A Second Inheritance System: The Extension of Biology through Culture

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A Second Inheritance System:
The Extension of Biology through Culture

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Abstract

By the mid-twentieth century (thus following the ‘Modern Synthesis’ in evolutionary biology), the behavioural sciences offered only the sketchy beginnings of a scientific literature documenting evidence for cultural inheritance in animals – the transmission of traditional behaviours via learning from others (social learning). By contrast, recent decades have seen a massive growth in the documentation of such cultural phenomena, driven by long-term field studies and complementary laboratory experiments. Here I review the burgeoning scope of discoveries in this field, which increasingly suggest that this ‘second inheritance system’, built on the shoulders of the primary genetic inheritance system, occurs widely amongst vertebrates and possibly in invertebrates too. Its novel characteristics suggest significant implications for our understanding of evolutionary biology. I assess the extent to which this second system extends the scope of evolution, both by echoing principal properties of the primary, organic evolutionary system, and going beyond it in significant ways. This is well established in human cultural evolution; here I address animal cultures more generally. The further major, and related, question concerns the extent to which the consequences of widespread animal cultural transmission interact with the primary, genetically based inheritance systems, shaping organic evolution.

1. Introduction

1.1 A second inheritance system

To introduce the concept of a ‘second inheritance system’ [1] discussed in this review, consider the example of chimpanzees (*Pan troglodytes verus*), who across a swathe of far-West Africa use natural hammer materials to crack open a variety of nuts [2,3] (figure 1). Together with the use of other tools to harvest additional resources, this skill provides a sufficient proportion of the nutritional and energy intake during the dry season, when the favoured fruit diet of the apes is depleted, to suggest it plays a crucial adaptive role in the successful occupation of the habitats involved [10,11]. However, the behaviour is not present in the repertoire of chimpanzees across the greater part of their range, which extends to Tanzania and Uganda in the east [5]; nor does it occur even within the range of the *verus* subspecies to the east of the great Sassandra river in Ivory Coast [6], despite studies establishing that appropriate nuts and hammer materials are available there and at other sites where the technique is absent [6,7] (figure 1). Such variation thus appears to defy explanation by either environmental or genetic differences, suggesting instead that the behaviour, once invented, has been inherited not via genetics but instead spread by a second inheritance system: observational learning. This would make nut-cracking a local ‘cultural variant’ [5, 12], or tradition, analogous to regional variations in human percussive technologies.

< insert figure 1 about here >

Convergent evidence is invaluable to test such inferences. These include differences in seasonal preferences for hammer materials documented even between neighbouring chimpanzee communities that are living in similar habitats and subject to much genetic mixing [13,14]. Further support comes from a suite of experimental investigations in both wild and captive communities [8,15]. In one of the latter, East African chimpanzees, who do not naturally crack nuts, were studied in an isolated island sanctuary and either exposed to an expert nut-cracking model or, in a baseline control group, saw no model [8]. Nut-cracking developed in a majority of those who viewed the model but not in the control individuals, and after both groups were exposed to the expert nutcracker, all began to crack nuts, with increasing frequency as their skill grew (figure 1).

In this example of nut-cracking, there are thus multiple convergent sources of evidence assuring the conclusion that social learning underlies the occurrence of the behaviour, such that the regional variations in Africa are fundamentally cultural. It is this social learning that provides chimpanzees with a ‘second inheritance system’ whereby they may benefit from the inventions of rare individuals, that may thus spread across and between communities, a capacity further diffusion experiments with captive apes have confirmed [16, 17]. Archaeological excavation at one nut-cracking site has revealed that such beneficial behaviour has been transmitted for at least 4,300 years [18] (figure 2), making it an evolutionarily significant phenomenon.

< insert figure 2 about here >

I earlier promoted the expression ‘second inheritance system’ to refer to such a process in the context of the issue of *Nature* reporting the chimpanzee genome [1], where the term seemed an obvious counterpoint to what is assumed to be the evolutionarily prior, or ‘primary’ system that relies on genetic inheritance, the ‘secondary system’ being built on the shoulders of that pre-existing primary system. This assumption seems reasonable insofar as, despite increasing demonstrations of the widespread occurrence of social learning in varied animal taxa (reviewed below), the phenomenon remains to be reported in the vast majority of living forms, including funghi, plants and most of the major phyla and classes of animals, both unicellular and multicellular, all of which display dependence on the primary system.

Labelling social learning *the* ‘second’ inheritance system might be questioned in the context of other conceptualisations and discussions of non-genetic forms of inheritance [19-25] including those reviewed in this present themed Issue. For example, individuals inherit environments resulting from the activities of their parents or others (‘ecological inheritance’), and these may be substantial contributions, as in beavers’ dams and lodges, or termite mounds [19,20]. Nevertheless, Odling Smee et al. [20, p. 181] suggest that ecological inheritance “more closely resembles the inheritance of territory or property than it does the inheritance of genes”, the former thus not transmitting information in the same sense that genes do. By contrast social learning does transmit information (as in the case of genes, between generations; but in addition via horizontal transmission within biological generations, discussed further below). In that sense social learning merits being seen as a second, significantly analogous information transmission system. Genetic and cultural transmission are therefore commonly seen as particularly comparable, as in Dawkins' concept of gene-like cultural 'memes' [26,27] as well as other, non-memetic conceptualisations [28,29]. What these systems share is the crucial Darwinian 'algorithm' of replication (of either genes or memes, that have the power to shape behaviour in particular ways), and hence repeated cycles of variation and selection on the resulting consequences, that can produce long term transmission and evolution. This will be discussed further below in section 4. Beaver dams will evolve only if the behaviour required to re-create them is transmitted over generations through information carried in genes or culture, or both. Darwin himself [30] highlighted the similarities between the evolution of living systems and the cultural evolution of phenomena like human languages, each dependent on the inter-generational inheritance of information. We shall return to such comparative issues concerning cultural and other forms of inheritance and evolution in further discussions below.

1.2 The extension of biology through culture

The creation of the modern, neo-Darwinian evolutionary synthesis occurred most potently in the period 1936-1947 [31,32]. As noted above, the parallels between biological/genetic and (*human*) cultural evolution were already well-recognised before this time; however, the notion of culture amongst non-human animals was not yet in the frame. The first stirring of attention to such phenomena began to appear only later, in the 1950s and 1960s, in such reports as the diffusion of milk-bottle opening by tits [33], socially learned dialects in songbirds [34] and the spread of foraging novelties in Japanese macaques [35]. Since then, the evidence for animal social learning and culture has grown exponentially, as long-term field studies (which in primates, for example, were achieved in only the last 50 years or so) matured, and increasingly sophisticated experimental and other methodological approaches developed [36]; such evidence now extends to all major classes of vertebrate and several invertebrate taxa too, overviewed in section 3 below. However, these broad manifestations of a second inheritance system, its evolutionary implications and core terminologies, have remained strikingly absent from the indexes, glossaries and content of many prominent authors' treatises on evolution, several quite recent [32, 37-40]. Where there *is* treatment, it is typically minimal, referring, for example, to a few restricted topics like birdsong and ape tool use [41]. The common exception is *human* culture, which has seemed to be an evident analogue in some respects to bio-genetic evolution [37], picked out by concepts such as memes [26] or that of the last 'major evolutionary transition' [42]. Even proponents of an extended evolutionary theory linking niche construction, biological evolution and culture have often focused treatment of culture on the human variety [19]. A major aim of the present paper is thus to explore how the reams of increasingly pervasive evidence of animal culture may contribute to contemporary extensions of the scope of biology and evolutionary theory.

