PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

From fish to fashion: experimental and theoretical insights into the evolution of culture

K. N. Laland, N. Atton and M. M. Webster

Phil. Trans. R. Soc. B 2011 **366**, 958-968
doi: 10.1098/rstb.2010.0328

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

Phil. Trans. R. Soc. B (2011) **366**, 958–968
doi:10.1098/rstb.2010.0328

Research

From fish to fashion: experimental and theoretical insights into the evolution of culture

K. N. Laland*, N. Atton and M. M. Webster

Centre for Social Learning and Cognitive Evolution, School of Biology, University of St Andrews, Queen's Terrace, St Andrews KY16 9TS, UK

Recent years have witnessed a re-evaluation of the cognitive capabilities of fishes, including with respect to social learning. Indeed, some of the best experimental evidence for animal traditions can be found in fishes. Laboratory experimental studies reveal that many fishes acquire dietary, food site and mating preferences, predator recognition and avoidance behaviour, and learn pathways, through copying[1] other fishes. Concentrating on foraging behaviour, we will present the findings of laboratory experiments that reveal social learning, behavioural innovation, the diffusion of novel behaviour through populations and traditional use of food sites. Further studies reveal surprisingly complex social learning strategies deployed by sticklebacks. We will go on to place these observations of fish in a phylogenetic context, describing in which respects the learning and traditionality of fish are similar to, and differ from, that observed in other animals. We end by drawing on theoretical insights to suggest processes that may have played important roles in the evolution of the human cultural capability.

Keywords: culture; social learning; tradition; fishes; gene-culture coevolution; teaching

1. INTRODUCTION

Humans are a remarkably successful species, both demographically in terms of our burgeoning numbers, and ecologically in terms of the broad range of terrestrial environments in which we thrive. Our capacity for culture is the major factor underlying these accomplishments [1,2]. By 'culture' we mean the ability to acquire valuable knowledge and skills from other individuals through social learning and teaching, and to build on this reservoir of shared knowledge, iteratively, generation after generation, building ever more efficient solutions to life's challenges [3]. Other animals, including fishes, are capable of social learning and traditionality in behaviour, and in many respects these resemble aspects of human culture and cognition. Nonetheless, the fact remains that humans alone have sequenced genomes, built satellites and Large Hadron Colliders, written plays and novels and composed moonlight sonatas, while the most culturally accomplished non-human animals sit naked in the jungle cracking nuts. It may be tempting to view culture as the faculty that sets humans apart from the rest of nature—and to some extent this is justifiable. However, the human cultural capability obviously must have evolved too.

Herein lies a major challenge facing the biological and social sciences: how could the extraordinary and unique human capacity for culture have evolved out of something resembling the simple behavioural traditions observed in other animals? While a comprehensive answer to this question may still be some way off, we will endeavour in this paper to provide a sketch of some factors that we believe to be important. Our position is informed by both experimental studies of social learning, innovation, diffusion and tradition in animals, and by theoretical studies that use mathematical models to investigate aspects of human social evolution.

We will concentrate disproportionately on the insights into animal traditions that can be gained from experimental studies of fishes. Our 'fishy focus' is only partly because other contributors to this Special Edition have been given the remit to cover alternative taxonomic groups. Fishes provide, we believe, highly informative and practical model systems for experimental investigation of the biological bases of culture. Naturally, we understand that to most social scientists, as well as to the layperson, fishes seem so distant—both intellectually and taxonomically—from humans, that it is extremely difficult to envisage how the study of their behaviour could shed light on human cognitive evolution. However, the cognitive capabilities of fishes have historically been underestimated, and in many respects their intellectual faculties are comparable to birds and mammals [4,5]. Recent years have witnessed a shift away from the belief that animal intelligence mirrors the degree of relatedness to humans towards the notion of convergent evolution of intelligence in distinct taxonomic

* Author for correspondence (knl1@st-andrews.ac.uk).

One contribution of 26 to a Discussion Meeting Issue 'Culture evolves'.

groups [6,7]. This has the dual implication that, among the 28 000 species of fishes, there might well be some with interesting cognitive capabilities, and that the blanket dismissal of cognitive prowess of an entire taxon based on experimental studies of a small number of species would be scientifically unjustifiable.

As we describe in the following sections, there is now extensive experimental evidence that social learning and tradition play an important role in the behavioural development of many fishes, and frequently underlie differences in the behavioural repertoires of different populations. Most fishes are social animals and, like other vertebrates, their behaviour is far from rigidly controlled by a genetic programme, but constantly and flexibly adjusted to exploit information and resources in their social and asocial environment. The behaviour of others constitutes important sources of information to many fish species, providing them with valuable clues as to what to eat, where to find it, how to process it, what a predator looks like, how to escape, how to move safely through their environment, whom to mate with and many other challenges. Social learning is now known to play an important role in all of these domains in many fishes.

Given the knowledge that fishes are both competent at, and naturally widely reliant on, social learning and tradition, experimental studies of fish behaviour take on a new light. That is because fishes offer practical advantages over many other vertebrates for the study of social learning. After all, the diffusion of innovations and animal traditions are group-level phenomena, and if they are to be studied reliably researchers require not just replicate animals but replicate populations of animals. While it would be economically and practically challenging to set up large numbers of replicate populations of chimpanzees or Japanese macaques, it is extremely straightforward and cheap to set up large numbers of populations of small fishes in the laboratory, and subject them to experimentation. For instance, guppies are commercially available, thrive in simple aquaria, and cost virtually nothing to buy and keep, while sticklebacks are ubiquitous in the temperate Northern Hemisphere, can easily be fished out of local streams, and are equally effective laboratory subjects. Fish experimentalists enjoy the twin luxuries of the multiple conditions that good experimental design frequently demands and good statistical power, bringing experimental rigour to any social learning investigation.

Before we turn to a consideration of the social learning capabilities of fishes, we note in passing that biological interest in 'animal culture' goes beyond interest in reconstructing the evolution of human culture [8]. This is of relevance, because most of the experimental work that we will describe was not motivated by a wish to throw comparative light on human cognitive evolution. Biologists have their own agenda in studying animal traditions and culture. Perhaps, the most obvious determinant of biological interest is the observation that social learning is a source of adaptive behaviour; individuals can efficiently acquire solutions to problems such as 'what to eat?' and 'with whom to mate?' by copying others. But the recent fascination of biologists with culture also relates to its capability to propagate behaviour in a manner that is to some degree independent of the ecological environment, generate patterns of phenotypic variation in space, allow arbitrary and even maladaptive information to spread, and underpin niche construction. The social sciences may have been studying culture in humans prior to biologists, but they no longer have a monopoly of interest. The challenge that we laid out at the outset of this paper, to understand the evolution of culture, is fundamentally a multi-disciplinary challenge, and a satisfactory solution will require a genuinely multi-disciplinary research effort.

2. SOCIAL LEARNING IN FISHES

We begin this review with a brief account of how social learning is used by fishes under several different contexts, including moving through space, finding food, avoiding predators and choosing a mate (see [4,5] for more extensive overviews).

(a) *Fish migrations*

For most fish species, biologically important locations, such as profitable foraging sites, areas safe from predation, resting sites, suitable areas to find mates and reproduce, as well as safe routes between these locations, must be learned. Many fishes are now known to exhibit traditionality in their use of mating sites, preferred schooling sites, resting sites, feeding sites and pathways through their natural environments [4,5]. A straightforward method for acquiring knowledge of the location of important resources is simply to follow others and in the process to learn the site or route for themselves.

