Poster **Vocal imitation in killer whales: A preliminary report**

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Socal learning in cetaceans has been reported for bottlenose dolphins (Tursiops truncatus) and recently for belugas (Delphinapterus leucas). Although previous observational evidence suggests that killer whales (Orcinus orca) are capable of vocal learning, the extent of the capacity for vocal imitation in this species has not been investigated experimentally. In this study we tested vocal imitative learning of sounds emitted by a conspecific and by a human in one killer whale. We used a 'do-as-I do' paradigm where the subject first listened to a conspecific demonstrator's performance that included 3 familiar and 3 novel sounds, and was asked to copy. The sounds were presented in two formats, performed by a killer whale model and played through a speaker. Then the subject also listened to 3 familiar and others 3 novel sounds, but now they were produced by a human demonstrator. The subject reached to copy all vocalisations emitted by both conspecific and human models for both familiar and novel sounds. This study provides experimental evidence for vocal learning imitation, including vocal production imitation in killer whales. The findings suggest that imitative learning may underpin some of the group-specific dialects through a process of cultural transmission reported in killer whales in the field.

Poster **An Experimental Test of Algae Scooping in Captive Chimpanzees**

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Wild chimpanzees in the Bossou community of south-eastern Guinea use tools to feed on aquatic algae. This behaviour has been suggested to demonstrate complex forms of social learning between individuals (Humle et al. 2011). In this study we presented two groups of naïve, captive chimpanzees with all the ecological materials of algae scooping to observe the origins and transmission methods of this behaviour. Naïve chimpanzees in both groups spontaneously used tools and a scooping technique very similar to their wild counterparts, despite never having been exposed to this behaviour before. This suggests that algae scooping is within the species Zone of Latent Solutions, or the behavioural limit to the solutions an individual can invent without any social learning. Thus, this tool-use behaviour will emerge spontaneously when individuals are provided with the appropriate ecological materials, and social learning probably only plays a minimal role. Further research into which tool-use behaviours are within chimpanzees Zone of Latent Solutions may also aid in informing our understanding on the evolution of early human material culture and cognition.

Poster **Evidence for dominance-biased social learning in wild vervet monkeys**

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Biases in whom animals learn from can have important implications for the spread of behaviours throughout social groups. Whilst previous studies have found biases towards copying dominant individuals over low-ranking individuals in captive primates (Horner et al. 2010; Kendal et al. 2014), this has yet to be shown in a wild population. By utilizing a novel methodology incorporating remote-controlled 'artificial fruits', we trained dominant and low-ranking females from each of three wild groups of vervet monkeys to prefer one colour of dyed apple whilst rejecting the other. These models then demonstrated their preferences to group members 50 times before the whole group was presented with large amounts of each colour of apple. Significant differences related to rank and social network were found in the composition of the audience for the females demonstrations. During the test phase, significantly more monkeys first chose the colour preferred by the dominant female in their group, than that preferred by the low-ranker (Binomial test, n=45, p=0.016). These results suggest a bias towards copying the foraging choices of dominant females over low-ranking females in wild vervet monkeys and provide the first evidence of a dominance based-bias in social learning in wild primates.

Paper **Why don't baboons have culture? Constraints on information transmission in wild baboon groups**

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The formation of culture in animal societies, including humans, relies on the social transmission of information among individuals in a group. While the cognitive capacities for social transmission of information appear to be present in a wide range of animal species, culture has only been described for handful of species. Whether or not a novel behaviour becomes adopted by an entire group to form a culture may depend on how individuals acquire and use social information. In this regard, two points are particularly important: (i) not all individuals will have the same opportunities to acquire social information because of differences in their social connections, and (ii) individuals may differ in their propensities to use such information once they have acquired it. In this study, we tested this hypothesis by introducing two novel tasks to groups of wild baboons. We investigated the effect of social network position, personality, dominance rank, age and sex on baboons' propensities to initially solve the task; opportunities to acquire social information about the task; and propensities to subsequently solve the task after having had opportunities to acquire social information. We discuss the implications of the results for the formation of culture in baboon groups.

Poster **Population-specific semantic shifts in wild chimpanzee auditory gestures. A case of observational learning?**

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"The vocal repertoire of great apes and other nonhuman primates seems highly constrained. We suggest that in several wild chimpanzee populations the meaning of specific auditory gestures has been modified (shifted) without changing the form of the gestures, resulting in new vocabulary items. This development would provide an alternative to creating additional vocalizations.We propose a scenario for the emergence of these population-specific semantic shifts, based on observational learning: the usage of an existing and generally used communicative signal (e.g., general attention-getters like leaf-clipping or knuckle-knocking) is reduced to and reliably associated with a specific context (e.g., display or sexual solicitation) within a population. That is to say, it is not the form of a signal that is learned but the use of an existing signal in a newly restricted context (contextual imitation). These shifts, resulting in new vocabulary items, would allow for more effective communication under specific social and ecological circumstances (e.g., time pressure on signalling, constrained vision) and thus might provide an adaptive benefit for sender and recipient. We examine the evidence for these shifts and propose possible benefits. Systematic studies are needed to determine the range and usage of the shifts in wild chimpanzees and other species."