1.3 Major questions

Set against the background briefly reviewed above, sections 3, 4 and 5 below deal with three major questions. In Section 3 I ask how widespread in the animal kingdom, and thus potentially influential in shaping the nature of evolution, are social learning and culture? The evidence is now sufficiently voluminous that only selected studies can earn mention, but I aim to indicate the nature and variety in the types of evidence now accumulated, and its distribution across major animal taxa. Next, in Section 4, comes a question I believe has not been addressed in any depth to date in the case of non-human animal cultures: the extent to which properties of the second inheritance system reflect those of the primary, genetic system, and the way these different processes shape evolution. We then examine some of the principal ways in which cultural evolution extends biology by introducing new evolutionary phenomena. Section 5 finally explores types of answer to the important question of how the primary and secondary systems may interact [19-23, 25].

2. Definitions

Social learning is essentially learning from others, which provides the foundation of our second inheritance system. More formally it has been defined as 'learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products' [43]. This last phrase acknowledges that individuals may learn from the effects of what others achieve, as when it was shown that birds would learn to open bottle tops from the torn holes that others left behind [44]. Note, however that 'observation' needs to be interpreted broadly to include the auditory as well as the visual channel.

By no means all that is acquired by social learning is further transmitted to others such that a larger result that we may recognize as 'culture' appears. Much that is socially learned, such as which tree is currently in fruit, will be ephemeral rather than giving rise to a tradition. According to one oft-cited if minimal definition, a *tradition* is 'a distinctive behavior patterns shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning' [45 p. xiii].

Culture is more variously defined than tradition. Many authors in the biological sciences treat 'culture' simply as a synonym for 'tradition' as defined above, and for the purposes of this review, that will be adequate. However it is important to recognize that some authors offer additional criteria for referring to culture [46], such as the existence of multiple, diverse traditions that constitute what we call a 'culture' in the human case [47].

In the present article, we are finally concerned with *evolution* – and the second inheritance system invoked by the existence of social learning and traditions arguably does not yet constitute evolution. Although Jablonka and Lamb [23, p. 158] defined cultural evolution as a 'change, in time, in the nature and frequency of socially transmitted preferences, patterns or products in a population', this may not satisfy all readers, who expect 'evolution' to entail some progressive elaboration, perhaps coupled with tree-like branching diversity, corresponding to the richness of evolved and evolving organic nature. Jablonka and Lamb's definition requires only *change* over time. However, it should be remembered that some changes we generally accept as 'evolutionary' involve a reduction in complexity, such as loss of sight in subterranean animals and the loss of limbs in certain reptiles and cetaceans. Standard definitions of evolution include "change in the properties of groups of organisms over the course of generations " [41, p. 2] that often lead "to erratic change and to diversification, rather than progress toward any particular end point" [40, p. 10]. Clearly, human cultures often echo the pervasive cumulative complexity and branching diversification that characterizes organic evolution as a whole, but not always; and in Section 4 we need to address the senses in which non-human animal culture (henceforth 'animal culture') fit and extend the scope of the evolution of forms of life.

3. Animal Cultures

Discoveries about animal social learning, traditions and cultures have accelerated over recent decades, and the present century alone has already spawned a literature far too voluminous to detail here. A recent survey of publications in the field for 2012-2014 alone recorded publications from over 100 research groups working on 66 species, spanning a great variety of mammals, birds, fish and insects both in the field and laboratory [48]. A survey of specifically 'cultural diffusion' animal experiments identified 30 in 2009-2015, compared to 33 for the whole period 1972-2008 reported earlier, and included eight different species of primates, plus other mammals, birds and insects [49].

Accordingly the overview that follows cannot provide a comprehensive account, but rather is designed to illustrate through selected examples (i) the diversity of taxonomic groups implicated; (ii) the diversity of functional contexts involved; and (iii) the range of observational and experimental approaches and kinds of evidence that have contributed. All these converge to underline the pervading role of culture across a broad span of animal life.

Discussion of this growing corpus of findings could be organized in various ways, such as by types of tradition or patterns of cultural transmission. Here I opt instead to focus on selected taxonomic groups, in part because the scope and significance of cultural phenomena appear to vary much in different taxa, as is well illustrated in the contrasts between the first two, primates and cetaceans, that have been the subjects of extensive recent research attention [50, 51].

3.1. Primates

Following a number of field researchers' attempts to chart the growing evidence that chimpanzee behavior varies significantly in different communities, coupled with circumstantial evidence of observational learning, a collaboration of workers from nine field sites achieved a more definitive survey [5]. An initial set of 65 potential cultural variants were consensually defined and were then coded for their prevalence at different sites, allowing 39 to be recognized as putative cultural variants, common in at least one community yet absent in at least one other, and not apparently explicable by genetic or environmental variations. Locally common variants were found to display unique profiles, thus suggested to be ‘cultures’ differentiated by their array of constituent traditions, and exhibiting a rich variety that spans foraging and food processing techniques, tool use, grooming, sexual and other social elements. Many other local behavioural variants have been published since, several reviewed in [52] but not yet systematically collated.

This approach has since been used as a template for similar surveys for other apes, first orangutans [53] and most recently gorillas [54], identifying 24 and 23 cultural variants respectively. One of the sequelae to the orangutan study included additional direct measures of genetic and ecological variations across the sites [55] and found neither of these predicted the distribution of the 24 putative cultural variations. In the New World, spider monkeys have been studied in the same way [56], identifying 22 different traditions. The same concept has been applied to the very specific and apparently functionless behavior of provisioned Japanese macaques’ ‘stone-handling’, identifying 39 variant forms that match the criterion of being customary at some, yet absent at other, locations [57].

Whilst a fruitful, arguably essential, first step in charting the potential cultural repertoire of a species, this ‘exclusion’ method of ruling out genetic and ecological explanations is of course vulnerable to failing to identify such factors, for example where the environmental effects are subtle. However, these exploratory studies have provided the foundations for suites of other approaches that have provided convergent and supportive evidence. These can be illustrated for chimpanzees, the best studied case, in the following: (i) Neighbouring communities in the wild, that experience genetic cross-mixing and live in similar habitats, have also now been shown to differ in both foraging and social behavior patterns [13,14,58]; (ii) Neighbouring communities in the same sanctuary, that appear environmentally and genetically homogenous, have also developed cultural differences in foraging and social behavior [59,60]; (iii) Intragroup spread of recognized innovations has been documented [61,62]; (iv) Intergroup transfer has resulted in the spread of foraging techniques from one community to another [63]; (v) male-female differences in juveniles' attention to maternal techniques predicted later relative competence [64] (moreover, documentation of juvenile orangutans' close 'peering' at complex manipulative techniques has recently been shown to be associated with multiple effects predicted from its hypothesized role in skill learning [65]); finally (vi) 'diffusion experiments' in which alternative techniques to deal with the same foraging problem are seeded in individuals in captive groups have demonstrated both intra-group and inter-group diffusion [16, 17]. Interestingly, when communities that habitually use sticks for foraging and others that do not (yet do make and use leaf-sponges) were presented with the same problem of extracting honey from vertical holes in wood, the first applied sticks but the latter applied only leaf sponges, that were inherently less effective [66], an effect the authors attribute to conservatism in their existing cultural cognition.

In sum, there is weighty convergent evidence from a welcome diversity of methodological approaches for the reality of multiple-tradition cultures in chimpanzees and several other primate genera, inherited through social learning, and affecting many areas of these animals' lives [67].

3.2. Cetaceans

Perhaps surprisingly, given how difficult it can be to observe the behavior of whales and dolphins compared to primates, this second mammalian group has also provided a wealth of evidence for culture that has recently received comprehensive book-length evaluation. Whitehead and Rendell, greatly updating their influential review of 2001, conclude pithily that "culture, we believe, is a major part of what the whales are" [51, p. 17].

One reason that such conclusions can be reached in ocean-based research is that unlike primates such as chimpanzees, cetaceans display complex vocalizations – 'songs' - that can vary much in both space and time. Whales may also undertake very long annual migrations between breeding and feeding grounds, to which they are often very faithful. Both of these phenomena can be well recorded at sea and have provided evidence for cultural transmission. For example, humpback and bowhead whale songs have been documented to change progressively over years, yet at any one time songs are shared across whole populations, implying cultural diffusion of each change [68,69]. Clearly these differences cannot be genetic, and indeed the humpback population-song off Australia has been observed to change so rapidly it has been described as a ‘cultural revolution’ as much as a case of gradual evolution [70]. Most remarkably, such radically new songs have been documented crossing the Pacific Ocean in progressive East-shifting waves over successive years [71] (figure 3).