Laland & Williams [9] trained 'demonstrator' guppies to take one of two alternative routes to a food source over repeated trials in laboratory aquaria. They then introduced naive subjects into the populations, who tended to shoal with their demonstrators, and thereby take the same route to food. After 5 days of trials, the subjects were tested alone, and showed a significant preference for taking the same route as had their demonstrators, despite there being an alternative route of equal distance and complexity (figure 1*a*). Thus simply by shoaling with knowledgeable conspecifics individuals can learn a route to food. Laland & Williams [9,10] then went on to demonstrate how this simple process could underlie the natural migratory traditions that are observed in many fishes. They conducted experiments using a transmission chain design, where small shoals were trained to take one of two routes, and these trained founders were then gradually replaced by naive individuals to see if the route preferences were retained. Several days after the trained founders had been removed the route preferences were maintained in the groups (figure 1*b*). Even when one route was substantially longer, and more energetically costly, than the alternative, the longer route was still being widely used by individuals whose founders had previously been trained to take it.

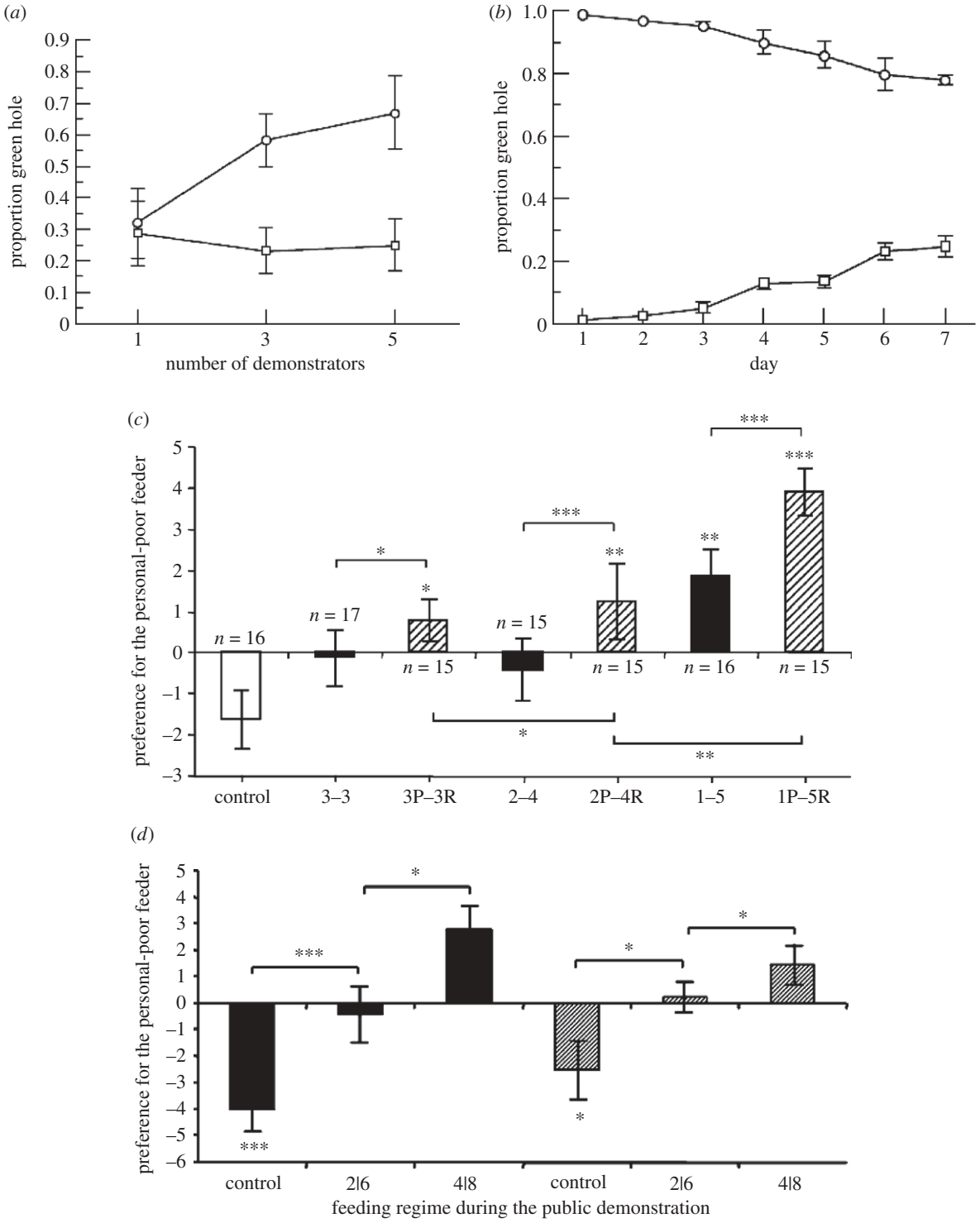

Figure 1. (*a*) The proportion (mean ± s.e.) of trials in which observer guppies tested singly took the green hole to a food source, given that their demonstrators were trained to take the green (circle) or red (square) hole, and that they had one, three or five demonstrators. (*b*) The proportion of trials in which subjects took the green hole to a food source, in transmission chains where founder populations were trained to take the green (circle) or red (square) hole. Each point represents the mean of the pooled performances of the fish in each group. (*c*) Mean (± s.e.) preference for the personal-poor feeder (time spent near the personal-poor feeder minus time spent near the personal-rich feeder from instantaneous sampling every 6 s for 90 s) in the personal-information only condition ('control', white bar), the social-information only conditions (black bars, where 3–3 denotes three fish shoaling at one feeder and three fish at the other feeder) and the public-information conditions (hashed bars, where 3P–3R denotes three fish feeding at the public-poor feeder and three fish at the public-rich feeder, respectively). See text for full details. Asterisks above bars indicate a significant difference from the control group; horizontal lines indicate orthogonal pairwise comparisons between groups. $*p < 0.05$, $**p < 0.01$ and $***p < 0.001$. (*d*) Mean (± s.e.) standard error difference (personal-poor minus personal-rich) in the number of instances that the fish was present in the 'goal zone' around each feeder (from instantaneous sampling of the fish's location every 6 s for the first 90 s following the start of the choice test), in fish trained on a 6|2 (i.e. 6 and 2 deliveries to rich and poor feeders, respectively; black bars) or 8|4 (hashed bars) regime and subsequently exposed to either a 2|6 or a 4|8 public demonstration (denoted as '2|6' or '4|8', respectively). Controls received no public demonstration (see text for full details). Asterisks denote either a significant difference from zero (in controls) or a significant difference between groups: $***p < 0.001$, $*p < 0.05$. (Reproduced with permission from [9] (*a*,*b*), [11] (*c*) and [12] (*d*).)

While many animals, notably chimpanzees [13], orangutans [14] and capuchin monkeys [15], exhibit behavioural traditions in nature (see [16–18]), the evidence that these are underpinned by social learning is, at best, circumstantial, leading to considerable controversy over the legitimacy of claims of animal culture [8,19]. In contrast, for fish there exists highly compelling experimental evidence that natural traditions are maintained through social learning, stemming from transplant experiments (see also [20]). Helfman & Schultz [21] transplanted French grunts, *Haemulon flavolineatum*, between populations and found that the moved individuals subsequently learn the daily migration routes between the foraging and resting sites used by resident conspecifics. The transplanted individuals only needed to follow the informed residents twice before being able to navigate the route themselves in the absence of all previous residents. Migratory traditions have also been shown to be present in bluehead wrasse, *Thalassoma bifascatum*, which have mating-site locations that remain in place over many generations. When entire populations were removed and replaced with transplanted populations, the wrasses were observed to establish entirely new mating sites, which remained constant over the 12-year period of the study [22]. However, when Warner replaced newly established populations after one month, he found the introduced fish re-used the same sites as their immediate predecessors [23]. Thus, these sites are not fully determined by habitat structure; rather, Warner's findings suggest that site use is initially based on resource assessment but then preserved through social learning.

