




Review

Information cascades spread adaptive and maladaptive behaviours in group-living animals



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Information cascades have been used to explain a variety of collective behaviours in nonhuman animals, including mate selection, antipredator responses and social foraging. A taxonomically widespread phenomenon, information cascades occur in many group-living animals from ant colonies to schools of fish and social mammals. Here we review the animal behaviour literature for examples of information cascades. We found that the literature on information cascades in animals is limited by inconsistent terminology that fails to adequately describe the differences between cascade types. We propose a classification framework, adapted from behavioural economics, to describe information cascades in behavioural ecology. Our framework consists of three types of information cascades derived from individual level fitness outcomes (adaptive, maladaptive or neutral) and a further two cascade types based on the transmission mechanism of cascading social information (signals or cues). We use a selection of past studies to illustrate the diversity of information cascades and we apply our framework to real world examples. We also discuss four mechanisms used by group-living animals to minimize the spread of maladaptive information cascades and propose avenues for future research.

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Life is full of difficult decisions, from finding a mate to choosing a nest site. Decision making can be improved through the use of information, where ‘information’ can be any event, cue or signal that reduces uncertainty and increases fitness by lowering an individual’s likelihood of making an erroneous decision (Danchin et al., 2004; McNamara & Dall, 2010). When making a decision, individuals can use private information, acquired from past experiences, and/or social information obtained from surveying the decisions and behaviours of others.

The use of social information can sometimes result in ‘information cascades’ where social information is sequentially adopted by observers and then spreads throughout a group to produce identical behavioural responses (Bikhchandani et al., 1992). Information cascades are a widespread phenomenon that drive a variety of collective behaviours in humans (Tump et al., 2020), including panic buying (Yuen et al., 2020), stock market crashes (Anderson & Holt, 1997; Bikhchandani et al., 1992) and crowd stampedes (Bikhchandani et al., 1992). While they differ in their specifics, at their core, information cascades occur when individuals adopt social information and conform to the behaviour of the crowd (Alevy et al., 2007; Helbing & Mukerji, 2012).

Information cascades are an emergent phenomenon of group living and are widespread among animal taxa. Group living confers several advantages to group members, including access to social information that improves foraging efficiency, mate choice and predator avoidance (Ioannou, 2021; Ward & Webster, 2016). Living in groups also incurs costs such as competition for resources like food or reproductive opportunities, disease transmission (Ioannou, 2021; Ward & Webster, 2016) and exposure to erroneous social information (e.g. false alarms) (Giraldeau et al., 2002).

Exchanges of social information among group members drives collective behaviours, where a global response emerges from successive local level interactions between individuals. Key to the emergence of collective behaviours is a propensity for group-living animals to copy one another or alter their individual behaviours to align with the actions of their neighbours (Webster & Ward, 2011). This tendency for behavioural conformity may arise from simple rules, such as ‘copy-the-majority’ or ‘copy-successful-individuals’ (Claidière & Whiten, 2012; Laland, 2004), which drive the adoption of social information by group members and generates many recognizable information cascades such as synchronous schooling fish and flocks of birds. For group-living animals, information cascades allow groups to rapidly disseminate socially acquired information with minimal acquisition costs to the recipients. Group-

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living animals, for example, use information cascades to rapidly warn the entire group of a nearby threat (Pays et al., 2013; Treherne & Foster, 1981) and, in some ant species, social information in the form of pheromone trails allows the rapid spread of information about the location of new food sources (Beckers et al., 1990).

When social information is inaccurate, deceptive or out of date (Giraldeau et al., 2002; Laland & Williams, 1998), information cascades can lead to decreases in the fitness of information recipients through the spread of misinformation, which results in poorer decision making (McNamara & Dall, 2010). For example, animals in groups may encounter false alarms, where an antipredator response is unnecessarily triggered, resulting in error cascades that reduce foraging time and increase energy expenditure (Beauchamp & Ruxton, 2007; Gray & Webster, 2023; Quinn & Cresswell, 2005). In humans, for example, error cascades have been used to explain the slow adoption of better performing crop varieties and suboptimal medical treatment decisions (Foster & Rosenzweig, 1995; Zhang, 2010). In economics, information cascades may rapidly accelerate individual trading decisions that drive asset pricing bubbles and market crashes (Dufwenberg et al., 2005; Kim & Meschke, 2011). With the emergence of digital systems, the reach of information cascades can be dramatically amplified, potentially driving globally influential error cascades, a significant concern in human systems as technology and artificial intelligence become increasingly integrated into daily life (Bak-Coleman et al., 2021).

In the animal behaviour literature, information cascades have been variously described as social/cultural transmission (Duboscq et al., 2016; Laland & Williams, 1998; Sherry, 2008), social copying (Auld & Godin, 2015; Oro, 2020), behavioural cascades (Rosenthal et al., 2015) and misinformation cascades (Franks et al., 2007). This variability in terminology conceals the differences between information cascades and makes comparing cascades between systems difficult. In this review, we synthesize and classify examples of information cascades from animal behaviour. We define different types of information cascades by the characteristics of the causal information and the fitness outcome of cascades on the information recipients. We discuss the behavioural mechanisms that limit maladaptive information cascades and conclude by suggesting avenues for future research.

DEFINING INFORMATION CASCADES

Information cascades were first described in behavioural economics and subsequently adopted to describe collective phenomena in an array of systems, including nonhuman animal behaviour. In economics, information cascades emerge where individuals copy the behaviour of the preceding individuals without regard to their private information (Anderson & Holt, 1997; Bikhchandani et al., 1992; Ziegelmeyer et al., 2010). Economists distinguish information cascades from ‘herding behaviour,’ where individuals make identical decisions but do not necessarily disregard their private information (Çelen & Kariv, 2004).