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Turning to the learning of migratory routes, the young of both humpback and right whales have been observed to follow their mothers from low latitude breeding grounds to distant feeding grounds, sometimes following her back the next year, and continue to adhere to the particular maternal migration routes for the remainder of their lives [72,73]. Analyses of the mitochondrial DNA that passes only through the female line have shown, moreover, that individuals may continue to associate with their maternal kin while following these socially inherited routes [73].

Evidence concerning the social learning of other behavior such as foraging techniques is naturally more elusive in the ocean, but for one behavior, ‘lob-tail feeding’, in which a humpback smacks its tail on the surface, apparently facilitating the compression of a ball of prey fish before cooperative capture, the earliest occurrences were recorded, followed by charting of its spread to hundreds of other whales over a period of 27 years [74]. The diffusion of the technique was shown to spread along social networks, consistent with a process of cultural transmission.

A very extensive range of other evidence ranging across dolphin tool use, putative teaching and cultural co-evolution with human maritime hunters is surveyed in [51]. Potentially the most culturally differentiated behavioural repertoires in cetaceans – and indeed among non-human species at large – are those of killer whales, or orcas. Orcas have evolved into a range of ‘ecotypes’ that are differentiated by a suite of characteristics attributed to cultural transmission, notably foraging strategies, migratory habits and song repertoires. Some populations specialize in hunting seals, others specialize in fish, and there are also significant variants within these two main categories [51, 75]. For obvious reasons cetacean research cannot match the power of experimental studies with primates outlined above, but in the case of orcas we do have recent experimental evidence that they, like dolphins tested before them [76], have an impressive capacity for social learning, extended to learning a 'Simon-says', 'Do-as-I-do' game and imitating bodily actions, even of human trainers [77]. Until humans reached Antarctica, killer whales and sperm whales, the cetaceans that have offered the most evidence to date for cultural repertoires, were the most widespread species on the planet, possibly as a result of their cultural sophistications [51].

Interestingly, these different cultural complexes are often sympatric, with the important implication for their evolutionary biology that migration between them becomes difficult [51, 75]. If you are in a culture characterized by hunting fish schools and a cluster of other migratory and vocal dimensions, it becomes less easy to transfer into a culture that specializes in a set of alternative behaviours, like the techniques needed to catch seals. The possibility is raised that vocal repertoires even function to actively differentiate such population units, a phenomenon familiar as 'symbolic marking' of one's culture in humans [51, 78.] Potential consequences for such major biological matters as speciation are discussed further below in sections 5.3 and 5.4.

3.3. Birds

The two major domains of song and migration available to cetacean researchers also provide avian data on cultural transmission, again differing interestingly from the corpus of primate research. As with cetaceans, the primary evidence for the social learning of migratory routes is circumstantial – the documentation of juveniles initially travelling with parents or other experienced birds on their first migrations, then subsequently remaining faithful to the routes travelled. For example, great bustards were found to travel as families on their initial migration to the wintering grounds, with females subsequently migrating along with other females too, whereas males progressively integrated into male parties and flew with them [79]. The authors interpreted these association patterns and the habitual routes resulting as evidence of the 'social transmission of migratory patterns' [79], paralleling the evidence for cetaceans [51]. Such initial travel of juveniles with experienced others and establishing long term fidelity to the routes flown appear to be not uncommon patterns in migratory birds [79], indicating a potentially very significant realm of cultural transmission insofar as around 40% of the approximately 10,000 species of birds are migratory.

However we know that even isolate juvenile birds of many species show restlessness directed at the normal migratory orientation of their population and thus appears independent of social learning; some, of which young cuckoos are perhaps the most marked example, migrate successfully without any parental guidance. The field would therefore benefit if the circumstantial and correlational data of early co-migration were complemented by experimental manipulations, such as cross-fostering (an approach well suited for animals where clutches of eggs can simply be swapped [80]). In the absence of such studies, we can fortunately turn to successful efforts to imprint young geese, swans and cranes onto micro-lite aircraft, which are subsequently flown to guide them over routes that they have then adopted in later migrations [81] (figure 4). The planes effectively act as surrogate migratory parents, demonstrating cultural transmission of migratory routes [81].

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An allied effect is birds' use of 'public information' on the breeding success of others to select their own future breeding habitat. Transferring flycatcher nestlings between nests enabled researchers to show that initially resident birds were more likely to migrate to other habitats on reduction of either the quantity or quality of chicks they could locally observe, whereas potential immigrants with less access to such information were positively influenced by the local quantity but not quality of chicks [82].

The most substantial and long-standing corpus of research on cultural transmission in birds concerns song-learning [34,83,84]. Laboratory studies have demonstrated that songs are socially learned from existing singers in numerous species of songbirds, so social learning is thought to underlie both regional variations typically referred to as 'dialects' [34, 83], and the ways in which songs may change from year to year whilst being shared within a local population [83,84], echoing this phenomenon in cetaceans, noted earlier in this article. Regional dialects were documented early in birdsong research [34] and have since been demonstrated in numerous species, the most recent book-length collation [83] listing over 84 different studies reporting and analyzing patterns of bird-song dialects. An illustrative example is shown in figure 5a [85] and a case of changes over time in figure 5b [86]. However the species studied to date can stand only as minimal representatives of the approximately 4,000 different species of song-bird that accordingly may also display these kinds of manifestations of cultural transmission. In the reference listing of [83], the term 'cultural evolution' occurs repeatedly. We postpone to section 4 consideration of the justifications that may be required for applying this expression.

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The variations in bird-song resulting from these processes are not thought to enhance dealing with local ecological circumstances, any more than do differences in human languages around the globe, although there is evidence of adaptation in the sound qualities themselves to transmission properties of different habitats [87]. By contrast, cultural transmission of migratory routes appears functional in guiding naïve individuals to critical locations that are often distant and may be inherently difficult to discover by oneself. Other instances of adaptive outcomes delivered through cultural transmission come from a variety of other methodological approaches and behavioural domains. One such approach has been cross-fostering across closely related species, such as great tits and their smaller relatives, blue tits [80]. When birds came to feed their own chicks, individuals that had been reared by the other species tended to reveal the preferences of their foster-parents, with the smaller blue tits offering larger prey than normal and the great tits offering smaller prey. The authors conclude that "the fact that young birds learn from their foster parents, and use this experience later when subsequently feeding their own offspring, suggests that foraging behavior can be culturally transmitted over generations in the wild" (p. 969). Similar effects on sexual imprinting, alarm calls and song have also been reported by this research team [80].

Cultural transmission of foraging techniques has been revealed in a different approach which involved 'seeding' alternative behaviours to extract food from hoppers in different communities of great tits within a marked population of which over 400 individuals participated [88]. The two alternative foraging behaviours initially demonstrated by pairs of trained community members spread differentially and with high fidelity in the respective communities, continuing into the following season and even evidencing the enhanced dispositions to copy others that characterize social conformity.

3.4. Fish

A famous quip in 2003 declared that there was stronger evidence for culture in fish than in primates [89]. The rationale was that it had been possible to translocate not only individuals but whole communities between sites (not feasible with, for example, either chimpanzees or whales), revealing that in French grunts these novices soon followed and adopted existing preferences of resident fish for travel routes between resting and foraging sites [90]. Conversely when bluehead wrasse were translocated only once residents were removed from their habitual mating sites, the incomers established new sites; and they then maintained them over a further 12 years of study [91]. Complementary laboratory studies with guppies were able to further show that naïve fish put with those who already learned to swim one of two alternative routes would first shoal with and then later independently display the preference they socially inherited in this way [92]; moreover repeated additions of naïve fish and removal of experienced ones until all the original models had gone, showed the tradition would be sustained across these simulated generations [93]. This was even the case when fish were adopting the less efficient of two optional routes [93]. In nature, such a maladaptive bias may eventually be overturned, but its existence, alongside other indicators of conformist dispositions even in such experiments of limited duration demonstrates how potent a force social learning can be in animals like these [94].