Paper **Performance of bonobos and human children on a novel action copying task**

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A central question regarding the evolution of culture is whether humans are the only great apes who imitate novel actions when physical information is absent from demonstrations. To date, two studies with chimpanzees have addressed this problem, both with negative results. Here, we explored the imitative performance of our other closest living relative, the bonobo. We compared the performance of 3-5 year old children and bonobos (ranging from juvenile-adult) on a two-action copying task. The non-enculturated and untrained bonobos were housed at a forested African sanctuary. A human demonstrator performed two arbitrary actions on or next to a small box before opening it to reveal a reward. Both familiar and novel actions were used as targets. The majority of children performed at least one the observed actions whereas no bonobo of any age performed either of the observed actions. Instead, the bonobos attempted to open the box using species-typical methods (e.g. pounding, biting). These results provide evidence that highlights core differences in action copying between humans and our closest living relatives. The fact that these differences occurred with untrained bonobos living in a naturalistic environment further highlights the fundamental differences between the imitative capacities of humans compared to non-human apes.

Poster **Behavioural flexibility and conservatism in captive chimpanzees (Pan troglodytes): Building on an established foraging technique to improve efficiency**

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Whilst evidence for culture in non-human species continues to grow, there are few examples of cumulative culture outside of our own uniquely complex behaviours. The prerequisites for cumulative culture include not only the ability to build on established behaviours but also to relinquish old solutions and flexibly switch to more productive or efficient ones. Here, we established an inefficient solution to a foraging task in five captive chimpanzee groups (n = 19). In three groups a conspecific model seeded an alternative, more efficient solution to the same task. When participants could still successfully forage with their previously established behaviours, individuals did not switch to this more efficient strategy; however, when their foraging method became highly inefficient relative to the available alternative, chimpanzees with socially-acquired information (four of whom were exposed to additional human demonstrations) relinquished their old behaviours in favour of the more efficient method (One-tailed Wilcoxon signed-rank test: Z=-2.410, N=10, P

Paper **A new experimental approach probes cumulative cultures in young children**

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"Human culture is uniquely complex, with cumulative increases in technology occurring over generations. This results in products too complicated for any one individual to produce alone. Researchers interested in the evolution and development of cumulative culture have attempted to replicate cultural ratcheting in vitro by examining how groups of animals make small-scale improvements to their behaviour to gain better rewards. This experiment expands that methodology, applying it to a more complex environment than typically used in social learning experiments. Our small worlds' apparatus offers four different exits, at four increasingly difficult levels, which can be manipulated with a number of different tools to extract rewards. To test cumulative culture over generations a replacement transmission chain was run with four-five year old children (n=66). One child, of a group of three, was replaced every five minutes until an entirely new group of children was present, with each chain run for 20 minutes. While there was little evidence for cumulative improvements along these chains, there was success at more complex levels in some. Cultural differences did develop between groups (Mann-Whitney, p= 0.0054), suggesting this novel and complex approach may enable us to better explore children's social learning in the wild."

Paper **Temporal properties of social influence on nut cracking in wild bearded capuchin monkeys (Sapajus libidinosus): considering a new dimension of social learning**

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Social facilitation and local enhancement while watching another perform an activity play important roles in transmission and maintenance of tradition in animals. However, very little attention has been given to the dynamics of these effects. What happens after the demonstration ends? In the first study of the dynamics of social influence of a natural behavior in the wild, we collected data on bearded capuchins (Sapajus libidinosus) in a nut-cracking population. Using a novel method, we continuously recorded the behavior of 16 immature monkeys and the activity of their groupmates around them, focusing on interactions with nuts and stones. Young monkeys manipulated nuts and stones at rates about four times higher, and spent about three times more of their time near anvils, while others in the group cracked nuts around them compared to other times. Both effects declined exponentially in the minutes following the end of others' nut-cracking activity. Those dynamics differed in juveniles according to age, with the older juveniles showing a slower rate of decline. Regarding social input as a continuous influence akin to the effects of positive reinforcement will enable development of quantitative predictive models of social influence on the spread of behaviors.
Supported by National Geographic Society.

Paper **Young children do not copy the majority when doing so leads to over-imitation**

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"Objective: The human tendency to over-imitate causally irrelevant actions is a well-documented, puzzling and surprisingly robust experimental phenomenon. However, theoretical investigations suggest that we should be strategic about whom and what we copy. The tendency to copy the majority is considered a key strategy in the acquisition of effective and reliable behaviour. Here we test whether previous evidence for majority-biased copying in children extends to the adoption of irrelevant actions.

