Understanding the multiple factors governing social learning and the diffusion of innovations

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What animals learn from social interactions with others can profoundly shape their behaviour across a range of ecologically relevant contexts. In recent years, there has been a call for better efforts to identify social learning in wild animals, followed by a surge in observational and experimental studies. Here, I review the range of contexts in which social learning has been documented in wild animals, and argue that that the use of social learning is restricted by its adaptive utility; including when there is opportunity for social interactions during sensitive developmental periods, when personal information is hard or risky to obtain, and when social information can outperform asocial learning. I conclude by highlighting the further potential for social learning to act as a mechanism by which populations can exhibit behavioural responses to changing environments, via the diffusion of innovations.

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Current Opinion in Behavioral Sciences 2016, 12:59-65
This review comes from a themed issue on Behavioral ecology
Edited by Andrew Sih and Alex Kacelnik
For a complete overview see the Issue and the Editorial
Available online 24th September 2016
http://dx.doi.org/10.1016/j.cobeha.2016.09.003
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Introduction
In many species, learning is a vital form of behavioural plasticity that lets individuals fine-tune their response to local environmental conditions [1–3]. In social animals, social learning in particular can provide a valuable source of adaptive information, allowing individuals to exploit the previous experience of others [3]. The process by which animals acquire new behaviour, information, skills and techniques from the observation of others [4] has been most intensively studied by research directed towards two broad goals. First, by comparative psychologists seeking to understand species differences in the capacity to socially learn and the psychological mechanisms underpinning learning; and second, by evolutionary anthropologists interested in explaining the evolution of complex culture in humans. However there is a growing recognition that social learning also plays a significant role in the behavioural ecology of many animals [5–8].

Here, I focus on two emerging themes from this literature. First, I review studies implicating social learning in the development and expression of behaviour across a range of ecological contexts. Although widespread, the use of social learning is not ubiquitous, and I use these examples to explore what social and ecological variables predict its occurrence. Second, I highlight the potential for social learning to act as a mechanism by which populations can respond to changing environments, via the diffusion of innovations [9]. We still have little understanding of when innovations are likely to spread and establish in populations, and I conclude by arguing that we need to develop a better integrative framework to understand the social dynamics underlying these processes.

The ecological significance of social learning
Social learning has now been implicated in the expression of behaviour across a wide range of taxa, from cetaceans [10] and fish [11] to insects [12,13]. It has further been documented across a range of ecologically relevant contexts, including courtship and mate choice [14], vocal communication [15], predator [16**] and brood parasite avoidance [17], movement [18**], settlement decisions [19], migration [20**], tool use [21,22], and foraging [6]. When socially learned information is shared by members of a community to form group-typical behaviours that persist over time [23], it can be further considered a culture or social tradition. Cultural behaviour has been long studied in primates [22,24**,25], but potential examples also include other mammals [10,26,27], birds [28**,29,30] and fish [31]. However perhaps the best studied non-human example occurs in passerine bird song: while bird song involves both learnt and innate components, many species can be considered social learners of song, usually via transmission from father to offspring [14,32,33]. This results in regional dialects, with different populations developing distinct song characteristics over multiple generations [34–36], and with vocal similarity between populations dependent on connectivity [37].

Yet there are many other cases where social learning does not appear to be involved in shaping species’ behavioural repertoire. These patterns can vary even between closely related species [5,38] and across different ecological contexts in the same species [19,39]; for example the importance of social learning in song acquisition varies considerably across bird taxa [40]. So how can we explain...
this variation? Cognitive constraints seem unlikely — under laboratory conditions, most species exhibit the capacity for some form of social learning. This even appears to be the case for those species that are largely solitary in the wild, for example in the red-footed tortoise (Geochelone carbonaria) [41], and has led some authors to argue that social learning relies on generic psychological processes, present in any species capable of learning [42,43,44**]. Instead, evolutionary theory suggests that there could be trade-offs to the use of social learning, restricting its adaptive utility to specific circumstances [45,46]. The variation within and between species in the use of social learning therefore give clues as to when we might expect selection for its use.