The greater bulk of such findings in fish appear to be associated with such route following, but there is some, more limited evidence for a role of social learning in anti-predator behaviour, aggressive interactions and mate-choice [95]. Relatively few studies have addressed whether particular behaviour patterns might be socially learned, but there is suggestive experimental evidence that it can play a role in archer fishes' shooting of prey such as insects above the water surface [96]. Perhaps the best evidence of behavioural copying in fish comes from experiments in which models were trained to enter a vertical tube to forage, an unusual behaviour that naïve fish failed to show until they observed the models, when they acquired the technique [97]. Once again, repeated addition of naïve fish and removal of experienced fish successfully simulated intergenerational transmission.

3.5. Insects

There is some scattered evidence for social learning in other invertebrates [98], but for insects the evidence has in recent years become substantial and compelling [99,100]. The celebrated phenomenon of the honey-bee dance is itself a case of social information transfer, although the way in which the information about distant foraging sites is coded in the configuration of the dance means it is more commonly classed as communication, and could arguably be thought of as a form of coded teaching.

More akin to the forms of social learning in other taxa reviewed above is observational learning, where bees have been shown to utilize the public information of which flowers other bees are preferentially feeding on [100,101]. Likewise, fruit flies chose egg-laying sites preferred by a majority of experienced flies they interacted with, even when the interaction itself took place spatially separated from the laying sites and thus likely depended on olfactory cues of the preferred medium [102].

In this latter study, second-order observers who interacted with flies that had been through their first social learning experiences tended to adopt these first-order learner's preferences, thus providing minimal evidence for transmission across cultural 'generations', although the arbitrary preference for one medium over the other soon faded as individual exploration over-rode the socially acquired preferences. A more thorough demonstration of such cultural diffusion, this time in bumble-bees, involved not a preference for one of two arbitrary trained options, but instead the adoption of a quite challenging behavioural technique very rarely achieved by naïve bees presented with the problem [103]. The novel behaviour involved pulling a string to drag an artificial flower from under a cover, thence to drink from it, and this procedure was introduced stepwise to models who when proficient were introduced singly into interactions with a colony of naïve bees, in controlled pair-wise encounters. In contrast to the near-absence of string-pulling in naïve bees, a majority of those to whom observational learning was available went on to master the technique; moreover, acquisition of the technique spread across up to three cultural 'generations' of experienced/naïve pairs, eventually becoming distributed across two thirds of each seeded colony before the experiment was terminated.

A capacity for social learning may thus be widespread in insects and some other invertebrates too; moreover as in this experiment, the potential for cultural diffusion has been demonstrated in at least some insects. What remains unclear is the implications of these laboratory findings for insect life in the wild. In bumble-bees, for example, only queens may survive through a high latitude winter, so any seasonally achieved 'wisdom of the hive' suggested by experiments like that described above [103] will perish. This means the scope for substantial cultural inheritance and evolution in invertebrates remains unclear. It could well exist in colonies with more continuity, such as those of tropical ants and termites with their sometimes gigantic and cumulatively built nests, but this has yet to be subjected to intensive research from this perspective.

4. Culture: Both a second inheritance system and second evolutionary system?

As we have seen above, the evidence for social learning is now both strong and widespread across a range of both vertebrate and invertebrate species. There is also widespread evidence for the existence of abilities to sustain repeated cultural transmission, such as in the bumblebee experiments reviewed immediately above. In short, a vast research effort in the last half century has revealed the operation of this second inheritance system to be a widely pervading phenomenon among animals.

But does this second inheritance system generate a second or further forms of *evolution* also? Not necessarily. What is socially learned may be useful but only temporarily so – such as what is currently a good food patch to exploit [47]. Even where cultural transmission occurs repeatedly so that a tradition is formed, this may have a limited lifetime such that the likelihood of any evolutionary change is accordingly constrained. As discussed above, the scope for cultural evolutionary change may be restricted in this way for insects, by contrast with the 4 evidence of nut-cracking in chimpanzees extending back over several millennia [18].

4.1. Parallels between animal culture and organic evolution

Given such potential for long term cultural evolutionary change, we can make comparisons with a prior analysis of the ways in which *human* culture echoes the core principles of organic evolution as set out by Darwin in the *Origin* [28]. Mesoudi et al. [28] listed these principles as variation, inheritance, competition/selection, adaptation, geographic differentiation, convergent evolution and changes of function. I now consider each of these from the perspective of 'animal culture' – I believe the first time such questions have been explored.

Variation and Inheritance. Inheritance is here a given, instantiated in plentiful evidence of social learning as reviewed above. The element of *variation* in the contents of behaviours that are culturally transmitted has also been extensively documented in realms of behaviour that include local repertoires of bird [83] and cetacean [68] song. However, those involve variation between spatially separate populations. For competitive selection to operate, variants need to compete in the same space, so intra-group variation documented in, for example, styles of chimpanzee termite fishing [64] and vervet monkey food-cleaning techniques [104] would be more relevant, as would adjacent cultural variants like those attributed to killer whales [51, 75]. The interaction of these two factors, variation and cultural inheritance, can give rise to evolution in the limited sense of change over time, via processes of drift created by such factors as imperfect inter-generational copying. Geographic divergence in bird-song dialects, for example, appears to be commonly explicable at least in part to 'mutations' [86] in copying, so that as song repertoires become geographically distant from each other they evolve different forms [83,85].

Competition and Selection. When we add to variation and inheritance the third core feature of the Darwinian process, selection amongst elements that are in some sense in competition with each other, we may get not only evolutionary change but some degree of elaboration of the feature at stake, as we see in the broader evolution of increasingly diverse and often more complex organic life forms. Such processes of selection are predicted to shape the outcomes to be *adaptations* to their respective niches.

However such evolutionary change is often slow and may even include long periods of stasis. Accordingly some of our best documented examples of 'evolution in action' are consequences of short term environmental perturbation by humans, as in the classic text-book case of peppered moths evolving to show dark camouflage during the sooty industrial revolution, then paler morphs again as the environment was cleansed. Perhaps the kind of cultural changes we can be alert for on this count may be particularly likely to arise from human interventions, including experimental ones. For example, Menzel et al. [105] exposed three juvenile chimpanzees to two different objects that the youngsters were disinclined to approach. Then at two month intervals one individual was replaced by a fresh one, so that trios three steps apart had totally different compositions. Nevertheless, habituation rose across generations and eventually stabilized (figure 6). Thus, bolder behavior developed in some juveniles (see discussion of 'guided variation' below), competed with shyness, and was selected for because the objects were not dangerous; these shifts were then inherited via social learning so that the eventual habituated steady state represents a simple case of cultural evolution via variation, competition, selection and (cultural) inheritance. A counterpart was recorded in the wild when two chimpanzees from a community already habituated to human observers migrated to a newly studied community and through these same processes of variation, competition, selection and cultural transmission produced a measurable enhancement in the pace of habituation underway there [106]. Such changes and processes appear to have received little explicit empirical investigation to date [67] but the examples above suggest that both observational and experimental investigation is feasible and now deserves to be pursued more systematically.