(b) *Foraging*

Social learning is also a means by which fishes increase their foraging efficiency [5]. For instance, when a fish discovers a food patch, the foraging behaviour of that individual will frequently attract others to the same area. Fish also often appear attuned to the feeding movements of others. For example, juvenile Atlantic salmon, *Salmo salar*, dart to the water's surface to catch prey items from their benthic foraging stations. This darting motion is used as a cue by conspecifics that indicate food is available [24]. Fishes do not just learn of the location of food socially, but have been found to learn novel food types [24,25] as well as to acquire novel foraging behaviour. A striking example of the latter is provided by Schuster *et al.* [26], who demonstrate experimentally that archer fish (*Toxotes jaculatrix*) can learn to shoot down moving aerial prey through observation of the successful performance of conspecifics.

(c) *Anti-predator behaviour*

Fishes also learn anti-predator behaviour from conspecifics. One mechanism by which this can be attained in fishes is via a chemical cue, known as Shreckstoff, released as a result of damage to the skin [27] or, in some species, voluntarily, as 'disturbance pheromones' [28]. When these cues are detected by conspecifics, or heterospecifics, the receivers typically exhibit an anti-predator response [29]. Extensive experimental evidence, in multiple species, has established that fish can learn the identity of predators through associating predator cues with the detection of Schreckstoff released by other fish. For instance, Hall & Suboski [30] found that control of the alarm reaction could be transferred to previously neutral stimuli via paired conditioning and could provide a mechanism whereby naive animals learn to recognize predators without ever coming into direct contact with them. Similarly, Chivers & Smith [31] demonstrated that minnows could associate these alarm substances with chemical cues emanating from predators.

Minnows also learn to exhibit anti-predator behaviour in response to olfactory cues from a novel predator when these cues are received at the same time as seeing a fright response from conspecifics [32]. They can associate spatial areas, and even chemical cues associated with the water, with predator risk through the same mechanism [33], allowing fishes to recognize habitats with high predation risk. Chivers & Smith [34] and Suboski *et al.* [32] recorded that naive minnows (*Pimphales promelas*) and zebra danios (*Danio rerio*), respectively, receiving visual cues of a fright response from demonstrators through a clear barrier, acquire anti-predator responses to predator cues, if experiencing them simultaneously. It is also known that the observed fright behaviour of one individual will induce a similar response in others despite them having not seen the predator themselves [35]. This phenomenon is known as the 'Trafalgar effect' [36]. Shoaling fish are therefore made aware of a potential predator earlier than they would if solitary and the shoal can respond to the threat more effectively with coordinated evasion behaviour [35]. Magurran & Higham [37] discovered that minnows, *Phoxinus phoxinus*, even though unable to see the predator, exhibited predator avoidance behaviour upon observing the fright reaction of conspecifics to a model pike, *Esox* sp.

(d) *Aggressive interactions*

Social learning also allows fishes to learn about the fighting potential of rivals. Male Siamese fighting fish, *Betta splendens*, monitor aggressive interactions between neighbouring conspecifics and use the information to guide subsequent aggressive interactions with the males they have observed [38]. Similarly, green swordtails (*Xiphophorus helleri*, Poeciliidae) were less likely to initiate fights, escalate fights or win against the winners of the contests they had observed [39]. This exploitation of communicated signals in a network has become known as 'eavesdropping' [40]; it provides a means whereby individuals can gain information about the social status of others without having to expend energy or risk injury in social contests. Grosenick *et al.* [41] report that, following observation of conspecific fights, the cichlid (*Astatotilapia burtoni*) deploys an impressive capability for transitive inference to compute a linear hierarchy among its rivals, which then influences which fish it fights.

(e) *Mate choice*

Social learning has also been shown to influence mate choice in several species of fish including species from

at least four families [5]. Perhaps, the most widely known example of mate-choice copying is in the guppy. Dugatkin [42] conducted a series of experiments in which two males were secured at either end of an aquarium, with a model female residing near one of the males. A focal female was then placed into the middle of the tank and allowed to observe the males. After the model female was removed, the focal female was then allowed to swim freely within the aquarium during which time it was observed that focal females would spend a significantly larger amount of time with the male that had been near to the model female. This effect was upheld even when the male's locations were reversed after the observation period, strong enough to reverse prior preferences [43], and increases with the size, and hence age, of the model female [44]. It is also observed in mollies, where it has been demonstrated in a native river, establishing that it is no laboratory artefact [45]. Interestingly, male Atlantic mollies (*Poecilia mexicana*), which also exhibit mate-choice copying, have been found to court the lesser preferred of two females when watched by an observing male, an act of deception thought to function to alleviate sperm competition [46].

3. LABORATORY STUDIES OF FISH OBSERVATIONAL LEARNING AND TRADITION

We now switch to describing some experimental studies from our own laboratory, which illustrate some interesting and relevant features of fish social learning and tradition.

(a) *Laboratory 'traditions' and the role of conformity*

Stanley *et al.* [47] demonstrated that foraging techniques can be maintained as traditions in laboratory populations of guppies, as well as in another poeciliid, the platy (*Xiphophorus maculates*). Demonstrator fish were trained to collect food from inside vertical tubes, requiring them to swim in a vertical position not normally observed. Demonstrators were initially trained to feed by swimming into horizontal tubes to collect food held at the far end. Over a period of several exposures these tubes were rotated to vertical. This was a foraging task that the fish could not solve by themselves without training; while trained fish reliably fed from these tubes, no naive fish presented with a vertical tube learned to feed from it on its own. When placed in groups with experienced demonstrators however, naive fish readily learned to feed from the vertical tubes, establishing the social transmission of a novel feeding behaviour. When the experienced demonstrators were gradually removed and replaced with further naive fish, other group members continued to exploit the feeding tubes. Larger groups of fish showed more stable transmission of this behaviour than smaller groups, although this was found to be related to their slower rate of turnover rather than a direct effect of group size.

The Stanley *et al.* [48] and Laland & Williams [9,10] studies show that simple traditions can be established in the experimental laboratory. While these laboratory traditions are short-term, lasting days or weeks rather than years, such experiments suggest potential mechanisms for the cross-generational transmission of arbitrary behavioural preferences to be maintained within fish populations, as observed in the aforementioned field experiments of Helfman & Schultz [21] and Warner [22,23]. Such traditions are stable because the natural shoaling tendencies of the fish bring about a simple form of conformity. Fish prefer to join and follow large shoals compared with small shoals [48], thereby lending them a tendency to adopt the majority behaviour that becomes stabilized through positive frequency dependence, generating the 'cultural inertia' that can characterize behavioural traditions [1]. This process is sufficiently powerful that it can maintain arbitrary and even maladaptive traditions [10], which helps explain why the mating and schooling sites of natural populations cannot always be predicted from features of the environment [23].

Lachlan *et al.* [48] showed that individual guppies preferred to follow larger groups of conspecifics over smaller ones, and that by following such a group on just three occasions they were able to learn the route to a food patch. Conformity effects are stronger in larger groups, where more individuals are available to act as demonstrators. For example, Day *et al.* [49] found that the latency of the first and focal fish to find food was lower in larger shoals compared with smaller shoals when foraging in open water. However, when fish were required to pass through a small hole in an opaque barrier to locate food the opposite was seen; the latency for the first and focal fish to reach the food patch was now significantly higher in the larger groups compared with smaller groups. They suggest that this is a consequence of conformity; individuals may be unwilling to break visual contact with the shoal, with the effect that, at least early on in the diffusion, the tendency to remain with the shoal discourages individuals from leaving to locate the prey patch, with large shoals exerting more pull than small shoals. This prediction was confirmed in a second experiment, where a transparent rather than opaque barrier was used. Here, fish no longer had to break visual contact with their shoal mates, and, as in the open water trial, the latency of the first and focal fish to find the food was once again lower in larger shoals compared with the smaller ones.

