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REVIEW

Distributed social learning hypothesis: a driving mechanism for filling the missing fragments of innate complex patterns

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Abstract
Social learning and communication enable animals to enhance their adaptability and behavioural flexibility in response to changing environmental conditions. This paper examines current perspectives on the diversity of social learning mechanisms, their ecological significance, and the behavioural mechanisms underlying the spread of novel behaviours within animal groups, with particular attention to the relationship between innovativeness and intelligence and the potential for innovative behaviours to spread through social learning. Within this framework, I highlight the distributed social learning (DSL) hypothesis, which posits that the initial performance of a complete behavioural pattern by a few individuals promotes its spread among conspecifics that possess only dormant fragments of the same behaviour. These fragments consist of short, neutral action sequences that, under favourable conditions, can be integrated into a coherent and functional pattern. Drawing on a wide range of research on social learning, I propose that DSL functions as a form of 'folk culture', blending innate, previously dormant behavioural components with learned ones. This process may enable animals to assemble novel behavioural patterns by recruiting and integrating pre-existing latent fragments of behaviour more efficiently than would be possible through entirely de novo acquisition.

Introduction

In his science fiction story *Lymphater's Formula*, Stanisław Lem (1961) describes a mathematician, Ammon Lymphater, who is inspired by the observations of a myrmecologist studying ants that, after their container breaks, find themselves in an unfamiliar desert environment and promptly begin catching the jumping mites present there. Some members of the colony possess an 'innate knowledge' of hunting techniques, whereas others appear to complete their hunting repertoire by observing successful hunters. The story goes on to describe how, based on these observations, the mathematician creates an artificial intelligence so powerful that he ultimately has to destroy it to prevent the destruction of human civilisation. As a child, I was captivated by this story. It sparked my enduring fascination with ants and, later, with the problem of social learning in animals. Almost half a century later, a strikingly similar observation in my own research inspired me to formulate the distributed social learning (DSL) hypothesis, which may help explain the rapid spread and consolidation of cultural traditions in animal communities. DSL, a hypothesis first proposed by (Reznikova and Panteleeva 2008), suggests that initial performances by a small number of individuals possessing a complete behavioural pattern promote the spread of that behaviour among others who possess only dormant fragments of it. These dormant fragments consist of short chains of actions that are neutral and non-functional on their own but can, under favourable conditions, be assembled into a coherent, goal-directed behavioural pattern.

In its broadest sense, social learning occurs when direct or indirect social interaction facilitates the acquisition of a novel behavioural pattern. It typically involves an experienced individual (the demonstrator) performing a behaviour that enables a naive animal (the observer) to subsequently expresses the same behaviour sooner or more effectively than would be possible through individual learning alone. More generally, social learning encompasses any situation in which the behaviour, presence, or products of one individual's behaviour influence the learning of another (Caldwell and Whiten 2002; Hoppitt and Laland 2013). Members of many species spend a significant part of their time in the company of conspecifics and can acquire essential information simply

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by observing others: when, where and what to eat, with whom to mate, whom to fear, and even how to spend leisure time, if any exists. Importantly, social learning serves both social and informational functions. Conformity may allow individuals to integrate into social groups, where *informational conformity* is employed to access the best information available about reality, and *normative conformity* helps regulate social interactions (Harrison et al. 2024).

Social learning has considerable adaptive value because it enhances behavioural flexibility in changing environment. In many natural situations, however, the boundary between flexibility and conservatism is blurred. Behaviour acquired through social learning may become intertwined with the expression of innate patterns. Furthermore, socially acquired behaviours may develop into stable behavioural traditions, some of which become paradoxically conservative and may be difficult to distinguish, in their expression, from innate forms of behaviour. If we want to determine which part of an animal's behavioural repertoire is attributable to social learning, this cannot be inferred intuitively; rather, it requires developmental studies and targeted experiments.

In modern ethology and comparative psychology, the study of social learning has developed into a rapidly expanding field with its own concepts, definitions, theoretical frameworks, and experimental approaches. Numerous forms of social learning have been identified, ranging from relatively simple ones, such as social facilitation, to the most complex, including tutoring and the maintenance of behavioural traditions in animal societies.

This review examines current perspectives on the diversity of social learning mechanisms, their ecological significance, and the behavioural processes underlying the spread of novel behaviours within animal groups. It also explores the relationships between innovativeness, intelligence, and the social transmission of innovations. Within this framework, I revisit the DSL hypothesis. First documented in ants, this form of social learning may occur more widely across the animal kingdom than has previously been recognised. Drawing together evidence from diverse taxa, I propose that DSL functions as a form of 'folk culture', blending innate, still-dormant behavioural components with learned ones. This process may enable animals to assemble novel behavioural patterns from dormant fragments more efficiently than by acquiring them entirely *de novo*.

Various types of social learning: terms, notions and examples

Social learning is widespread in the animal kingdom – from crickets and ants to whales and elephants – and is involved in behaviours ranging from navigation and predator avoidance to mate choice and foraging. Most research into social learning has been conducted using group-living animals as subjects. However, at least in many mammals and birds, adult members of almost all species, whether social or solitary, interact with their offspring and/or siblings when social learning is of significant importance. Whether social species have evolved enhanced capacities for social learning remains an open question (Kendal et al. 2018). Nevertheless, a growing body of research has documented social learning in animals that do not habitually live in social groups (Reader and Lefebvre 2001; Webster 2023).

Many authors distinguish different forms of social learning based on the mechanisms involved, particularly the extent to which they depend on complex cognitive processes. In this review, I examine these forms, beginning with those generally regarded as the most cognitively demanding, and revisit some of the key concepts underlying their classification.

Imitation (observational learning)

In his influential article 'The question of animal culture', (Galef 1992) noted that in the absence of of convincing evidence for true imitation or teaching, certain behaviours observed in birds or chimpanzees could not be said to be cultural. One consequence of this view was the emergence of a general model of *cumulative culture* in which such a form of cultural propagation was impossible without 'true imitation' (Tomasello 1999). Another development motivated by this debate was the introduction of the experimental artificial fruit two-action task, which provided the first robust evidence of imitation learning in animals and young children (Huber 2002; Whiten et al. 1996) for a review see (Suwandschieff et al. 2023). This paradigm subsequently inspired a wide range of comparative studies exploring social learning and cultural transmission across a wide diversity of species.

Teaching

Conceptually, teaching is a category of behavioural adaptations for transmitting knowledge and skills to others. The persistence of culturally transmitted behaviour may be supported not only on social learning but also on the actions of individuals that actively facilitate its transmission. The evolutionary approach developed by (Caro and Hauser 1992) treats *teaching* in animals as a specific type of social learning, where a knowledgeable individual engages in behaviour that is costly, or at least provides no immediate benefit to itself, while enabling a naïve individual to acquire knowledge or skills more rapidly. These authors proposed a working definition of teaching: an individual actor (A) can be said to teach if it modifies its behaviour only in the

presence of a naive observer, B, at some cost, or at least without obtaining an immediate benefit for itself. A's behaviour encourages or punishes B's behaviour, provides B with experience, or sets an example for B. As a result, B acquires knowledge or learns a skill earlier in life or more rapidly or efficiently than it might otherwise do or would not learn at all. When teaching is defined in such functional, rather than intentional, terms, numerous examples have been described across birds, mammals, and insects (Hoppit et al. 2008; Brandl et al. 2023; Thornton and Clutton-Brock 2011; Troisi 2017). However, as discussed below, the diversity of terminology —particularly in studies of insects—often blurs the boundaries of the concept. I therefore propose restricting the use of the term 'teaching' and distinguishing it clearly from the broader concept of information transmission. This distinction can be illustrated by the following examples.

Parental teaching of hunting skills One of the best natural models for studying teaching is parental behaviour in predatory species. A substantial body of evidence describes how predators, from whales to rodents, facilitate the development of their offspring's hunting skills. At the same time, members of many other species become successful hunters without parental instructions. Why do species, such as ferrets, grasshopper mice and frogs require no training in complex hunting actions, whereas others, according to classic studies, including cats (Lorenz 1952) and falcons (Tinbergen 1942) appear to teach their offspring step by step? Answering this question requires species-specific investigations to determine whether parents actively shape the development of hunting behaviour.

For example, it has long been known that, in felids and other carnivores, mothers modify their predatory behaviour in a series of stages. Leyhausen and Toinkin (1979) described how adult female domestic cats pursue, capture, kill, and eat prey in a smooth sequence with minimal hesitation between actions. However, when these cats become mothers and their kittens begin to leave the nest, they modify their behaviour, performing the sequence in a way that—logical from a human perspective—clearly appears to shape the kittens' hunting skills progressively. Under controlled laboratory conditions, (Caro 1980) tested the hypothesis that this maternal behaviour functions as teaching. He found it difficult to determine whether maternal behaviour responded to developmental changes in the kittens, because the two processes appeared to proceed in parallel. Later, by studying interactions among mothers, cubs, and prey in wild cheetahs, (Caro 1994, 2005) showed that the coordination between the mother's actions—particularly her provisioning of prey—and the cubs' developing hunting skills resembled the parallel processes observed in domestic cats rather than a behavioural 'dialogue' between mother and offspring.