< insert figure 6 about here >

Adaptation. These chimpanzee examples exemplify adaptation because the objects and observers were not in fact dangerous, so habituation was beneficial. Three different categories of adaptation facilitated by cultural transmission can be noted, with illustrative examples. First, adaptation may be to the physical environment: for example, long-tailed macaques exploiting coastal shores in Thailand use a variety of stone tools to smash certain shellfish and prise others off rocks at low tide, opening up possibilities in this intertidal niche otherwise inaccessible to them [107]. Such adaptive significance will likely apply for many animals that learn about tool use by observation, but are not, of course, limited only to tool use. Second, sexual selection may mould behaviours that thence come to be adaptations enhancing mating and reproductive success. For example, there is evidence from several species of birds that greater male song repertoires are preferred by females and confer enhanced reproductive success [83]. Third, socially transmitted behaviours may be adaptations to social life. For example, among white-faced capuchins a range of intimate social customs arose and diffused across groups, including acts risky and likely costly to participants, such as plucking hair and placing fingers in the other's nostrils and eye sockets, which were thought to serve a bonding function [108].

Accumulation of modifications. In the human case we are confronted with manifestations of cumulative culture across innumerable aspects of human life, from languages to technologies to institutions, with the cumulation often occurring along with differentiation in different regions [109-111]. This has created cultural evolutionary trees that echo what is familiar in the realm of organic evolution – the 'tree of life'. In the case of animal cultures we see such differentiation in examples like the birdsong dialects discussed above. However as noted above this appears to involve only evolutionary *change*, rather than *cumulation* of the kind that generates increasingly complex or elaborate forms that build on ancestral ones. Indeed, many authors state that cumulative culture is what distinguishes humans from other animals [e.g. 109-111].

Others interpret some of the evidence for animal culture as potentially or actually demonstrating some cumulative build up, even if on a small scale compared to human achievements. For example, Jablonka and colleagues [23, 112] suggest that Japanese macaques' famous sweet potato washing tradition evolved through stages involving shifts from stream to sea, seasoning items in the salt water, swimming and fish-eating: "through the accumulation of social transmitted variations over time, the macaques have acquired a new life style" [112, p. 99]. Many of the tool-sets used by wild chimpanzees may likewise reflect cumulative build-up, such as the making of deep tunnels to subterranean termite nests using stout sticks, followed by fishing the termites out using long stems brought to the site that are first prepared by oral and manual processing to have more efficient brush-tips [113]. To researchers familiar with chimpanzees it seems difficult to imagine that this behavioural complex, applied to the extremely opaque problem of harvesting deeply subterranean prey, has come about other than by step-wise elaboration over long periods. However, in most such cases we cannot check such inferences via the kinds of archaeological or historical records that chart cumulative culture in our own species. An alternative approach is to bring the question into the laboratory and create the conditions for cumulative change, well pioneered in human experiments [114]. This has now begun to be explored in non-human species, particularly in chimpanzees, with evidence to date indicating only minimal foundations of cumulation at best [115-117].

Geographic distributions. Organic evolutionary differentiation, for example between subspecies, tends to be associated with geographic spacing, including differences between islands like those of the Galapagos. So too for human cultures, with variance in aspects of material and linguistic culture correlating with both geographic and genetic separation [118]. Likewise measures of cultural variance and geographic distance were found to covary strongly in gorillas [54] and differences in bird song dialects on 'islands', whether separated by water or other barriers, are well documented [83].

Convergent evolution. Cases of convergent organic evolution are predicted and evidenced where similar combinations of the key Darwinian forces discussed above are at play in geographically dispersed locations. Again, parallels in human culture abound, from important cases like handwriting to more trivial ones like the neotenisation of teddy bears and Mickey Mouse [28]. The use of stones to smash open food items presents a nice primate example, having appeared and spread locally in small populations of chimpanzees in Africa, capuchin monkeys in Brazil and long-tailed macaques in Thailand [119].

Change of function. Changes of function in organic evolution such as the fish swimbladder evolving into lungs are again paralleled by numerous examples in human material culture, so much so that Basalla [120] concluded his extensive survey by suggesting that few major human technologies were originally designed for the function they eventually came to serve. Few cases of animal culture have been tracked for long enough to hope to detect such changes, but the Japanese macaque saga indicates that this can occur, if on a small scale, when cleaning the sweet potatoes gave way to biting and salting them in the sea [112]. Boesch [121] presents evidence that the leaf-clipping display of chimpanzees has evolved to serve different functions such as courtship and play initiation in different regional communities.

4.2 Cultural transmission creates new forms of evolution

Culture extends evolutionary biology not only through these analogies with organic evolution, but also by incorporating additional dimensions of inheritance and evolution. This has been well recognized in the sphere of human culture, elucidated in some detail in the works of Boyd and Richerson [122, 123]. In the present focus on animal culture I discuss two issues they highlighted: the nature of the transmission processes, and the way in which these processes may be fine-tuned by selective information processing,

Forms of inheritance. Analyses of human cultural evolution have noted that in addition to vertical, parent-to-offspring social transmission paralleling genetic transmission, cultural transmission may be horizontal within a generation, or oblique, via non-kin across generations [122,123]. In species where parental care occurs and especially where it is intense or extended, there is plentiful evidence for vertical inheritance, for which the great apes with their long period of mother-infant dependence provide good examples [67]; moreover as in the human case [67], a trend may be common for substantial initial learning from parents, followed by horizontal and oblique learning from a widening array of other conspecifics who may display more varied forms of expertise [65]. Horizontal and oblique transmission are often not distinguished, but plentiful evidence of them is available from diffusion experiments in a wide range of species [49], from primates [16] to birds [88] and bees [103], as well as through non-interventive studies in the wild, such as those described above for whales [74] and apes [62]. These processes can provide much faster dispersion of beneficial innovations than can genetic evolution; the latter study, for example, traced the diffusion of an innovation in tool use in a chimpanzee community across a period of six days [62].

Genetic inheritance occurs in packages transmitted at conception, even though activation may later be contingent on environmental factors; by contrast social learning can operate often with considerable flexibility through the lifetime, and refine adaptation further through individual-level learning processes, sometimes in cycles of social and asocial learning (like practice) [8]. This provides what has been called ‘guided variation’ [122], which unlike random genetic mutation can steer learning to greater adaptation within the lifetime. In turn, such improvements can be inherited through social learning from others, in a Lamarckian-like fashion [23, 112].

Fine-tuning via ‘transmission biases’. Further selective fine-tuning is offered through a variety of ways in which social learning can be sensitive to context, variously called transmission biases [122], directed social learning [124] or social learning strategies [125]. Rendell et al. [126, figure 1] distinguish as many as 23 such potential biases. For space limitations I here illustrate only a handful of examples from five of these, where most empirical evidence exists [36, Table 8.1]. ‘When’ social learning strategies are those conditional on circumstances. A critical illustration of ‘when asocial learning is costly’ is learning about predators from others rather than through risky personal experience, experimental evidence of which ranges from fish [127] to primates [128], and an illustration of ‘when uncertain’ is naïve rats’ but not experienced rats’ disposition to learn diet preferences from others [129]. ‘Who’ strategies represent rules of whom to best learn from. These include conformity or ‘copy the majority’, that takes various forms illustrated by route choice in fish [130], foraging method in birds [88] and apes [131] and diet choice in monkeys [132]. ‘Copy success’ ranges from nest site choice in birds [82] to foraging sites in apes [133]. Finally there are biases in ‘what’ to preferentially learn about, from songbirds learning song from conspecifics rather than heterospecifics [134] to learning about natural predator types rather than random objects in birds [135] and primates [128]. All these biases give the second inheritance system a continuing adaptive finesse beyond that provided by the primary genetically based system.

5. Interplay between cultural and organic evolutionary systems

5.1 Functional traditions may enhance fitness

Many behaviour patterns that are acquired through cultural transmission appear likely to be beneficial to the biological fitness of the animals concerned, which is what shapes evolution. This includes cases of foraging knowledge and skills, predator avoidance, tool use, migratory routes and song. Indeed, in a majority of cases, repeated episodes of cultural transmission are likely to be maintained *because* the outcomes are functionally significant. For example, many forms of tool use in primates permit the exploitation of embedded food sources otherwise unavailable to the tool-users and relevant competitors; there is evidence that without this extension to their niche, chimpanzees would be significantly limited in the marginal habitats they utilize [10]. Taking another example from a very different domain of behaviour, birdsong has been shown to function in both territory defence against competitors, and the attraction of mates; for example, larger song repertoires in great reed warblers can result in higher breeding success, sometimes extending to extra-pair copulations [83]. Where culturally transmitted behaviour makes up a significant proportion of a species' repertoire it may thus provide a critical contribution to an individual's fitness. Of course this is not straightforward to rigorously test, but now begs for more concerted quantitative analysis.