Methods: Children aged 4- to 6-years-old (N=260) were assigned to one of four experimental conditions, or a baseline control. In the experimental conditions, participants watched four demonstrators retrieving a reward from a puzzle box, before retrieving the reward themselves. The first condition determined whether children copied the majority when choosing between two causally equivalent relevant actions. In the remaining conditions, we systematically varied the number of demonstrators performing an irrelevant action. Results and conclusion: Children copied the majority when the majority solution was causally equivalent or more efficient than the minority solution. However, majority-biased copying disappeared when children witnessed a majority who demonstrated a less efficient solution than the minority. These findings emphasise the adaptive flexibility of social learning strategies and question the robustness of over-imitation in real-world settings."

Poster **The Social Brain Hypothesis: Are social woodpeckers bird-brains?**

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The Social Brain Hypothesis is well known for determining the positive relationship between group size and brain size in primates, however, in order to be an all-encompassing theory of the evolution of intelligence, the trend must be shown to exist in all animal taxa. Interestingly, previous research has found that, in birds, it is not social complexity but rather pair bonding that drives brain size differences. This research project addressed the hypothesis in a previously unstudied, homogenous and yet socially diverse bird family - woodpeckers (Picidae). After conducting phylogenetically corrected analyses on the relationship between sociality and relative cranial volume, no significant difference was found between pair bonded and simply monogamous or social species. However, a significant difference did emerge between social and monogamous species, suggesting that in this bird family, sociality allows birds to get away with having a smaller cranial capacity. As such, this research suggests that long-term pair bonding may not account for brain size differences across all bird families while also suggesting that social living may alleviate some of the cognitive demands of social species.

Paper **The influence of social tolerance on social learning in wild Malagasy primates**

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The social environment an animal lives in can facilitate social learning because social tolerance may positively influence the spread of information. In this study we compared the spread of social information between hierarchically organized ringtailed lemurs (Lemur catta) and comparatively more egalitarian redfronted lemurs (Eulemur rufifrons). We first operationalized social tolerance in a co-feeding experiment, revealing that redfronted lemurs were more socially tolerant. We therefore predicted that social learning of a new foraging technique would be facilitated in the more socially tolerant redfronted lemurs. To test this prediction, we presented four wild groups of redfronted lemurs and three groups of ringtailed lemurs with a feeding-apparatus that could be opened with two different techniques. In two groups of each species we trained a demonstrator to use one of the techniques. The probability of learning the task was higher in the more tolerant redfronted lemurs. Interestingly, in the presence of a demonstrator redfronted lemurs were less likely and ringtailed lemurs were more likely to learn the task. However, the presence of a demonstrator did not influence the speed of learning and redfronted lemurs learned the task more quickly. Thus, social tolerance indeed influences the spread of a new foraging-technique in these primates.

Paper **The driving forces of cultural complexity: non-humans, humans, and the question of population size.**

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The demographic and technological success of humans is often attributed to their capacity to generate increasingly complex technologies, and to accumulate large amounts of useful information that can be passed between individuals and between generations. However, exactly what has driven this cultural accumulation is hotly debated. At the heart of the debate is the question of what genetic, demographic, or social features of behaviourally modern humans (as opposed to, say, chimpanzees, Neanderthals, or even early humans) allowed culture to accumulate to such an unprecedented level. Answering this question would allow us to explain the emergence of human behavioural modernity, the changing rate of cultural evolution observed across human evolutionary history, and the variability in cultural complexity among modern human groups. Here we show, using both an analytical model and an agent-based simulation model, that a full understanding of the emergence of behavioural modernity, and cultural evolution more generally, depends on first understanding and untangling the complex relationships between culture, genetically-determined cognitive ability, and demography.

Paper **Testing the Cultural Intelligence Hypothesis in Orangutans: an Evolutionary Perspective**

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In order to explain human intelligence we need to understand its presence and causal mechanisms in animals. Here we present a study investigating the cultural intelligence hypothesis by using orangutans as a model taxon. Because intelligence is largely constructed developmentally, the cultural intelligence hypothesis focuses on the social inputs and opportunities for interacting with the physical environment during ontogeny. It predicts that the more of such inputs an individual experiences, the more learned skills it acquires, but also the better it gets at solving problems. This prediction can be tested at developmental and evolutionary time scales. First, the developmental perspective predicts differences between individuals depending on exposure to social learning experienced during a lifetime. Data from wild orangutans strongly support this idea in that more gregarious populations possess more enhanced skill sets and innovations. Moreover, is it supported by the difference we are observing between wild and captive orangutans, the latter exposed to artificially high social density as well as human social inputs. Second, from a evolutionary perspective species with systematically richer social environment may over time evolve to become more

intelligent, reflected by larger brain size. We performed an across zoo study on two closely related species; Sumatran, Pongo abelii (N=19) and Bornean, Pongo pygmaeus (N=13). The homogenous and similar environmental conditions provided by zoos should allow us to detect any intrinsic differences between these two species. At nine European zoos mother-reared orangutans were examined on their novelty response as well as their cognitive performance, in the form of a set of tasks assessing problem solving ability. Results suggest an intrinsic difference in how the two pongo species apply their learning ability, with Sumatrans being more likely to show necessary problem solving skills. Thus Pongo abelii may have experienced higher selection on learning mechanisms.