In raptorial birds, teaching behaviour likewise appears plausible when adults release live, often injured, prey near juveniles, allowing them to practise hunting. However, several studies illustrate how difficult it is to disentangle the respective roles of maturation and parental investment in the development of hunting behaviour. For example, in ospreys (*Pandion haliaetus*), (Meinertzhagen 1954) described adults encouraging fledglings to catch fish from their very first hunting attempts during the first six days after fledging. These observations provide apparently strong evidence for parental teaching. However, hand-raised young ospreys were found to catch fish successfully within 3 days to 3 weeks after release into the wild, despite having received no parental instruction (Schaadt and Rymon 1982). (Howard and Hoppitt 2017) tested whether osprey parents increasingly brought live prey to the nest as their offspring matured, thereby allowing them to practise prey handling in a manner analogous to the progressive teaching described in meerkats (Thornton and McAuliffe 2006). Contrary to this prediction, they found the opposite trend, indicating that ospreys do not teach their young at the nest.

In summary, elaborate teaching behaviour occurs in some predatory mammals and birds, yet effective hunting techniques may also develop in its absence. Nevertheless, the evolution of this costly behaviour suggests that it provides adaptive benefits, for example by enabling juveniles to acquire hunting skills more rapidly and thereby increasing their chances of survival (Ruaux et al. 2020). Teaching is expected to be favoured by natural selection when opportunities for individual learning are limited or costly and when passive social learning is ineffective. For instance, meerkat pups seldom encounter mobile prey and therefore have few opportunities to refine their prey-handling skills (Thornton and Clutton-Brock 2011). Moreover, some prey, such as scorpions, are dangerous to handle, and because successful prey capture requires repeated motor practice, observation alone is insufficient. Consequently, adults provide pups with opportunities to handle live prey that would otherwise be unavailable (Thornton and McAuliffe 2006).

These examples show that the education of hunters conforms closely to the functional definition of teaching proposed by (Caro and Hauser 1992). Is teaching restricted to hunting, or does it occur in other behavioural contexts? Interestingly, Thornton and co-authors (Thornton and Raihani 2008; Thornton and Clutton-Brock 2011) regarded certain behaviours in ants (Franks and Richardson 2006) and pied babblers (Raihani and Ridley 2008) as clear examples of teaching, whereas they did not reach the same conclusion for raptorial birds, cetaceans, or primates. Similarly, (Hoppitt et al. 2008) considered teaching to occur in bees, ants, babblers, meerkats, and other carnivores, but not in chimpanzees—a striking taxonomic distribution that the authors

argued is consistent with viewing teaching as a form of altruism. More recent reviews (Brandl et al. 2023; Troisi 2017) include numerous examples from birds, cetaceans, and carnivores, yet they continue to cite tandem-running ants and waggle-dancing honeybees as classic examples of teaching, while the existence of teaching in chimpanzees remains controversial. It is striking that social insects remain among the strongest candidates for animal teaching, whereas the teaching abilities of our closest living relatives continue to be debated. Throughout this review, I therefore adopt Caro and Hauser's (1992) functional definition, because broadening the concept risks blurring the distinction between teaching and the more general process of information transmission through social learning.

Can insect teach? All the reviews discussed above treat two insect behaviours as examples of teaching. The first is tandem running in *Temnothorax albipennis*, in which an informed individual leads a naïve nestmate to a food source (Franks and Richardson 2006). The second is the honeybee waggle dance, which has traditionally not been regarded as teaching but has been interpreted by (Hoppitt et al. 2008) as functionally analogous to tandem running. However, these two cases illustrate information transfer, not teaching. In the behavioural literature, the terms 'teaching', 'tutoring', 'information transfer', and even metaphors such as 'scaffolding' are often used interchangeably (Whiten 2022), although they refer to distinct concepts.

I suggest distinguishing between the ethological notions of 'teaching' defined as a costly transfer of knowledge or skills which remains with a pupil and has a long-lasting effect, and '*information transfer*' – the purposeful relaying of messages from a signaller to a receiver through specific communication channels that influence the receiver's immediate behaviour see (Reznikova 2020, 2023). This definition includes the transfer of information through odour trails, vocal signals, and other forms of communication. Information transfer should not be equated with tutoring as an act of instruction. Rather than producing long-lasting changes in behavioural competence, it typically conveys information about immediate environmental circumstances.

Returning to tandem running in ants as an example of teaching, let us consider its place among other ant communication systems. Among the approximately 15,000 described ant species, foraging strategies range from solitary foraging to highly coordinated group retrieval (Hölldobler and Wilson 1990), and the distribution of cognitive responsibilities within a colony depends on the recruitment strategy employed. Tandem running, in which an experienced scout leads a single recruit to a previously discovered resource (Wilson 1959), is generally regarded as the most primitive form of recruitment, although it occurs widely across the ant phylogeny (review in (Schultheiss et al. 2015). Recent classifications distinguish four principal recruitment strategies (Kolay et al. 2020; Reznikova 2020): (1) Mass recruitment, in which scouting individuals broadcast guidance information to their nestmates in the form of a scent trail; (2) Tandem running; (3) Group recruitment: a scouting ant may lead a group of several individuals to a goal; (4) 'Leader–scouting' system in which a scout communicates the location of a distant resource directly to foragers without relying on pheromone trails or physical guidance. The leader–scouting forager system in ants and the waggle dance in honeybees, see (Chittka and Rossi 2023; Dong et al. 2023; von Frisch 1947, 1967) represent exceptionally sophisticated forms of information transfer, enabling the communication of spatial information about distant targets.

Do these behaviours qualify as teaching? In my view, they do not. Whether one considers the relatively simple tandem-running system or the far more elaborate communication systems of leader–scouting ants and honeybees, all function primarily to convey information about an immediate, context-specific objective. Although in tandem running, the leader appears to 'instruct' the follower, the information conveyed concerns the location of a particular resource at a particular time rather than a generalisable behavioural skill. This differs fundamentally from the examples of teaching discussed elsewhere in this review, where the learner acquires behavioural skills or knowledge that persist beyond the immediate context and can be applied in future situations.

Can apes teach? Here, I consider teaching from the ethological perspective, applying the functional criteria proposed by Caro and Hauser (1992). Even within this framework, convincing evidence for active teaching in chimpanzees remains lacking (Moore and Tennie 2015). Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) are the closest living relatives of *Homo sapiens*, sharing a common hominin ancestor approximately 6 million years ago (Duda and Zrzavý 2013). Nevertheless, the mechanisms of social learning and cultural transmission in humans and chimpanzees appear to differ substantially, and these differences may extend to the ways in which knowledge is transmitted between individuals. Human infants are capable of faithful imitation to a degree not observed in chimpanzees (Whiten et al. 2009). At the same time, Whiten (2022) argues that non-human animals possess sufficient long-term cultural fidelity to support at least limited forms of cumulative cultural evolution.

Teaching could be particularly advantageous in apes because some complex skills appear to have a restricted developmental window. For example, chimpanzees that fail to acquire nut-cracking between approximately three

and five years of age do not subsequently learn the technique and instead obtain nuts by scrounging from proficient individuals (Matsuzawa et al. 2001). Despite this apparent opportunity for teaching, convincing evidence remains elusive. Although (Boesch 1991, 2012) reported several observational cases interpreted as teaching, studies at other long-term field sites have not reached the same conclusion (Moore 2013; Moore and Tennie 2014). Lonsdorf's (2006) study of the ontogeny of termite fishing at Gombe found that mothers tolerated their offspring observing termite fishing and occasionally even tolerated interference or tool theft, but they did not actively facilitate learning. Likewise, an experimental study found no evidence of teaching in chimpanzees under conditions in which young children readily instructed one another (Dean et al. 2014). Further evidence comes from comparisons among wild populations. (Musgrave et al. 2020) examined two chimpanzee populations differing in the complexity of termite fishing. At Goualougo, where termite fishing is more elaborate, adults frequently transferred tools in response to requests by younger individuals, actively facilitating possession changes. At Gombe, by contrast, requests for tools were typically refused. These findings suggest that tolerance and active facilitation increase with the complexity of the task, although they still fall short of demonstrating teaching in the strict ethological sense. Similarly, (Bandini et al. 2021), studying the acquisition of nut-cracking in naïve orangutans (*Pongo abelii* and *P. pygmaeus*), concluded that non-copying forms of social learning are sufficient to modulate and stabilise tool traditions across generations.

In the absence of consensus, several researchers have adopted a more conservative analogy to describe knowledge transmission in wild chimpanzees. First proposed by Matsuzawa (Matsuzawa 2011; Matsuzawa et al. 2001) and later adopted by (de Waal 2001) and (Boesch 2012), the analogy is that of the traditional Japanese sushi apprenticeship. Apprentices spend years observing a master before attempting the craft themselves, receiving little or no explicit instruction. Silent, but tolerated, observation replaces active teaching.