5.2 Sexual selection

In songbirds, there is evidence that aspects of culturally transmitted songs provide an important basis for female selectivity in mate choice, with variables such as song complexity providing honest, difficult to fake information about a male's quality, correlated with such factors as the adequacy of their breeding territory and food supply [83]. Such sexual selection may hence shape not only further cultural evolution in this respect but also associated aspects of organic evolution, such as the enhanced neurogenesis that has been found to be associated with song repertoire size [136] and that may also be correspondingly associated with females' ability to recognize and evaluate such song qualities. Similar phenomena may well be associated with cetacean song, but here there is an unsurprising lack of the kind of experimental finesse that has been possible in the avian studies.

5.3 Behavioural drive, cultural drive and organic evolution

The hypothesis that behavioral innovation may allow animals to invade or construct a new niche-space, that then exerts new selective pressures that further shape future organic evolution, has been explored in varied ways from a theoretical perspective over the last century, from early ideas that became known as the Baldwin Effect, to genetic assimilation and the concept of behavioural drive [47, 137-139]. Empirical evidence for such effects has remained sparse by contrast, but this is arguably unsurprising given the nature of the phenomena, with organic evolutionary consequences slow to emerge compared to the lifetimes of scientists, and evidence of the initial proposed behavioural innovations often simply buried in the past. However empirical investigations exist, a striking one being that first explored by Wilson and colleagues [137,138] in demonstrating an almost perfect correlation of r = 0.97 between relative brain size (i.e. corrected for body size) and the rate of change in measures of organic evolution across taxa ranging from reptiles to mammals (and see [140] for a substantial related avian study).

Where the initial behavioural drive is delivered by the kinds of cultural processes discussed in the present review, the phenomenon can be called ‘cultural drive’ [138] and with a particular focus on human culture has been discussed further under the rubric of ‘cultural niche construction’ [19].

What of the non-human animal case? As a potential case of such cultural drive, Whitehead and Rendell [51] present the case of killer whales ecotypes outlined above. These authors present compelling evidence that these are based on culture and that this has had correlated effects in anatomy, such as in the stronger jaw structures of those populations that focus on the more substantial prey of seals. However, if genetic variations are now responsible for the jaw differences, can we be confident the same is not true of the other, behavioural differences? We know from experimental studies in birds such as the Galapagos woodpecker finches that use twigs to fish for insect prey, social learning is not essential [141], a scenario difficult to experimentally address in killer whales, concerning their predatory expertise. However unlike the case of the finches, experimental evidence of more general bodily imitation has been published for the killer whales [77]. Whitehead and Rendell review a variety of other arguments that in this example we are looking at the primary effects of cultural transmission, and associated organic adaptations.

Another potential effect of cultural transmission occupying a substantial role in a species’ adaptations to its ecological niche is in the organic, notably neuronal, underpinnings of the requisite learning abilities [136]. A ‘Cultural Intelligence Hypothesis’ was initially put forward to explain the marked encephalization of great apes [47, 142], but is equally relevant to other taxa in which culture plays a particularly prominent role, such as cetaceans [51]. Testing this hypothesis is challenging, but there is evidence that Sumatran orangutans, that are more social and apparently culturally rich than their Bornean counterparts, also exhibit the superior asocial learning abilities predicted [143,144], and have brain sizes typically 2-12% larger [144].

Humans likely constitute a special case of such a hypothesis, on the basis that the growing reliance of evolving humans on cultural transmission explains the hyper-development of human cognition, cultural transmission processes and tripling in brain size compared to other apes [110, 145]. There is a large literature on this anthropocentric and often controversial topic [see for example 110, 111, 145-149], but this is principally focused on comparisons of our own species with only our closest ape relatives, whereas the present review aspires to survey a broad range of species, so does not further address the subject here.

5.4 Culturally driven genetic differentiation and speciation

A corollary of scenarios like that of the killer whales outlined above suggests that as such ecotypes diverge culturally, differentiation in population genetics may follow ('culture leads, genes follow') or genes and culture may co-evolve in double helical fashion, driven either by drift or by active selection (as in the case of stronger jaws in seal-hunting killer whales) [51,75]. Effects interpreted in this way are now becoming increasingly common in the cetacean literature [150-151] and a parallel case, supported by modelling, has been made that cultural processes can generate multi-level structured societies of the kind found in sperm whales [152]. Compelling cases of gene-culture co-evolution are increasingly well established in the case of human culture [153,154], but these often rest on firm historical evidence of the critical cultural change, such as in the famous instance of dairy farming and lactose tolerance. Such relatively direct evidence of cultural history is more difficult to obtain in the proposed animal cases, but genomic analyses are becoming increasingly sophisticated in the inferences they can offer about the role of such factors as population bottlenecks, drift and selection, and are producing compelling cases for culture being key in these evolutionary effects [75,150,151].

Related hypotheses and empirical data have been also been developed in the avian birdsong literature [83], with the added bonus of experimental evidence of the role of selection. Thus Grant and Grant [155] showed experimentally that populations of a finch species from different islands in the Galapagos chain responded with significantly different levels of intensity to songs sufficiently different to their own, leading the authors to conclude they are "well advanced along the path of speciation" [155, p. 545], full speciation thus being a logical and plausible ultimate scenario following from such findings. Elsewhere, in discussing the question of how songs and responses to them diverge in such apparently incipient species, these authors discuss five different factors likely involved, an analysis too elaborate to summarise here, but which highlights the scope of the evolutionary processes now being explored [155-156].

To date the study of the effects of culture on genetic and organic differentiation between populations appears limited to ecotypes and songs in cetaceans, and birdsong; it has not been reported in the only other taxon – primates - in which there is sufficient evidence of cultural variance to warrant exploration of this phenomenon, although as in some songbirds [84] there is evidence that in chimpanzees, as seems predictable [118], greater cultural and genetic variance is correlated across greater degrees of geographic separation [157].

6. Summary Conclusions

As reviewed in Section 3 of this article, recent decades have witnessed an accelerated accumulation of evidence of social learning in animals, including both vertebrates and invertebrates (principally insects). The effects of such learning may be transient, but repeated and sustained cultural transmission has also been documented in many vertebrate species, generating long-standing traditions. These cover a diverse range of types of behavior including migration, vocal communication, tool use, and foraging and predator avoidance techniques. Because these involve a (second) form of inheritance, display inter-individual variance and can shape adaptation (often more quickly than can genetic change), they deserved to be integrated into contemporary understanding of the scope of biology and the phenomenon at its core, evolution. Yet classic texts, even quite recent ones, show stark omissions in this regard [30-31,36-39,41].

In section 4 of this article I therefore pursued what I believe is the first exploration in non-human species of the extent to which, for the moment setting aside attention to genetic and organic evolution, animal culture displays key properties of evolutionary systems, as human culture has been amply shown to do. Some empirical evidence of each of eight such properties can be offered, even though these often pale in comparison to what we see in the case of human culture. It is to be hoped this exploration nevertheless focuses some research effort on such matters, and on the ways in which the prevalence of culture introduces new evolutionary characteristics such as horizontal transmission and adaptive transmission biases .

In then further exploring the scope of gene-culture interaction in the animal case, I suggest the most important conclusion is that cultural processes may shape adaptation in significant ways, thereby changing the dynamics of evolution at a broader level. In some cases this may shape genetic and organic differentiation between culturally variant populations, perhaps even leading to speciation. Empirical investigation of such processes is inherently difficult because of such factors as the long time scales that may be involved, but with the accumulated discoveries of animal culture now building through decades of research, this exciting prospect begs further attention.

