualisms that have been central to the evolution of life on Earth (reviewed in Bronstein, 2015), numerous cases of human-wildlife mutualism are ecologically and economically important, such as bats that eat insect pests attracted to our homes, numerous species that pollinate our crops, and vultures that eat our waste (Gangoso et al., 2013; Ghanem & Voigt, 2012; Kremen et al., 2004). The narrower subset of human-wildlife mutualisms that we term human-wildlife cooperation is specifically defined by their coordinated cooperative behaviour, in addition to mutual benefits.

2 | CASES OF HUMAN-WILDLIFE COOPERATION

2.1 | The greater honeyguide

In parts of sub-Saharan Africa, the greater honeyguide (*Indicator indicator*, hereafter 'honeyguide') bird regularly cooperates with human 'honey-hunters' to locate and access the nests of bee species (mostly African honeybees, predominantly *Apis mellifera scutellata*, but in some places also meliponine stingless bees; Isack & Reyer, 1989, Spottiswoode et al., 2016). The interaction

BOX 1 Glossary

- **Amensalism:** an interaction between two species in which individuals of one species are negatively impacted and individuals of the other species experience no net effect.
- **Commensalism:** an interaction between two species in which individuals of one species receive a net benefit, and individuals of the other species experience no net effect.
- **Cue:** an incidental source of information in the environment that may influence the behaviour of an observer, but has not evolved for that function. Contrast with signal.
- **Domestication:** a sustained, multigenerational relationship in which one species (typically humans) assumes control over the reproduction or care of a plant or animal to secure a more predictable supply of a resource.
- **Human-wildlife mutualism:** an interaction between a wild animal and a human in which the individuals involved in both species experience a net benefit. These may range from diffuse interactions without deliberate behavioural cooperation between species (e.g. human waste disposal or pest removal by wild animals), to deliberate, cooperative one-to-one interactions (see: Human-wildlife cooperation).
- **Human-wildlife cooperation:** a subset of human-wildlife mutualisms in which the mutual benefit is achieved through cooperative behaviour in participants of both species. The participating human and animal coordinate the interaction by altering their behaviour in response to the partner species' actions in order to achieve a common goal.
- **Kleptoparasitism:** a parasitic interaction (in which one animal receives a net benefit and the other incurs a net cost) where one animal takes resources from another.
- **Mutualism:** any interaction between two species in which individuals of both species experience a net benefit. Mutualisms need not include active cooperative behaviour from either party.
- **Neutralism:** an interaction between two species in which individuals of both species experience no net benefit or cost.
- **Net effect, net benefit or net cost:** The final impact, after accounting for all the combined costs and benefits. For example, if an interaction has both a benefit and a cost which are equal, then the net result is neutral. These types of costs and benefits are typically considered in terms of evolutionary fitness.
- **Signal:** An act that influences the behaviour of another individual and is produced specifically to achieve that effect. Contrast with cue.
- **Wild animals:** any animal that lives freely in nature without its behaviour or reproduction being deliberately controlled by humans.

begins when a honeyguide approaches a human (usually a man, but women occasionally honey-hunt, Wood et al., 2014), sometimes attracted by the human producing a stereotypical sound. These sounds vary geographically and can involve shouting, whistling, blowing into a hollow object or chopping wood (Gruber, 2018; Isack & Reyer, 1989; Spottiswoode et al., 2016; Wood et al., 2014). The honeyguide signals to the human with a 'chattering' call that is used only in this context, and flies in the direction of a bees' nest (Isack & Reyer, 1989; Spottiswoode et al., 2016; Wood et al., 2014). The honey-hunter (or typically, small group of honey-hunters) follows until he or she locates the bees' nest, commonly in a tree, rock crevice or termite mound. The honey-hunter harvests the nest using tools, such as an axe, to fell the tree or excavate the nest, and fire and smoke to subdue the bees. After the harvest, the honeyguide supplements its insectivorous diet by feeding on beeswax, which (unlike humans and most bird species) it is able to digest. Regular cooperation is now restricted to only a few known areas (Figure 1; Table S1) but infrequent interactions occur throughout the honeyguide's range, suggesting this partnership was likely once widespread. Rarely, honeyguides guide humans to dangerous animals, which is believed by some cultures to function as a punishment for not sharing beeswax on previous occasions

(Isack, 1999). Whatever the true function (if any) of this behaviour, such a belief could play an important role in maintaining the interaction by ensuring those participating reward the honeyguide. Reports that honeyguides guide humans to other food sources (e.g. carrion) or similarly cooperate with other honey-eating mammals (such as honey badgers *Mellivora capensis* and baboons *Papio* spp.) are not well-supported (Dean et al., 1990; Friedmann, 1955).

2.2 | Dolphins

Humans currently or historically cooperated with at least three species of wild dolphins (Figure 1): Irrawaddy dolphins *Orcaella brevirostris* in the Ayeyarwady river in Myanmar (currently active; Tun, 2004), Lahille's bottlenose dolphin *Tursiops truncatus gephyreus* or *Tursiops gephyreus* (subject to ongoing taxonomic debate, Wickert et al., 2016; Wang et al., 2021) in Brazil (currently active; Simões-Lopes, 1991), and Indo-Pacific bottlenose dolphins *Tursiops aduncus* in Australia (ended in 1930; Neil, 2002). Although details of the cases differ, the basic interaction is similar and we therefore outline them together. At all locations, people fishing (hereafter 'fishers') cooperate with dolphins to catch fish