This analogy captures an important characteristic of ape social learning. Mothers generally tolerate their offspring observing their activities, but rarely modify their behaviour to facilitate learning and seldom even establish eye contact during these activities. Indeed, numerous studies indicate that learning in great apes is overwhelmingly initiated by the infant rather than by the parent (Lonsdorf 2006). A striking contrast is provided by the cooperative-breeding callitrichids (marmosets and tamarins), in which adults actively facilitate the acquisition of foraging skills by juveniles (Byrne and Rapaport 2011; Humle and Snowdon 2008). Being cooperative-breeders, callitrichids outperform their independently breeding sister taxa (squirrel monkeys) and capuchin monkeys, which show an intermediate breeding system, in the socio-cognitive domain, including social learning, communication, teaching-like behaviours, understanding of gaze and communicative cues as well as in cooperative problem solving (Burkart and (Burkart and van Schaik 2010). Overall, despite decades of intensive field observations and experimental studies, compelling evidence for active teaching in great apes remains scarce. By contrast, teaching-like behaviour appears to have evolved more readily in cooperative-breeding primates, suggesting that social organisation, rather than phylogenetic proximity to humans, may be the stronger predictor of the evolution of teaching.

Over-imitation

Over-imitation is the tendency to copy elements of a demonstrated action that are irrelevant to achieving its goal. The phenomenon was first demonstrated by (Horner and Whiten 2005), who showed that, unlike chimpanzees, young children faithfully reproduce actions that appear causally unnecessary. In their study, 3- to 4-year-old children and young chimpanzees were presented with a puzzle box containing a hidden reward. An experimenter demonstrated a sequence of both causally necessary and causally irrelevant actions for retrieving the reward. When the box was opaque, preventing the subjects from identifying which actions were functionally important, both chimpanzees and children tended to copy the entire sequence. A striking difference emerged when the box was transparent. Chimpanzees omitted the visibly unnecessary actions, whereas children continued to reproduce them with high fidelity, even though these actions were clearly unrelated to obtaining the reward. Since this seminal study, over-imitation has become the subject of extensive research in developmental psychology and comparative cognition. By contrast, relatively few studies have examined the phenomenon in non-human animals. (Clay and Tennie 2018), for example, directly compared large samples of bonobos and young children in an action-copying task involving visibly causally irrelevant actions. Children aged 3–5 years readily copied the irrelevant actions, whereas bonobos did not. More recently, (Mackie and Huber 2023) reported evidence of over-imitation in dogs. In their experiments, dogs copied the causally irrelevant actions performed by their human caregivers, suggesting that the phenomenon may be facilitated by the unusually close social relationship between dogs and humans. Over-imitation is widely considered a hallmark of human social cognition. By faithfully copying not only actions that are causally effective but also those that appear unnecessary, children acquire conventionalised behavioural sequences that support rituals, social norms,

and other culturally transmitted practices. This tendency has also been proposed as one of the cognitive foundations of cumulative technological culture.

Contagious behaviour

Contagious behaviour represents one of the simplest forms of social influence and is exemplified by rules such as '*If others are fleeing, flee too.*' When two or more animals engage simultaneously in the same species-typical behaviour, this coordination is often attributed to behavioural contagion. In such cases, the behaviour of one individual acts as a releaser for the innate behaviour of others (Thorpe 1963; Zentall 2006). Examples of contagious behaviour include flight responses, movements in flocks or shoals, and chorusing by birds, frogs, and dogs. Antipredatory behaviour can also be considered contagious when it involves the coordinated movement of a group of animals for defensive purposes. When this coordinated behaviour is aggressive (i.e., directed toward rather than away from danger), it is known as *mobbing*.

Social facilitation

Initially, the theory of social facilitation was developed by Zajonc to explain the effects of an audience on human performance. (Zajonc 1965) argued that the presence and behaviour of others may influence an individual's motivation, ultimately leading to improved performance. In its broad sense, social facilitation is defined as an increase in the performance or frequency of a specific behaviour resulting from the presence of others. Applying the logic of social facilitation to ethology, (Clayton 1978) defined social facilitation as an increase in the frequency of a behavioural pattern in the presence of others simultaneously displaying the same behavioural pattern. She suggested that social facilitation in animals could be due to the reduction of isolation-induced fear. For instance, in ground squirrels, the presence and behaviour of conspecifics affect juveniles' responses to alarm calls. Visually isolated juveniles were less likely to respond to playback alarm calls than juveniles tested in the presence of conspecifics (Mateo 1996). Another example comes from naïve ants reared in isolation from both socially experienced nestmates and the symbiotic aphids that provide them with honeydew. These ants displayed species-specific patterns of aphid tending earlier and more effectively after observing experienced aphid-tending nestmates (Reznikova and Novgorodova 1998). Many authors consider social facilitation to be a basic form of social learning that, through relatively simple mechanisms, can explain phenomena previously interpreted as evidence of animal culture, such as milk bottle opening by tits (reviews in (Aplin et al. 2015; Galef 2004). Unlike imitation or teaching, social facilitation does not require the acquisition of a novel behavioural pattern; instead, it increases the likelihood that an existing behaviour will be expressed in the presence of others.

Stimulus enhancement

Stimulus enhancement (Galef 1988; Spence 1936) is said to occur when the presence or actions of an individual draw an observer's attention to a particular object, thus enhancing the observer's opportunity to learn about it. The result of this narrowing of behavioural focus is that the individual's subsequent behaviour becomes concentrated on that object or its salient features. For example, (Lorenz 1935) found that ducks enclosed in a pen did not react to a hole large enough to allow escape unless they happened to be near another duck as it was escaping. The sight of a duck passing through the hole in the pen appeared to draw attention to the opening. Thus, one could ask whether observing a ball roll through the hole, for example, would produce a similar effect. If so, it would not be interpreted as social learning (Zentall 2022). *Generalised stimulus enhancement* focuses the observer's attention on an object as a whole, while *localised stimulus enhancement* focuses only on a functional part of the object. However, the observer does not copy the demonstrator's actions, and the observer's behaviour is acquired through trial and error. For example, (Avarguès-Weber and Chittka 2014) showed that bumblebees given the opportunity to associate the actions of conspecifics with rewarding flowers rapidly developed a preference for flowers of that type, and subsequently visited both occupied and unoccupied flowers sharing the same characteristics (stimulus enhancement). Notably, social facilitation and stimulus enhancement mediated by more experienced individuals can serve as proximal mechanisms that promote the safe incorporation of novel foods, the spread of information about predators and other dangers, and even facilitating more efficient mate choice.

Observational conditioning

This form of learning occurs when an observer acquires an association between an environmental event and a reinforcer by observing the behaviour of another individual. For example, a rat may learn to approach a lever after observing a demonstrator press it and receive food. Although such conditioning must take the form of higher-order conditioning (because the observer does not directly experience the unconditioned stimulus), there is evidence that higher-order conditioning can occur even in the absence of a demonstrator. For example, pigeons presented with a localised light followed shortly by the presentation of inaccessible grain, spontaneously initiated pecking at the light. The presence

of a demonstrator drawing additional attention to the light (by pecking at it) and to the reinforcer (by eating) may further enhance associative processes without requiring imitative learning see (Zentall 2015). Socially transmitted food preferences (Galef 1988) represent a particularly well-studied case of observational conditioning. The underlying mechanisms include fundamental associative-learning processes (e.g., learned safety or the habituation of neophobia to novel tastes), for which a conspecific may serve as a catalyst. A classic example of observational conditioning is the acquisition of fear of snakes by laboratory-reared monkeys exposed to a wild-born conspecific in the presence of a snake (Mineka and Cook 1988). Presumably, a fearful conspecific serves as the unconditioned stimulus, and the snake serves as the conditioned stimulus. Exposure to either a fearful conspecific or a snake alone is insufficient to produce fear of snakes in the observer.

Goal emulation

Goal emulation is a form of social learning in which an observer understands that an observed action has a particular outcome while recognising that the same goal can be achieved by different behavioural means (Whiten and Ham 1992). Whereas stimulus enhancement alters the salience of specific stimuli in the environment, emulation alters the salience of particular goals (Byrne 2005). In 'emulation', the learner gains information from observing a demonstration, but in achieving the same goal, may use a different method. The study that prompted the recognition of this process involved chimpanzees learning from a trained conspecific how to rake food items into a cage (Tomasello et al. 1987). The data showed that chimpanzees exposed to a skilled demonstrator learned how to use the rake, unlike controls, who were unsuccessful despite manipulating the tool just as often. However, the animals did not copy the precise strategy employed by the trained conspecifics. Instead, the observers learned functional properties ('affordances') of the tool from the demonstration. The concept of emulation learning (Call and Tomasello 1994) has since been broadened to encompass observational learning about the properties of objects and the potential relationships between them. Emulation can also account for findings of observational learning that were earlier interpreted as imitation (Tennie et al. 2006).

Ecological aspects of social learning

The opportunity to exchange information among individuals is one of the principal benefits of group living. Species differ in their abilities to use socially acquired information, particularly their capacity through traditions. Members of social groups often monitor the behaviour of conspecifics to gain information about the location of foraging sites or the approach of predators. By exploiting social cues inadvertently provided by individuals engaged in efficient performance (*inadvertent social information*, ISI), animals can also use *public information* (PI), which provides a critical source of information for assessing resource quality by monitoring the performance of others (Danchin et al. 2004; Valone 1989). In many cases, the only socially acquired information available to group-living animals comes from the behavioural actions of others, which reveal their decisions rather than the initial stimuli on which those decisions are based. Consequently, individuals must choose between using socially generated cues or relying on a personally acquired information derived directly from the environment. Social and personal information are not weighted equally; animals switch between these sources according to their relative reliability and the costs associated with obtaining them (Taborsky and Oliveira 2012).