While the aforementioned studies are strongly suggestive of conformist learning, they do not provide unequivocal evidence for it. However, Pike & Laland [12] showed that ninespine sticklebacks (*Pungitius pungitius*) do indeed follow a 'copy-the-majority' or conformist social learning strategy. Fish were trained to expect greater prey yield from one food patch, then were given conflicting public information from foraging conspecifics that another food patch was richer, and finally tested for their patch choice. Pike & Laland found that as the number of demonstrators at the patch demonstrated to be richer increased, so did the likelihood that the observer would select this patch. Moreover, this likelihood increased disproportionately and not linearly with increasing demonstrator number (figure 1*c*), a definitive feature

of conformist social learning [1]. Control experiments in which the demonstrators received no food, ruled out the possibility that this was simply a shoaling response. Pike & Laland's finding provides clear support for the predictions of theoretical analyses, which suggest that animals should exhibit conformist behaviour when basing decisions upon social information [1,50].

(b) *Public information use and efficient copying in ninespine sticklebacks*

The aforementioned Pike & Laland study is the latest in a series of studies that we have carried out to investigate public information use in sticklebacks. 'Public information use' refers to the capability of an animal to assess the quality of a resource vicariously, through monitoring the success and failure of others interacting with it [51]. It allows individuals to collect information, for instance, about the richness of a foraging patch, without the costs associated with personal sampling, such as increased exposure to predators and travel time incurred between patches to make comparisons.

This capability was first demonstrated in a fish, the ninespine stickleback, *P. pungitius*, by Coolen *et al.* [52]. We placed observer fish in a central compartment from where, through transparent partitions, they could observe two groups of demonstrators being fed through artificial feeders at different rates. The observer could not see the food in the feeder, only the reactions of the demonstrators to the food. After a period of 10 min, all demonstrators and remaining food items were removed from the tank and the observer was released. It was observed that the observers spent a significantly larger proportion of time in the feeding zone that formerly housed the demonstrator group that was fed at the faster rate, and disproportionately chose to enter this goal zone first, implying that they were able to use the behaviour of the demonstrators to establish which of the two foraging patches was the more profitable. Coolen *et al.* [52] compared public information use in the ninespine stickleback and the closely related threespine stickleback (*Gasterosteus aculeatus*), finding that only the ninespines were able to use public information about patch quality when tested later in the absence of demonstrators. This species difference seems robust, with public information use seen in ninespines in a number of subsequent studies, described below, while several recent investigations have found no evidence for public information use in threespines, in spite of the fact that threespines are capable of other forms of social learning [53,54].

We believe that the explanation for this species difference may be related to the observation that threespines possess greater armour, in the form of lateral plates and longer dorsal spines [55], than do ninespines. Indeed, this morphological difference is to such an extent that predatory fishes have been shown to display a preference for consuming ninespines over threespines [56]. The superior defences of threespines mean that they are more likely to withstand the higher predation risk associated with personal sampling and therefore benefit more from maximizing their opportunities to feed. In contrast, the ninespines are more vulnerable to predation and hide in refuge when predators are near. Seemingly, natural selection has fashioned the ninespines' ability to use public information as a means of acquiring valuable foraging information through observation, from the safety of refuge.

Coolen *et al.* [52] also demonstrated that ninespines are not only capable of using public information in a foraging context from conspecifics but from the heterospecific threespines as well. As these fish were collected from the same rivers and streams, and are sympatric throughout their range, this finding raises the possibility that the opportunity to acquire public information from heterospecifics may underlie a preference in the ninespines for mixed-species shoaling. We have collected ninespine and threespine sticklebacks from all round the world, assaying them for public information use, and also raised both species in the laboratory under a variety of rearing conditions. We have found no other aspect of the fishes' ecology, morphology, social system or rearing conditions that affect the incidence of public information use. Rather, we observe a robust species difference, with ninespines always, and threespines never, exhibiting this capability.

Building on our Coolen *et al.* [52] study, we have adopted the ninespine stickleback as a model organism for studying public information use and social learning strategies, using the aforementioned procedure and apparatus. The advantage of this paradigm is that it is extremely flexible, allowing us to vary, for example, the ratio of food delivered by each feeder in order to simulate rich and poor feeding patches, the number, phenotype or species of the demonstrators, or to provide the observer with various forms of prior experience (or 'private information') about one or both of the patches. This approach enables us to investigate the social learning strategies that govern the ways in which individuals weight different sources of information when they are in conflict.

Such studies reveal that ninespines are capable of adaptive tradeoffs in their reliance on social and asocial sources of information, mixing their own prior knowledge of patch quality with the information gleaned from observation of others, in a surprisingly sophisticated way. For instance, van Bergen *et al.* [57] first gave ninespine subjects the opportunity to learn through direct foraging that one of two prey patches either consistently or on average yielded a larger number of prey items, followed by conflicting public information which implied that the previously lower yielding patch was now richer. Subjects were then tested as before. We found that fish that had received reliable private information ignored public information and chose the patch they had previously experienced to be richer, while those which had unreliable (noisy) private information were more inclined to copy, and base their patch choice at test on the richer patch for the demonstrators. Moreover, the magnitude of copying increased with the degree of noisiness in their private information. A second experiment devalued the private information in a different way, by manipulating its age, but to similar effect. Fish would base

their patch choice on private information in preference to conflicting public information if only 1 day had elapsed since they last sampled the patch, but as the private information got more and more out-of-date, they increasingly ignored their private information and copied the demonstrators. If 7 days had elapsed since they last updated their private information, subjects had switched completely to using public information, and copied at the same rate as individuals that had not previously sampled the patches. Thus, these fish are not always or mindlessly using public information, but rather switching between reliance on different sources of information according to their probable reliability.

Use of this paradigm reveals evidence for theoretically predicted optimal learning strategies in our fish. Kendal *et al.* [58] found that ninespines deploy a 'hill-climbing' social learning strategy when they exploit public information. Specifically, they saw that fish with previous experience of finding food at one prey patch switched patch preferences when the prey capture rate of demonstrators suggested that the yield of the alternative patch was greater than that at the rich patch according to their private experience. Conversely, they were far less likely to switch to the alternative patch if the prey capture rate of the demonstrators was lower than that of the 'rich' patch based on their private information. Such a strategy, if widely deployed, potentially allows individuals in a population to steadily increase their foraging efficiency by gradually homing in on the most profitable foraging locations, which lends it a 'hill climbing' quality. Pike *et al.* [11] showed that the probability of an observing fish selecting a demonstrated richer prey patch was proportionally dependent solely upon the returns to the foraging demonstrators (in terms of prey item yielded by the patch). The degree of copying by the observing fish increased with the absolute rate of feeding by the demonstrators (figure 1*d*). What is particularly interesting about this finding is that the ninespines behaviour is precisely that predicted by an evolutionary game theory analysis conducted by economist Karl Schlag [59]; theory of course developed to predict humans' behaviour. In other words, humans and a species of stickleback exhibit the same optimal learning rule when they copy, a rule that Schlag terms 'proportional observation'—they both follow a *payoff-based* copying strategy. Schlag's analysis demonstrated that 'proportional observation' is an optimal social learning strategy, which will take populations to the fitness maximizing behaviour. The use of a relatively simple rule by individuals (proportional copying) could lead to a surprisingly complex outcome in a population (cumulative knowledge gain). In this respect, these results may be of general significance, since they establish that the proportional observation rule, which possesses the hill-climbing properties necessary to allow optimal solutions to be reached over repeated iterations, is actually observed in nature. The deployment of a strategy with this potential ratcheting quality has, to our knowledge, never been demonstrated before in a non-human, and has hitherto been considered absent in animals. Utilization of such a strategy by ninespine sticklebacks may allow them to exhibit cumulative increases in the efficiency with which they exploit diverse prey in their natural environments, for instance, as they colonize new regions.