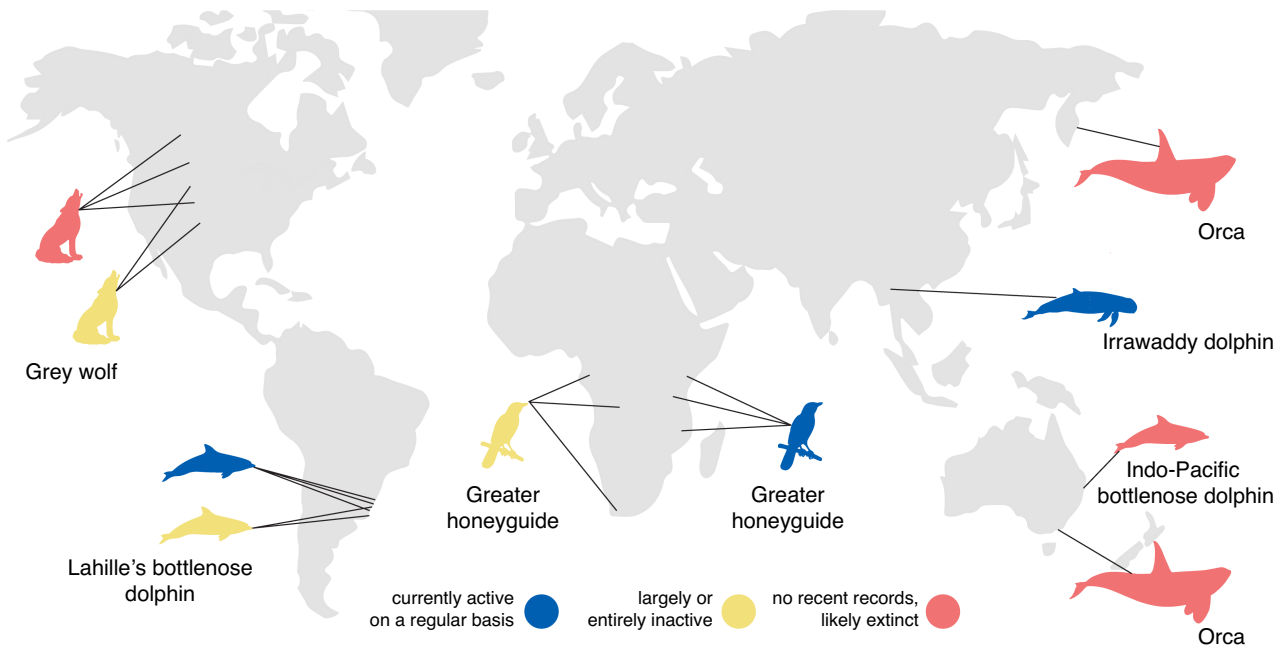


FIGURE 1 The locations of active and historical cases of human-wildlife cooperation known to the scientific community. See Table S1 for references and Table S2 for additional potential cases. Active human-honeyguide cooperation, in particular, is likely to be more widespread than indicated here.

(primarily migratory mullet species; Mugilidae). Precise characterisation of the interactions is challenging in the murky water where these interactions typically occur, but the dolphins appear to herd fish from deeper waters to the surface or shoreline, and in the process provide cues or possibly signals to the fishers about when and where the fish are available (Simões-Lopes, 1991; Smith et al., 2009; Tun, 2004). The fishers then deploy their fishing gear (cast- or hand-nets) at the concentrated schools, and the dolphins target the fish evading the nets (Neil, 2002; Simões-Lopes et al., 1998; Tun, 2014; Valle-Pereira et al., 2022). Fishers reportedly used acoustic signals to attract Indo-Pacific dolphins in eastern Australia, and still do so with Irrawaddy dolphins in Myanmar (Neil, 2002; Tun, 2004). Once the fishers and dolphins are prepared, the cooperative fishing practice is always initiated by the dolphins herding fish towards the fishers (Neil, 2002; Simões-Lopes et al., 1998; Tun, 2004).

2.3 | Orcas

Cooperative hunting between humans and orcas *Orcinus orca* historically occurred in at least two locations: Chukotka in Russia and Twofold Bay in Australia (Bogoslovskaya et al., 2007; Neil, 2002). In both cases, orcas would herd whales and other marine mammals to the surface or shoreline and trap them, increasing their accessibility to hunters (Table S1). At Twofold Bay, up to 30 individually recognisable, named orcas cooperated with humans, beginning around 1830. Several orcas would harass a baleen whale while others sought local whalers, signalled to them by splashing, and led them to the prey

(Clode, 2002; Neil, 2002). Whaling crews included Scottish immigrants and members of the Yuin aboriginal community. After harpooning the whale, they allowed the orcas to eat the tongue before harvesting the carcass (Clode, 2002). Cooperation at Twofold Bay ceased in 1926. Dwindling whale populations and petroleum reducing the demand for whale-oil caused the interaction to decline, but the major cause of its end appears to have been the deliberate killing of two orcas by settlers, which led to the pod's departure (Clode, 2002). Although orcas are delphinids (and the orca's closest living relative is the Irrawaddy dolphin, McGowen, 2011), human-orca cooperation is markedly different to human cooperation with other dolphin species, and we hereafter exclude orcas when we refer to dolphins.

2.4 | Wolves

Domestic dogs *Canis lupus familiaris* regularly cooperate with humans for tasks including hunting, gathering, transport and protection (Dounias, 2018), but present-day examples involving captive training do not demonstrate that humans similarly cooperated with dogs' wild ancestors. Scientific observation of cooperation between humans and wolves *Canis lupus* has been made impossible by persecution of wolves and forced assimilation of indigenous communities with whom wolves may have cooperated (Fogg et al., 2015; Pierotti & Fogg, 2017). However, numerous accounts from indigenous groups detail important cultural attitudes towards wolves and close interactions that include cooperation. Humans reportedly learnt from wolves how to hunt

by driving prey off small cliffs or into ravines or deep snow, and subsequently cooperatively took part in this activity alongside wolves (Barsh & Marlor, 2003). Scientific hypotheses for ancient human-wolf cooperation have been generated, which are compatible with indigenous accounts, with the complementary abilities of the two species, and with the appearance of early anatomical changes associated with wolf domestication in the fossil record (Schleidt & Shalter, 2003; Shipman, 2015a, 2015b). These hypotheses propose that wolves located, pursued and exhausted large prey including elk *Cervus canadensis*, bison *Bison* spp. and mammoths *Mammuthus* spp. Wolves were fast enough to run down and corner large prey, but had difficulty killing them. Humans followed the wolves and were much more effective at killing large prey, especially proboscideans, using tools (e.g. spears and bows, Shipman, 2015b). As such, humans would have avoided costly pursuits and wolves would have avoided injuries sustained while killing dangerous prey. The people involved ensured they left a share of the meat for the wolves, a practice that appears to have persisted even where cooperative hunting has ceased (Pierotti & Fogg, 2017). Most evidence consistent with human-wolf cooperation involves North America, but similar interactions may have occurred in Europe and Asia (Table S2).