The role of social learning in foraging

The idea that animals may observe others to gather information about resource quality arose primarily in foraging contexts. Animals can use socially gained cues in the context of searching patchy distributed food or making decisions about food availability and appropriateness (reviews in: (Danchin et al. 2004; Frith and Frith 2012; Thornton and Clutton-Brock 2011). In experiments on foraging decisions of guppies, (Kendal et al. 2004) provided the first experimental evidence for the role of social conformity—in its simplest form, 'follow the majority'—in foraging when personal and social information conflict. Their findings suggest that conformity can promote social learning in naïve individuals. In contrast, prior experience may buffer individuals against conformity, as long as the costs of relying on that experience remain small. Experiments with nine-spined sticklebacks provided empirical support for using PI in foraging (Kendal et al. 2009). The propensity to increase food consumption in the presence of co-eaters has traditionally been attributed to social facilitation review in (Kelly et al. 2020).

It is worth noting that social sampling information can be challenging to use and requires a more nuanced assessment of its costs. (Rieucau and Giraldeau 2011) addressed the possibility that only a fraction of group members provides social information at any given time. Their results suggest that animals are more selective in their use of social information than previously assumed, challenging the traditional view that all group members simultaneously search for resources while monitoring the success of others. Nevertheless, few studies have examined whether apparently

high-quality social information, when combined with reliable but contradictory asocial information, can induce individuals to disregard their own asocial information as predicted by the theory of informational cascades, thereby leading to potentially suboptimal decisions.

Mate-choice copying

Mate choice copying occurs when the probability of an individual selecting another as a sexual partner increases because a conspecific of the same sex has chosen the same partner (Gibson and Höglund 1992). The extent to which social information influences mate choice remains one of the most intriguing questions in behavioural ecology reviews by (Galef 2004; Ryabko and Reznikova 2015; Jones and DuVal 2019). Mate-choice copying was originally proposed as an explanation for the marked skew in male mating success observed in many lekking species. Manipulation experiments with guppies suggested that females follow a simple rule: 'If this male is good enough for another female, he is good enough for me.' Thus, females use the presence of another female near a male as an indication of his quality. However, females also evaluate the male's own characteristics. In guppies, tail colouration is particularly important. When males differ only slightly in this trait, females prefer the more popular male; however, if a male has a pale-coloured tail, he has no chance of being selected by a female (Dugatkin and Godin 1993). (Galef and White 1998) devised an elegant experiment with Japanese quail (*Coturnix japonica*), in which they artificially introduced a novel male trait—a white hat. Females that observed successful matings involving these artificially ornamented males subsequently preferred males wearing similar white hats.

According to (Ryabko et al. 2023), mate choice may be one of the most cognitively demanding problems an animal faces. This is because the task indirectly requires predicting what mates are going to be attractive in the next generations (a variable that itself may depend on the environment)—and doing so at least as well as the competing members of the population. As in food-choice decisions, informational cascades based on reliable information about mate quality may facilitate the spread of socially acquired mate preferences throughout a population of potential copiers review by (Varela et al. 2018).

Socially transmitted information about danger

Acquiring information about dangers, such as predators, through social cues can substantially decrease the risk of mortality for group-living animals (Brown and Laland 2003; Caro 2005). The general tendency to copy the flight responses of an entire group (flock, herd, or shoal) is called *social contagion*. A panic reaction by a single individual can trigger similar responses in other group members. Individuals react to the flight responses of their neighbours rather than directly to the approaching predator itself. Synchronous predator responses are cooperative in some species. Fish schools, which are thought to be primarily an antipredator adaptation, provide a good example of collective escape behaviour. Schools of sand eels can execute diverse, coordinated escape manoeuvres, such as splitting, joining, or forming an hourglass shape. In herring, the type of escape formation depends on the approach angle of the threat reviewed in (Evans et al. 2019). (Doran et al. 2022) conducted a field study investigating the antipredator benefits of waves produced by fish at the water surface when they collectively dive down in response to attacks by avian predators. Fish engaged in surface waves that were highly conspicuous, repetitive, and rhythmic, involving many thousands of individuals for up to 2 min. Experimentally induced fish waves doubled the time birds waited before launching their next attack, substantially reducing the frequency of attacks.

Nevertheless, we know little about collective information processing in animal groups. For example, many groups appear to show increased sensitivity in the presence of a perceived threat, as evidenced by the increased frequency and magnitude of repeated cascading waves of behavioural change often observed in fish schools and bird flocks. However, the mechanisms underlying these context-dependent changes in collective sensitivity remain poorly understood. (Sosna et al. 2019) addressed this question using schooling fish as a model system. The authors found that even though perceived risk increases the probability that individuals will initiate an alarm, the context-dependent change in collective sensitivity predominantly results not from changes in how individuals respond to social cues, but from changes in group spatial organisation and, consequently, in the topology of the interaction network.

In addition to rapid fear learning in response to innate fear-relevant stimuli, *social fear learning* (SFL) has been documented across a wide variety of species, including birds, rodents, ungulates, cats, dogs, and primates reviews in (Debiec and Olsson 2017; Eilam 2005). A recent field experiment investigated how juvenile vervet monkeys rely on others when responding to danger (Mohr et al. 2023). Primate alarm calls are primarily hardwired, but individuals must adapt their calling behaviour according to the situation. Such learning necessitates recognising locally relevant dangers and may occur through either personal experience or the observation of conspecifics. The authors exposed juvenile vervet monkeys to unfamiliar raptor models in the presence of audiences that differed in experience and reliability. Juveniles remained silent when accompanied by

vigilant mothers, but gave alarm calls when their mothers ignored the predator. In contrast, juveniles remained quiet when their siblings ignored the predator, but alarm-called when siblings were vigilant. Despite the small sample size, the study suggests that juvenile vervet monkeys, confronted with unfamiliar and potentially dangerous raptors, rely on the behaviour of socially relevant group members to decide whether to alarm call, demonstrating that the identity and reliability of social models may play a crucial role in the ontogeny of primate alarm-call behaviour.

Distribution of novel behaviours within animal communities

This section considers how novel behavioural patterns become established in animal communities across varying levels of social cohesion, from fission–fusion societies—where groups continuously form and split—to highly social and eusocial systems characterised by stable, cooperative group structures reviews by (Couzin 2006; Reznikova 2007). The spread of novel behaviours can be underpinned by different proximate mechanisms, ranging from cultural transmission based on imitation to the sophisticated integration of innate and socially acquired behavioural fragments.

Culture, traditions and innovations

Some researchers distinguish between the concepts of 'traditions' and 'culture' in animal societies. Based on massive field data obtained from chimpanzees (Whiten et al. 1999) and orangutans (van Schaik 2004), (Whiten and van Schaik 2007) defined animal culture as the possession of multiple traditions spanning different domains of behaviour, such as foraging techniques and social customs. More specifically, (Whiten 2021) defines culture as all that is learned from others and is repeatedly transmitted across individuals, forming traditions that can be passed on to successive generations. Based on the *distributional approach to culture*, (Acerbi et al. 2022) proposed identifying a species as 'cultural', examining the distribution of behavioural and/or artefact forms among different groups of the same species, using the so-called method of exclusion. According to this approach, if a behaviour is present in group A, but not in group B (or occurs there only at a very low frequency), and if this pattern is unlikely to be explained by genetic and/or environmental differences, then the behaviour is inferred to be socially transmitted, and the species may therefore be regarded as possessing culture. Cognitive mechanisms underlying complex forms of social learning include the capacity for faithful imitation, which is relatively rare in animals. Human cultural transmission is characterised by the so-called ratchet effect, in which modifications and improvements are retained within a population until further changes ratchet things up again. However, animals possess sufficient long-term cultural fidelity to support at least limited forms of *cumulative cultural evolution*(CCE; (Whiten 2022).

What does it mean to be an animal innovator?

Innovation in animal studies involves the discovery of novel solutions to environmental or social problems. In their pioneering paper on primates' innovating behaviour, (Kummer and Goodall 1985) defined innovation as ''a solution to a novel problem, or a novel solution to an old one; a communication signal not observed in other individuals in the group or the existing signal used for a new purpose; a new ecological discovery such as a food item not previously part of the diet of the group." These authors were the first to propose that innovations could provide a useful measure of cognition in the wild. Animal innovation is highly diverse, and the cognitive flexibility that underpins it appears to depend less on overall brain size than on specialised neural organisation. In particular, corvids and parrots solve many complex cognitive tasks at the same level as primates review by (Güntürkün et al. 2024); the processing capacity of insects' brains enables ants (Reznikova 1982, 2018) and bumblebees (Bridges et al. 2023; Loukola et al. 2017) to demonstrate the cognitive flexibility required for innovation-based social learning.