Paper **Long-term declarative memory for imitative actions in dogs**

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"Deferred imitation involves replicating an action after a delay, relying on declarative memory. This was shown in dogs after intervals up to 10 minutes (Fugazza and Miklósi 2014). In the present study we used the Do as I do paradigm combined with the two-action procedure to investigate on dog's (N=12) memory for imitative actions after intervals from 1 to 24 hours. Our results show that dogs' imitative performance does not differ significantly between dogs that are asked to imitate immediately and dogs that are asked to imitate after a delay (Likelihood ratio test of GLMMs: Ï‡2 = 2.68, df = 3, P = 0.443), suggesting presence of long-term declarative memory of imitative actions in dogs.We also assessed what information dogs (N=16) recall preferentially between the location where the demonstration is executed and the object manipulated by the demonstrator, by making spatial and object information incongruent, so that dogs can only match either the location or the object.

When they match the location, action matching performance decreases compared to when they match the object (GLMM of action matching, effect of condition: Ï‡2 = 59.70, df = 6, P < 0.0001), indicating that the object is an important cue for recall.

Paper **Similarities and differences etween motherese and doggerel. An acoustic analysis**

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There has been growing evidence that pet talk (doggerel) and infant directed speech (motherese) have similar acoustic characteristics such as high-pitch register, repetitiveness, and attention-getting devices. It is still unclear, however, whether doggerel and motherese have gender, age or context dependent acoustic and/or linguistic features. In the present study we collected infant directed (ID), dog directed (DD) and adult directed (AD) speech samples in four different speech situations (calling attention, object manipulation, teaching and predetermined sentences) from parents of 0-30 months old infants (N=20 mother-father pairs) who also had pet dogs. In agreement with earlier findings we found that AD signals are markedly different from ID and DD signals, while there are only minor differences between the latter two. Both ID and DD signals were characterized by a higher fundamental frequency mean (F0) compared to AD in both female and male participants independently of context. However, women exhibited a higher F0 range in their DD compared to AD speech samples whereas men used the same F0 range towards dogs and adults. Interestingly, the acoustic features of the DD speech are more similar to that of used towards 19-30 month-old babies than ID speech toward younger ones. (Supported by OTKA K-112138).

Paper **Not all cues are created equal: how picky eaters are influenced by social cues, but fearful birds are not**

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In human-disturbed environments, animals encounter novel foods and novel threats. Individuals can vary in response to new foods by either consistently consuming them (Adventurous Consumers; AC), or refusing to incorporate them into their diet despite repeated feeding opportunities (Dietary Conservative consumers; DC). Individuals also vary in how willing they are to take risks. We investigated whether a wild population of individually-marked jackdaws (Corvus monedula) had distinct classes of AC and DC individuals, and whether social cues guided food choices and approaching threatening stimuli. We presented groups of birds with combinations of novel and familiar food types placed in risky and non-risky locations and measured how long they needed before approaching and consuming novel foods reliably. This the first study to look at dietary conservatism in corvids, a highly neophobic, but generalist forager. We found wild individuals varied in approaching and consuming novel foods, and varied in whether they ate in a risky location. Novel food choices were influenced by social cues, but social cues did not facilitate risky foraging. These results demonstrate that similar social cues may not equally facilitate behavior towards different types of novelty.

Poster **The role of social learning in structuring signature whistle characteristics of bottlenose dolphins.**

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The signature whistle is an individually distinctive whistle type within a dolphin's repertoire that broadcasts the identity of the owner. They are used to facilitate group cohesion and address conspecifics. Vocal learning plays an important role in signature whistle development whereby dolphins draw on their auditory experience of their acoustic environment, including whistles from con-specifics, to help generate an unique whistle contour. We conducted a large scale geographic comparison of bottlenose dolphin signature whistles to investigate how social learning, environmental factors, morphological or genetic variation explain differences in signature whistle repertoires between populations. We identified differentiation in a range of signature whistle characteristics between populations. Body length predicted most of the variability related to absolute and adopted frequency of signature whistles. In most populations, high degrees of divergence were detected in the frequency modulation pattern of whistle types, indicative of signature whistle development maximizing diversity for individual recognition. However in Zanzibar, most dolphins converged on an upsweep whistle type with subtle but consistent variation between individuals. Differing ecological and social pressures appear to drive the variation in modulation diversity observed at the population level, whereas morphological variation underlines the observed differences in other frequency parameters.

Paper **New trends in the animal culture debate: integrating ecological variation and representational perspective to understand how ape behavioural differences are connected to human cultures**

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The question of animal culture has been predominant in the social learning literature particularly during the last two decades, with ape data from both wild and captive groups making a substantial contribution to the debate. Today, the debate is no longer on whether apes have culture or not. Rather, empirical researchers and theorists now attempt to decipher how much ape cultures compare to the human phenomenon, and the evolutionary relatedness between the two phenomena. Here I will address some of the new trends in the debate and attempt to integrate them with more classic questions on animal culture. Specifically, while the debate has been mainly about social learning mechanisms up to now, researchers are now attempting to analyse both the influence of environmental variations and genetics on cultural behaviour. How ecology influences the appearance, maintenance and disappearance of cultural behaviour has therefore become a hotspot for research. Second, human cultures are inherently representative. Therefore, it appears necessary to evaluate this aspect in animal cultures through the adoption of a representational perspective, to allow uncovering the biological roots of human cultures. I will use data from both wild and captive wild-born apes to propose answers to these questions.