3 | CANDIDATE CASES OF HUMAN-WILDLIFE COOPERATION

3.1 | Corvidae

At least two members of the Corvidae family (including ravens and crows) reportedly provide humans with information about the location of food sources, although these interactions have received little attention from the scientific community. Multiple reports suggest that hunters in North America and Europe consider common ravens *Corvus corax* an indicator of the location of prey, and the ravens benefit by scavenging on hunters' kills (Freuchen & Solomonsen, 1958; Heinrich, 1999). New Caledonian crows *Corvus moneduloides* may similarly indicate the cryptic location of inaccessible beetle larvae to the local Kanak people, who harvest the insects by chopping open tree-trunks using axes (N.T.U., pers. obs.). In all of these cases, evidence that the corvids cooperatively seek or signal to humans remains limited, and the birds may instead merely provide passive cues of prey locations.

3.2 | Other honeyguide species

There are reports that humans in sub-Saharan Africa cooperate with other wax-eating honeyguide species in the Indicatoridae family in a similar manner to the partnership with the greater honeyguide, including lesser *Indicator minor*, scaly-throated *I. variegatus* and dwarf honeyguides *I. pumilio* (Table S2, Ivy, 1901; Friedmann, 1955; Kajobe & Roubik, 2006; Brisson, 2010; Dounias, 2018). Details of their

potential interactions with humans, including the behaviour of the bird involved, require further investigation.

4 | HOW DOES HUMAN-WILDLIFE COOPERATION FUNCTION AND WHAT ARE ITS CONSEQUENCES?

In this section, we review the functional commonalities, benefits, costs, and wider ecological effects of human-wildlife cooperation. For both partners, the key benefit in all identified cases is enhanced foraging efficiency: the animal locates or aggregates a dispersed food resource, and the human then uses tools to increase its availability to both parties. However, cases of human-wildlife cooperation that have yet to be identified by the scientific community could involve other benefits, including shelter, protection or acquisition of inedible resources of economic or cultural value. While some cases rely on signals from at least one species (Spottiswoode et al., 2016), in other cases, cues may be sufficient to allow the human or animal to detect the presence and behaviour of the inter-species partner, and coordinate their own actions accordingly. All known cases are facultative rather than obligate for both the human and animal species. The humans involved can access the resource (and other food sources) through other means, and are thus not available frequently enough for the interaction to fully support the animal partner. However, it is likely that human groups that engage in human-wildlife cooperation historically relied on the interaction much more than they do now, and reliance is particularly high when other foods are scarce (Wood et al., 2014).

Quantitative studies have revealed that the benefits humans gain from engaging in human-wildlife cooperation are substantial. Honey-hunters from the Boran, Yao and Hadza communities increase the rate of finding bees' nests up to five-fold when guided by a honeyguide compared to searching for bees on their own (Isack & Reyer, 1989; Wood et al., 2014). Honey located with the help of honeyguides provides up to 10% of the calorific intake of members of the Hadza community in northern Tanzania, and has important economic benefits for the Yao honey-hunters in Niassa Special Reserve, Mozambique (Spottiswoode et al., 2016; Wood et al., 2014). Similarly, cooperating with Irrawaddy dolphins in Myanmar, and with Lahille's bottlenose dolphins in Brazil, increased fishers' catches between three- and seven-fold compared to fishing without interacting with dolphins (Santos et al., 2018; Simões-Lopes et al., 1998; Smith et al., 2009; Tun, 2005). While the benefits of cooperating with orcas have not been quantified, participants reported that the interaction substantially reduced the number of people and boats required to land a whale (Clode, 2002).

The benefits to the animal partner are more challenging to quantify. Beeswax is an energy-rich food which honeyguides can efficiently digest (Friedmann, 1955). Without cooperating with humans that can access bees' nests inside cavities and subdue the bees, honeyguides would have very limited opportunities to eat beeswax and would risk being stung to death (Isack & Reyer, 1989; Short & Horne, 2001). Individuals of the three dolphin species that

cooperate(d) with humans are thought to increase their foraging success because the fishing gear limits the escape options for prey or disrupts their anti-predator defences by splitting the school (Simões-Lopes et al., 1998; Tun, 2004). Fishers at Amity Point in Australia reportedly gave Indo-Pacific bottlenose dolphins fish directly from their spears (Fairholme, 1856), but this type of active reward rarely or never occurs at other locations (Simões-Lopes et al., 1998; Smith et al., 2009). At Laguna in Brazil, cooperating with humans is correlated with smaller home ranges and higher survival for Lahille's bottlenose dolphins (Bezamat et al., 2019; Cantor et al., 2018). Finally, participating in human-wildlife cooperation may itself be a pleasurable experience or strengthen social bonds, for both species (Machado, Cantor, et al., 2019; Santos-Silva et al., 2022). Such non-material benefits are unlikely to have driven the first emergence of the interaction, but could be important for its persistence (Machado, Daura-Jorge, et al., 2019).