The phenomenon of innovation provides some of the clearest evidence for striking inter- and intraspecific differences in cognitive performance. The idea that innovative individuals might be 'smarter' than non-innovative ones has received considerable attention in the experimental literature on innovation. A compelling illustration of exceptional individual cognitive performance is provided by Nicolas, a striped field mouse that consistently outperformed all of his cage mates in quantitative discrimination tasks (Reznikova et al. 2019b). In another experiment in which striped field mice were given the task of choosing a smaller (i.e., safe to hunt) number of tasty, but biting, ants, he was the only one to offer a solution that spared him the painful experience. The experimental paradigm exemplifies the tension between aspiration and apprehension. The experimental setup was as follows (Panteleeva et al. 2013). The experimenters recycled transparent plastic water bottles to make tunnels containing different quantities of live ants actively moving inside. The tunnel openings were fitted with elastic lids containing narrow slits that allowed mice, but not ants, to pass through. Mice were tested individually in an arena with two tunnels attached to their sides (Fig. 1). So, mice could enter, kill and eat ants in the tunnel and then

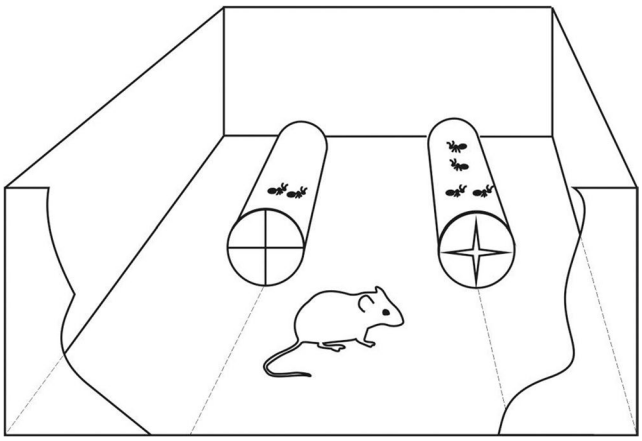

Fig. 1 Experimental setting used: tunnels contain different number of live ants. It is shown in the right tunnel how crosswise slits allow a mouse to pass in and out by applying its own weight. Note that in reality mice had to choose between 5 and 15 ants (and so on, see the text), and never between 2 and 4

leave, whereas ants were locked up. The subject could see and compare the contents of the two tunnels simultaneously, such as 5 vs 15, 10 vs. 30, and so on. The authors relied on the spontaneous hunting behaviour of mice with no prior experience of ant predation, see (Panteleeva et al. 2013) for details. Most mice captured ants in the tunnel containing fewer individuals, killed and consumed the aggressive insects, then quietly left the tunnel and, after a short interval, returned to hunt again. When confronted with a large number of biting ants, however, they typically jumped out of the tunnel and rarely revisited it (Fig. 2). A previously unpublished result presented here concerns Nicolas in particular. Unlike his cage mates, he did not engage with the task as the experimenters had intended. Instead, he devised his own alternative strategy. He first inspected both tunnels, apparently assessing the conditions. He then lay on his side,

Fig. 2 With too many biting ants within a tunnel, striped field mice jumped out of the tunnel containing many ants and rarely revisited it

hooked a claw under the tunnel lid to create a small opening, extracted ants one by one, and consumed them calmly. After finishing with one tunnel, he proceeded to the other, applying the same method consistently across trials (Fig. 3a, b). Taken together with his exceptional performance in a separate series of experiments on numerical discrimination of geometric shapes (Reznikova et al. 2019b), Nicolas may reasonably be regarded as an unusually capable individual. Remarkably, innovative behaviour is not restricted to taxa traditionally regarded as cognitively advanced. For example, (Osuna-Mascaró 2026) recently reported experimental evidence of flexible, egocentric tool use in a pet cow (*Bos taurus*), Veronika, which used a deck brush to scratch itself.

Nevertheless, innovativeness and intelligence are not synonymous. Cognitive sophistication is not necessary for all innovation, and simple processes are likely to be expected and essential, even in human innovation. In particular, neophilia, tolerance to unrewarded acts, motor flexibility, motivational responses or perception can also predict innovativeness (Reader et al. 2016). For instance, in Thornton and Samson's 2012 study, wild meerkats *Suricata suricatta* solved food-extraction tasks in their natural habitat. Most successful individuals solved tasks more than once and learned to inhibit ineffective responses across successive presentations of the same task. However, they did not learn to manipulate functional parts of the apparatus more efficiently, nor did they extract general rules allowing them to solve novel tasks faster. In contrast to recent claims that innovation requires complex cognitive effort, these results indicate that straightforward, well-established learning mechanisms combined with dogged perseverance may suffice to generate solutions to novel problems. Some unexpected findings appear at odds with the well-established view that animal innovators are both faster and more flexible learners. In their experiments with Indian mynas, *Sturnus tristis*, a highly successful worldwide invader, (Griffin et al. 2013) tested the prediction that inter-individual variation in innovation propensity measures behavioural flexibility. Results revealed that mynas that solved an extractive foraging task more quickly learned to discriminate between a cue that predicted food. However, fast innovators were slower to change their behaviour when the significance of the food cues changed. (Griffin et al. 2013) speculate that fast, innovative learners and non-innovative, slow, flexible learners constitute two separate individual strategies underpinned by enhanced neural processing power. These individuals may differ consistently in 'cognitive style', differentially trading off speed against accuracy in cognitive tasks. In particular, innovation and reversal learning would capture two separate dimensions of cognitive ability, each associated with a different constellation of personality traits.

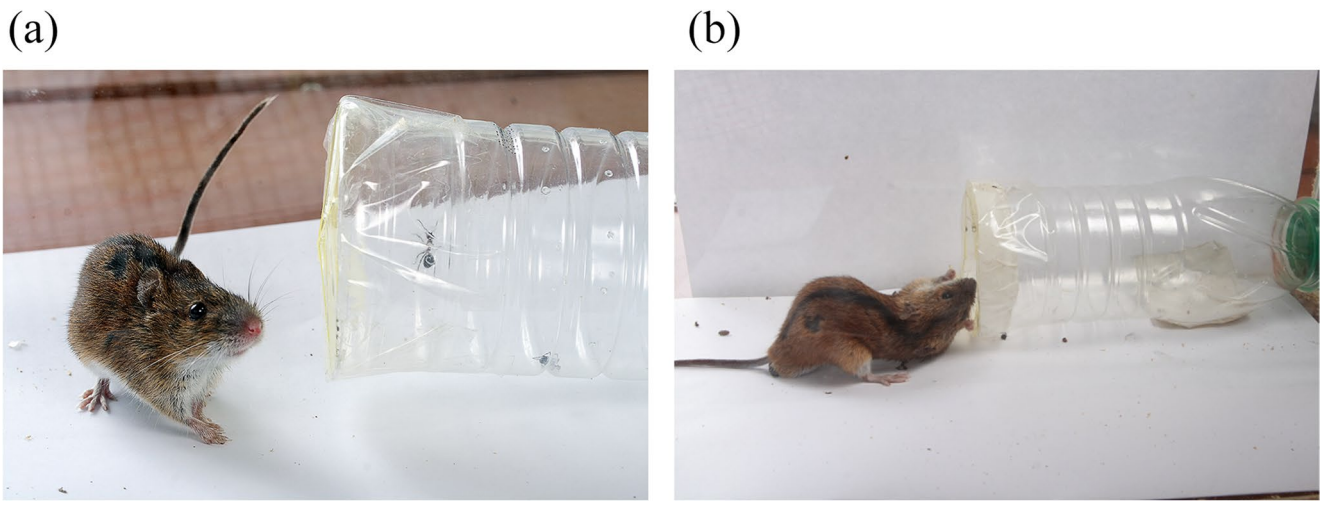

Fig. 3 (**a**) Nicolas, the striped field mouse, examines transparent tunnels with tempting, but dangerous, prey and assesses the situation. (**b**) Nicolas lay down on his side, opened a crack in the tunnel lid, hooking it with one claw, took out the running ants one at a time and ate them calmly

It has become clear that cognitive processes involved in innovation are moderated by general-purpose cognitive mechanisms such as attention and inhibitory control, motivational systems such as perseverance, reactions to novelty (neophilia and neophobia) and play (Tebbich et al. 2016). Long-term field studies by (Perry et al. 2017) on innovation in wild capuchin monkeys (*Cebus capucinus*) in Costa Rica further demonstrate that innovativeness is influenced not only by cognitive abilities but also by age, sociality, and life history. Older, more social monkeys were more likely to invent new forms of social interaction. In contrast, younger monkeys were more likely to innovate in other behavioural domains (foraging, investigative, and self-directed behaviours). Sex and rank had little effect on innovative tendencies.

Summarising these and other studies on inter-relations between innovativeness and intelligence, we can consider 'cognitive style' an essential component of innovative behaviour. In this context, a study on orangutans (van Schaik et al. 2016) is an excellent example bridging another major hypothesis concerning the factors that promote innovation. As the study reports, wild orangutans are not innovative. Young orangutans are highly neophobic, avoid independent exploration and show a preference for social learning. Accordingly, they acquire virtually all their learned skills through socially induced exploration. Adult exploration rates are also low. In striking contrast, zoo-living orangutans actively seek novelty and are highly exploratory and innovative, probably because of positive reinforcement, active encouragement by human role models, increased sociality and an expectation of safety, which strongly reduces exploration costs. However, in nature, most populations have large innovation repertoires because innovations, once made, are retained well through social transmission. Comparisons strongly suggest that significant innovations are made where ecological opportunities are propitious.

The '*necessity drives innovation hypothesis*' has been another significant driving hypothesis for much of the work on innovation in non-human animals (Reader and Laland 2003). Many examples support this hypothesis, including the new observation of Japanese macaques capturing swimming fish and aquatic insects (Takenaka et al. 2022).