First and foremost, the transmission of information takes place in a social context [47–49]: species or individuals with limited opportunity for interaction will thus also show more limited social learning [50]. For example, migration routes in species where there is limited opportunities for learning on-route appear to be initially determined with genetically coded directional information and then modified by experience, for example, in cuckoos and some songbirds [51]. This contrasts with taxa that migrate socially, such as cranes [20**], waterfowl [52] and cetaceans [53], where specific migration routes can be maintained as social traditions over many generations. It seems likely that social learning would be further enhanced in species where these social interactions are with kin [54], and where juveniles are social during sensitive development periods (whether with kin or others). This is illustrated by cooperatively breeding meerkats (Suricata suricatta), where young learn a whole suite of behaviours from adults during a period of juvenile dependency [54–56]. Finally, within species, individuals can also differ in their opportunities for social learning depending on their social network structure [48,57,58]. There are few empirical examples, but two occur in great tits (Parus major) and chacma baboons (Papio ursinus) where individuals with more central network positions enjoy better access to information about new food sites [59,60**].

Second, models for the evolution of learning have proposed that agents should use social learning when behaviour needs to be plastic to fluctuations in the temporal or spatial environments [61–63], and when personal information is relatively hard to obtain [4,45]. These predictions are also increasingly supported by empirical evidence [64], with one example coming from interactions between two sympatric species: pied flycatchers (Ficedula albicollis) and great tits (Parus major). Pied flycatchers returning from migration use social information from resident great tits when selecting nest sites. A series of experiments have demonstrated that flycatchers copy the preference of tits for such arbitrary features as symbols on nest-boxes [19], and preferentially copy individuals with larger clutches [65]. Late arriving birds used more social information, likely because they have less opportunity for gathering personal information [19]. This contrasts with resident tits, who use little social information in their nest site choice [66], but will show much more extensive social learning than flycatchers in other ecological contexts; including mate choice, song learning and foraging behaviour [5,6,38,39,67] (see Box 1). Social learning in great tits may be particularly facilitated by their winter social ecology (as discussed above), as juveniles can acquire a range of behaviours when flocking with adults [28**].

Evidence from empirical studies is also consistent with the hypothesis that social learning will evolve when obtaining personal information is risky or costly [68,69]. For example, animals often use social learning to avoid potentially poisonous foods: in vervet monkeys, learnt avoidance of a particular food type will persist as a local tradition over multiple generations [24**], while in rats, pups acquire their mother’s learnt food preferences directly from her milk [70]. Interestingly, there is less evidence for an ecologically significant role of social learning in predator avoidance, where genetically fixed fear responses seem predominant [54]. However social learning may still act to refine pre-existing dispositions through learning of new alarm calls [16**] or predators [71]; one notable example occurs in American crows where social learning spread knowledge of a particular ‘dangerous’ masked person over geographic space and across generations [72].

Third, the use of social learning gives the opportunity to access collective information, and its use may therefore be favoured under circumstances where such collective sensing will significantly improve or outperform personal information [16**,61]. For example, in the superb fairy-wren (Malurus cyaneus) naïve individuals are initially unresponsive to cuckoo models, but will alarm-call and mob a cuckoo after observing experienced group-mates doing so [73]. This recognition mechanism has population-level outcomes, as sub-populations of fairy-wrens that have not been parasitized for several generations stop responding to cuckoos [74]. Similarly, reed warblers (Acrocephalus scirpaceus) will up-regulate their behavioural response to cuckoos after observing a mobbing neighbour [17,75]. Behavioural responses to cuckoos can be costly if individuals are over-ready to reject nests, eggs or chicks [17], and using social learning may thus allow a better collective assessment of the local level of threat.