Clarifying the costs incurred by cooperating members of both species is important for our understanding of how cooperation trades off with other activities and how stable the interaction is. Although these costs remain poorly understood, the basic functioning of the interaction could expose one or both parties to at least five potential costs. First, both parties could incur opportunity costs whilst locating a willing partner, particularly when they are at low densities. Second, both parties could incur direct costs by interacting with an uncooperative or low-quality partner. For example, orcas and dolphins have been deliberately or accidentally killed whilst cooperating with humans, and wolves are capable of killing humans (Clode, 2002; Thomas et al., 2019). In many cases, opportunity costs and the risk of harm are likely reduced by the human participants' customs and knowledge, including signals of willingness to cooperate which reduce search times and uncertainty about the interaction (Pryor & Lindbergh, 1990; Smith et al., 2009; Spottiswoode et al., 2016). Third, such signalling could itself incur costs. Honeyguides are small birds at risk of predation by raptors, and are brood parasites that lay their eggs in the nests of 'host' species. Conspicuous signalling to a honey-hunter can lead to detection and attack by host species (Isack, 1987), or to attack by competitors or potentially predators. Fourth, participation in all known cases of human-wildlife cooperation is at least partially learnt (rather than innate), and learning itself can incur costs (Uomini et al., 2020). Whilst learning, individuals may expend time and energy without gaining significant benefits, or face fatal risks, such as (for dolphins) accidental entanglement in nets (Simões-Lopes et al., 2016), and (for honeyguides) conspecific or heterospecific aggression. Finally, for the humans involved, participation may be costly where more efficient methods of gathering the resource or earning an income are available.

Beyond its benefits and costs for the species directly involved, human-wildlife cooperation may also have significant broader ecological impacts. All cases of human-wildlife cooperation increase access to a prey species, and could therefore reduce local abundance of this species and affect its associated food web. In some cases, the animal partner is capable of having a larger impact on its environment

by influencing the actions of a tool-using human. For example, human-honeyguide cooperation involving tree-felling and fire ignition could play a role in ecosystem regulation, because honeyguides influence which bees' nests are harvested, which trees are felled, and when and where potential wildfires are ignited (Tinley, 1977). Human-dolphin fisheries in Brazil produce almost no bycatch of unwanted species, demonstrating that human-wildlife cooperation can result in much smaller ecological impacts than alternative practices (Zappes et al., 2011).

5 | WHAT MECHANISMS REGULATE THE ANIMAL BEHAVIOURS INVOLVED IN HUMAN-WILDLIFE COOPERATION?

The proximate mechanisms governing animals' participation in human-wildlife cooperation likely involve sensory, cognitive and neuroendocrine traits, though these are poorly understood. In many cases, the animal collects information about a food resource using acute sensory capabilities that exceed those of humans. For example, dolphins use echolocation to locate prey in murky water, while wolves and potentially honeyguides use olfaction to locate dispersed prey and cryptic bees' nests, respectively (Lord, 2013; Parker, 2018). These sensory abilities, combined with their locomotion (e.g. swimming, flight), enable the animal to provide information that would be costly or impossible for humans to acquire alone.

Human-wildlife cooperation appears to require flexible cognition which permits the animal to process relevant information and coordinate with human partners. For example, wolves are able to respond appropriately to human gestures without training, and their pronounced tolerance and attentiveness towards humans is likely to have been important in the development of human-wolf cooperation (Range & Virányi, 2015). Honeyguides appear to store and process spatial and temporal information about bees' nests (Corfield et al., 2013; Isack & Reyer, 1989), and New Caledonian crows (for which cooperation with humans remains unconfirmed) demonstrate exceptional cognitive flexibility during foraging tasks (Weir et al., 2002). Dolphins and orcas exhibit some of the largest relative brain sizes and cognitive capacities of all non-human mammals (Marino et al., 2007; Whitehead & Rendell, 2014), and their cooperation with humans may arise from their ability to innovate (Patterson & Mann, 2011), communicate (Janik, 2013), socially learn new foraging techniques (including how to force prey into enclosed areas, Guinet & Bouvier, 1995) and cooperate (with each other and non-human species, Zaeschmar et al., 2013). Clarifying the cognitive processes required for human-wildlife cooperation should provide insights into why some animal species regularly cooperate with humans and others do not.

Understanding the neural and endocrine factors associated with an animal's participation in human-wildlife cooperation could also shed light on the traits that may have permitted the behaviour to first arise. Most wild animals ignore or actively avoid humans, yet those involved in human-wildlife cooperation seek human

proximity. The neural basis for this tolerance or attraction to humans is unclear, but may resemble reduced neophobia in other species, which can similarly allow individuals to access novel foraging opportunities (Mueller et al., 2014). In wolves, dolphins and orcas, the ability to engage in human-wildlife cooperation may depend on pre-existing abilities to socialise and cooperate, which in other mammals are associated with variation in the expression of key neuroendocrine receptor genes (e.g. French et al., 2016). Clarifying the neuroendocrine, genetic and epigenetic mechanisms underpinning these animals' cooperation with humans could help us understand individual and population-level variation in propensity to cooperate.

6 | HOW DO HUMAN-WILDLIFE COOPERATION BEHAVIOURS DEVELOP, AND HOW DOES THEIR DEVELOPMENT IMPACT THE INTERACTION?