In this review, we consider the key feature of information cascades in nonhuman animals to be the sequential nature of behavioural imitation. We consider all instances where individuals imitate the behaviour of one (or a few) focal individuals to be information cascades. This definition encompasses what others have described as ‘blind copying’ among animals (Coolen et al., 2005; Kendal et al., 2009; Leadbeater & Chittka, 2007) and allows for cases where individuals do not weigh socially transmitted information against private information before imitating a behaviour, for example when an animal reacts to an alarm call without validating the presence of a threat.

In economics and animal behaviour, information cascades are further categorized by the fitness consequences for the

participants. When considering the fitness outcomes of information cascades in animal groups, we disregard the outcome for the initiator(s) of the cascade and consider only the resulting fitness of those that subsequently follow. In some cases, the selective advantages or disadvantages for the initiator and participants of a cascade may not align. For example, a deceptive alarm call may benefit the signaller but be disadvantageous to the receivers of the signal (Flower, 2011; Gray & Webster, 2023). Where a deceptive alarm call generates an information cascade, we would consider the fitness outcome of the cascade to be negative, as most participants engaged in a disadvantageous behaviour.

We also note that information cascades can be initiated actively or passively. Some cascades involve active information transmission by the initiator (signaller) while others involve behavioural copying without active signalling. For example, animals such as peahens, *Pavo cristatus* (Nichols & Yorzinski, 2016) and vervet monkeys, *Chlorocebus pygerythrus* (Cheney & Seyfarth, 2018) use alarm calls to signal the approach of a predator; this is an example of active information transmission. During active transmission, individuals need to make two decisions: the first is whether or not to act on the signal (e.g. by hiding or fleeing) and the second is whether or not to transmit information to the group by repeating the alarm call.

In contrast, passive information cascades occur when individuals simply mimic the behaviour of those around them. For example, when confronted by a predator, some schooling fish will turn and swim away rapidly, a behavioural cue imitated by neighbouring fish, leading to an information cascade as the fleeing behaviour spreads sequentially throughout the school (Magurran, 1990). During passive transmission, the responder is not actively deciding to transmit information; it is simply responding to the information it has observed. Information transmission thus happens as a passive consequence of information adoption. Put another way, passive cascades occur when individuals respond and transmit information via cues (behaviours that unintentionally modify the behaviour of recipients) while active information cascades occur when individuals respond to signals (traits that have evolved specifically for communication).

BUILDING AN INFORMATION CASCADE FRAMEWORK

The literature describing information cascades in animal systems features inconsistent terminology that hinders the identification of information cascades, makes comparison between different systems difficult and impedes transdisciplinary communication. To resolve the existing inconsistencies, we developed a framework to better capture the diversity of information cascades in nature and improve the testability of hypotheses regarding the fitness outcomes of different information cascades. We returned to the behavioural economics literature, the field where information cascades theory was first developed, to build a framework suitable for biologists.

For the purposes of this review, we first attempted to identify comparable examples of the different types of information cascades established by economists in animal systems. Economists define information cascades by both the behavioural response of those that receive social information, and whether responding to the information has positive or negative effects on individual well-being. Up cascades and down cascades describe the manner of information transmission during a cascade, where social information is sequentially adopted during an up cascade and rejected during a down cascade (Bikhchandani et al., 1992). Examples include the widespread adoption of behaviours that lead to panic buying (up cascade; Yuen et al., 2020) or disregarding medical advice leading to the rejection of health protective measures during a pandemic

(down cascade; Allington et al., 2020). Economists further classify cascades as either forward cascades or reverse cascades depending on the outcome of an up or down cascade on the recipients. A forward cascade propagates beneficial behaviours, while reverse cascades have negative outcomes for recipients (Anderson & Holt, 1997; Nöth & Weber, 2003; Seiler, 2012).

We encountered a number of studies that described the equivalent of forward (adaptive) cascades and reverse (maladaptive) cascades in animal systems; however, all instances of information cascades among animals were most readily understood as ‘up’ (adoption) cascades, and we failed to identify any definitive examples of ‘down’ (rejection) cascades. While further research may be necessary to determine whether down cascades are present in animal systems (Appendix 1), for applicability, we omitted down cascades in our framework (Fig. 1).

While we considered directly adopting the ‘forward’ and ‘reverse’ cascade terminology from economics, we found it difficult to remember and unintuitive in the context of biological systems. In the interest of clarity, we apply biological terms that better encapsulated the phenomenon they describe. We therefore replaced forward cascade with adaptive cascade and reverse cascade with maladaptive cascade. In addition, we include a new term, which to our knowledge has not previously been suggested in the field. Several of the information cascades we identified in animals appeared not to have obvious adaptive or maladaptive outcomes but none the less caused widespread behavioural copying. We decided to call such cascades ‘neutral cascades’ as they appear to have neutral selective effects.

In total, we implement three terms to describe the fitness outcomes of information cascades among animals: adaptive cascades, maladaptive cascades and neutral cascades, all of which may occur as active cascades via signals or passive cascades via cues (Fig. 1). We acknowledge that information cascades encompass a vast array of behaviours in diverse fields of animal behaviour, many of which have detailed and extensive vocabularies of their own. We do not seek to reconstruct these fields within the framework presented here but rather highlight that information cascade theory provides

a broad, overarching framework that describes phenomena occurring in many systems.