Paper **Innovation and flexibility in chimpanzees in response to a changing foraging task.**

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"Previous studies reported conservatism in chimpanzees' approach to foraging tasks (Hrubesch, et al. 2009; Marshall-Pescini & Whiten 2008). More recent work recorded apes responding to changing tasks with cumulative, progressive solutions (e.g. Lehner et al. 2011).

Captive chimpanzees at the Chimfunshi Wildlife Orphanage, Zambia, were offered an extractive foraging task consisting of a tube partially filled with juice, and a variety of tool materials including sticks and cloth. Chimpanzees could access the device as a group. After 10 hours of testing, the tube was made narrower, restricting available solutions. After a further 20 hours of this restricted condition, the most successfully used tool material was no longer provided, and the task was presented for a further 10 hours.

In one group an individual used a novel, combinatorial tool technique to extract juice in the restricted, narrow tube stage of the task. Two further individuals were then observed using this same technique, having observed the original innovator. When one tool component of this technique was no longer provided, one of these secondary individuals substituted an alternative material to solve the task. This minority of chimpanzees solved the novel task using a combinatorial tool technique, and flexibly modified it when circumstances required."

Paper **The neuromolecular correlates of social learning from informants of differing social rank**

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While our knowledge of the emergent properties of social influence in animals and humans is well established, the mechanisms by which social experience is translated into behavior are poorly understood. The neurobiological mechanisms that mediate social influence are effectively unknown, despite this being the primary cognitive link translating experience into behavior across taxa. We use the cichlid Astatotilapia burtoni, is a model system in social neuroscience, to investigate the neuromolecular mechanisms of social learning. Males of this species have distinct phenotypes – dominant and subordinate – and we use these different phenotypes to act as social informants in group association learning tasks. Although subordinate males are the least connected individuals in their social networks, groups led by these males learned most quickly - significantly faster than for dominant males or naive groups. We then used immunohistochemical analysis of immediate early gene (IEG) induction across brain regions important in learning and social behaviors, the putative homologs of the hippocampus (learning and memory), lateral septum (social interactions) and basolateral amygdala (emotional processing) to examine neural activation patterns when individuals learn from informants of differing social relationships.

Paper **An investigation of social learning through open diffusion in Orange-winged Amazon parrots**

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This study investigates the social transmission of a novel foraging technique in Orange-winged Amazon (OWA) parrots using an open diffusion technique. Data was collected on three separately-housed groups of captive parrots. A two-action artificial fruit was used to test whether subjects would be more likely to successfully open the apparatus if they had the opportunity to observe a competent demonstrator and, if so, whether they would be more likely to use the demonstrated method. Two experimental groups observed trained demonstrators open the apparatus door using either a pull (n = 15) or slide action (n = 22), while control groups (n = 17; n = 20) did not. Results showed that experimental parrots interacted significantly more with the box (26/37) than controls (3/37), with more experimental birds successfully opening the box (10/37) than controls (0/37). The demonstrated method (pull or slide) was not used significantly more than the non-demonstrated method by birds in the experimental groups. Although strong evidence of stimulus enhancement was found, there was no evidence that the OWAs imitated the demonstrated method. This study shows that when presented with a problem in a naturalistic group setting, stimulus enhancement and individual learning are sufficient to support problem solving.

Poster **Preliminary results from a computational multi agent modelling approach to study humpback whale song cultural transmission.**

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The empirical investigation of cultural transmission phenomena in the animal kingdom is often a challenging task, especially if carried out on wild populations with vast home ranges. Humpback whales (Megaptera novaeangliae) present a striking example of cultural transmission. Within a population, all males in acoustic contact conform to a similar song; however, this can disappear quickly if a new song is introduced. Our project aims to explore the mechanisms behind the cultural transmission of humpback whale songs using a computational multi-agent modelling approach. This methodology is used to simulate real-world phenomena using digital entities (agents) capable of interacting with each other following pre-determined rules. We created a spatially-explicit model in which agents (whales) move following simple rules derived from flocking algorithms. These rules are implemented to mimic migratory movements observed in the wild. While moving, agents sings their own song and learns other agents songs based on geographical distance and song similarity. Preliminary results suggest that parameters such as agent acoustic active space and breeding ground size influence the degree of population song conformity. Future work will address implementing different learning strategies, a more realistic representation of humpback whale song structure and the introduction of song innovation.