The *Cognitive Buffer Hypothesis*(CBH; (Allman et al. 1993) posits that the essential role of the brain is to buffer animals against environmental variation. Support for the CBH comes from research showing that bird species with the highest innovation rates are the likeliest to invade novel or variable environments successfully (Sol et al. 2016). Many studies indicate that individuals primarily innovate if their existing behaviour pattern no longer provides a benefit or when they have no other option. Therefore, the most likely innovators are those for whom the benefits of increased resources are the highest (Brosnan and Hopper 2014). The results obtained on great tits suggest that the processes underlying innovative problem-solving performance are critical in determining foraging efficiency during egg laying, when food is scarcer and when males feed their mates. This idea was supported by the finding that the size of the area around the nest used to search for food (the home range) was half as large for birds who were good problem-solvers compared with poor problem-solvers review in (Morand-Ferron and Quinn 2015). Taken together, these findings suggest that innovation is not a unitary cognitive trait but emerges from interactions among cognitive abilities, motivational dispositions, personality, social learning opportunities, and ecological conditions.

How innovations spread within populations and societies?

Studying social learning using the 'artificial fruit two-action task' experimental paradigm mentioned above, experimenters effectively create animal 'innovators' themselves (Huber 2002). They choose active, exploratory animals with high rank in their groups, train them to solve a problem, and then allow them to transmit the acquired behaviour to the naïve members of their social groups. This method of experimental investigation helps illuminate the process of social learning and explore its underlying mechanisms across various species. However, this approach does not provide insight into how innovations disseminate throughout wild populations. It remains unclear whether such 'innovators' are particularly creative individuals, those exposed to appropriate environmental contingencies, or individuals in a specific motivational state reviews by (Griffin 2016; Reader et al. 2016). Studies on passerine birds have found a correlation between individual-level innovativeness and problem-solving success (Cole and Quinn 2012; Prasher et al. 2019).

An intriguing question is whether a single prodigious individual or several particularly innovative members can initiate and propagate a new tradition within an animal community. To observe how novel behaviours spread through groups, detailed observations of natural populations are essential and should be complemented by experiments conducted in captivity. Occasionally, researchers are fortunate enough to witness the gradual emergence and establishment of a new tradition. A good example is the 'grooming handclasp', a unique grooming posture in which two individuals sit facing one another, simultaneously raise one arm overhead and support each other's forearm by holding hands or wrists to create an 'A-frame' posture. (McGrew and Tutin 1978) first observed the grooming handclasp in a chimpanzee community inhabiting the Mahale Mountains in Tanzania. In contrast, the same pattern was absent in chimpanzees at Gombe Stream, located only 170 km to the north. The authors considered it 'unlikely that the two populations had time to differentiate markedly through genetic drift' (McGrew and Tutin 1978). (de Waal and Seres 1997) tracked how one female chimpanzee propagated this tradition within a captive group of 20 chimpanzees over a period of 5 years. Initially, handclasps were always initiated by the same adult female, Georgia. She began the posture mainly with her adult female kin. In the second year, Georgia initiated the pattern with several partners, mostly immediate adult kin. In later years, these relatives began initiating the pattern at rates similar to or higher than Georgia's. Over the years, the behaviour increased in frequency and duration, spreading to the majority of adults, as well as to a few adolescents and older juveniles. The pattern persisted even after the apparent originator, Georgia, was removed from the colony (but see the next section).

Notably, even when the behaviour appears non-adaptive, as is the case for many of the behavioural traditions observed in non-human primates, including handclasp grooming in chimpanzees (McGrew and Tutin 1978; van Leeuwen 2021) and stone-handling in macaques (Huffman and Hirata 2003; Leca et al. 2012), such traditions may still be adaptive by preserving group cohesion or reinforcing group identity.

Field observations and experiments conducted under natural conditions have demonstrated that the establishment of new feeding techniques and habits in wild populations often occurs through relatively simple forms of social learning. For example, the famous sweet potato washing behaviour of Japanese macaques on Koshima Island is widely distributed within the population and is temporally stable (Kawai 1965; Kawamura 1959). (Nagell et al. 1993) suggested that the spread of this habit is partly due to stimulus enhancement. The attention of a naïve monkey can be drawn to a potato when it sees another monkey pick one up. The naïve monkey may then pick up its own potato and, for social reasons, follow the experienced monkey into the river. At this point, the naïve monkey may accidentally learn the benefits of placing the potato in the water see also (Hirata et al. 2001; Matsuzawa 2015). Reviewing over 60 years of field studies on Koshima monkeys, (Schofield et al. 2018) classified this behavioural tradition as an example of 'cumulative culture', albeit in a relatively simple form.

The extensive spread across the United Kingdom of birds opening milk bottles and drinking the cream from the surface of the milk is often regarded as a classic case of social transmission. However, the original investigators were cautious in their interpretation of the diffusion process (Fisher and Hinde 1949). Based on their experiments with black-capped chickadees, (Sherry and Galef 1984, 1990) suggested social facilitation as the primary mechanism responsible for the origin and spread of milk-bottle opening among birds. Sherry and Galef's results indicated that two simple socially mediated responses – feeding from milk bottles that others had opened and the simple presence of conspecifics near milk bottles – facilitated the acquisition of milk bottle opening by naïve birds. Importantly, such simple forms of social interaction may well underlie many traditional behaviours in animals (Galef 2004).

An interesting example of mechanisms 'simpler than true imitation' underpinning the spread of a novel behavioural tradition (stimulus enhancement, in this case) comes from pinecone-stripping behaviour in black rats. In a series of studies (Zohar and Terkel 1996) see review in (Aplin 2016), researchers demonstrated that a population of black rats exploits human-established pine plantations in Israel using a unique foraging technique: stripping pinecones to extract

and consume the seeds. Juveniles acquire this behaviour by interacting with partially stripped cones left by experienced individuals and, as a result, are able to exploit an otherwise inaccessible food resource. Because pinecone stripping has not been observed in other populations of black rats, it is widely regarded as an innovation, although the original innovation event remains unknown. Further research is needed to determine the evolutionary significance and long-term persistence of this behavioural tradition.

There is a growing body of data on ecological changes resulting from the cultural transmission of behaviour in local populations. In the years following the start of the seminal study on potato washing in macaques, several other newly acquired behaviours (e.g. begging, stone-handling, hot-spring bathing) emerged and spread through different groups of macaques in different regions of Japan following patterns of acquisition dependent mainly on age, sex, and kinship review by (Matsuzawa 2018). Recent years have seen an enormous expansion**o**f research into the cultural diffusion of behavioural tradition within and between generations of animals. There are two main approaches to studying cultural diffusion: (1) identifying and tracing behavioural traits within natural populations, tracing and (2) social diffusion experiments conducted in the laboratory or the field, based on Network-Based Diffusion Analysis (NBDA), in which diffusion follows the lines of social networks, implicating transmission via social learning from close associates review by (Whiten et al. 2016).

In social diffusion experiments, researchers observe how information spreads within a group, sometimes by seeding new behaviour into the population. (Curio et al. 1978) conditioned blackbirds to make alarm calls in response to novel stimuli and demonstrated that such responses could be transmitted through a chain of six successive pairs of birds (A–B, B–C, C–D, and so on). The authors interpreted these results as support for a 'cultural transmission hypothesis'. The following controlled diffusion experiments concerned foraging behaviour in pigeons and rats. (Lefebvre 1986) released pigeons trained to peck through food covers into whole flocks of naïve birds. He showed that the piercing technique was learned rapidly by some observing birds, whereas control birds that had not observed a demonstrator failed to acquire it as readily. In the seeded population, the behaviour continued to spread over subsequent weeks. (Laland and Plotkin 1990) applied the principle of the linear diffusion chain to the transmission of digging up pieces of hidden food through consecutive expert–novice pairings of rats. (Whiten and Mesoudi 2008) considered the open diffusion paradigm the 'gold standard' for demonstrating the spread of behaviours through groups of animals. These experiments have high ecological validity and involve the release of a trained demonstrator into a group of naïve observers, together with the provision of the substrates necessary to perform the target behaviour. (Whiten and Mesoudi 2008) reviewed 33 animal diffusion experiments conducted from 1972 to 2008, encompassing fish, birds, primates, and rodents. In some cases, group members preferentially adopted a relatively rare innovation rather than the one repeatedly demonstrated by the trained demonstrator. The mechanisms responsible for biased transmission, where one cultural trait is more attractive or successful than another, have been the subject of extensive theoretical and conceptual discussion (Mesoudi 2021).

The expressive examples with whales include tracing the diffusion of 'lob-tail feeding' from its first occurrence in humpback whales to its spread along the networks of 653 whales over 27 years, based on over 73,000 observations (Allen et al. 2013). (Foote et al. 2016), based on population genomic data from killer whales, showed the correlation between genetic structure and culturally inherited foraging behaviour. The authors suggested that founding groups may have expanded into new foraging niches through innovation and social learning, and then diverged due to natural selection, assortative mating, and genetic drift. Recently, (Filatova et al. 2024) applied the same technique to reveal a cultural tradition in Baird's beaked whales, whose cultural behaviour has never been studied. They reported that a local population of Baird's beaked whales in the Commander Islands regularly used a shallow area of the shelf slope with depths less than 300 m, which is uncharacteristic for this species. The authors have concluded that knowledge of the shallow regions is transmitted horizontally through social learning as a local cultural tradition. At the other extreme, the invention and diffusion of using moss as a tool for sponging water by wild chimpanzees was tracked across a sequence of just days by a variant of this network-based technique (Hobaiter et al. 2014; Whiten 2014).