We also note that the classification framework proposed here is not intended to provide rigid definitions but instead highlights the nature of the causal information (active or passive) and fitness outcomes (adaptive, maladaptive, or neutral) which drive the cascade. We explore the dynamic nature of information cascades, the fitness outcomes of which may shift as environmental or informational conditions change over time.

METHODS AND RESULTS

We used the databases Google Scholar and Web of Science to identify studies describing information cascades in animal behaviour. Searches were conducted between July 2021 and October 2022. Across both databases, we used the search terms ‘information(al) cascade’, ‘forward/reverse/up/down cascade’, ‘error cascade’, ‘misinformation cascade’, ‘behavioural cascade’, ‘cascading failure’, ‘error copying’, ‘social information use’, ‘information conflict’, ‘maladaptive information’ and ‘social transmission/diffusion’. Papers containing one or more of these key terms were scrutinized to determine whether an information cascade was present according to our definition. In Google Scholar, relevant papers were selected from within the first 100 search results, comprising five pages, due to the large number of search results returned. In addition, we found the most relevant papers appeared within the first five pages. We also used the search terms to identify further articles by searching the ‘cited by’ lists of important and highly cited articles. In Web of Science, we applied relevant Category filters to search queries, including ‘Ecology’, ‘Biology’, ‘Behavioural Sciences’ and ‘Zoology’. All returned search results were assessed in Web of Science.

Overall, we identified several papers that described information cascades driving a diverse suite of behaviours in nonhuman animals (Table 1). In the next sections, we describe examples of different information cascade types.

		Action	
		Behavioural transmission via cues	Behavioural transmission via signals
Fitness outcome	Positive	Passive adaptive cascade Adopting the behaviour of successful foragers to locate the best feeding patches (Cortés-Avizanda et al., 2014)	Active adaptive cascade Following calls made by foraging birds allows consecutive individuals to locate foraging patches (Martínez et al., 2018)
	Neutral	Passive neutral cascade Transmission of behaviours via cues has evolutionarily neutral effect	Active neutral cascade Transmission of novel song variants in songbirds has evolutionarily neutral effects (Otter et al., 2020).
	Negative	Passive maladaptive cascade Copying new foraging behaviours in dolphins increases negative interactions with humans and risk of injury and death (Donaldson et al., 2012)	Active maladaptive cascade Foraging ants may become trapped in ‘death spirals’ after adopting out-of-date social information (Kronauer, 2020)

Figure 1. Information cascades can be classified by the nature of the causal information (signals or cues) and by the fitness outcome experienced by participating individuals (excluding the initiator(s)). Adaptive, neutral and maladaptive cascades occur when participants experience selectively beneficial, neutral or maladaptive outcomes, respectively. Information cascades may be active cascades when behaviours are transmitted via signals or passive cascades when transmitted via cues.

Table 1
Cascade types with examples in animal systems

Cascade type	Description	Behaviours and species displaying cascade type	Recruitment type
Adaptive cascade	Socially transmitted information is adopted resulting in a positive outcome	Food recruitment in vultures (Cortés-Avizanda et al., 2014)	P
		Foraging patch selection in nine-spined sticklebacks, <i>Pungitius pungitius</i> (Coolen et al., 2005)	P
		Shoaling behaviours in three-spined sticklebacks, <i>Gasterosteus aculeatus</i> (Doran et al., 2022; Ward et al., 2008)	P
		Collective predator avoidance in fish (Doran et al., 2022; Treherne & Foster, 1981)	P
		Antipredator response in insects (Treherne & Foster, 1981)	P
		Cultural conformity in great tits, <i>Parus major</i> (Aplin et al., 2015)	P
		Mate choice copying (Auld & Godin, 2015; Varela et al., 2018)	P
		Mixed-species foraging (Martínez et al., 2018)	P
		Response to false alarms by semipalmated sandpipers, <i>Calidris pusilla</i> (Beauchamp, 2010)	P
		Response to false alarms by redshank, <i>Tringa totanus</i> (Quinn & Cresswell, 2005)	P
Maladaptive cascade	Socially transmitted information is adopted resulting in a negative outcome	Response to false alarms by treehoppers, <i>Umberonia crassicornis</i> (Hamel & Cocco, 2012)	A
		Spontaneous startle responses in golden shiners, <i>Notemigonus crysoleucas</i> (Rosenthal et al., 2015)	P
		Bobolinks, <i>Dolichonyx oryzivorus</i> , and Savannah sparrows, <i>Passerculus sandwichensis</i> , adopting poor-quality nesting sites (Nocera et al., 2009)	P
		Poor-quality nest site selection in the black-throated blue warbler, <i>Setophaga caerulescens</i> (Betts et al., 2008)	A
		Maladaptive information transfer in guppies, <i>Poecilia reticulata</i> (Laland & Williams, 1998)	P
		Poorer feeding patch selected by nutmeg mannikins, <i>Lonchura punctulata</i> (Rieucan & Giraldeau, 2009)	P
		Army ant death-mills (Kronauer, 2020)	A
		Inflexible decision making in <i>Temnothorax rugatulus</i> ants (Sasaki et al., 2015)	A
		Suboptimal nest site selection in <i>Myrmecina nipponica</i> ants (Cronin, 2013)	A
		Suboptimal feeding-patch selection in stingless bees (Schmidt et al., 2006)	A
		Initiate or worsen ecological traps; observed in dolphins (Donaldson et al., 2012)	P
		Red crossbills, <i>Loxia curvirostra</i> , prematurely abandon profitable foraging patches (Smith et al., 1999)	P
		Cultural transmission of new songs in white-throated sparrows, <i>Zonotrichia albicollis</i> (Otter et al., 2020)	A
		Cultural transmission of new songs in humpback whales, <i>Megaptera novaeangliae</i> (Noad et al., 2000)	A
		Neutral cascade	Selective outcome is neutral

Examples labelled 'P' or 'A' represent passive and active cascades, respectively.