Paper **Competitive constraints on social information use**

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Animals are expected to collect and use social information in favour of personal information when the former facilitates more efficient acquisition of resources. However, the heterogeneous and uncertain nature of resource distribution that promotes social information use will also generate competition between individuals. Such competition may act to constrain or facilitate an individual's ability to use social information. We conducted a feeding experiment using wild chacma baboons (Papio ursinus) to investigate how an individual's freedom to access resources can affect its freedom to use social information. We demonstrate that constraints on an individual's ability to use social information, driven by low social rank, can have a strong impact on its performance relative to others. However, we also show that when resources exhibit some stability in their spatiotemporal distribution, individuals with low competitive ability can decouple their use of social information from the competitive context in which it was collected. Our experiment stresses the importance of considering the levels of competition and uncertainty faced by individuals as distinct but interdependent processes, underpinned by the spatiotemporal distribution of resources. Taking this approach will allow us to understand both the causes and consequences of individual constraints on social information use.

Paper **Emergent conformity in cumulative culture**

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Cumulative culture, the ability to progressively build on the achievements of previous generations, is possibly one of the key aspects that set human culture apart from non-human animal culture. We investigated the evolution and dynamics of cumulative culture in a realistic setting with a large-scale dataset of computer code resulting from a series of collaborative programming competitions run over a 15-year period. We were interested in the extent to which copying takes place, and its consequences on the diversity of culture. Results show that as improvement in complex tasks becomes progressively difficult, and valuable information accumulates, populations focus on copying and improving the current best entry. We observed patterns of convergence, punctuated by leaps from one idea to another. This convergence leads to a decrease in cultural diversity over time, as the population performs increasingly similar behaviours. When complex solutions are built over time through cumulative culture, conformity does not necessarily have to be the result of a complex cognitive process that drives individuals to copy the majority - it could simply be an emergent pattern in a population of individuals independently copying the best idea at the time. The question of whether this emergent conformity is optimally adaptive remains open.

Paper **Social learning and cooperation across societies**

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The human capacity to learn from others drives mankind's ecological success. Social learning facilitates accumulation of technological advances over time and can help solve collective action problems. Despite the importance of social learning for human adaptation and cooperation, its genetic and cultural determinants are poorly understood. While psychological surveys suggest that collectivism promotes conformist attitudes, it remains unclear whether and how culture shapes people's learning behaviour. Here we show with behavioural experiments conducted using collectivist (China) and individualist (UK) subject pools (total n=540) that social learning in cooperation settings strongly varies across societies. Chinese subjects base their cooperation decisions on peer information more often than British subjects. Moreover, our results reveal remarkable societal differences in the type of peer information that people consider. In a social dilemma situation, Chinese subjects tend to be success-oriented, adopting peer behaviour that leads to higher payoffs. By contrast, Western subjects are more frequency-oriented, cooperating only if sufficiently many peers do so as well. These differences indicate that the effects of social learning on the emergence and maintenance of group cooperation are largely culture-specific. Our study demonstrates that culture shapes learning strategies in cooperative settings and challenges the view that Eastern societies cultivate conformist behaviour.

Paper **Assessing Targeted Helping Behaviour and Mutualistic Cooperation in Bonobos and Chimpanzees**

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"Given that most research examining prosociality in nonhuman primates is focusing on chimpanzees and studies including the bonobo are scarce, we are specifically comparing bonobos with chimpanzees. Both species are differing on several types of behaviours such as social tolerance and stress reactivity, which are thought to influence expressions of prosociality. In this study, six bonobo and chimpanzee pairs are presented with an instrumental helping design to understand whether individuals are transferring tools to a conspecific. The level of cognitive complexity underlying such helping is additionally examined. More specifically, if helpers are able to demonstrate a self-other distinction, hence, understand that the other might need a different tool to the one currently needed by themselves. Behavioural measures of the recipient are taken to examine their relationship to the occurrence of tool sharing. By using an ABA design, we are first assessing whether helping is occurring even though no benefit results for the helper. Subsequently, while keeping the set up constant, the pairs are presented with a mutual cooperation task in which rewards can only be acquired by transferring the correct tool to the receiver. Finally, the A part is presented again to assess corresponding changes in the rate of helping.- This study is currently ongoing."

Poster **Exploring an associative account of imitation in children and capuchin monkeys (Sapajus apella**)

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The problem of how sensory information about an action performed by another is converted to a matching motor action has long vexed researchers. An associative account suggests sensorimotor experience may forge links between sensory and motor representations of the same action facilitating future imitation. Examining automatic imitation, the tendency of a perceived action to aid the performance of that action while interfering with incompatible action, we tested predictions of an associative account of imitation in human children and capuchin monkeys. In one study we trained monkeys to respond to an action stimulus with either the same action (imitation) or a different action (counter-imitation) and found that monkeys initially performed better when imitating. However, counter-imitation training abolished any subsequent imitative bias, highlighting the contribution of sensorimotor experience to action matching. A further study with children examined if previous sensorimotor experience influenced automatic imitation as predicted by an associative account. Using a stimulus-response compatibility procedure we found that actions children often perform in synchrony (e.g. clapping) showed greater automatic imitation effects when compared to actions for which experience of synchronous performance is likely to be more limited (e.g. pointing). These results support the idea that domain-general processes facilitate imitative ability in primates.

