

Association for the Study of Animal Behaviour (ASAB) Winter Meeting 3-4th December 2015
Zoological Society of London, Regents Park

Social Learning and Culture

<http://synergy.st-andrews.ac.uk/solace/asab-winter-conference-2015/>

Programme (see below for talks abstracts)

ASAB Day 1 Thursday 3rd December 2015

- 09.00 Reception Desk open.
10.00 Introductory remarks: Kevin Laland
10.05 Plenary Talk: Luke Rendell (St Andrews).
"The cultural lives of cetaceans"
10.50 COFFEE
CHAIR – Marc Feldman (Stanford)
11.15 Etienne Danchin (Toulouse) (with A C Dagaëff, A Pocheville, S Noebel, & G Isabel).
"Cultural transmission in *Drosophila melanogaster*"
11.40 Rose Thorogood (Cambridge) (with N B Davies).
"Cuckoo host assess risk by integrating personal and social information"
12.05 Will Swaney (Liverpool) (with S M Reader).
"Population variation in social learning in fish: A case for adaptive specialization?"
12.30 Award of ASAB Medal: Professor Pat Monaghan, University of Glasgow
12.35 LUNCH
CHAIR – Lars Chittka (QMU London)
14.15 Plenary Talk: Thomas Bugnyar (Vienna).
"Social information transfer in corvids"
15.00 Ellen Garland (St Andrews) (with L Rendell, M M Poole & M J Noad).
"Song learning in humpback whales: Lessons from song hybridisation events during
revolutionary song change"
15.25 Tore Slagsvold (Oslo).
"On the significance of early social learning in titmice"
15.40 TEA
CHAIR – Neeltje Boogert (St Andrews/Cambridge/Oxford)
16.10 Nicole Creanza (Stanford) (with L Fogarty & M W Feldman).
"Correlated evolution of song repertoire size, mate choice, and learning modes"
16.35 Corina Logan (Cambridge) (with A J Breen, A H Taylor, R D Gray & W J E Hoppitt).
"How New Caledonian crows solve novel foraging problems and what it means for cumulative
culture"
17.00 Alex Thornton (Exeter) (with E Zwirner).
"Cognitive requirements of cumulative culture: Teaching is useful but not essential"
17.25 Posters and wine reception
19.00 Leave: Dinner with speakers

Overleaf: ASAB Day 2

ASAB Day 2 Friday 4th Dec

- 09.30 Reception Desk Open
- 10.00 Introductory remarks: Andy Whiten
- 10.05 Plenary Talk: Elli Leadbeater (London).
“Insights about social learning from the insect world”
- 10.50 Coffee
- CHAIR – Alex Thornton (Exeter)
- 11.15 Sylvain Alem (London) (with C J Perry, X Zhu, T Ingraham & L Chittka)
“Learning the ropes: Social spread of string pulling in an insect”
- 11.40 Noa Truskanov (TelAviv) (with A Lotem).
“Social learning of foraging techniques by young house sparrows: Observational learning or stimulus enhancement?”
- 12.05 Claudio Tennie (Birmingham) (with A Acerbi).
“The neglected factor of cultural stabilization: Redundant copying”
- 12.30 LUNCH
- CHAIR – Tim Birkhead, ASAB President (Sheffield)
- 14.00 Tinbergen Lecture: Prof Nina Wedell (Exeter)
“Sex, conflict and selfish genes”
- CHAIR – Hal Whitehead (Dalhousie)
- 15.00 Nina Kniel (Germany) (with S Bender, C Dürler, V Heinbach & K Witte).
“Sex-specific use of public information in zebra finches”
- 15.25 Marco Smolla (Manchester) (with T Galla, T Gilman, S Shultz).
“Competition resources can explain patterns of social and individual learning”
- 15.40 TEA
- CHAIR – Rachel Kendal (Durham)
- 16.10 Lucy Aplin (Oxford) (with R McElreath & B Sheldon)
“Cultured Birds? The interaction between individual-level learning rules and group-level processes in the emergence and resilience of cultural behavior”
- 16.35 Neeltje Boogert (Oxford) (with D R Farine & K A Spencer)
“Early life stress triggers juveniles to switch social learning strategies”
- 17.00 Hal Whitehead (Dalhousie).
“Gene-culture coevolution in whales”
- 17.25 Closing remarks: Kevin Laland & Andy Whiten