Applying the Information Cascade Framework: Examples in Animal Systems

Active and passive adaptive cascades drive social foraging

Adaptive cascades occur when a socially transmitted behaviour enhances the fitness of group members. Social foraging is a key benefit of group living and improves the efficiency of finding resources, as well as potentially revealing their quantity and quality (Ward & Webster, 2016). The exchange of social information among group members during foraging drives information cascades in many animal groups. For example, adaptive cascades allow hundreds of vultures to locate carrion within hours of its initial discovery. A change in flight pattern inadvertently broadcasts a cue to watching vultures and generates an information cascade as successive vultures navigate towards the feeding site (Dermoddy et al., 2011). As successive vultures join, a passive information cascade radiates from the food site, further sharing the cue and driving recruitment (Cortés-Avizanda et al., 2014).

Adaptive cascades also drive collective foraging in group-living insects. Many ants, for example, communicate social information via pheromone trails, which signal the location of food to nest-mates. In contrast to the vulture example, pheromone trails actively signal the location of resources to fellow ants and as successive ants follow the trail an active cascade emerges. Bees also generate active

cascades during foraging and use visual signals (the waggle dance) to communicate the location of profitable resources. The information cascades that drive the social foraging methods of eusocial insects like ants and bees are powerful adaptations that make them highly successful in many environments. Social information pertaining to foraging behaviour may also be used interspecifically, driving complex multispecies information cascades (Appendix 2).

Adaptive cascades establish local cultures

Cultural evolution, or the establishment of local traditions, has been described in numerous nonhuman animals (Allen et al., 2013; Aplin et al., 2015; Canteloup et al., 2020; Whiten, 2019). In some cases, information cascades may facilitate widespread social learning and transmit novel behaviours from a limited number of innovators to the broader population. Aplin et al. (2015) found that a novel foraging technique seeded in two individual great tits, *Parus major*, quickly spread throughout the local population via social learning. Here, information cascades, where tits imitated the novel foraging behaviour displayed by neighbours, facilitated the spread of the behaviour and its eventual adoption by the majority of the local population. The high level of behavioural copying among tits was linked to their propensity for social conformity, where individuals favoured the first behaviour they observed and continued to rely on social information instead of changing their foraging

technique as they gained personal experience (i.e. private information). In this way, social conformity maintained the stable use of the novel behaviour over two generations (Aplin et al., 2015). The tit example highlights the role of conformity in facilitating the emergence of information cascades, which are likely to appear where conformity bias (i.e. copy the majority/most common behaviour; Canteloup et al., 2020) drives the adoption of a behaviour at a group level.

Passive adaptive cascades facilitate group-wide synchronized behaviours

Perhaps the most recognizable information cascades in animals are the mesmerising synchronized movements of schooling fish, herds of mammals and flocks of birds and bats (Camazine et al., 2020; Miller et al., 2014). In each system, the behaviour of one or a few individuals spreads rapidly to direct collective action, giving rise to complex and often large-scale behavioural patterns (Miller et al., 2014). In foraging golden shiners, *Notemigonus crysoleucas*, Strandburg-Peshkin et al. (2013) found that schools with experienced fish more rapidly located potential foraging sites compared to schools of solely uninformed individuals. The transmission of information from informed to uninformed fish occurred rapidly and radiated spatially from a single initiator to its neighbours in a wave-like pattern, in a manner characteristic of information cascades.

The almost instantaneous sharing of information observed in schools, swarms and flocks has led some to describe information cascades as 'autocatalytic responses' wherein the behaviour of a small number of individuals stimulates a group level response which is continually reinforced as more individuals adopt the behaviour (Ioannou et al., 2011). Under changing conditions this enables groups to rapidly adopt adaptive behaviours informed by weak or ambiguous stimuli that may only be detected by a small subset of the population. However, as with information cascades, autocatalytic behaviours remain vulnerable to noise and false alarms because they are informed by others' behavioural responses rather than an assessment of the stimulus itself (Ioannou et al., 2011). In roosting semipalmated sandpipers, *Calidris pusilla*, for example, collective alarm responses allow flocks to rapidly escape by observing the departure of neighbouring birds. While this is an adaptive behaviour in most instances, sandpipers frequently experienced maladaptive passive cascades when false alarms caused by the departure of a few birds triggered an erroneous group-wide response (Beauchamp, 2010).

Passive information cascades emerge readily but are fragile

In the vulture, fish, and sandpiper examples above, individual animals rely on cues: information produced inadvertently by neighbouring animals, such as the movements of nearby conspecifics or the sudden departure of a flock mate. Information cascades driven by cues produce passive cascades where information is transferred unintentionally to neighbouring animals, in contrast to intentional information transmission via signals. The diffuse nature of information sharing during passive information cascades produces more opportunities for information cascades to form, as information is unintentionally broadcast and is not modulated by decisions of when to emit or repeat signals (as in active cascades). As a result, passive information cascades may emerge frequently in some animal groups.