Paper **Whom should I copy? Biased social learning and the diffusion of innovations**

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"Many animals socially learn in order to develop and survive in their environment. When social learning is of high fidelity it can lead to the diffusion and maintenance of behaviours over many generations; the process of cultural transmission. Theory suggests that in order to be adaptive social learning should be used strategically. Copying specific individuals in a social group based on observable traits such as success, familiarity or age is a widely observed and well studied form of strategic social learning. These biases in social learning influence the transmission of behaviour in groups and are therefore likely to shape population level cultural patterns. Here we study the maintenance and diffusion of cultural traits as an emergent process of adaptive social learning in an evolutionary context. We present an agent-based simulation model of a difficult learning task in a complex, variable environment. Agents adopt different social learning strategies and compete to learn and exploit the most valuable behaviours. We show that a preference to copy the young and successful is particularly advantageous and can outweigh many other strategic decisions. Additionally we find that selection on learning behaviour leads to the emergence of cultural systems characterised by the rapid diffusion of innovations."

Poster **What do children learn through making together?**

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As they grow up, children everywhere develop skills and acquire knowledge under the influence of those around them. This way they become full participants in the social traditions of their group. And by participating in the social traditions they may preserve and change them over historical time. One way in which children may learn under social influence is by engaging hands-on in a playful activity of making an artefact together with a more skilled maker. This is similar to situations of apprenticeship but limited in its duration and formal commitment. In this study we ask what children learn when they participate in such an activity. The making activity we investigated is a modified version of a regular workshop that the Life Science Centre (Newcastle, UK) offers to local school groups and has been conducted by an instructor with children visiting the Centre in August 2015. We provide evidence that, in the activity, children may (1) become familiarised with novel tools and materials, and recognize their normative affordances; (2) learn how to operate a novel tool effectively; and (3) learn about the necessary steps to make an artefact (in this case, a vehicle) using simple materials.

Paper **Does social learning from multiple sources scaffold innovative tool-making in children?**

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Cumulative culture requires both the invention of novel traits (innovation) and the transmission of these traits between individuals (cultural transmission). Both innovation and cultural transmission have been investigated in children with regard to tool use, but the combination of these two abilities, namely the possibility that social learning might facilitate innovation, remains underexplored. Here, children were tested on their ability to modify a tool following a demonstration by one or two models, or in a baseline condition with no demonstration. Preliminary results suggest that children were able to combine two demonstrated techniques to construct a novel tool and retrieve a reward, outperforming children provided with no information. Furthermore, these children were equally and, in some cases, better able to solve the task than those provided with a complete demonstration of the solution (a model building the novel tool using both techniques). Results suggest that children may use their well-developed capacity for social learning to scaffold their less developed ability to innovate tools. The role of such combinative learning is discussed in relation to cumulative culture.

Paper **Young children's ability to copy cumulative culture in a construction task**

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One factor argued to separate humans from other animals is our ability to accumulate improvements in cultural products over time. However, we still know little about the ontogenetic origins of cumulative culture. Cumulative culture is based on two main cognitive capacities: Innovation and imitation. This talk will focus on the imitative aspect and present studies exploring whether 1) young children are able to copy cumulative culture in a construction task and 2) what kind of social information they need to do so. In study 1, 34 children between 4 and 5.5 years built a construction from sticks and plasticine that was as tall as possible. The action demonstration group observed the experimenter build a tower possessing features going beyond what children in a baseline group reached individually. Results showed that the demonstration group built taller constructions than the baseline group and, crucially, that some children copied the complex technique shown, suggesting that 4- to 5-year-old children are able to imitate cumulative culture. We also present results from study 2 (ongoing), in which we compare action and end state only demonstrations, investigating whether children would still be able to copy cumulative culture even when they don't have the opportunity to imitate actions.

Paper **Food sharing and its implications for teaching behaviour in wild golden lion tamarins**

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"There is currently considerable interest in animal teaching, yet, there are only three nonhuman species that fulfil Caro and Hauser's (1992) functional definition of teaching. None of these are primates. However, there is suggestive evidence of teaching in golden lion tamarins (Leontopithecus rosalia) in a food-sharing context.

The aim of this study was to investigate candidate teaching behaviour of golden lion tamarins in wild populations in Brazil. We test the hypothesis that food sharing is a form of teaching, whereby provisioning novel foods to juveniles teaches them what to eat in the future.

We evaluate the evidence that food sharing fulfils Caro and Hauser's three criteria that behaviour qualifies as teaching if: a) it is costly or not beneficial to the tutor; b) it is modified in the presence of a naive pupil; and c) results in learning in the pupil. Results show that adults transfer more novel food compared to familiar food to juveniles, and that this is not due to an increase in juvenile motivation to obtain novel food, supporting criterion b). Using Bayesian modelling, I assess whether receiving food has an effect on juveniles later foraging choices, and whether this persists into adulthood, thus assessing criterion c)."