Ultimately, such socially learned behaviour can be transmitted across generations, as cultural ‘inheritance’ or ‘memory’ [76], even potentially forming a second inheritance system to genetic evolution [76,77]. Perhaps the best illustration of cultural inheritance comes from studies in primates, where populations of chimpanzees, orangutans and capuchin monkeys differ in a suite of
behaviours, including in tool-use [22, 25]. Recent archaeological evidence suggests that these differences group-typical behaviours may be long-lasting [78**]. However patterns of migration and movement also provide intriguing examples of how ecologically relevant information can be shaped through across-generation transmission of information. For example, in painted turtles (Chrysemys picta), individuals follow precise routes between water sources [18**], and juveniles learn routes by following the paths of older turtles. As individuals appear to be unable to locate these vital water sources by exploration alone, specific routes become local traditions. Yet cultural preferences can also be relatively arbitrary, with social learning serving to facilitate group activities [79**]. This was most clearly demonstrated in a study of blue-headed wrasse (Thalassoma bifasciatum), where local populations used specific mating-sites that were stable over time. When populations were translocated between reefs, individuals established new mating sites that were used over subsequent generations, demonstrating that specific mating sites were culturally inherited [31]. It seems possible that many specific movement pathways or migratory routes could be refined and shaped over generations of use, however more research is needed to fully understand this process [77].

**The diffusion of innovations**

In contrast to the stabilizing effect of inter-generational traditions, social learning can act as an agent of change when the behaviour transmitted is an innovation [9]. The social transmission of innovations can enable populations to exhibit rapid behavioural responses to new opportunities or novel challenges; it may thus be a vital mechanism by which animal populations adapt to human-induced environmental change [80]. The diffusion of innovations can also potentially lead to population-level niche shifts, ultimately with evolutionary consequences [81, 82**]. While, as yet, no study has convincingly described this

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**Box 1 Cross-fostering experiments in great and blue tits (Parus major and Cyanistes caeruleus)**

A long-term study cross-fostering nestling great tits and blue tits has shown that the development of a variety of behaviours are affected by species-imprinting in the nest. These include mate choice [38], song (Figure 1b) [67], and foraging behaviour (Figure 1c) [5, 6]. Cross-fostering has a lasting effect on behaviour, and behaviours could be potentially transmitted to following generations, for example as cross-fostered individuals deliver differently sized food items to their own young (Figure 1d).

**Figure 1**

(a) Photograph showing mixed brood of great tits and a blue tit. (b) Graph adapted from Johannessen et al. [87] comparing example sonograms of control song (i,iii) to the song of cross-fostered birds (ii,iv). (c) Graph adapted from Slagsvold and Wiebe [6] comparing the foraging height of juveniles (open bars) and adults (filled bars) in August–September after differ rearing conditions. (d) Graph adapted from Slagsvold and Wiebe [6] comparing prey volume relative to body size that were fed to chicks by birds that were previously themselves cross-fostered (filled bars) or not (open bars).
pathway from innovation and social transmission to population-level niche shift (Box 2), several have partially either observed the process in wild populations or replicated it in cultural diffusion experiments [83, 84**,**85**,86].

Perhaps the most famous observation of an apparent spread of innovation was in parids (Parus major and Cyanistes caeruleus), piercing the foil caps of milk bottles to eat cream [29, 87] (Box 2). This behaviour first observed in southwest England in 1921, and spread over much of the country in the following 26 years of observation, before disappearing when changes in milk-bottle design made the resource inaccessible. Yet little is known of the exact social dynamics underlying this particular event, or what the evolutionary or ecological consequences might have been if the behaviour had continued [88]. Diffusion dynamics are better understood for the spread of a new ‘lob-tail’ feeding technique that has been observed over the last 27 years in a population of in humpback whales (Megaptera novaeangliae). Here, known social networks were used with network-based diffusion analysis [89] to infer rates of social transmission [90**], with estimates that social learning increased acquisition rates from 2.7 to 32 times over asocial learning [90**]. Again, the initial innovation event was unknown; as is what long-term effect this new foraging technique may have on population dynamics.