While passive information cascades may emerge readily, they are also fragile and attenuate quickly, and as a consequence may have comparatively minor negative fitness outcomes when erroneous social information is broadcast. Ioannou et al. (2011) highlighted that information cascades allow groups to respond to weak signals, and perhaps this reliance on weak or ambiguous stimuli

allows passively initiated cascades to dissipate quickly compared to more 'persuasive' signals broadcast during active cascades. In economics, the scale and duration of an information cascade were found to be related to the informativeness of the broadcasted information. Less informative stimuli generated unstable cascades that were more likely to occur frequently and attenuate quickly (Goeree et al., 2007). In group-living animals, cues broadcast by neighbours may not explicitly communicate the nature of the stimulus generating a behaviour, so responding to cues often entails a degree of uncertainty (Lima, 1995). In schooling golden shiners, for example, alarm cascades are initiated by a startle response in neighbours. The fish must make rapid binary decisions (adopt or ignore behaviour) and are unable to distinguish between startle responses produced from real or false alarms, suggesting that false alarms may be an unavoidable by-product of rapid passive cascades. Consequently, passive cascades in the fish dissipated quickly and varied dramatically in the number of group members involved (Rosenthal et al., 2015). This is potentially explained by the inherent ambiguity in broadcast cues, where an inability to distinguish genuine and false alarms drives spontaneous information cascades of varying length and duration (Lima, 1995). In contrast, we highlight in the following sections how communication through signals may generate active cascades that are difficult to halt and may lead to maladaptive outcomes when environmental conditions change.

Active and Passive Maladaptive Cascades can Exacerbate Ecological Traps

Maladaptive cascades occur when the adoption of social information results in negative fitness outcomes for the participants. In comparison to adaptive cascades, maladaptive cascades often occur when a change in environmental or informational conditions causes the spread of maladaptive behaviours in a system adapted for the transmission of information via adaptive cascades. Army ants, for example, exhibit an unusual behaviour whereby a circling vortex of ants marches until it dies from exhaustion or dehydration, known as a suicide- or death-mill (Kronauer, 2020; Schneirla & Piel, 1948). Death-mills occur because army ants, like many ant species, use powerfully attractive pheromones (social information) to rapidly recruit conspecifics to resources such as food or to maintain group cohesion during raids (Couzin & Franks, 2003; Kronauer, 2020). Under novel environmental conditions the information cascade leads to the spread of maladaptive behaviours, such as the creation of a death-mill, which is reinforced with pheromones as they march (Kronauer, 2020). Maladaptive cascades like the death-mill highlight the danger of information cascades as sharing out-of-date social information may prevent individuals from obtaining new, up-to-date information, potentially trapping populations in suboptimal or fatal behaviours (Bernardo & Welch, 2001). Thus, maladaptive cascades can exacerbate 'ecological traps' where previously adaptive behaviours become maladaptive under new environmental conditions.

The danger of information cascades and ecological traps is further exemplified in bottlenose dolphins, *Tursiops truncatus*, where individuals learned to obtain food from recreational fishers, a behaviour that was passively acquired through social learning by observing the behaviours of other dolphins. In systems without human interference, social learning is beneficial to dolphin pods because it allows them to exploit new food resources and share novel feeding strategies in an adaptive manner. In this case, however, the spread of new behaviours resulted in increased death and injury because of the higher risk of boat strikes and entanglements with fishing gear (Donaldson et al., 2012). The dolphins are an example of an adaptive cascade that becomes maladaptive due to

a change in the environment (the presence of boats and fishing gear). Importantly, social learning driven by passive information transmission allowed the ultimately detrimental behaviour to become imbedded within the local population.

Neutral Information Cascades and Cultural Drift

During our review of the literature, we encountered examples of information cascades in animal systems that could not be strictly defined as adaptive or maladaptive (Garland et al., 2022; Noad et al., 2000; Otter et al., 2020). These examples were centred within the cultural transmission literature; a phenomenon where a range of socially learned behaviours propagates through an animal system (Garland & McGregor, 2020; Laland & Janik, 2006). Numerous animal groups exhibit cultural transmission, including but not limited to the song dialects of birds (Otter et al., 2020) and cetaceans (Garland & McGregor, 2020; Noad et al., 2000), and tool-making cultures among primates (Whiten et al., 1999). Explaining the evolutionary processes driving the formation and preservation of culture in nonhuman animals presents an ongoing challenge to biologists. While cultural transmission often spreads advantageous behaviours, as seen in great tits (Aplin et al., 2015), and occasionally maladaptive behaviours (Laland & Williams, 1998), a definitive link between culturally transmitted information and improved survival or reproductive success is yet to be ascertained (Aplin, 2019). To that end, the ‘neutral model’ of cultural evolution has been proposed to act as a null hypothesis for testing whether culturally transmitted behaviours arise from natural selection or via drift-like processes (Bentley et al., 2004).

Neutral cascades spread song variants in whales and birds

In humpback whales, *Megaptera novaeangliae*, a song variant spread rapidly when whales from a neighbouring ocean basin exposed an isolated population to a new song (Noad et al., 2000). The adoption of the new song was driven by an information cascade, as the behaviour was seeded by a small number of individuals and subsequently spread to entirely replace the original song dialect of the unexposed population. However, the adaptive benefits of this cascade remain open to debate. While the process of change in whale song is considered cultural evolution, the rapid adoption of new song variants was not linked to fitness benefits such as improved reproductive success (Garland et al., 2022). In a similar example, a novel song variant spread at a continental scale throughout white-throated sparrows, *Zonotrichia albicollis*, in North America (Otter et al., 2020). A new ‘doublet ending’ song variant replaced the ‘triplet ending’ song in Canadian populations and was transmitted during the seasonal intermix of populations at overwintering grounds. Like the whale example, the new song did not appear to confer any fitness benefit to birds that adopted the song, and suggests that cultural drift may cause the spread of new songs in this species rather than positive selection (Logue & Leca, 2020). To that end, the information cascade driving the adoption and establishment of new songs among whales and white-throated sparrows can be considered neutral cascades. In both examples, the spread of the songs cannot be linked to positive selection and highlights that information cascades may spread arbitrary cultural traditions that have neutral fitness outcomes (Franz & Matthews, 2010; Logue & Leca, 2020; Otter et al., 2020).