In both the human and animal parties of all known examples of human-wildlife cooperation, the skills required to participate appear to be at least partially socially learnt. Honey-hunters in Kenya and Cameroon and fishers in Brazil and Myanmar report learning to participate in the local human-wildlife cooperation from their fathers, or occasionally other close (usually older male) relatives, or friends (Gruber & Sanda, 2019; Isack, 1999; Peterson et al., 2008; Silva et al., 2021; Spottiswoode et al., 2016; Tun, 2004). It is more challenging to characterise behavioural development in the animals involved, but the available evidence is consistent with a similar role for social learning. Preliminary observations suggest that the skills can be transmitted from mother to calf in Lahille's bottlenose dolphins in Brazil and Irrawaddy dolphins in Myanmar (Simões-Lopes et al., 1998, B.D.S., pers. obs.; Tun, 2004). Such vertical social learning, in addition to horizontal social learning among peers, is also the most parsimonious explanation for stereotyped cooperative behaviours that are group-specific and maintained across generations (Daura-Jorge et al., 2012; Simões-Lopes et al., 2016; Whitehead & Rendell, 2014). In contrast, honeyguides appear to genetically inherit an innate tendency to guide humans, because juvenile honeyguides attempt to do so and are unlikely to learn from their parents given their brood-parasitic lifestyle (i.e. young are raised in the nests of other species). However, subsequent refinements to guiding behaviour (such as recognition of human signals directed at honeyguides) are most likely learnt, given that they are specific to local human culture, and given that juvenile honeyguides are reportedly less likely to successfully guide humans to bees' nests and less responsive to human signals than adults (Spottiswoode et al., 2016). One goal of current work is to determine whether such learning is purely individual (i.e. learnt from trial-and-error attempts to guide humans) or also social (i.e. learnt from observing other conspecifics guiding humans). Little is known about how wolves and orcas learn to cooperate with humans, but both are capable of socially learning novel foraging strategies (Brent et al., 2015; Holzhaider et al., 2010; Range & Virányi, 2014).

The importance of social learning in the behaviours' development in both species has implications for the persistence of human-wildlife cooperation. First, socially-learnt behaviours can spread more rapidly than those learnt individually or inherited genetically (Hoppitt & Laland, 2013). Second, although able to spread quickly, socially-learnt traits are also susceptible to rapid loss, because their persistence relies on naïve individuals having an opportunity to learn (Thornton & Malapert, 2009). This risk is more severe when naïve individuals can only learn from a limited number of demonstrators that are repositories of knowledge (McComb et al., 2001). At two locations in Australia, cooperation between humans and orcas, and between humans and Indo-pacific bottlenose dolphins, both reportedly ended after outsiders killed recognisable animals that previously cooperated with humans (Clode, 2002; Neil, 2002). Human-honeyguide cooperation is less susceptible to such sudden disappearance, because of its likely partially innate component and wide geographical spread. Third, human socially-learnt practices relating to human-wildlife cooperation can stabilise the interaction. For example, many cultural groups that cooperate with honeyguides, cetaceans, wolves and potentially corvids have taboos against killing the animal or cheating the partnership (Bergier, 1941; Clode, 2002; Heinrich, 1999; Isack, 1999; Neil, 2002; Pierotti & Fogg, 2017; Thein, 1977; Usik, 2015; Wood et al., 2014). Furthermore, some groups resist abandoning the practice in favour of alternative livelihoods because doing so would be incompatible with their culture and way of life. For example, while bee-keeping may provide a more reliable source of honey than wild honey-hunting (Gruber, 2018), some communities consistently avoid apiculture (e.g. because they are nomadic), and instead maintain an active partnership with honeyguides (Laltaika, 2021). Clarifying the socially-learnt cultural factors that lead to contrasts in commitment to human-wildlife cooperation will thus help us understand which cases are at risk of decline, and develop and implement strategies to safeguard them (van der Wal, Gedi, & Spottiswoode, 2022; van der Wal, Spottiswoode, et al., 2022).

The role of social learning in the development of the skills involved in human-wildlife cooperation can also have consequences at larger scales, by creating geographic variation in the associated behaviours. For example, aspects of both human-honeyguide and human-dolphin cooperation vary with human culture, including the signals used to coordinate the interaction (Laltaika, 2021; Simões-Lopes et al., 2016; Spottiswoode et al., 2016; Wood et al., 2014), the tools used by humans to access the resource (Laltaika, 2021), the prey species targeted (Fogg et al., 2015; Simões-Lopes et al., 1998; Spottiswoode et al., 2016), whether humans reward the animal (Laltaika, 2021; Neil, 2002; Nelson, 1983; Spottiswoode et al., 2016; Wood et al., 2014), and human sentimentality towards the animal (Pierotti & Fogg, 2017; Silva et al., 2021). The result is a geographical mosaic of behavioural variation propagated by (potentially social) learning in participants of the two species. Allopatry resulting from habitat fragmentation could further enhance this geographic variation. Consequently, a human or animal attempting to cooperate outside their local area may suffer reduced efficiency or be entirely

unable to engage due to their incompatible behavioural repertoire. As such, these interactions, like many other types of mutualisms, may both promote adaptive diversification and enforce local isolation (Vamosi & Vamosi, 2010). Geographical variation therefore has implications for our understanding of the functioning, consequences and conservation status of cases of human-wildlife cooperation, all of which may not be generalizable across locations.

Local human cultural traits interact with aspects of human-wildlife cooperation, and an anthropological perspective can provide insights that would otherwise remain obscure. A detailed review is beyond the scope of this paper, but briefly, participation in human-wildlife cooperation can be shaped by the local human culture because activities and attitudes involving nature are determined by cultural and social factors including gender, religion, wealth, and livelihood (Anderson et al., 2011; Deb, 2015; Hoppitt & Laland, 2013; Kirksey & Helmreich, 2010; Mullin, 1999; Schlesier, 1987). Some communities feel a spiritual connection with nature, which is likely to stabilise human-wildlife cooperation because it promotes trust, reciprocity and sustainability towards the natural world (Anderson, 2000; Armstrong Oma, 2010; Ingold, 2002; Marshall, 1995). Reciprocally, the interaction may alter the human culture within which it operates, by generating new customs and beliefs. For example, in some groups that report cooperating with orcas or wolves, the animal became a 'cultural keystone species', vital to the community's sense of identity and cultural integrity (de Castro, 1998; Fogg et al., 2015; Holzlehner, 2015; Pierotti, 2011). The affectionate relationships developed with individual animals can lead to people ascribing them names and personalities, which in some cases invoke a belief in reincarnation of ancestors as cooperative animals (da Rosa et al., 2020; Neil, 2002; Peterson et al., 2008; Silva et al., 2021; Tun, 2004). Although comprehensive ethnographic analyses of these interactions are lacking for most relevant human groups, it is clear that human-wildlife cooperation can take on moral and cosmological significance that influences the behaviours involved and goes beyond the material benefits of central interest to evolutionary ecologists.