NB “Back to back” Primate Society of Great Britain Winter Meeting,
2nd December 2015
Zoological Society of London, Regents Park

Primate Social Learning and Culture

<http://synergy.st-andrews.ac.uk/solace/psgb-winter-conference-2015/>

ASAB Winter Meeting Talks Abstracts (alphabetical, by speaker name)

Learning the ropes: Social spread of string pulling in an insect

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Social learning is accepted to be widespread among animals and can enable novel behaviours to spread between individuals. Pollinating insects can acquire flower preferences from each other's, but robust tests of social intelligence would require an observation of copying behavioural routines that are not part of the normal behavioural repertoire. As an example of such routines, string-pulling tasks have long been used to assess cognitive abilities in comparative psychology. We present experimental evidences of the acquisition of such a technique through social learning in an insect, the bumblebee (*Bombus terrestris*). We used a stepwise protocol to train bumblebees to solve a string-pulling task in order to obtain a reward, and 82% of the bees successfully learned the technique. We subsequently explored whether this newly acquired technique could spread socially through demonstration-observation. Only 11% of naïve bees spontaneously solved a string-pulling task, but after observing a trained demonstrator from a distance, 60% of the bee tested with the string task obtained the reward. In providing the first experimental demonstration of social learning of novel and non-ecological behaviour in insects, our results also suggest that the miniature brains of bees might possess the essential cognitive prerequisites for culture.

Cultured Birds? The interaction between individual-level learning rules and group-level processes in the emergence and resilience of cultural behaviour.

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To what extent socially learnt behaviours are transmitted, spread and persist will be partly determined by the adaptive use of social learning strategies. However while multiple learning strategies have been identified in animals, how these learning biases co-occur within populations or vary between individuals is rarely considered. Here we use cultural diffusion experiments in wild parids to investigate the interaction between two adaptive learning strategies that are potentially important in cultural evolution: pay-off biased learning and frequency-dependent learning. We show that a) parids use conformist social learning when acquire novel foraging techniques; b) this leads to the establishment of group-level traditions; and c) when techniques differ in their pay-off, populations adaptively shift to the more rewarding behaviour. In order to investigate the mechanisms underpinning these group-level patterns, we apply statistical models to estimate learning rules for each individual. We find that while most individuals are conformist, individuals vary in their degree of bias. This variation, combined with heterogeneous social structure and personal reinforcement, allows more adaptive information to invade otherwise resilient traditions. We thus provide experimental evidence for cultural behaviour in wild birds, examine individual variation in learning strategies, and explore the effect of such variation on population-level outcomes.

Plenary Talk
Social information transfer in corvids

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Social learning has been studied in a variety of species, focusing on questions about mechanism, function and evolution. We are currently experiencing a new wave of research that profits from recent advancements in methods and techniques. Focusing on birds, I here review some of these developments that, in my opinion, offer the opportunity for both i) integrating different levels of analysis within social learning research; and ii) combining questions of social learning with those of cognition and personality research. Specifically, I argue that birds provide an excellent model group for taking into account cognitive capacities and social constraints, as well as consistent individual differences/preferences in understanding mechanisms and patterns of information transmission. I advocate the use of the comparative approach in phylogenetically closely and distantly related species, in order to back up or avoid taxon-specific interpretations.