Interestingly, the adoption of novel songs has been linked to selective benefits in some birds (Ríos-Chelén et al., 2012), while the failure to learn specific songs may incur fitness costs due to lowered reproductive success in others (Crates et al., 2021). This highlights that although information cascades may drive similar behavioural patterns in different groups, the fitness consequences of cascades cannot be easily inferred in other systems. Instead, there may be

dramatic differences in the fitness benefits of information cascades based on the qualities of the group, the species in question, and the informational or environmental conditions.

Minimizing Maladaptive Cascades in Animal Systems

Since maladaptive cascades have negative fitness outcomes, animals that use social information are expected to have evolved mechanisms to prevent maladaptive cascades from spreading. We identified four common strategies that animals employ when using social information to avoid maladaptive cascades: following and transmitting social information only from a trustworthy source; following and transmitting social information only when personal information is unavailable or unreliable; the evolution of negative feedback mechanisms that suppress the transmission of information; and using quorum sensing to minimize the spread of unprofitable behaviours. In the next section, we discuss each of these mechanisms in detail.

Only use information from trustworthy sources

On average, animal signals must be honest to be reliable (Johnstone & Grafen, 1992). Where signals are error prone, animals may employ strategies to minimize responses to unreliable signallers. When information recipients can recognize individual signallers, maladaptive cascades can be prevented by ignoring information from unreliable signallers (Pollard, 2010). Nichols and Yorzinski (2016) found that peahens discriminated between individual alarm calls based on their record of reliability. When exposed to repeated false alarm calls (in the absence of a threat) from a particular individual, peahens stopped responding to those calls but continued to respond to alarms given by new callers. Similarly, when false alarms were played repeatedly to vervet monkeys, groups learned to ignore calls made by unreliable individuals but responded if the identity of the signaller or the nature of the advertised threat changed (Cheney & Seyfarth, 1988).

Flexible use of social and personal information

Animals may avoid maladaptive cascades by prioritizing personal information (in the form of memories) over socially acquired information (signals or cues) when personal information is more reliable or contains richer information. Doing so reduces the probability that an individual will adopt and transmit a behaviour based on out-of-date or incorrect socially acquired information.

In honey bees, *Apis mellifera*, for example, the waggle dance is a form of communication that allows foragers to communicate the location and quality of a food source to nestmates (Grüter & Farina, 2009). However, bees that remember foraging sites of satisfactory quality tend not to follow waggle dances, thus limiting their exposure to potentially unreliable social information (De Marco et al., 2008). When a food source becomes unrewarding, bees will increase their observation of waggle dances, thereby prioritizing social information. Honey bees therefore appear to rely on social information only when personal information about high-quality food resources is unavailable. Furthermore, Leadbeater and Chittka (2007) note that honey bees avoid maladaptive cascades when selecting new nesting sites by independently verifying the site's suitability before advertising its location via waggle dance. In doing so, honey bees avoid sharing social information regarding unsuitable sites which might occur if decisions were made by blindly copying others (Leadbeater & Chittka, 2007; Seeley & Visscher, 2004a). In a similar manner to honey bees, the ant *Lasius niger* prioritizes personal information (memories) over social information (pheromone trails; Czaczkes et al., 2019). However, *L. niger* foragers will prioritize social information in situations where personal information is unreliable, for example when low

light conditions prevent accurate visual navigation (Jones et al., 2019).

Negative feedback mechanisms

Negative feedback mechanisms can suppress maladaptive cascades by reducing or modulating the positive feedback that accumulates during an information cascade (Couzin, 2009). Negative feedback signals can stop others from following adverse social information. For example, pharaoh ants, *Monomorium pharaonis*, deposit a 'no entry' pheromone at trail forks to deter nestmates from following unrewarding foraging routes (Robinson et al., 2005). Similarly, honey bees use a stop signal that prevents other bees from advertising dangerous locations via a waggle dance (Jack-McCollough & Nieh, 2015; Nieh, 2010). The stop signal effectively limits recruitment to dangerous foraging sites (Nieh, 2010) and so minimizes the propagation of dangerous information. Stop signals are also used by the treehopper *Umbronia crassicornis*, whose nymphs live in family groups guarded by their mother. When a group of nymphs produces an alarm call in the absence of a threat, adult treehoppers use a negative feedback signal that dampens the signalling and stops the spread of false alarms (Hamel & Cocroft, 2012). Signalling from the mother also increases the threshold for subsequent alarm calls among the offspring thus reducing the risk of maladaptive alarm cascades in future (Hamel & Cocroft, 2019).