4. THE PSYCHOLOGICAL PROCESSES UNDERLYING FISH SOCIAL LEARNING

Thus far, we have focused upon functional aspects of social learning, such as where to forage, and what route to follow. We now briefly consider the psychological mechanisms that underlie such behaviour, drawing on Hoppitt & Laland's [60] classification of social learning processes.

The above studies imply that route preference learning, described for both laboratory studies of guppy shoaling behaviour [48] and in the wild in several species of reef fishes [21–23], is underpinned by simple local enhancement mechanisms, whereby an observer is attracted to a location where it detects or has recently detected the presence of others. Conversely, mate choice copying, widely reported in poeciliid fishes, is probably brought about through stimulus enhancement, whereby the presence of receptive demonstrators interacting with potential mates cause the observer to become more likely to interact with mates with similar phenotypes to themselves. Public information use, described above for foraging ninespine sticklebacks, might operate through observational conditioning, in which observation of a demonstrator exposes the observer to a relationship between stimuli at t_1, and exposure to this relationship effects a change in the observer detected, in any behaviour, at t_2. A 'simple' case of local enhancement is ruled out because observers were not responding to the mere presence of demonstrators but to the rate of feeding itself. One plausible explanation is that observers formed S–S associations of different strengths between each food patch and food, as a result of a previously formed association between the sight of a feeding conspecific and food. Anti-predator learning (e.g. [61]) may also be supported by observational conditioning, or possibly observational R-S learning, in which observation of a demonstrator exposes the observer to a relationship between a response and a reinforcer at t_1, and exposure to this relationship effects a change in the observer detected, in any behaviour, at t_2. Finally, learning to exploit novel foods (e.g. [24]) may be brought about by response facilitation, where the presence of a demonstrator performing an act increases the probability of an animal that sees it doing the same.

We know of no convincing laboratory evidence that fish are capable of imitation, that is, learning to produce particular bodily movements through observation of others, although there is plenty of experimental evidence for observational learning in fishes [26,41,52], and several studies produce evidence consistent with imitation, although other mechanisms are perhaps more likely (e.g. [26,47]). Suggestive circumstantial evidence of imitation is also provided by Mazeroll & Montgomery's [62] report that in the local migrations of brown surgeonfish (*Acanthurus nigrofuscus*, *Acanthuridae*), followers not only take the route

of leaders but reproduce their postural changes (e.g. dips and rolls). However, it is a feature of animal social learning that simple processes are sufficient both to allow individuals to acquire adaptive information, and to mediate behavioural traditions in populations.

5. FROM ANIMAL TRADITION TO HUMAN CULTURES

In this final section, we endeavour to place the social learning of fishes in a more general context, before going on briefly to address the issue of the evolution of human culture. While this account is inevitably speculative, we describe the theoretical findings that lead us to favour this argument.

The preceding sections establish a number of points about the social learning capabilities of fishes. First, social learning is widespread in fishes, as demonstrated by extensive and rigorous laboratory investigation. Second, while much social learning in fishes results from simple local enhancement or following mechanisms, as it does in other animals, many fishes are highly competent social learners, exhibiting forms of learning that are reliant on seemingly more complex forms of social learning. For instance, we have described cases of observational learning, conformist learning, proportional observation and acquisition of novel motor patterns through observation. Third, the social learning exhibited by individual fish species is frequently expressed across multiple domains. For instance, in guppies alone, experimental evidence reveals the social learning of routes to food sites, food patch preferences, natural and artificial predator evasion behaviour, female mating preferences, and predator inspection. This means that some fish species cannot accurately be characterized as 'one trick ponies' [63]. Fourth, not just social learning, but also the diffusion of innovations through populations [64,65] and the maintenance of traditions, has been reproduced and investigated in the laboratory. Fifth, the social learning of fishes is not restricted to the experimental laboratory: field experiments demonstrate that social learning is used under natural conditions [45,66] while relocation experiments provide clear evidence that fish traditions are underpinned by social learning [21–23]. Finally, fishes are excellent model systems for studying social learning, and there is much still to be done, for instance, concerning the biological basis, development and phylogenetic history of social learning capabilities where fishes could usefully be deployed. When we add to this the broader recent insights into fish Machiavellian intelligence [67], tracking third-part relations [38], computing transitive inference [41], tool and substrate use [68] and cooperation [69,70], we witness a far richer conception of fish cognition than hitherto conceived.

Notwithstanding the above, the observation that fishes in general exhibit much richer social learning than might be predicted on the basis of examinations of relative brain size among the animalia need not, in and of itself, lead us to challenge our conceptions of fish intelligence. The most probable explanation for this pattern is that social learning and tradition do not inherently require complex cognition. A major finding of the social learning strategies tournament [71] is that even random copying is typically far more effective than trial-and-error learning, which explains why social learning is widespread in nature, not just in vertebrates but even in crickets, bumblebees and fruitflies [72]. However, another clear conclusion from Rendell *et al.*'s [71] analysis is that the strategic use of copying is far more effective than random copying, and that there are fitness benefits associated with copying efficiently. Such strategic copying is now widely reported in fishes [11,12,57,73].

In many respects, the social learning of fishes is very much comparable to that of birds and mammals. Similar experiments in mammals and birds, such as transmission chains or diffusion studies, generate broadly similar patterns, and appear to be reliant on similar processes, as those described in fishes [74–77]. While individual species or genera of primates, such as chimpanzees, orangutans, macaques and capuchins, may arguably exhibit more sophisticated cultural capabilities, there is little reason to suppose that the social learning of fishes is any less impressive than that observed in, say, bushbabies, lemurs or gibbons. A broad sweep of the social learning capabilities of animals in general suggests convergent selection in distinct lineages for those cognitive capabilities that might be considered the rudimentary foundations of culture, a perspective that receives support from a recent meta-analysis of primate intelligence [78]. Certain lineages have apparently witnessed selection for more strategic forms of copying, such as payoff-based rules like proportional observation, or effective sampling rules like conformity, which gave individuals an edge over their competitors. There is now considerable evidence that strategic copying is a general feature of animal learning [79,80].

The Great Apes are one such lineage, and it is here that we envisage certain feedback processes began to operate, or to operate at a greater pace, triggering the cascade of events that culminated in our own extraordinary culture (see [17] for a similar argument). One process that we believe to be important is a 'cultural' or 'behavioural drive' [81]. Reader & Laland [82] found that, across non-human primates, the incidence of behavioural innovation and social learning increases positively with brain size, controlling for research effort, phylogeny and a number of other factors. This led them to endorse the argument, originally conceived by Allan Wilson [81], that the ability to invent new behaviour, and to copy the inventions of others, would give an individual a selective advantage in the struggle to survive and reproduce. As these abilities must have some neural substrate, Wilson argued that innovation and social learning would generate selection for larger and larger brains among primates, culminating in humans—the most innovative and culturally reliant species with the largest relative brain size. (Whiten & van Schaik [83] make a similar argument.) However, while Reader & Laland's data are consistent with Wilson's hypothesis, we believe that the primate lineage leading to humans is not just characterized by more and more social learning, but rather better and better social learning. Indeed, these factors are probably related, since more efficient

forms of social learning will allow for greater amounts of socially transmitted information. Moreover, big brains allow for a number of capabilities that enhance the efficiency of copying, including better perceptual systems (allowing copying from distance and supporting accurate imitation), more cross-modal mapping allowing integration across modalities and generalization across modular structures, better comprehension of the goals of the demonstrator, and the ability to monitor payoff or compute frequency-dependence.