There is some evidence of cultural diffusion in insects. (Battesti et al. 2012) demonstrated that previous social interactions influence the choice of oviposition site in *Drosophila*. Naïve observer flies develop a preference for the same egg-laying medium as experienced demonstrator flies conditioned to avoid one of two equally rewarding media. (Danchin et al. 2018) found that fruit flies can transmit mating preferences culturally across generations, potentially fostering persistent traditions in mating preferences. A transmission chain experiment validates a model of the emergence of local traditions, indicating that such social transmission may initially lead to neutral traits becoming adaptive, thereby strongly selecting for copying and conformity. (Alem et al. 2016) demonstrated cultural diffusion in bumblebees through an exceptionally challenging behavioural technique: pulling a string to drag an artificial flower from under a cover before obtaining the reward. Only a

small minority 'innovated' and solved the task spontaneously, but most bees could learn to pull a string when trained stepwise. In addition, naïve bees learnt the task by observing a trained demonstrator from a distance. In cultural diffusion experiments, the skill spread rapidly from a single knowledgeable individual to most of a colony's foragers. The authors observed that there were several sequential sets ('generations') of learners so that previously naïve observers could first acquire the technique by interacting with skilled individuals and, subsequently, themselves become demonstrators for the next 'generation' of learners, so that the longevity of the skill in the population could outlast the lives of informed foragers. This suggests that, so long as animals have a basic toolkit of associative and motor learning processes, the key ingredients for the cultural spread of unusual skills are already in place and do not require sophisticated cognition.

Network-based diffusion analysis (NBDA) allows researchers to test whether information spreads over a social network (Boogert et al. 2014). (Aplin et al. 2015) combined cultural diffusion experiments based on food extractive tasks with NBDA to understand how novel skills diffuse within animal groups. They introduced novel foraging techniques into wild sub-populations of great tits. The authors employed automated tracking to map the diffusion, establishment, and long-term persistence of seeded behaviours. An automatic device allowed each bird to solve a problem associated with getting food in a particular way. The authors further applied the NBDA to examine social factors influencing diffusion dynamics. Birds learned specific solutions from their individual demonstrators, and these solutions spread rapidly throughout the populations, just as the milk bottle-opening innovations did. In a population without the demonstrator, birds used the two available solutions equally; so they did learn how to solve the problem, but without a demonstrator, different individuals solved it using different solutions. This study thus presented convincing experimental evidence that innovative behaviours can spread rapidly from just a few individuals via social learning, and these behaviours can be maintained by social conformity when the majority of individuals use the same behaviour. Following the same procedure as (Aplin et al. 2015), (Chimento et al. 2021) tested the alternative hypotheses by providing great tits that had already learned one solution with a new, more efficient solution, which allowed the birds to open the device faster. The researchers manipulated a fundamental demographic process –*population turnover*– while experimentally controlling it in the lab. The results showed that gradually replacing individuals with naive immigrants significantly increased the probability that a more efficient behaviour would invade the population's cultural repertoire and outcompete an established inefficient behaviour. Fine-scale, automated behavioural tracking revealed that population turnover did not increase innovation rates but did affect adoption rates, as immigrants disproportionately sampled novel, efficient behaviours relative to the available social information. These results provide evidence for cultural group selection sensu (Richerson et al. 2016) for animal efficiency and highlight the mechanism linking population turnover to this process.

Recent study on complex dynamics of social learning in groups of wild Arabian babblers (Aljadeff et al. 2025) suggests that even when there are no major differences in the value of alternative task solutions, naïve group members may play a critical role in shaping group culture when innovations appear. Both naïve birds and demonstrators learn socially from each other, as well as through individual trial-and-error learning, which enables naïve individuals to become demonstrators themselves and influence the pattern of social transmission. This process mostly leads to a homogenous group behaviour, but one that cannot be predicted by the seeded demonstration.

In a changing environment, innovativeness can be an advantageous behavioural adaptation. As (McGrew 1992) noted, many documented cases of innovation within populations are associated with key environmental changes, such as food shortages or forced migrations. Under these conditions, novel behaviours introduced by a few innovators may become more valuable than previously adaptive, species-typical patterns. However, this does not imply that other group members will readily adopt these new behaviours. Innovations must spread in a viscous social environment populated by individuals expressing innate, species-specific behavioural patterns. Typically, animals respond to unusual actions of conspecifics with curiosity, yet they often remain reluctant to adopt them.

Distributed social learning (DSL) as a possible driving mechanism of animal culture

A central challenge in the study of social learning is to understand how socially acquired information interacts with species-specific behavioural programmes. I hypothesise that innate behaviours may sometimes facilitate the social learning process as animals may only need to learn particular components of new behaviours instead of acquiring entirely new behavioural sequences. This is the distributed social learning (DSL) hypothesis, which may contribute to a faster spread and consolidation of cultural traditions in animal communities. Below, I consider examples and potential explanations for how DSL may operate.

Many years after my first reading of Lem's story mentioned in the Introduction, we observed a remarkably similar phenomenon to that described by the fictional myrmecologist (Reznikova and Panteleeva 2001, 2008). Surprisingly, even the proportion of *Myrmica rubra* ants possessing the innate ability of how to catch difficult-to-handle jumping prey closely matched the proportion predicted by the science fiction writer. The hunting pattern of *Myrmica* ants directed at jumping springtails includes selecting a victim, approaching it, and performing the 'tip-and-run attack': the ant attacks the prey, bends the abdomen and head towards the thorax, jumps towards the springtail, and falls abruptly, much like a fox pouncing on a mouse. In the field experiments, we placed containers with live springtails, each near 11 colonies of *M. rubra*. Only the members of colonies inhabiting sites rich in springtails displayed effective hunting (Reznikova and Panteleeva 2001). Developmental experiments (Reznikova and Panteleeva 2005, 2015) showed that naïve ants raised from pupae of hunting families treated springtails peacefully, like their nest-mates (Fig. 4). These results enabled us to reject the hypothesis that the presence of this particular prey species alone acts as a releaser for ant hunting. In another series of experiments, we identified, among hundreds of naïve ants, a small number of individuals that possessed a fully formed complex behavioural pattern ('born hunters'), together with others that exhibited only fragments of this pattern (approximately 3% of colony members). We therefore hypothesised that distributed social learning (DSL) plays an essential role in the spread of new traditions within animal communities: initial performances by a few individuals possessing the complete hunting pattern can propagate this behaviour among individuals that possess only dormant fragments of it (Reznikova and Panteleeva 2008). The spread of these behaviours throughout the population is based on relatively simple forms of social learning, such as social facilitation. To be triggered, carriers of dormant fragments of the relevant hunting pattern must be exposed to performances of this behaviour with sufficient frequency. It is easier to reconstruct a complete behavioural pattern from a dormant fragment than to learn the entire behavioural sequence from scratch. According to the DSL hypothesis, social learning therefore operates by activating genetically based predispositions to acquire specific sequences of behavioural acts.

Fig. 4 Naive ants raised from pupae of hunting families treated potential victims (springtails) peacefully, like their nest-mates

The study of ritual courtship behaviour in *Drosophila* (Pan and Baker 2014) provides additional support for the DSL hypothesis. Pan and Baker demonstrated that males lacking a gene essential for normal mating behaviour were nevertheless able to acquire appropriate courtship behaviours when kept in a group, ultimately achieving successful mating. I conjecture that, in both the ant and *Drosophila* studies, social learning serves as the driving mechanism that activates dormant behavioural fragments, enabling the full expression of innate behavioural programmes.

Recently, (Reznikova et al. 2019a, 2017, 2022) identified advanced hunting patterns in facultatively predatory rodents, which may serve as a useful model for studying the fragmentation of innate behavioural patterns that may underpin DSL. The authors reported skilful predatory attacks on highly mobile insects in 13 herbivorous and granivorous species of voles, mice, hamsters, and gerbils that lack specialised adaptations for predation. They subsequently investigated hunting behaviour in laboratory-reared descendants of wild animals that had never encountered live prey, in order to determine whether hunting behaviour comprises both rigid and flexible components. Using a data-compression approach to the comparative analysis of hunting patterns as biological 'texts', (Levenets et al. 2020) showed that herbivorous and granivorous species retain in their behavioural repertoire—and display in full detail—hunting patterns similar to those of specialised predators such as grasshopper mice. For instance, the Tuvinian silver vole, a herbivorous species from the Baikal Mountains, proved to be among the most proficient hunters in these experiments. Voles exhibited a relatively primitive 'core' hunting pattern, relatively primitive hunting scheme, typically initiating attacks with their teeth. Gerbils, in contrast, efficiently use both paws and teeth to initiate an attack, bringing their hunting behaviour closer to that of specialised rodent predators. (Reznikova et al. 2022) hypothesised that the divergence and specialisation of predatory behaviour in rodents may arise from the natural fragmentation of ancestral hunting patterns, through the loss or recombination of specific behavioural elements. This raises the question of which fragments of the hunting pattern are retained, modified, or lost in different rodent species? The authors found flexible segments within

the key bite–grasp–handle bouts. In gerbils and hamsters, the bite–grasp bout proved to be the most flexible segment of the hunting pattern. If the grasping component is omitted after the bite, the hunting pattern becomes incomplete in hamsters and voles, whereas gerbils can still complete a successful attack. When attacking an insect, gerbils do not need to use their jaws initially; capturing the prey with their forepaws alone is often sufficient. Studies on neurophysiological mechanisms of insect hunting in mice and rats (Comoli et al. 2005; dos Santos et al. 2012; Han et al. 2017) led (Reznikova et al. 2022) to suggest that different genes might regulate the flexible and stable parts of the hunting pattern in rodents. Similar to *Myrmica* ants (Reznikova and Panteleeva 2008), some gerbils are 'born hunters', successfully catching and killing prey on their very first encounter. Others, which initially display incomplete hunting patterns, may eventually acquire the missing behavioural elements, whereas still others never do.