Quorum responses

In comparison to negative feedback mechanisms that actively suppress runaway positive feedback, quorum responses reduce the initial speed at which social information spreads, limiting the propagation of erroneous information (Ward & Webster, 2016). During a quorum response, animal groups down-weight the adoption of rare behaviours (Ward & Webster, 2016). However, once a critical prevalence is reached (the quorum threshold), the likelihood that others copy the behaviour increases sharply, and positive feedback drives rapid adoption. In this way, the trend of behavioural adoption during a quorum response is nonlinear, being slow when a behaviour is uncommon and accelerating once the quorum threshold is met (Sumpter & Pratt, 2009). By limiting the adoption of minority behaviours that occur below the quorum threshold, a group limits the probability that an individual member triggers a maladaptive cascade as the behaviours of misinformed individuals are less likely to become sufficiently prevalent and meet the quorum threshold (Ward & Webster, 2016). Quorum responses are widespread in nature and regulate behaviours including nest site selection in honey bees (Seeley & Visscher, 2004b) and ants (Franks et al., 2015; Pratt et al., 2002; Sasaki et al., 2015), and direct the collective behaviour of schooling fish (Ward et al., 2008).

SYNTHESIZED FINDINGS AND KEY THEMES

This review has revealed that information cascades are widespread among a diverse array of animal systems. Like humans, many group-living animals conform to the behaviour of their neighbours and frequently encounter information cascades that initiate systemwide behavioural changes. Information cascades offer a highly efficient mechanism for rapidly sharing beneficial social information with group mates, a key evolutionary advantage of group living. We find information cascades driving advantageous group level foraging, mate selection and predator avoidance in animals. However, despite information cascades driving many behavioural phenomena, the literature is incohesive. To that end, the conceptual framework we provide and deploy in this review can be used to draw together future studies and standardize the definitions and characteristics of cascades occurring across different taxa.

A key pattern that emerged during this review is the potential for adaptive cascades to operate in a maladaptive state given the correct conditions. While the adaptive benefits of information cascades are numerous, the 'blind copying' that often emerges during a cascade may fail to provide relevant or useful information as conditions external to the group change over time, potentially exposing a group to maladaptive cascades. In Table 1, we see a significant list of maladaptive cascades (one that outnumbers the list of adaptive cascades); however, each of these maladaptive cascades emerges from a system evolved to provide adaptive benefits to the group. While some maladaptive cascades may occur infrequently, such as army ant death-mills (Kronauer, 2020), others may occur often, in some instances outnumbering adaptive cascades, as seen with the collective alarm responses of some birds (Beauchamp, 2010; Gray & Webster, 2023). The magnitude of adverse effects of maladaptive cascades may also vary significantly and range from a slight loss of foraging time or unnecessary energy expenditure, to cascades that result in collective injury and death.

The persistence of maladaptive cascades in animal systems is likely explained by the strong fitness benefits conferred when they are operating in an adaptive state, which outweigh the deleterious impacts of maladaptive cascades. However, group-living animals also employ several mechanisms that limit and regulate the emergence or propagation of maladaptive information cascades, suggesting their adverse effects have been selected against over evolutionary time.

A novel discovery we found was the existence of information cascades that appeared to fall outside an adaptive/maladaptive binary. This necessitated the introduction of the new term 'neutral cascade' to describe examples of information cascades that had no clear adaptive or maladaptive fitness outcome. In comparison to other cascade types, neutral cascades appear to be relatively rare in animal systems (Table 1) and may be a result of strong social conformity that drives collective behaviours in animal groups (Claidière & Whiten, 2012). Neutral information cascades, however, have been little studied in nonhuman animals, despite the documented transmission of neutral traits in some animal groups (Whiten, 2019). This presents opportunities for future research, especially as neutral cascades in nonhuman animals present interesting comparisons to human systems, where similar cascades drive cyclical and unpredictable fads and trends (Golman et al., 2022).

Future Research

Information cascades drive highly significant group level behaviours in human and nonhuman animal groups, making them a timely subject for future research endeavours. Moving forward, comparative studies investigating how differences in group communication and organization affect information cascades offer a very interesting avenue for future research. Factors influencing cascades include group structure, the characteristics of the causal information (i.e. cues or signals) and the surrounding environmental conditions. Even cascades that feature similar behaviours may have vastly different outcomes, as seen in songbirds, where song learning may have beneficial, neutral or maladaptive fitness effects depending on the species concerned (Crates et al., 2021; Otter et al., 2020; Ríos-Chelén et al., 2012).

Improving our knowledge of information cascades in animal systems may have important implications for conservation and ecosystem management. Information cascades act as force-multipliers, where the behaviour of one individual affects the actions of many others, with fitness-related consequences. As we have highlighted here, adaptive cascades can quickly shift to maladaptive ones when environmental conditions change, and social

information becomes out of date. As we continue to see shifts in other cascading phenomena (Damien & Tougeron, 2019; Vitasse et al., 2021), understanding which behaviours emerge from cascading social information is key to determining and potentially predicting how species will respond to new conditions and emerging ecological traps.

Lastly, using knowledge from cascades in animal groups may provide insights into complex problems faced by humans. This includes the rapid spread of harmful information in human systems, a largely unresolved challenge in modern society (Lazer et al., 2018; World Economic Forum, 2013). The rapid expansion of social networks has accelerated the speed and distance humans can share social information, including mis- and disinformation (Bak-Coleman et al., 2021; Vosoughi et al., 2018). The increasing speed of daily life in human societies (social acceleration) impedes our ability to accurately judge information quality (Sultan et al., 2022) and has worrying implications for the spread of maladaptive cascades (Tump et al., 2020). Broadening our understanding of how animal systems modulate information sharing, such as scaling alarm calls based on individual trustworthiness (Cheney & Seyfarth, 2018; Nichols & Yorzinski, 2016), could inspire novel solutions to the pernicious problem of misinformation spread in human-designed systems.