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Figure Captions

Figure 1. Evidence for nut-cracking as a cultural variant in chimpanzees. Nut-cracking using natural hammer materials is spread across a large area of West Africa white stars) yet absent elsewhere (dark stars) [3-5], despite independent studies confirming availability of raw materials [6,7]. Experiments with East African chimpanzees show they can acquire nut-cracking through observational learning [8,9]; see text for details.

Figure 2. Nut-cracking continuity confirmed by archaeology. Christophe Boesch holds material evidence of nut-cracking excavated to a time-depth of at least 4,300 years ago, corresponding to that currently produced by chimpanzees on the surface here in the Taï Forest [18]. Photo credit: Julio Mercader.

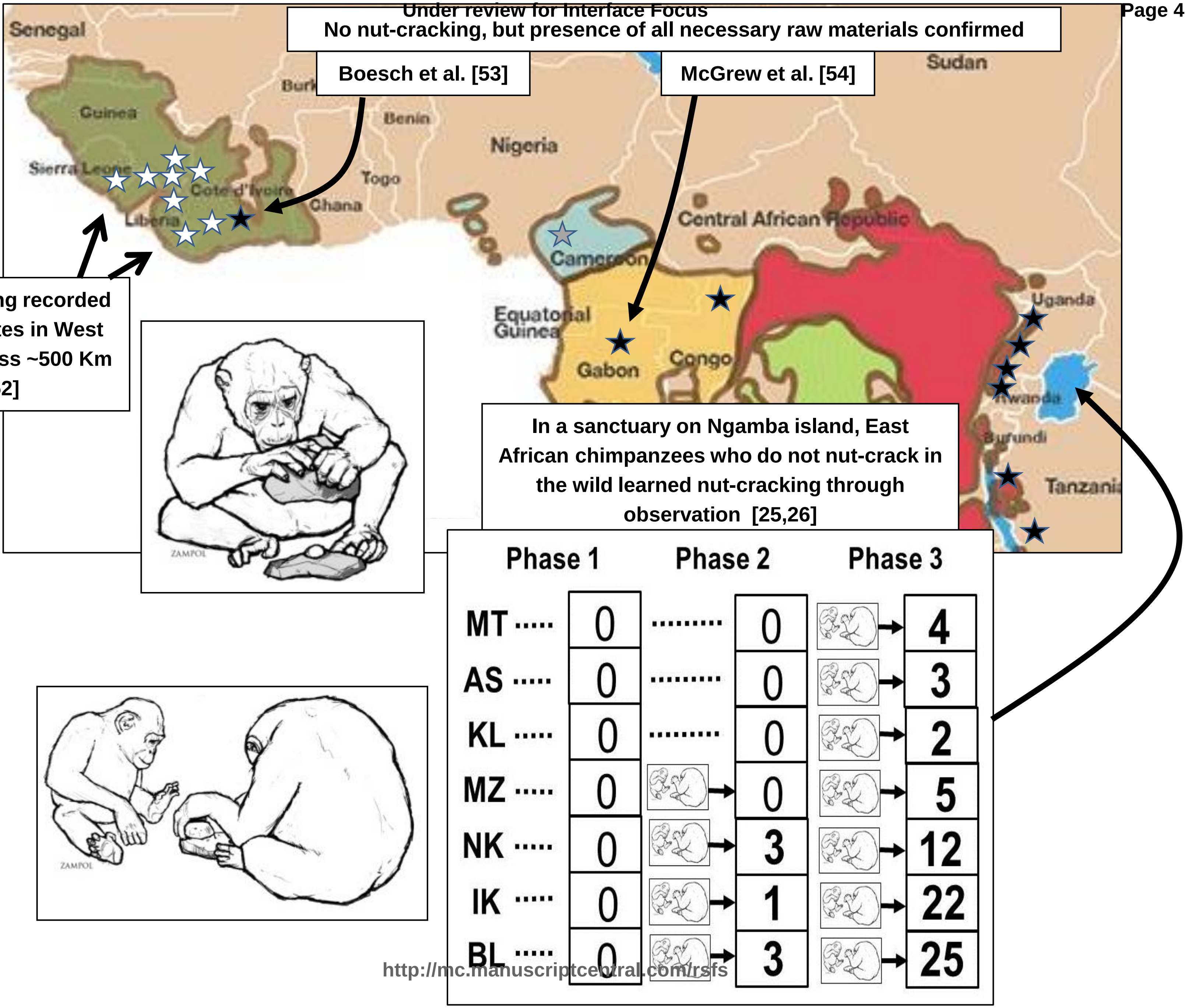
Figure 3. Diffusion of whale songs in space and time. Different humpback whale songs, here colour-coded for simplicity, were first recorded near East Australia and passed in successive waves across the Pacific ocean [after 51, modified with additions after 71, with permission of Chicago University Press].

Figure 4. Micro-lite aircraft to which juvenile birds imprint have acted as surrogate parents to demonstrate migratory routes, confirming a role for cultural transmission as birds adopt the routes in later seasons. Cover illustration of Whooping Cranes in the study of Mueller et al., with permission of American Association for the Advancement of Science [81].

Figure 5. (a) Regional dialect differences illustrated by sonograms of white-crowned sparrows [83, modified from 85 with additions, with permission of Cambridge University Press]; (b) Behavioural change over time through ‘cultural mutations’ in the socially inherited songs of saddlebacks [86].

Figure 6. An example of Darwinian cultural change? Three young chimpanzees, ABC, were exposed to two initially alarming objects, ‘swing’ and ‘satellite’.

Every two months, one chimpanzee was replaced by a naïve one, as indicated in the sequence BCD, CDE and so on. Adaptive bolder approaches were socially inherited and over time came to dominate, resulting in a culture of common contact with the objects [105].



No nut-cracking, but presence of all necessary raw materials confirmed

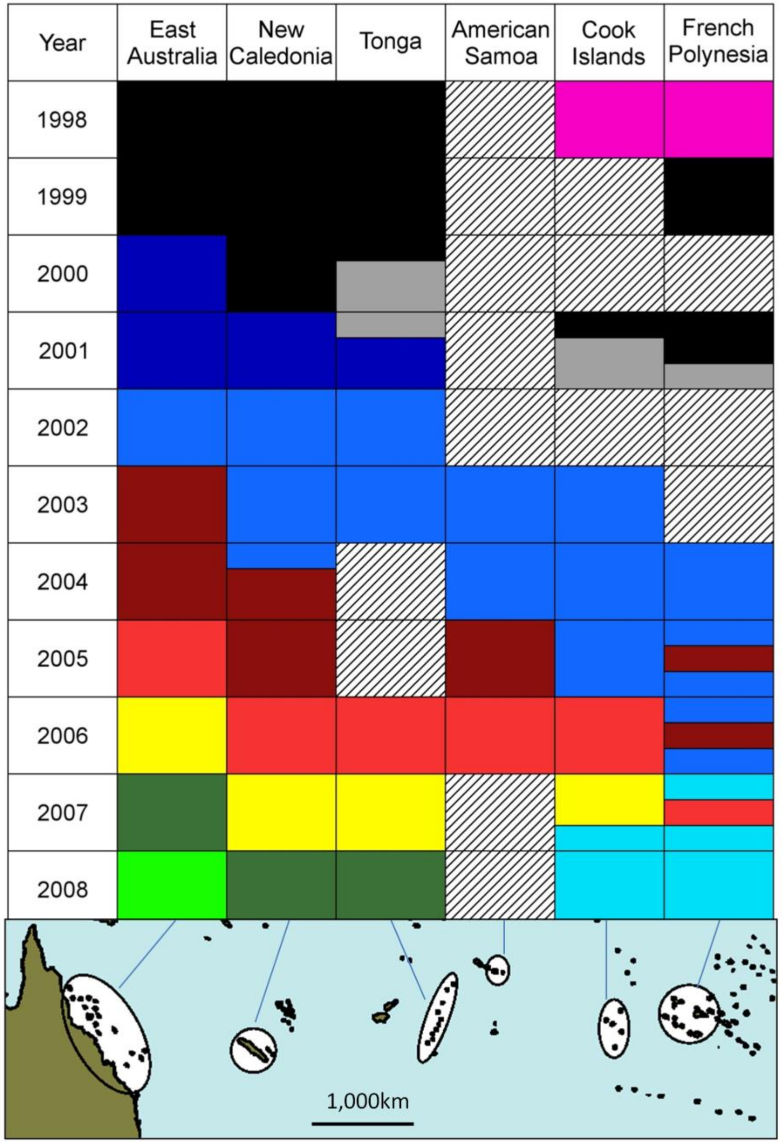
Boesch et al. [53]