The importance of improvements in the efficiency of social learning is another take-home message of the social learning strategies tournament [71], where strategies that copied highly strategically, timing their copying to be optimal so as to maximize their payoffs, thrived. The winning strategy engaged in a form of mental time travel, monitoring rates of change in the environment, and then evaluating information based on its age to devalue out-of-date knowledge, and judging how valuable its current behaviour will be in the future and whether further learning was likely to be profitable. We suspect that humans alone are capable of copying in this manner, although, as van Bergen *et al.*'s sticklebacks demonstrate, animals may well be capable of adjusting their reliance on information according to its age. However, efficiency in copying can be gained through other means, such as following conformity and payoff-based copying rules [1], as again illustrated by the sticklebacks [11,12].

Our thinking is also highly influenced by a recent theoretical analysis by Enquist *et al.* [84], which, through stochastic simulation, reveals an accelerating relationship between the fidelity or accuracy of information transmission during copying and the length of time that a cultural trait stays in a population. In simple terms, the study reveals that a small increase in fidelity can make a big difference to how long a cultural trait persists, with the knock-on consequence that high-fidelity transmission mechanisms support much more culture than low-fidelity mechanisms. Moreover, more culture, and more long-lasting culture, means greater opportunities for cumulative culture, since the longer cultural variants last the more likely an improvement or refinement will be devised, and the greater the opportunities there are for cross-fertilization of ideas from different cultural traits, leading to further accumulation. Common chimpanzees are reported to have 37 cultural traits [13] while the number of cultural variants possessed by humans is far too numerous to count. The Enquist *et al.* study suggests that a large part of the difference in the extent of chimpanzee and human culture can be attributed to differences in the fidelity of copying. In particular, humans, but not chimpanzees, possess a capacity for teaching, supported by language, which greatly increases the accuracy with which complex knowledge can be transmitted between individuals. Tomasello [85] was probably correct to link fidelity to cumulative culture. Moreover, theoretical work conducted in our laboratory suggests that cumulative culture broadens the conditions that favour teaching, which completes the feedback loop.

In summary, we believe that teaching, language and cumulative culture reinforce each other, each enhancing the utility and potency of the others. Teaching is far more effective with language, language becomes critical in a rich and diverse cultural context, and cumulative culture promotes reliance on teaching. The hominins, a taxonomic group that like other Great Apes was already comparatively rich in its social learning capabilities, were probably one of several primate lineages experiencing selection favouring more and more efficient and accurate copying, which led in turn to a richer culture. At some juncture our ancestors crossed a threshold when the fidelity of their copying was sufficient to support cumulative knowledge gain, and the aforementioned feedback mechanism kicked in. We now know that much recent human evolution was probably dominated by gene-culture coevolution, as humans evolved in response to their agricultural and other cultural practices, such as the domestication of animals and plants, and the new densities, diseases and diets these practices afforded [86]. Humans and their ancestors constructed a cultural niche, and evolved to excel in it [87].

Research supported in part by an ERC Advanced grant (EVOCULTURE, 232823) and NERC grant (NE/D010365/1) to K.N.L.

ENDNOTE

[1]By the term 'copying' we mean any form of social learning, and do not necessarily imply imitation.

REFERENCES

1 Boyd, R. & Richerson, P. J. 1985 *Culture and the evolutionary process*. Chicago, IL: University of Chicago Press.
2 Richerson, P. J. & Boyd, R. 2005 *Not by genes alone*. Chicago, IL: University of Chicago Press.
3 Laland, K. N. & Hoppitt, W. J. E. 2003 Do animals have culture? *Evol. Anthropol.* **12**, 150–159. (doi:10.1002/evan.10111)
4 Brown, C. & Laland, K. N. 2003 Social learning in fishes: a review. *Fish Fisheries* (Special Edn) **4**, 280–288.
5 Brown, C. & Laland, K. N. 2006 Social learning in fishes. In *Fish cognition and behaviour* (eds C. Brown, K. N. Laland & J. Krause), pp. 186–202. Oxford, UK: Blackwell Publishing.
6 Shettleworth, S. J. 2001 Animal cognition and animal behaviour. *Anim. Behav.* **61**, 277–286. (doi:10.1006/anbe.2000.1606)
7 Emery, N. J. & Clayton, N. S. 2004 The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science* **306**, 1903–1907. (doi:10.1126/science.1098410)
8 Laland, K. N. & Galef, B. G. 2009 *The question of animal culture*. Cambridge, MA: Harvard University Press.
9 Laland, K. N. & Williams, K. 1997 Shoaling generates social learning of foraging information in guppies. *Anim. Behav.* **53**, 1161–1169. (doi:10.1006/anbe.1996.0318)
10 Laland, K. N. & Williams, K. 1998 Social transmission of maladaptive information in the guppy. *Behav. Ecol.* **9**, 493–499. (doi:10.1093/beheco/9.5.493)
11 Pike, T. W., Kendal, J. R., Rendell, L. & Laland, K. N. 2010 Learning by proportional observation in a species of fish. *Behav. Ecol.* **20**, 238–244.