Author Contributions

Joseph S. McCormick: Conceptualization, Writing – Original draft, Writing – Review and editing; **Tanya Latty:** Conceptualization, Writing – Review and editing; **Thomas E. White:** Conceptualization, Writing – Review and editing; **Eliza J. T. Middleton:** Conceptualization, Writing – Review and editing.

Declaration of Interest

The authors have no conflicts of interest.

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APPENDIX 1: REJECTING REJECTION CASCADES

Information cascades driven by the sequential rejection of a behaviour are called ‘down cascades’ in economics. In contrast to up cascades where group members imitate the behaviour of the cascade initiator, down cascades emerge where group members do not copy the initiator’s behaviour and instead collectively reject their behaviour. Like cascades driven by the adoption of a behaviour, down cascades are known to have both beneficial and adverse outcomes in human groups. Examples of rejection cascades in humans include avoiding poor investment options by rejecting the unsuccessful choices of naïve entrepreneurs (adaptive rejection cascade; [Bernardo & Welch, 2001](#)) and rejecting common childhood vaccinations (maladaptive rejection cascade; [Kata, 2012](#); [Reich, 2018](#)).

In humans, rejection behaviours are relatively straightforward to decipher, as the motivation for following others’ behaviours can be determined via questioning whether a behaviour was sequentially rejected because of a perceived danger, risk or adverse outcome. However, it is challenging to identify rejection cascades among nonhuman animals, because of the complexity of disentangling individual level motivation alongside the fact that rejection cascades often involve not displaying a behaviour (i.e. collectively avoiding another’s mistake). The difficulty presented by rejection cascade identification among animals is further mirrored in the literature. Our searches failed to identify any empirical examples of rejection cascades operating among nonhuman animals. However, we note that some animal species reject behaviours exhibited by other individuals that are perceived to be poor performers ([Loukola et al., 2020](#); [Seppänen et al., 2011](#)). To our knowledge, cases where rejection behaviours are sequentially spread throughout a group have yet to be observed in nonhuman systems. This warrants further research to confirm whether the lack of rejection cascades is a true representation of the natural world or is an area that has been insufficiently studied.

APPENDIX 2: ACTIVE AND PASSIVE CASCADES DRIVE MIXED-SPECIES FORAGING

Adaptive cascades are not limited to intraspecific communication. Using information intended for others, or eavesdropping,

occurs among different species and provides a broad range of information that may be unobtainable from conspecifics alone ([Magrath et al., 2015](#)). [Martínez et al. \(2018\)](#) found that arthropods flushed out of the surrounding habitat by nomadic army ants attracted birds in multispecies foraging groups. The recruitment of foraging birds to army ant swarms was driven by information cascades that sequentially recruited species according to their feeding guild. Calls from bird species that exclusively feed during army ant raids (obligate species) attracted less specialized species (facultative species), which in turn, attracted birds that only sometimes feed at army ant swarms (occasional species). In this way, an information cascade involving several species from different guilds indirectly enhanced each other’s foraging success ([Martínez et al., 2018](#)). These flocks may contain 20 different species and emerge from a combination of active signalling and passive recruitment via cues (Fig. A1).

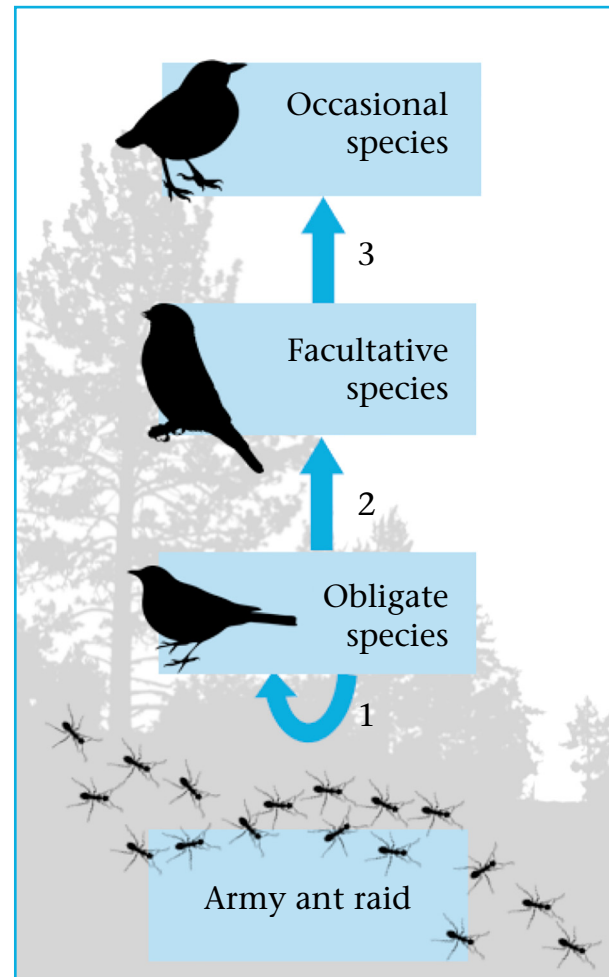


Figure A1. The flow of information (blue arrows) between different avian feeding guilds generates an information cascade as follows. Signals from obligate ant-feeding species generate an information cascade that attracts additional conspecifics. Eavesdropping on cues from obligate feeders propagates the information cascade and recruits facultative species to the army ant invasion front. The information cascade extends to species that occasionally feed on army ant raids which respond to cues from facultative species.