7 | HOW DID HUMAN-WILDLIFE COOPERATION EVOLVE?

A detailed understanding of the evolutionary histories of human-wildlife cooperation is challenging because behavioural traits do not fossilise, and current activity is not necessarily reflective of past practices. We therefore propose a conceptual framework for understanding the emergence of human-wildlife cooperation, by contextualising it within the diversity of human-wildlife interactions (Figure 2). This framework facilitates a discussion of the potential precursors of human-wildlife cooperation, of how cooperation could cease by shifting to another interaction type, and of the processes involved in these shifts, within the context of existing research on the evolution of mutualisms in general. First, we outline the evolution of human-wildlife cooperation by discussing its six potential precursors. These

include antagonistic precursors (e.g. parasitism), which have also been identified as precursors in other mutualisms (Thompson, 1994).

(i) *Commensalism with animal benefit as a precursor to human-wildlife cooperation*

Human-wildlife cooperation may arise from a commensalism in which an animal benefits from associating with humans, with no net effect experienced by the humans. Over time, either or both species adjust their behaviour such that the human begins to derive a benefit, and if these behavioural adaptations involve inter-species coordination, human-wildlife cooperation is established.

Two cases of human-wildlife cooperation could have originated from commensalisms in which the animal scavenges from the human. First, honeyguides may have scavenged wax from the messy harvests of honey-hunters, and followed them in anticipation of available wax (Wood et al., 2014). Honeyguides of many species know the location of bees' nests, and greater honeyguides may, over time, have learnt and/or been selected to call to humans, establishing the coordinated cooperation and reciprocal signalling present today. Second, wolves are proposed to have scavenged for waste scraps around human encampments approximately 12,000 years ago, and this began the 'commensal pathway' to the domestication of wolves (Coppinger & Coppinger, 2001). On this pathway, human-wolf cooperation is proposed to have started once humans learnt to cooperatively hunt with the wolves attracted by scavenging opportunities, and ultimately humans maximised the benefits they received from cooperating with wolves by controlling the wolves' lives and breeding, resulting in domestic dogs. This proposal for the origin of human-wolf cooperation is disputed because wolves reportedly rarely scavenge, and humans at that time may not have produced enough waste to attract wolves (Pierotti & Fogg, 2017). In some or all of the estimated six independent wolf domestications (Pierotti & Fogg, 2017), alternative pathways may have enabled human-wolf cooperation and subsequent domestication (see below).

(ii) *Commensalism with human benefit as a precursor to human-wildlife cooperation*

In this commensal interaction, humans benefit from interacting with an animal but have no net impact on the animal. There are two ways this could precede human-wildlife cooperation. First, these commensal interactions can occur when the animal's presence indicates the location of a resource so abundant that the human and animal do not compete for access. For example, fishers cannot easily directly observe the locations of fish schools in murky water, but they can observe the movements of foraging dolphins. Where the fish are sufficiently abundant (or the humans are unable to exhaustively catch them), the fishers' actions do not deprive the dolphins of food. Second, humans can benefit from interacting with, but not negatively affect, an animal if humans scavenge or share animal kills. Such sharing can occur without competition if humans and animals feed on different parts of a resource. Non-exclusive foraging may have occurred with