Correlated evolution of song repertoire size, mate choice, and learning modes

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Birdsong is a complex cultural and biological system, and the selective forces driving evolutionary changes song vary considerably among species. Studies to date have provided conflicting evidence regarding the extent to which syllable repertoire size is subject to sexual selection. In particular, females seem to prefer males with large repertoires in laboratory studies, but field studies have not consistently supported the hypothesis that repertoire size influences mate choice. However, some bird species crystallize their song repertoire before the first breeding season, whereas others continue to learn in adulthood. Repertoire size might be a better indicator of male fitness in species with open-ended learning. We re-reviewed the literature on mate choice and repertoire size with this distinction between open-ended and closed-ended learning in mind. We then use theoretical approaches to demonstrate that culturally transmitted song can be a niche-constructing trait, influencing the spread of other traits that are likely to have genetic underpinnings, such as those that affect neural development and mating preferences. Further, we perform phylogenetic analyses of repertoire size and learning mode across several families of songbirds and find evidence for correlated evolution: the rate of evolution of repertoire size is significantly higher in clades with open-ended learning.

Cultural transmission in drosophila melanogaster

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Animal culture is the part of phenotypic variation that is transmitted across generations through social learning. The literature identified four criteria that need to be fulfilled to demonstrate that a trait is inherited culturally. These criteria are 1) trait expression is acquired by some sort of "social learning", 2) such social transmission has a vertical component (i.e. occurs from older to younger individuals), 3) socially learned information is memorized for long enough to allow further social transmission (durability of socially learned information), and 4) socially learned information is generalized to similar situations (rule transmission). We adopted the most demanding definition of culture by only considering as culturally transmitted those traits that meet these four criteria simultaneously. We tested them in *Drosophila melanogaster* and found that female sexual preferences meet the four of them. However, a simple model showed that these four criteria are not sufficient to produce long bouts of cultural traditions of preferring a given male phenotype in a population. Such traditions only emerged after adding the fifth criterion that females learn to prefer one male phenotype in a conformist way (i.e. learning the preference of the majority). We then demonstrated that *drosophila* female sexual preference also verify this last criterion by ignoring rates of errors up to at least 33%. We conclude that *drosophila* have all the cognitive capacities to culturally transmit sexual preferences vertically, a trait potentially strongly impacting evolution. Cultural inheritance may thus have long been a major evolutionary process in a vast array of taxa.

Early-life stress triggers juveniles to switch social learning strategies

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In many species, juveniles use information provided by others to acquire essential skills. They can learn from peers (horizontal social learning), their parents (vertical social learning), or other adults (oblique social learning). So whom do juveniles choose to copy? We found that juvenile zebra finches socially learned novel foraging skills exclusively from adults. However, whether they copied their parents or unrelated adults was determined by their early-life experiences. We experimentally manipulated exposure to developmental stress by feeding half of the chicks in each of thirteen broods with stress hormones, while siblings received a control treatment. Once juveniles reached nutritional independence, we released them and their parents with other families into free-flying aviaries. While control juveniles learned novel foraging skills from their parents, their developmentally stressed siblings learned exclusively from unrelated adults. Thus, early-life stress triggered individuals to switch strategies from vertical to oblique social learning. Furthermore, a similar switch was observed in vocal learning strategies, where developmentally stressed juveniles were far less likely than their control siblings to copy their fathers' songs. Such alternative social learning strategies may allow developmentally stressed juveniles to avoid copying poor-quality role models and help them acquire more adaptive behaviours.

Song learning in humpback whales: Lessons from song hybridisation events during revolutionary song change

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Humpback whale songs are one of the most startling examples of transmission of a cultural trait and social learning in any non-human animal. Here, we investigate extremely rare cases of song hybridisation, where parts of an existing song are spliced with a novel, revolutionary song, to understand how songs are learnt. Song unit sequences were extracted from over 800 phrases recorded during a song revolution (French Polynesia 2005), to allow fine-scale analysis of composition and sequencing. Clustering of song sequences (i.e., phrases) using the Levenshtein distance indicated songs clustered into three song types; a single hybrid phrase was identified representing the transition of one singer between two of these song types. A predictive model was fitted to the data and tested against the only other known recordings of humpback song hybridisation: the eastern Australia 1996-97 song revolution. Songs change during revolutions through combining multiple complete phrases and themes from one song type, before transitioning through a hybrid phrase into the phrases and themes of a second song type. These extremely rare snapshots of song change represent the only known examples of song learning in over 20 years of data, spanning five populations of humpback whales where song revolutions occur.