The best examples of a long-term evolutionary or ecological change resulting from the cultural transmission of behaviour may be in black rats (Rattus rattus) [91] and killer whales (Orcinus Orca) [82**]. In a series of studies [91–93], researchers have shown that a population of black rats exploits human-established pine plantations in Israel using a unique foraging behaviour: pinecone stripping. Rats learn to strip and eat pinecones by interaction with the partially eaten food of knowledgeable individuals, and as a consequence have colonized an otherwise uninhabitable new habitat [93]. As this behaviour is not observed in other populations of black rats, it is assumed to be an innovation, although the initial event is unknown. More work is also needed to elucidate what evolutionary implications this novel behaviour may have. This aspect is better explored in an exciting recent study in killer whales. Here, population genomic data has been used to show that genetic structuring is correlated with cultural-inherited group differences in foraging behaviour. While the evidence is indirect, it suggests that genetically distinct groups may show altered natural selection regimes associated with a historic colonization of a novel niche, with colonization facilitated by behavioural flexibility and social learning [82**].

Yet despite these observed examples of how the social learning of innovations can lead to important changes in foraging behaviour, and its extensive study in other fields (e.g. in social science [94]); there is as yet no predictive framework for when would expect a novel innovation to successfully spread across animal populations. Cultural diffusion experiments (reviewed in [83, 84**]) give some clues, as do studies on the factors determining species and individual-differences in innovativeness [9]. For example, a series of experiments in great tits have demonstrated that: (1) juveniles and less competitive individuals are most likely to innovate solution to new foraging problems [95, 96]; (2) one or two initial trained ‘innovators’ are sufficient for information to spread rapidly through social network ties and establish at the sub-population level [28**], with juveniles learning faster than adults [28**,97], and that; (3) once novel innovations are established they are retained with high fidelity over the life time of individuals and transmitted across generations via oblique transmission [28**]. The rapid transmission of information may thus be restricted by age-dependent learning, but be facilitated by the fission-fusion flocking in this species [98]. Other hypothesized factors influencing the social transmission of innovations are detailed in Box 2 [99**].

**Conclusions**

What animals learn from interaction with others can profoundly shape their behaviour across a range of ecologically significant contexts. This requires a rethinking of traditional approaches to behavioural ecology, with even behaviours once thought to be entirely genetically fixed (e.g. nest building) now argued to contain a learnt component [100]. The use of social learning does not appear to be taxonomically restricted, nor restricted to the kind of long-lived species with extended parental care that we may have traditionally associated with such learning (e.g. primates). Rather its use is restricted by its adaptive utility, including when there is opportunity for social interactions during sensitive developmental periods, when personal information is hard or risky to obtain, and when social information can outperform asocial learning.

In addition to this role in the development of behaviour, social learning can facilitate the spread of innovations,
and thus is a potentially important source of adaptive plasticity for species invading new environments or confronting changed ones. The multiple factors constraining the process by which innovations transmit through populations have been understudied in animals, despite a long history of research in humans [94]. Cultural diffusion experiments have been valuable in identifying that social learning can act to transmit innovations through social network ties [84**]. Future work needs to build on this experimental foundation by moving outside the laboratory and refocusing on the interplay between social dynamics, cognition and ecology. We can then begin to develop an integrative framework to understand when and how innovations will arise, spread and establish in animal societies.

**Conflict of interest**
Nothing declared.

**Acknowledgements**
L.M.A was supported by a grant from the BBSRC (P.I. Prof. Ben Sheldon; BB/L006081/1), and by a Junior Research Fellowship at St John’s College, University of Oxford. Thank you to Prof. Louis Lefebvre for discussions, to Dr. Damien Farine for comments on the manuscript, and to Friederike Hillemann for use of her photograph in the first figure.

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