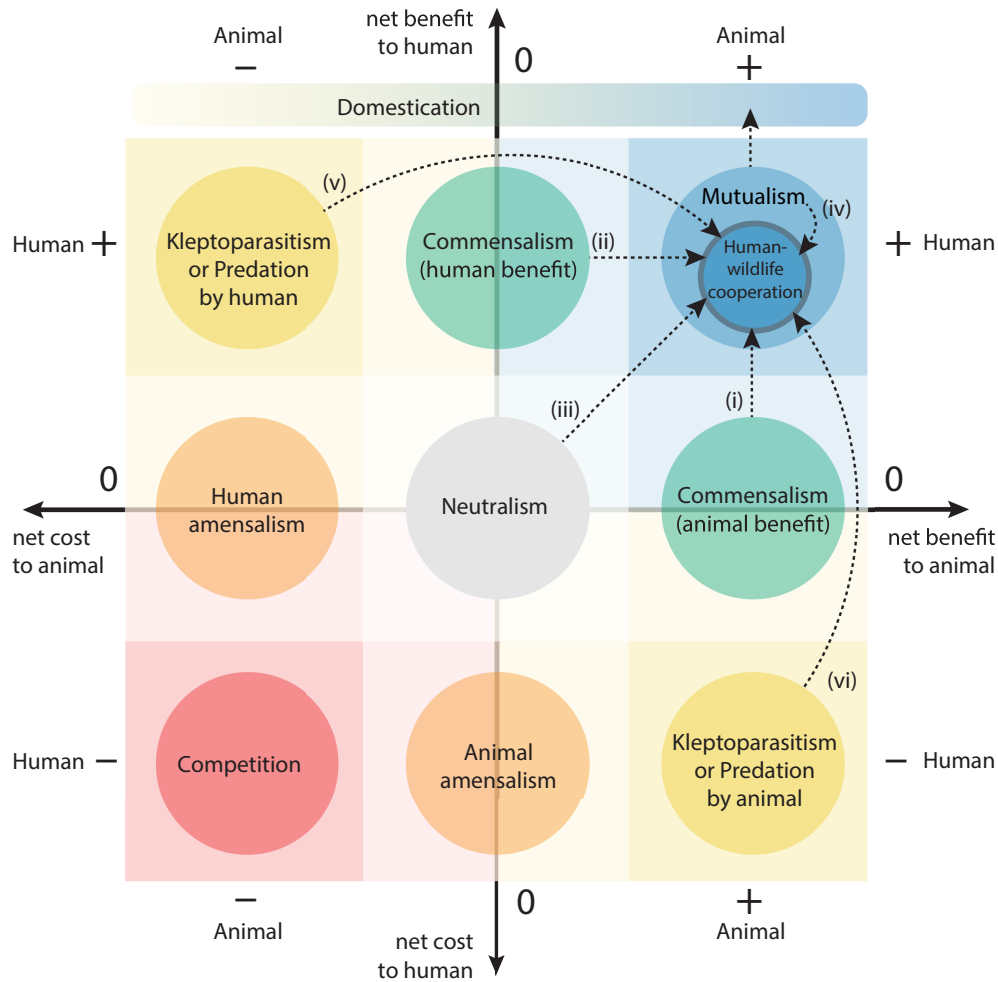


FIGURE 2 Routes by which human-wildlife cooperation could arise. Human-wildlife interactions are depicted in terms of the outcome for participating individuals of both species. The impact to the animal is shown on the x-axis (with negative on the left, neutral in the centre and positive on the right) and impacts for humans on the y-axis (with negative at the bottom, neutral in the centre and positive at the top). Human-wildlife cooperation is a subset of human-wildlife mutualisms, and the six feasible shifts to human-wildlife cooperation are shown by the numbered arrows from the precursor interactions: (i) commensalism with animal benefit, (ii) commensalism with human benefit, (iii) neutralism, (iv) other forms of non-cooperative human-wildlife mutualism, (v) kleptoparasitism by humans and (vi) kleptoparasitism by animals. A shift from human-wildlife mutualism to domestication (as may have occurred in wolves) is also shown.

orcas, which typically fed on the tongues of the whales they killed, leaving the blubber and meat for humans (Clode, 2002). Human use of foraging dolphins as cues of fish, or scavenging from kills made by orcas, could readily shift to human-wildlife cooperation because both parties may be able to increase their foraging efficiency by adapting their behaviour to cooperate with one another.

(iii) Neutralism as a precursor to human-wildlife cooperation

Neutralism, in which two species interact with no net effect on one another, could precede human-wildlife cooperation if a complex interspecific interaction exists between two non-human animal species, and this relationship is transferred to humans. For example, common ravens are thought to cooperate with wolves by leading them to prey and scavenging on the resulting carrion (reviewed in Dounias, 2018), and it has been suggested that potential human-raven cooperation may have begun when human hunters assumed the role of wolves in an

existing wolf-raven interaction (Table S2, Heinrich, 1999). Such partner replacements highlight that human-wildlife cooperation is a subset of mutualisms occurring between species, and that participants may engage, abandon, or switch partners according to the opportunities available and their associated net benefits.

(iv) Non-cooperative human-wildlife mutualism as a precursor to human-wildlife cooperation

Other forms of human-wildlife mutualism provide benefits to both parties without cooperative behaviour, but such cooperation could emerge if it increased the benefits to both. For example, prior to the emergence of human-honeyguide cooperation, a honeyguide's presence near a cryptic bees' nest may have provided honey-hunters with a cue of a source of honey. When these humans harvested the nest, both they and the bird gained a benefit, resulting in a mutualism driven by passive cues without coordination.

Such a mutualism based on cues could operate between humans and several other honeyguide species in the *Indicator* genus, many of which are typically cryptic except when near bees' nests (Archer & Glen, 1969; Cronin & Sherman, 1976). Subsequent adaptations including reciprocal signalling (Isack & Reyer, 1989; Spottiswoode et al., 2016) are likely to have increased the mutual benefits of the interaction by increasing the rate at which the humans located bees' nests, resulting in human-honeyguide cooperation.

Human-wildlife cooperation could be emerging from mutualisms currently without active cooperation in two further cases. First, Guiana dolphins *Sotalia guianensis* in south-east Brazil drive fish against unattended nets that fishers attach to posts in the water (see Table S2). This behaviour is thought to increase the catches of both the dolphins and the fishers, but as yet there is no evidence of coordination in this mutualism (e.g. dolphins actively indicating where or when to deploy the nets, and fishers actively attracting dolphins to the nets). Second, New Caledonian crows may provide a cue of hidden beetle larvae for the Kanak people who harvest them and make them more accessible to the birds (N.T.U., pers. obs.), but to our knowledge, active cooperation does not occur.

(v) *Kleptoparasitism by humans as a precursor to human-wildlife cooperation*

Kleptoparasitism by humans is an antagonistic interaction in which humans steal prey caught by wild animals. Kleptoparasitism could be a precursor to human-wildlife cooperation if the animal party adapted to derive a benefit from the interaction. The shift from human kleptoparasitism to human-wildlife cooperation may have occurred in several of the human-dolphin partnerships. Dolphins frequently hunt by driving fish against obstacles without human involvement (Hoese, 1971), and in some locations, fishers reportedly exploit this strategy by stealing the fish made accessible by dolphins (e.g. Indian Ocean humpback dolphins *Sousa plumbea*, Kumar et al., 2012). This kleptoparasitic interaction could lead to human-wildlife cooperation if the dolphins learn to coordinate their foraging to the fishers' actions and gain a benefit by catching fish with limited escape routes. It is thus a plausible precursor to cooperation between humans and Lahille's bottlenose dolphins at several locations in Brazil.

(vi) *Kleptoparasitism by wildlife as a precursor to human-wildlife cooperation*

Kleptoparasitism by wildlife is an antagonistic interaction in which animals steal prey caught by humans, which typically leads to human-wildlife conflict as humans protect their interests (e.g. Tixier et al., 2021). As a result, there is currently limited support for this pathway to human-wildlife cooperation. However, elements of kleptoparasitism need not prevent the persistence of mutualistic interactions between humans and wild animals, if humans tolerate associated losses because they are outweighed by the benefits of the interaction. For example, while cooperating with Lahille's bottlenose

and Irrawaddy dolphins, fishers tolerate the dolphins taking some fish from their nets (Simões-Lopes et al., 1998; Tun, 2004). Similarly, some human societies in northern Asia that herd and hunt antelope accept occasional wolf kills because wolves maintain herd cohesion (Stépanoff et al., 2017).