Sex-specific use of public information in zebra finches

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The use of public information in mate choice is widespread throughout the animal kingdom. An individual can gather public information about the quality of potential mates by observing a sexual interaction of its conspecifics. Thereby, it can copy the mate choice of the observed individual. However, if the observer is detected by the observed individuals, this could influence their behaviour, called audience effect. We performed separate experiments for mate-choice copying and the audience effect in both sexes of the zebra finch (*Taeniopygia guttata castanotis*) to investigate possible sex-specific aspects in the use of public information. For our experiments, we used artificial ornamentation to distinguish between genetically based preferences and those based on public information. We found that female zebra finches showed mate-choice copying for males of the observed phenotype, whereas males did not. Further, we found that male zebra finches showed an audience effect in the context of mate choice as a change of preference, whereas females did not change their preference, but showed a general decrease in choosing motivation in the presence of a same-sex audience. Therefore, we found a sex-specific use of public information in the context of mate choice in the zebra finch.

Plenary Talk
Insights about social learning from the insect world

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The insects have been latecomers to social learning research, perhaps because their learning abilities were once considered minimal, or because social learning was thought cognitively demanding. We now know that neither supposition holds entirely true, and numerous recent studies have highlighted social learning across the Hymenoptera, Diptera, Orthoptera and beyond. Insect worlds bring much more to the study of social learning than a simple widening of taxonomic scope, because they offer both types of social information and social environments that are rare or non-existent elsewhere. For example, in eusocial groups, social information has repeatedly evolved into signals, which provide tractable, easily manipulated natural tests of social learning theory. Here, I will discuss how natural selection shapes such systems to produce animals that rely on social information when it is useful and ignore it when it is not. Understanding the mechanisms behind flexible social information use is a major focus in the field of social learning, and I will argue that the potential contribution of insect societies is only just beginning to be realized.

How New Caledonian crows solve novel foraging problems and what it means for cumulative culture

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New Caledonian crows make and use tools and tool types vary over geographic landscapes. It is unknown to what degree social learning accounts for the maintenance of these designs. Indeed, little is known about the mechanisms these crows use to obtain information from others, despite the questions importance in understanding whether tool behaviour is transmitted via social, genetic, or environmental means. For social transmission to account for tool type variation, copying must utilise a mechanism that is action specific as well as context specific. To determine whether crows can copy a demonstrator's actions as well as the contexts in which they occur, we conducted a diffusion experiment using a novel non-tool foraging task. Two groups had demonstrators and one group did not. We found that crows socially learn about context: after observers see a demonstrator interact with the task, they are more likely to interact with the same parts of the task. In contrast, observers did not copy the demonstrator's specific actions. Our results suggest it is unlikely that observing tool-making behaviour transmits tool types. We suggest it is possible that tool types are transmitted when crows copy the physical form of the tools they encounter.

Plenary Talk
The cultural lives of cetaceans
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Our understanding of the evolution of social learning and culture is deepened by incorporating information from as wide a range of taxa as possible. In recent years evidence has accumulated that points to the major role of cultural transmission in the development of behaviour in cetaceans. Culture features in vocal communication, foraging tactics, habitat use and sexual selection across those species that have been best studied. I will illustrate this by presenting details of two areas of research. The first encompasses long-term studies of sperm vocal dialects from the Pacific and Atlantic Oceans and the 'island' population that lives in the Mediterranean Sea, exploring how multiple levels of their hierarchical social structure can be identified through variations in acoustic signals. The second focuses on the multiple roles of cultural transmission in humpback whale populations, illustrating how it allows them to adapt to ecological shifts and also how we are beginning to explore the transmission dynamics behind the remarkable wave-like propagation of songs across the South Pacific Ocean. Both examples derive from relatively well-studied species, and few cetacean species have featured in more than a handful of papers on behaviour, so there is an untapped potential for comparative insight within this group on questions ranging from the role of social learning in the evolution of individual vocal labels to the interaction between culture and the evolution of menopause.