12 Pike, T. W. & Laland, K. N. 2010 Conformist learning in nine-spined sticklebacks' foraging decisions. *Biol. Lett.* **6**, 466–468. (doi:10.1098/rsbl.2009.1014)
13 Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. 1999 Culture in chimpanzees. *Nature* **399**, 682–685. (doi:10.1038/21415)
14 van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S. & Merrill, M. 2003 Orangutan cultures and the evolution of material culture. *Science* **299**, 102–105. (doi:10.1126/science.1078004)
15 Perry, S. *et al.* 2003 Social conventions in wild white-faced capuchins: evidence for traditions in a Neotropical primate. *Curr. Anthropol.* **44**, 241–268. (doi:10.1086/345825)
16 Whiten, A. 2011 The scope of culture in chimpanzees, humans and ancestral apes. *Phil. Trans. R. Soc. B* **366**, 997–1007. (doi:10.1098/rstb.1993.0334)
17 van Schaik, C. P. & Burkart, J. M. 2011 Social learning and evolution: the cultural intelligence hypothesis. *Phil. Trans. R. Soc. B* **366**, 1008–1016. (doi:10.1098/rstb.1993.0304)
18 Perry, S. 2011 Social traditions and social learning in capuchin monkeys (*Cebus*). *Phil. Trans. R. Soc. B* **366**, 988–996. (doi:10.1098/rstb.1993.0317)
19 Laland, K. N. & Janik, V. 2006 The animal cultures debate. *Trends Ecol. Evol.* **21**, 542–547. (doi:10.1016/j.tree.2006.06.005)
20 Slagsvold, T. & Wiebe, K. L. 2011 Social learning in birds and its role in shaping a foraging niche. *Phil. Trans. R. Soc. B* **366**, 969–977. (doi:10.1098/rstb.1993.0343)
21 Helfman, G. S. & Schultz, E. T. 1984 Social transmission of behavioural traditions in a coral reef fish. *Anim. Behav.* **32**, 379–384. (doi:10.1016/S0003-3472(84)80272-9)
22 Warner, R. R. 1988 Traditionality of mating-site preferences in a coral reef fish. *Nature* **335**, 719–721. (doi:10.1038/335719a0)
23 Warner, R. R. 1990 Male versus female influences on mating-site determination in a coral-reef fish. *Anim. Behav.* **39**, 540–548. (doi:10.1016/S0003-3472(05)80420-8)
24 Brown, C. & Laland, K. N. 2002 Social enhancement and social inhibition of foraging behaviour in hatchery-reared Atlantic salmon. *J. Fish Biol.* **61**, 987–998. (doi:10.1111/j.1095-8649.2002.tb01857.x)
25 Brown, C. & Laland, K. N. 2001 Suboski and Templeton revisited: social learning and life skills training for hatchery reared fish. *J. Fish Biol.* **59**, 471–493. (doi:10.1111/j.1095-8649.2001.tb02354.x)
26 Schuster, S., Wohl, S., Griebsch, M. & Klostermeier, I. 2006 Animal cognition: how archer fish learn to down rapidly moving targets. *Curr. Biol.* **16**, 378–383. (doi:10.1016/j.cub.2005.12.037)
27 von Frisch, K. 1938 Zur Psychologie des Fisch-Schwarmes. *Naturwissenschaften* **26**, 601–606. (doi:10.1007/BF01590598)
28 Wisenden, B. D., Chivers, D. P., Brown, G. E. & Smith, R. J. F. 1995 The role of experience in risk assessment: avoidance of areas chemically labelled with fathead minnow alarm pheromone by conspecifics and heterospecifics. *Ecoscience* **2**, 115–122.
29 Brown, G. E. & Godin, G. J. 1997 Anti-predator responses to conspecific and heterospecific skin extracts by threespine sticklebacks: alarm pheromones revisited. *Behaviour* **134**, 1123–1134. (doi:10.1163/156853997X00098)
30 Hall, D. & Suboski, M. D. 1995 Visual and olfactory stimuli in learned release of alarm reactions by zebra danio fish (*Brachydanio rerio*). *Neurobiol. Learn. Mem.* **63**, 229–240. (doi:10.1006/nlme.1995.1027)
31 Chivers, D. P. & Smith, R. J. F. 1995 Free-living fathead minnows rapidly learn to recognize pike as predators. *J. Fish Biol.* **46**, 949–954. (doi:10.1111/j.1095-8649.1995.tb01399.x)
32 Suboski, M. D., Bain, S., Carty, A. E. & McQuoid, L. M. 1990 Alarm reaction in acquisition and social transmission of simulated-predator recognition by zebra danio (*Brachydanio rerio*). *J. Comp. Psychol.* **104**, 101–112. (doi:10.1037/0735-7036.104.1.101)
33 Chivers, D. P. & Smith, R. J. F. 1995 Fathead minnows (*Pimephales promelas*) learn to recognize chemical stimuli from high-risk habitats by the presence of alarm substance. *Behav. Ecol.* **6**, 155–158. (doi:10.1093/beheco/6.2.155)
34 Chivers, D. P. & Smith, R. J. F. 1994 Fathead minnows *Pimephales promelas*, acquire predator recognition when alarm substance is associated with the sight of unfamiliar fish. *Anim. Behav.* **48**, 597–605. (doi:10.1006/anbe.1994.1279)
35 Krause, J. 1993 Transmission of fright reaction between different species of fish. *Behaviour* **127**, 37–48. (doi:10.1163/156853993X00416)
36 Treherne, J. E. & Foster, W. A. 1981 Group transmission of predator avoidance behaviour in a marine insect: the Trafalgar effect. *Anim. Behav.* **32**, 536–542.
37 Magurran, A. E. & Higham, A. 1988 Information transfer across fish shoals under predator threat. *Ethology* **78**, 153–158. (doi:10.1111/j.1439-0310.1988.tb00226.x)
38 Oliveira, R. F., McGregor, P. K. & Latruffe, C. 1998 Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proc. R. Soc. Lond. B* **265**, 1045–1049. (doi:10.1098/rspb.1998.0397)
39 Early, R. L. & Dugatkin, L. A. 2002 Eavesdropping on visual cues in green swordtail (*Xiphophorus helleri*) fights: a case for networking. *Proc. R. Soc. Lond. B* **269**, 943–952. (doi:10.1098/rspb.2002.1973)
40 McGregor, P. K. 1993 Signaling in territorial systems—a context for individual identification, ranging and eavesdropping. *Phil. Trans. R. Soc. Lond. B* **340**, 237–244. (doi:10.1098/rstb.1993.0063)
41 Grosenick, L., Clement, T. S. & Fernald, R. D. 2007 Fish can infer social rank by observation alone. *Nature* **445**, 429–432. (doi:10.1038/nature05511)
42 Dugatkin, L. A. 1992 Sexual selection and imitation: females copy the mate choice of others. *Am. Nat.* **139**, 1384–1389. (doi:10.1086/285392)
43 Dugatkin, L. A. & Godin, J. 1992 Reversal of female mate choice by copying in the guppy (*Poecilia reticulata*). *Proc. R. Soc. Lond. B* **249**, 179–184. (doi:10.1098/rspb.1992.0101)
44 Dugatkin, L. A. & Godin, J. 1993 Female mate copying in the guppy (*Poecilia reticulata*)—age-dependent effects. *Behav. Ecol.* **4**, 289–292. (doi:10.1093/beheco/4.4.289)
45 Witte, K. & Ryan, M. J. 2002 Mate choice in the sailfin molly (*Poecilia latipinna*) in the wild. *Anim. Behav.* **63**, 943–949. (doi:10.1006/anbe.2001.1982)
46 Plath, M., Blum, D., Tiedemann, R. & Schlupp, I. 2008 A visual audience effect in a cavefish. *Behaviour* **145**, 931–947. (doi:10.1163/156853908784089225)
47 Stanley, E. L., Kendal, R. L., Kendal, J. R., Grounds, S. & Laland, K. N. 2008 The effects of group size, rate of turnover and disruption to demonstration on the stability of foraging traditions in fish. *Anim. Behav.* **75**, 565–572. (doi:10.1016/j.anbehav.2007.06.014)
48 Lachlan, R. F., Crooks, L. & Laland, K. N. 1998 Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Anim. Behav.* **56**, 181–190. (doi:10.1006/anbe.1998.0760)
49 Day, R. L., MacDonald, T., Brown, C., Laland, K. N. & Reader, S. M. 2001 Interactions between shoal size and conformity in guppy social foraging. *Anim. Behav.* **62**, 917–925. (doi:10.1006/anbe.2001.1820)

50 Henrich, J. & Boyd, R. 1998 The evolution of conformist transmission and between-group differences. *Evol. Hum. Behav.* **19**, 215–242. (doi:10.1016/S1090-5138(98)00018-X)

51 Templeton, J. J. & Giraldeau, A. 1996 Vicarious sampling: the use of personal and public information by starlings in a simple patchy environment. *Behav. Ecol. Sociobiol.* **38**, 105–114. (doi:10.1007/s002650050223)

52 Coolen, I., Van Bergen, Y., Day, R. L. & Laland, K. N. 2003 Species difference in adaptive use of public information in sticklebacks. *Proc. R. Soc. Lond. B* **270**, 2413–2419. (doi:10.1098/rspb.2003.2525)

53 Webster, M. M. & Hart, P. 2006 Subhabitat selection by foraging threespine stickleback (*Gasterosteus aculeatus*): previous experience and social conformity. *Behav. Ecol. Sociobiol.* **60**, 77–86. (doi:10.1007/s00265-005-0143-3)

54 Harcourt, J. L., Biau, S., Johnstone, R. & Manica, A. 2010 Boldness and information use in three-spined sticklebacks. *Ethology* **116**, 440–447.(doi:10.1111/j.1439-0310.2010.01757.x)

55 FitzGerald, G. J. & Wooton, R. J. 1996 The behavioural ecology of sticklebacks. In *Behaviour of teleost fishes* (ed. T. J. Pitcher), pp. 537–572, 2nd edn. London, UK: Chapman & Hall.