The processes involved in shifting to human-wildlife cooperation from the six precursors we identify above can influence aspects of the interaction itself, including its stability. As is true for mutualisms in general, some cases of human-wildlife cooperation may be more stable than others (Sachs et al., 2011). Shifts to human-wildlife cooperation may occur via individual or social learning, genetic or epigenetic changes, or require a combination of these processes. Human-dolphin and human-orca cooperation has arisen and been lost multiple times independently, with some cases thought to originate in recent decades (Simões-Lopes et al., 1998). This pattern is consistent with a central role for social learning and limited genetic change, which leaves the interactions vulnerable to rapid loss. By contrast, unlike for all other cases of human-wildlife cooperation, key elements of honeyguides' cooperation with humans appear to be innate in the birds. This suggests that the interaction is ancient, likely beginning prior to the emergence of *Homo sapiens* (around 300,000 years ago, Hublin et al., 2017), as honey-producing ancestral *Apis* species and wax-eating honeyguides have been present in Africa for at least 3 million years (Cridland et al., 2017; Spottiswoode et al., 2011). By ca. 2.6 million years ago (Plummer, 2004) hominins used stone tools that could have allowed them to break open bees' nests (Wood et al., 2014), but whether they did so presumably depended on their ability to protect themselves from bee stings. One possibility is that cooperation between hominins and honeyguides originated when *Homo erectus* first controlled fire, allowing them to use smoke to subdue the bees (possibly 1.5 million years ago, Wrangham, 2011; Gowlett, 2016). Another is that they placated the bees with techniques other than smoke, such as using leaves, fungal spores or water (Kraft & Venkataraman, 2015; Laltaika, 2021). While the date of the earliest human-honeyguide cooperation is still unknown, this discussion highlights that if an interaction is at least in part genetically controlled it could in theory be maintained for tens of thousands of generations or more.

Contextualising human-wildlife cooperation within the diversity of human-animal interactions can help us to understand the ways in which the partnership could end by shifting to another interaction type. First, as is the case for mutualisms in general (Chamberlain et al., 2014), human-wildlife cooperation is context-dependent. A change in ecological conditions (e.g. prey type or abundance, availability of alternative food) could shift the costs and benefits of the partnership and alter the interaction type. For example, prey scarcity may cause humans to alter their behaviour to maximise their own benefit and deprive the animal, resulting in antagonistic interactions (e.g. competition or kleptoparasitism). Prey scarcity may mean the fishers' gear deprives the dolphins of food, causing a similar antagonistic shift even without behavioural change in either party. Interactions in which the human and animal party feed on different parts of the food source may be more resilient to such conflict. For example, honey-hunters prefer honey while

honeyguides eat beeswax (although both appear to eat bee larvae, Isack & Reyer, 1989), and whalers ate blubber and meat while leaving the whale tongues for orcas (Clode, 2002), limiting the potential for interaction shifts driven by competitive exclusion. Second, the cooperative interaction could shift to domestication, as occurred for wolves. The domestication of wolves appears to have coincided with the rise of agriculture in human societies approximately 40,000 years ago, which may have shifted the benefits of the interaction away from cooperative hunting and towards an exchange of shelter for security (Germonpré et al., 2009; Pierotti & Fogg, 2017). By contrast, keeping honeyguides, orcas and dolphins in captivity would likely be too costly or jeopardise the benefits of the interaction, limiting the potential for a shift to domestication.

8 | CONCLUSIONS AND FUTURE DIRECTIONS

Our synthesis highlights that the coordinated behaviour involved in human-wildlife cooperation enhances access to resources for participants of both species, likely generates understudied impacts on the local ecological communities, and may have evolved via shifts from multiple other forms of human-wildlife interaction. Social learning plays a central role in maintaining many cases of human-wildlife cooperation, and cultural variation generates geographic mosaics of cooperative behaviour and provides a valuable sense of identity for the people involved. We urge researchers to address the key unanswered questions emerging from this review (Box 2: Outstanding questions for future research), by integrating ecological, evolutionary, and anthropological approaches to better understand and protect remaining cases of human-wildlife cooperation. In doing so, we will gain new insights into the diversity of our current and ancestral interactions with the natural world.

AUTHORS' CONTRIBUTIONS

This review paper was conceived by C.N.S., D.L.C., J.E.M.v.d.W., and N.U. with input from all co-authors; The writing was led by D.L.C. with significant support from C.N.S., J.E.M.v.d.W., N.U., and M.C., and contributions from all co-authors; M.C. created the figures with input from C.N.S., D.L.C., and J.E.M.v.d.W. All authors reviewed and approved the final version for submission.

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BOX 2 Outstanding questions for future research

- Are there other active, historical or emerging novel cases of human-wildlife cooperation, which are yet to be recognised by the scientific community?
- Can inter-species signalling in the context of human-wildlife cooperation tell us about animals' capacity for language, the potential for human-animal communication in other contexts, and the evolution of language more broadly?
- What, quantitatively, are the benefits of participating for the animal, relative to non-participation?
- What, quantitatively, are the costs of involvement in human-wildlife cooperation for members of both species, and can these drive shifts to antagonistic interactions?
- What are the impacts of human-wildlife cooperation on the local ecological community?
- Can the genetic and physiological regulation of animals' contribution to human-wildlife cooperation help us to understand the circumstances required for their evolutionary emergence, and to understand population variation in participation?
- What are the roles of phenotypic plasticity and social learning in maintaining these and other mutualistic interactions?
- What are the causes and consequences of geographical and cultural variation within human-wildlife cooperation systems?
- How can ecological, evolutionary, and anthropological insights into human-wildlife cooperation inform us as to the best practices for safeguarding them, or restoring them where they are lost?
- Can our understanding of human-wildlife cooperation inspire applications to cooperation between synthetic entities in robotics?

CONFLICT OF INTEREST

The authors declare that no competing interests exist.

DATA AVAILABILITY STATEMENT

Data sharing not applicable—no new data generated.

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