On the significance of early social learning in titmice
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Animals may acquire knowledge from others which is often manifested in behavioural traditions within populations that persist across generations. Social learning may help to cope with a fluctuating environment in a way that involves complex social interactions and contributes to cognitive evolution. In birds, there is ample opportunity for social learning because parents often provide care for the offspring for several weeks, and the juveniles may join flocks where social learning can continue. We aimed to study the significance of early social learning by using an avian model system in the wild, where we let the offspring of one species (blue tit) be raised by another species (great tit), and vice versa. This has let us study the significance of early social learning for a number of behaviours, including brood parasitism, sexual imprinting and hybridization, song, nest site selection, and foraging. I will summarize our main findings from 20 years of research, and present some new results on parental food provisioning of the offspring.

Competition for resources can explain patterns of social and individual learning in nature

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In nature, animals often ignore socially available information despite the multiple theoretical benefits of social learning over individual trial-and-error learning. Using information filtered by others is quicker, more efficient and less risky than randomly sampling the environment. Most previous models explain mixed learning strategies found in nature by penalising the quality of socially derived information (outdated, costly, poor fidelity). Competition for limited resources provides a compelling, yet hitherto overlooked, explanation for the evolution of mixed learning strategies. We present a novel model of social learning that incorporates competition and demonstrate that social learning is favoured when competition is weak, or when resource quality is highly variable but predictable. Surprisingly, the frequency of social learning in our models always evolves until it reduces the mean foraging success of the population. Additionally, we use the new framework to also investigate how population structure affects the success of social learning. Preliminary results indicate that the use of social learning is degree-dependent in random graphs, whereas small world networks generally support social learning. In combination with our previous results this will help us understanding how cumulative culture, an extreme form of social learning only found in humans, could evolve in a competitive world.

Population variation in social learning in fish: A case for adaptive specialization?

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While social learning can facilitate the acquisition of novel and beneficial behaviour patterns, it can also carry numerous costs, such as increased competition with conspecifics or the acquisition of disadvantageous behaviour. Such costs and benefits are likely to vary across environments, potentially resulting in population differences in social learning propensities. An open question is whether such population differences in social learning are domain-general or instead reflect specialization to particular contexts. To address this question, we compared social learning propensities in two feral populations of guppies established 20 years ago in two semi-natural pools. In one pool guppies have abundant food but are exposed to predators, in the other food is limited but predators are absent. We investigated how guppies living in these different habitats socially learn in two ecologically-relevant contexts, foraging and escape. Social learning was apparent in both populations, depending on context: predator-exposed guppies were superior at socially learning escape routes, while food-limited guppies were superior at socially learning feeding sites. These differences suggest adaptive specialization of social learning propensities to local environmental conditions and indicate that subtle and potentially adaptive population differences in social learning can emerge over relatively short timescales.

The neglected factor of cultural stabilization: Redundant copying

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Human culture at time B is very similar to culture at time A. How do we achieve such fidelity despite the fact that human culture presents complex behaviour which would not even exist outside a cultural context? As a solution we present a neglected factor of cultural stabilization: “redundant copying”. We define redundant copying as the ability to perceive, memorize and exploit multiple layers of information at once (i.e. even after single demonstrations). For example, a redundant copier might exploit action and results information at once (i.e., simultaneous imitation as well as emulation). Using an individual based model, we show that redundant copying outperforms several variants of non-redundant copying (e.g., non-redundant copying with repeated demonstrations over time or non-redundant copying with increased fidelity). Our results are also robust in light of different cost functions that might underlie redundant copying (e.g., higher costs for additional brain tissue). In addition, we show how our model either evolves toward human-like states (i.e. towards redundant copying) or towards non-human great ape like states (i.e. without redundant copying). We believe redundant copying is and was key to explain human cultural stability a necessary precursor to cumulative cultural evolution.

Cognitive requirements of cumulative culture: Teaching is useful but not essential.