In gerbils, 'seizing with the forepaws' rather than biting constitutes the critical component of the hunting pattern. They can seize an insect and go straight to eating, resembling the predatory strategy of a cat. The natural fragmentation of hunting patterns in rodents may therefore represent a possible evolutionary source of novel behaviours. Preliminary experiments on Mongolian gerbils (Fig. 5) suggest that some individuals can learn the missing fragments of the hunting pattern by observing conspecifics expressing the complete pattern, paralleling the process previously demonstrated in *Myrmica* ants (Reznikova and Panteleeva 2008, 2015). These findings provide preliminary support for the DSL hypothesis in mammals and suggest that distributed social learning may operate across phylogenetically distant taxa.

A useful conceptual bridge is provided by the notion of *exaptation*, originally defined by (Gould and Vrba 1982) as the co-option of traits for functions other than those for which they were originally selected. Developed in an evolutionary context, this concept extends naturally to behaviour: action components that initially serve one functional role may be recruited into new behavioural configurations under altered conditions. The observations cited above—of individuals expressing either complete hunting patterns or only partial fragments—support this view. These fragments are not merely incomplete expressions of a fixed programme; rather, they constitute latent functional units that can be can be recombined into novel, adaptive behavioural sequences.

Fig. 5 The preliminary results obtained on Mongolian gerbils suggest that some individuals can learn the missing fragments of the hunting behaviour by observing the carriers of the complete pattern

At the cognitive level, the framework proposed by (Gabora and Ranjan 2013) provides a plausible mechanism for such recombination. Although the authors do not explicitly frame this process in terms of exaptation, it is functionally equivalent: micro-features of experience are co-opted into new representational structures. Within this perspective, the behavioural fragments observed in ants and rodents described above can be understood as the outward expression of partially activated or recombined internal representations. However, this cognitive mechanism must be situated within an ecological and evolutionary context. (Sol et al. 2016) emphasise that innovation is not uniformly expressed but is shaped by environmental variability, opportunity, and constraint. Periods of ecological change—such as resource scarcity or habitat alteration—promote behavioural flexibility and increase the adaptive value of novel solutions. Viewed together, these ideas suggest that environmental pressures do not create behavioural novelty directly. Instead, they alter the selective conditions under which latent behavioural fragments are more likely to be recombined through exaptive processes, socially transmitted, and ultimately stabilised as behavioural traditions.

I hypothesise that species-specific predispositions may underlie animals' ability to acquire particular behavioural sequences through social learning, and that inherited motor patterns may form the basis of some well-known cases of animal 'cultural transmission.' Let us consider several examples:

(1) Tool manufacture in New Caledonian crows has often been cited as an example of cumulative culture (Hunt and Gray 2003). However, social input may not be necessary for the acquisition of basic tool-use skills. Developmental experiments by (Kenward et al. 2006, 2005) showed that, among four hand-raised chicks, one three-month-old individual ('Corbeau') manufactured a strip tool and used it as a probe on the first day of exposure to pandanus leaves. This case resembles the 'at once and entirely' expression of complex behavioural patterns described above for certain ants and rodents. (Kenward et al. 2005) concluded that basic tool manufacture and use can emerge from a predisposition to

manipulate tool-like materials to obtain otherwise inaccessible food, without requiring social learning. More recent studies point to multiple, mutually compatible mechanisms, including 'mental template matching' (Rutz and Hunt 2020), suggesting a substantial genetic contribution to tool-oriented behaviour in New Caledonian crows, while indicating that the acquisition of basic tool-use skills does not necessarily depend on social information.

(2) The stone-handling tradition in macaques (Leca et al. 2012; Nahallage et al. 2016) provides another example. Recent work has revealed cross-species genetic variation, with particularly high levels of sensorimotor proficiency in Nicobar and Burmese long-tailed macaques (Pal et al. 2018; Pelletier et al. 2017). This suggests that such behaviours may become established and persist preferentially in populations whose members possess the appropriate genetic predispositions for specific forms of sensorimotor activity.

(3) Handclasp grooming (McGrew and Tutin 1978; van Leeuwen 2021) remains one of the most enigmatic social traditions in chimpanzees. Using long-term data from two communities, (van Leeuwen and Hoppitt 2023) demonstrated that this behaviour is influenced by social transmission biases, including majority bias and dominance/prestige bias (Boyd and Richerson 1985; Waring and Wood 2021). Individuals converged on group-specific styles, with older and dominant individuals exerting greater influence, and both vertical and oblique transmission playing a role. These findings indicate that chimpanzee social behaviour is shaped by cultural transmission processes previously thought to be uniquely human. However, the possible contribution of inherited behavioural predispositions has not been excluded. As noted above, (de Waal and Seres 1997) described a female that appeared to express a complete 'at once and entirely' handclasp pattern and subsequently propagated it within a captive group. As in the case of stone-handling in macaques, such behaviours may become established in populations containing individuals with the relevant sensorimotor predispositions.

Taken together, these well-known examples of long-standing 'foci of culture' suggest that the mechanisms underlying the spread of traditions remain insufficiently understood. I hypothesise that new skills spread preferentially in populations containing individuals who carry dormant fragments of the relevant behavioural patterns, and decline where such carriers are absent. For example, in capuchin monkeys, the most efficient technique (the 'canine seam' method) for processing *Sonneratia apetala* fruits was introduced by an immigrant adult male and rapidly adopted by others (Barrett et al. 2017). Although some individuals switched to this technique and many younger individuals attempted it, the behaviour never reached fixation. I suggest that the absence of individuals carrying compatible latent fragments may have contributed to its eventual decline.

The problem of culturally transmitted skills is closely linked to the uneven taxonomic distribution of teaching—the most complex form of social learning. Teaching is widespread among predators, from meerkats to whales and falcons, yet appears limited or absent in chimpanzees, which do not actively facilitate skill acquisition in contexts such as termite fishing or nut cracking. I propose that, in the case of hunting behaviour, parental 'instruction' operates in parallel with the maturation of the offspring's behavioural repertoire, and that one function of teaching may be to activate dormant behavioural fragments. Repeated exposure to skilled conspecifics—through parental guidance in vertebrates or encounters with successful hunters in ants (Reznikova and Panteleeva 2008)—may progressively facilitate the assembly of complete behavioural patterns from dormant fragments.

Taken together, these considerations support a multilevel account of innovation. At the neural level, distributed representations enable the flexible recombination of features. At the behavioural level, this is expressed as the fragmentation and reassembly of action patterns, as described in the DSL framework. At the population level, ecological pressures determine which recombined patterns persist and spread. DSL therefore represents the behavioural mechanism linking these levels, providing a bridge between inherited predispositions, social transmission, and the emergence of animal traditions.

This synthesis generates several testable predictions. First, individuals exhibiting partial or fragmented behavioural repertoires should disproportionately contribute to innovation, acting as sources of novel recombinations. Second, the frequency of such recombination should increase under conditions of environmental instability, consistent with increased reliance on exploratory behaviour. Third, newly established behavioural patterns should retain identifiable structural elements of pre-existing actions, reflecting their exaptive origins. Finally, there may exist an optimal degree of fragmentation: excessive rigidity constrains innovation, whereas excessive fragmentation reduces functional coherence.

Concluding comments

Social learning plays a vital role in tuning behaviour in both group-living species and those that are largely solitary but maintain early-life contact with conspecifics. The readiness to acquire information from others reflects both the

conformity characteristic of animal societies and the flexibility required to cope with environmental change.

The capacity to learn from and about others reduces the costs associated with maintaining a fully pre-specified behavioural repertoire. Except in cases involving teaching, social learning in animals is typically based on the use of public information rather than deliberate information exchange. More complex forms, such as faithful imitation, remain relatively rare.

By providing additional guidance, social learning can enhance fitness and increase behavioural flexibility. Social learning may play a more fundamental role in evolutionary strategies than previously assumed. I highlight the distributed social learning (DSL) hypothesis, according to which socially acquired information activates inherited fragments of behavioural patterns that remain dormant until the appropriate social cues are encountered. Different individuals may carry different dormant fragments of the same behavioural pattern. Activation of these latent fragments may require repeated exposure to the corresponding behaviour expressed by conspecifics carrying the complete target pattern. This process may facilitate the expression of novel behaviours that would otherwise appear too complex to acquire without imitation. Thus, rather than residing entirely within individuals, the potential for behavioural innovation may itself be distributed across populations, where dormant behavioural fragments can be activated, recombined, and propagated through DSL. The diffusion of innovations may therefore rely on relatively simple mechanisms, such as stimulus enhancement, acting upon a population-wide substrate of latent, recombinable behavioural components.

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