McGrew et al. [54]

Nut-cracking recorded at eight sites in West Africa across ~500 Km [52]

In a sanctuary on Ngamba island, East African chimpanzees who do not nut-crack in the wild learned nut-cracking through observation [25,26]

	Phase 1	Phase 2	Phase 3
MT	0	0	4
AS	0	0	3
KL	0	0	2
MZ	0	0	5
NK	0	3	12
IK	0	1	22
BL	0	3	25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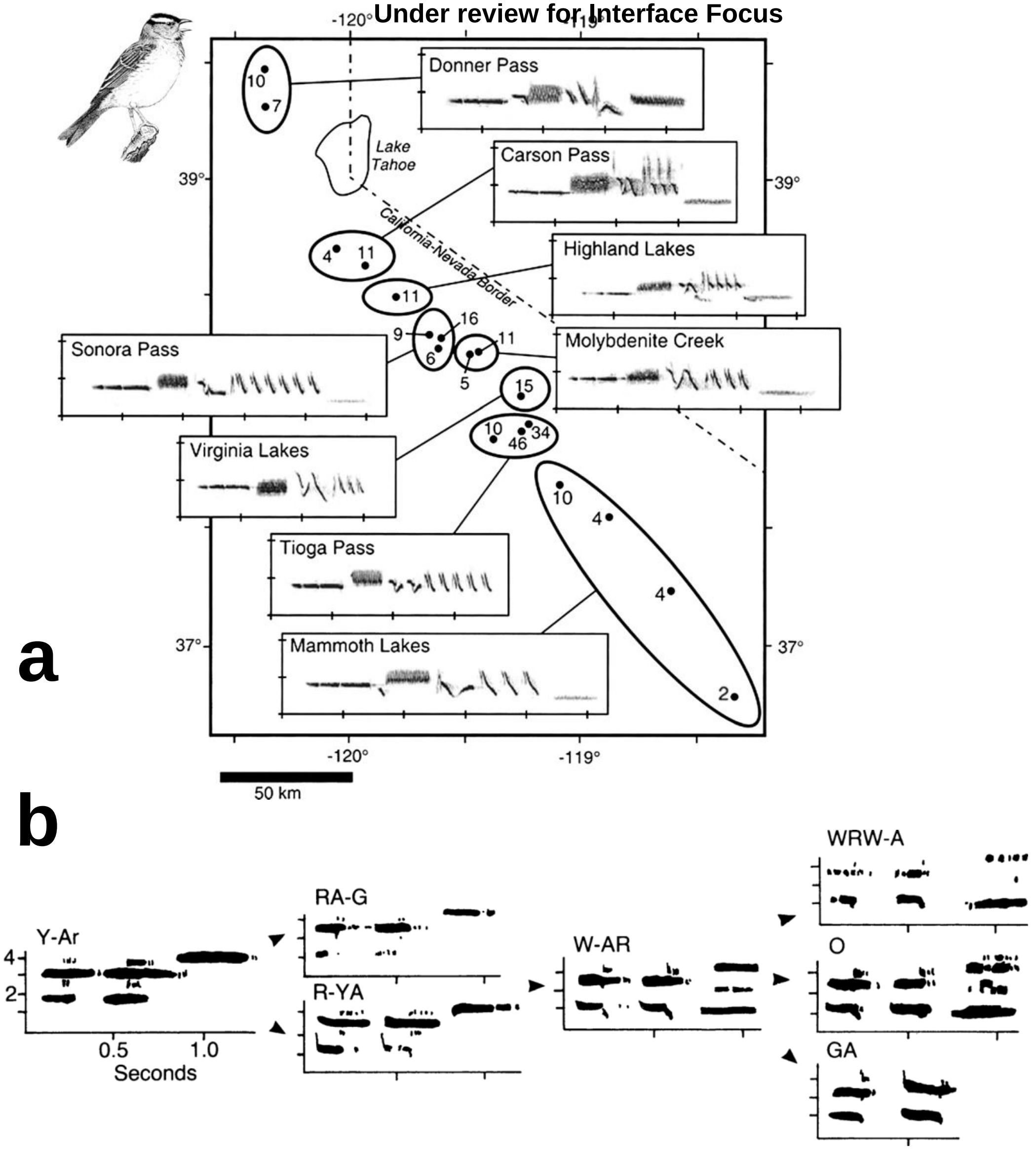
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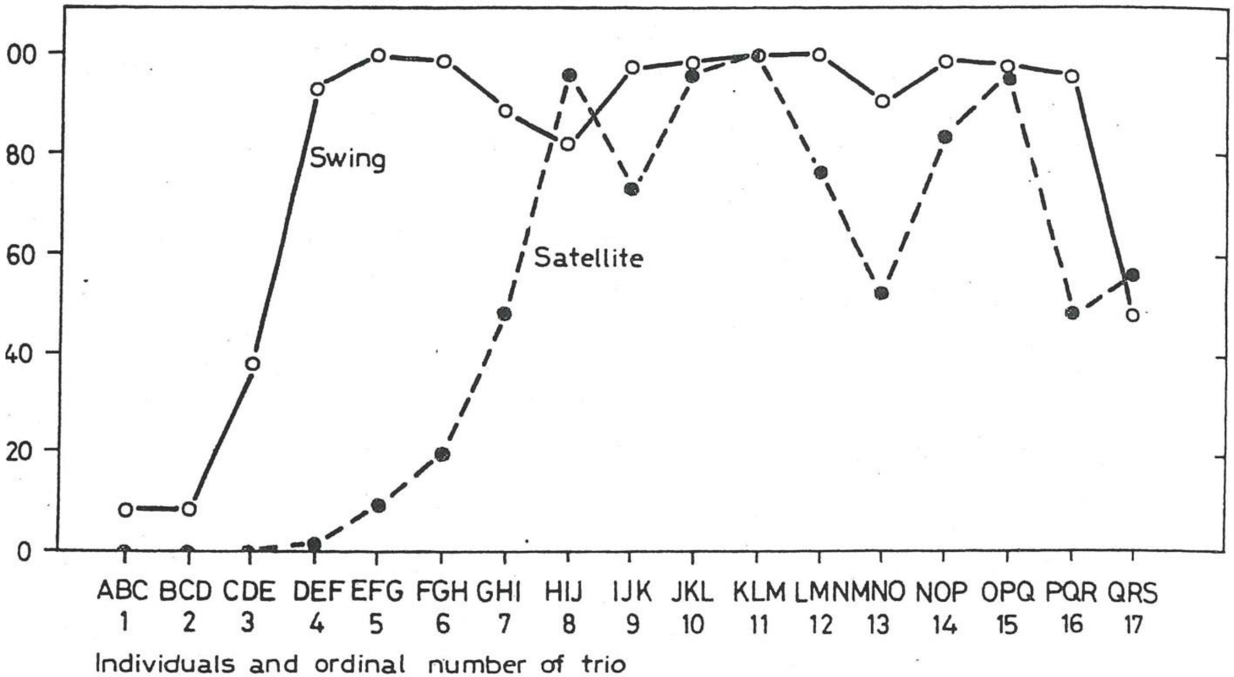
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PQR 16
QRS 17
Individuals and ordinal number of trio