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The cumulative nature of human culture is unique in the animal kingdom. Progressive improvements in tools and technologies have facilitated humanity’s spread across the globe and shaped human evolution, but the cognitive mechanisms enabling cultural change remain unclear. We show that, contrary to theoretical predictions, cumulative improvements in tools are not dependent on specialised, high-fidelity social learning mechanisms. Participants were tasked with building a basket to carry as much rice as possible using a set of everyday materials and divided into treatment groups with differing opportunities to learn asocially, imitate, receive teaching or emulate by examining baskets made by previous chain members. Teaching chains produced more robust baskets, but neither teaching nor imitation were strictly necessary for cumulative improvements; emulation chains generated equivalent increases in efficacy despite exhibiting relatively low copying fidelity. People used social information strategically, choosing different materials to make their baskets if the previous basket in the chain performed poorly. Together, these results suggest that cumulative culture does not rest on high-fidelity social learning mechanisms alone. Instead, the roots of human cultural prowess may lie in the interplay of strategic social learning with other cognitive traits including the ability to reverse engineer artefacts through causal reasoning.

Cuckoo hosts assess risk by integrating personal and social information

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Individuals often vary their defenses in response to perceived levels of predation or parasitism risk, but how do they assess such threat levels? In theory, information can be available either from personal experience, or from observing responses of others when personal information is costly to acquire. In nature, however, animals may do best by integrating both information sources. Recent work shows that hosts of brood parasitic cuckoos fine-tune their behaviour to best match spatial and temporal variation in parasitism risk. How do they 'know' when to risk rejecting a potential cuckoo egg from the nest, especially when it resembles their own? We used field experiments to test if reed warblers, hosts of the common cuckoo, rely on their own experience with cuckoos, pay attention to the behaviour of their neighbors', or instead combine these sources of personal and social information. We found that only when alerted by both social and personal information of local cuckoo activity did individuals reject an egg. We suggest that combining social and personal information for learning is likely to be common in the wild, as many animals that face varying levels of threat will have access to these two ways of obtaining information.

Social learning of foraging techniques by young house sparrows: Observational learning or stimulus enhancement?

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Social learning of foraging techniques is widespread among animals, but it is often not clear whether such learning is based on advanced processes, such as imitation, or on simpler mechanisms, such as stimulus enhancement. Using a two-action experimental design, we show that hand-reared house sparrows that follow a model of a mother demonstrator (a stuffed bird operated by the experimenter) were more likely to find seeds hidden under a leaf using the action demonstrated by the mother (either pushing the leaf or pecking it). This result suggests a role for imitation or observational learning. However, young sparrows exposed to the pushing demonstration were also much more likely to try to remove the leaf by pulling it with their beak, a behavior never demonstrated to them. This result suggests that learners paid attention to the contact area of the demonstrator's beak with the leaf, or to the resulted movement of the leaf, but not necessarily to the actions of the demonstrator. Put together, our study shows that positive results in a two-action experimental design cannot rule out fine-scale stimulus enhancement, which may in fact be indicated by the production of additional relevant actions that were not demonstrated.

Gene-culture coevolution in whales

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Culture has driven human evolution in important ways but gene-culture coevolution is rarely considered in non-humans, except cetaceans. Well-supported scenarios propose that cultural conservatism and xenophobia in orcas may have produced ecotypes that are behaviourally, ecologically and genetically distinct. However, as culture drives ecotypes into narrower niches, they become increasingly vulnerable. Orca evolution is thus a dynamic patchwork of ecotypes splitting, evolving, specializing and disappearing. The matrilineal species of toothed whale—in which females stay grouped with mothers—have mtDNA diversity about 10% of that in other whale species. I propose that this results from cultural hitchhiking in which selectively important cultural traits are shared by members of a matrilineal group. As these are transmitted in parallel with mitochondrial genes, the diversity of these functionally-neutral genes is reduced by a process analogous to genetic hitchhiking. Models show cultural hitchhiking can operate with multifaceted evolving cultures and some emigration between groups. New genomic data are consistent with cultural hitchhiking in sperm whales, although genetic signatures of bottlenecks and cultural hitchhiking are similar. I suspect that increasingly detailed behavioural observations together with powerful new genomic methods will reveal additional cases of gene-culture coevolution in cetaceans.