56 Hoogland, R. D., Morris, D. & Tinbergen, N. 1957 The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as a means of defence against predators (*Perca* and *Esox*). *Behaviour* **10**, 205–237. (doi:10.1163/156853956X00156)

57 van Bergen, Y., Coolen, I. & Laland, K. N. 2004 Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proc. R. Soc. Lond. B* **271**, 957–962. (doi:10.1098/rspb.2004.2684)

58 Kendal, J. R., Rendell, L., Pike, T. & Laland, K. N. 2009 Nine-spined sticklebacks deploy a hill-climbing social learning strategy. *Behav. Ecol.* **20**, 238–244. (doi:10.1093/beheco/arp016)

59 Schlag, K. H. 1998 Why imitate and if so, how? A boundedly rational approach to multi-armed bandits. *J. Econ. Theory* **78**, 130–156. (doi:10.1006/jeth.1997.2347)

60 Hoppitt, W. J. E. & Laland, K. N. 2008 Social processes influencing learning in animals: a review of the evidence. *Adv. Study Behav.* **38**, 105–165. (doi:10.1016/S0065-3454(08)00003-X)

61 Brown, G. E. & Chivers, D. P. 2006 Learning about danger: chemical alarm cues and predation risk assessment by fishes. In *Fish cognition and behaviour* (eds C. Brown, K. N. Laland & J. Krause), pp. 49–69. Oxford, UK: Blackwell Publishing.

62 Mazeroll, A. I. & Montgomery, W. L. 1995 Structure and organization of local migrations in brown surgeonfish (*Acanthurus nigrofuscus*). *Ethology* **99**, 89–106. (doi:10.1111/j.1439-0310.1995.tb01091.x)

63 McGrew, W. 2004 *The cultured chimpanzee*. Cambridge, UK: Cambridge University Press.

64 Reader, S. M. & Laland, K. N. 2000 Diffusion of foraging innovation in the guppy. *Anim. Behav.* **60**, 175–180. (doi:10.1006/anbe.2000.1450)

65 Swaney, W., Kendal, J. R., Capon, H., Brown, C. & Laland, K. N. 2001 Familiarity facilitates social learning of foraging behaviour in the guppy. *Anim. Behav.* **62**, 591–598. (doi:10.1006/anbe.2001.1788)

66 Reader, S. M., Kendal, J. R. & Laland, K. N. 2003 Social learning of foraging sites and escape routes in wild Trinidadian guppies. *Anim. Behav.* **66**, 729–739. (doi:10.1006/anbe.2003.2252)

67 Bshary, R. 2001 The cleaner fish market. In *Economics in nature* (eds R. Noë, J. van Hooff & P. Hammerstein), pp. 146–172. Cambridge, UK: Cambridge University Press.

68 Wirtz, P. 1996 Werkzeuggebrauch bei Lippfischen. *Aquar. Terr. Z.* **1**, 4–5.

69 Millinski, M. 1987 Tit for tat in sticklebacks and the evolution of cooperation. *Nature* **325**, 433–435. (doi:10.1038/325433a0)

70 Croft, D. P., James, R., Thomas, P. O. R., Hathaway, C., Mawdsley, D., Laland, K. N. & Krause, J. 2005 Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata*). *Behav. Ecol. Sociobiol.* **59**, 644–650. (doi:10.1007/s00265-005-0091-y)

71 Rendell, L. *et al.* 2010 Why copy others? Insights from the social learning strategies tournament. *Science* **328**, 208–213. (doi:10.1126/science.1184719)

72 Leadbeater, E. & Chittka, L. 2007 The dynamics of social learning in an insect model, the bumblebee (*Bombus terrestris*). *Behav. Ecol. Sociobiol.* **61**, 1789–1796. (doi:10.1007/s00265-007-0412-4)

73 Webster, M. M. & Laland, K. N. 2010 Reproductive state affects reliance on public information in sticklebacks. *Proc. R. Soc. B* **278**, 619–627. (doi:10.1098/rspb.2010.1562)

74 Curio, E. 1988 Cultural transmission of enemy recognition by birds. In *Social learning: psychological and biological perspectives* (eds T. Zentall & B. G. Galef), pp. 75–97. Hillsdale, NJ: Lawrence Erlbaum.

75 Laland, K. N. & Plotkin, H. C. 1991 Excretory deposits surrounding food sites facilitate social learning of food preferences in Norway rats. *Anim. Behav.* **41**, 997–1005. (doi:10.1016/S0003-3472(05)80638-4)

76 Laland, K. N. & Plotkin, H. C. 1993 Social transmission of food preferences amongst Norway rats by marking of food sites, and by gustatory contact. *Anim. Learn. Behav.* **21**, 35–41.

77 Lefebvre, L. & Palameta, B. 1988 Mechanisms, ecology, and population diffusion of socially-learned food-finding behaviour in feral pigeons. In *Social learning: psychological and biological perspectives* (eds T. Zentall & B. G. Galef), pp. 141–164. Hillsdale, NJ: Lawrence Erlbaum Associates.

78 Reader, S. M., Hager, Y. & Laland, K. N. 2011 The evolution of primate general and cultural intelligence. *Phil. Trans. R. Soc. B* **366**, 1017–1027. (doi:10.1098/rstb.2010.0342)

79 Laland, K. N. 2004 Social learning strategies. *Learn. Behav.* **32**, 4–14.

80 Kendal, R. L., Coolen, I., van Bergen, Y. & Laland, K. N. 2005 Tradeoffs in the adaptive use of social and asocial learning. *Adv. Stud. Behav.* **35**, 333–379. (doi:10.1016/S0065-3454(05)35008-X)

81 Wilson, A. C. 1985 The molecular basis of evolution. *Sci. Am.* **253**, 148–157. (doi:10.1038/scientificamerican1085-164)

82 Reader, S. M. & Laland, K. N. 2002 Social intelligence, innovation and enhanced brain size in primates. *Proc. Natl Acad. Sci. USA* **99**, 4436–4441. (doi:10.1073/pnas.062041299)

83 Whiten, A. & van Schaik, C. P. 2007 The evolution of animal 'cultures' and social intelligence. *Phil. Trans. R. Soc. B* **362**, 603–620. (doi:10.1098/rstb.2006.1998)

84 Enquist, M., Strimling, P., Eriksson, K., Laland, K. & Sjostrand, J. 2010 One cultural parent makes no culture. *Anim. Behav.* **79**, 1353–1362. (doi:10.1016/j.anbehav.2010.03.009)

85 Tomasello, M. 1994 *Chimpanzee cultures* (ed. R. Wrangham *et al.*), pp. 301–317. Cambridge, MA: Harvard University Press.

86 Laland, K. N., Odling-Smee, F. J. & Myles, S. 2010 How culture has shaped the human genome: bringing genetics and the human sciences together. *Nat. Rev. Genet.* **11**, 137–148. (doi:10.1038/nrg2734)

87 Odling-Smee, F. J., Laland, K. N. & Feldman, M. W. 2003 *Niche construction: the neglected process in evolution.* Monographs in Population Biology, 37. Princeton, NJ: Princeton University Press.