Poster **Cumulative Complexity in Chimpanzees' Mastery of Tool Technology**

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Cumulative culture describes the ability to build up the complexity of knowledge and technology over time through social learning. To date, very little experimental research has addressed whether chimpanzees are capable of iterated, cumulative learning. We investigated whether chimpanzees learned complex tool manufacture skills to extract distant rewards by building upon more simple behaviours. Chimpanzees (N=33) were exposed to four quadruplicate foraging puzzles ('Levels'), each containing four kinds of food exit ('Lift', 'Back Door', 'Trap Door', 'Ramp'). Levels were positioned at varying distances from the subject, such that the first and closet level ('Level 1') was accessible manually; 'Level 2' required a simple unmodified tool; 'Level 3' an elongated tool; and, 'Level 4' an elongated hook tool. Overall, chimpanzees (four groups, N=20) extracted 286 'Level 1', 117 'Level 2' and 78 'Level 3' rewards. No individual successfully extracted a reward from 'Level 4' four using a hook tool. One asocial control among eight, tested individually, also solved levels 1-3. However, failure of an additional group (N=5), exposed to Level 3 only, to extract a single reward suggests that cumulative learning, afforded by closer, easier, levels was essential for task progression.

Paper **Chimpanzees copy subordinate models as well as dominants**

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Chimpanzees can be innovative, yet observations of novel behaviours propagating between communities are uncommon. A bias towards copying dominant individuals has been proposed to explain this phenomenon, as the primary means of novel behaviours reaching a community are typically a) innovation by low-ranking individuals, or b) migrant females, who generally enter groups as low-rank. Previous work has shown that, given the choice between dominant or subordinate models, chimpanzees prefer to copy dominants. However, these two model types have never been compared in isolation from one another. Our study investigated whether observers are motivated to copy a subordinate model if no better option is available. In different groups, high- and low-ranking individuals were trained to use either of two possible methods of opening a puzzle box, and then modelled their technique in their group. All were then allowed to interact with the apparatus for 10 hours in an open-diffusion setting. Results demonstrate that observers were as likely to copy the method used by subordinate individuals as dominants, and more likely to copy either than to learn asocially. These findings call into question the hypothesis that rank-bias constrains the spread of novel behaviours in chimpanzees.

Paper **Vocal Learning in the Functionally Referential Food Grunts of Chimpanzees**

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"One standout feature of human language is our ability to reference external objects with socially-learned words. Exploring the phylogenetic origins of this capacity is key to understanding the evolution of language. While non-human primates can produce vocalizations that refer to objects in the environment it has been argued that their acoustic structure is strictly tied to arousal states, a key discontinuity with language. Here, we demonstrate vocal learning in the acoustic structure of referential food grunts in captive chimpanzees. Following the integration of two groups of adult chimpanzees, the acoustic structure of grunts produced for a specific food converged over 3 years. Acoustic convergence arose independently of preference for the food and social network analyses indicated this occurred only after strong affiliative relationships were established between the groups. This is the first evidence of non-human animals actively modifying and socially-learning the structure of a referential vocalization. Our findings indicate primate referential call structure is not simply arousal-based and that the socially-learned nature of referential words in humans likely has ancient evolutionary origins.

This study was first published as a Report in Current Biology (2015). Following recent correspondence (Current Biology, submitted), further analyses have been explored to support our findings.

Paper **Responding to conspecific injury cues reduces short-term mortality from predation in gammarids**

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Chemical cues passively released by injured individuals provide a source of social information to conspecifics on the presence, location and activity of predators. These have been widely studied in a range of aquatic species, including helminths, crustaceans, anurans and fishes, where they have been shown to induce a range of antipredator behaviours. Few studies, however, have explicitly tested whether responding to conspecific injury cues (CICs) actually reduces the likelihood of being captured by a predator. In this study I tested whether gammarids (Gammarus pulex), an aquatic amphipod crustacean, were less likely to be captured by predator fish if they were provided with CICs. Gammarids typically respond to CICs by reducing activity and hiding in cover, and are capable of learning associations between CICs and novel predator chemical cues. I found that gammarids tested in the presence of CICs did indeed survive for longer than did those tested without them. Control experiments ruled out prey odour-saturation as a factor influencing predator capture rates. This study demonstrates how responding to social information in the form of CICs can reduce short term mortality from predation.

Paper **Attention to rewards versus reward retrieval techniques in capuchins (Sapajus apella) and young children (Homo sapiens)**

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Studies investigating the (social) learning of foraging techniques in capuchins have shown mixed results. Potentially, capuchins may attend more to rewards than reward retrieval techniques (RRTs) hampering learning the latter. In this study a transparent artificial-fruit contained a reward placed Near (5cm) or Far (25cm) from one of two alternative RRTs performed by a human. Capuchins were less likely to watch the action and less successful at retrieving the reward, when the food was Far rather than Near the RRT (ps < .05). Capuchins showed limited evidence of learning from the demonstrator so long as the food was Near. Comparisons were made with 180 two- to four-year-old children. Children with no demonstrations were significantly more likely to acquire the reward when it was Near (60% success), rather than Far (23%, FET, p < .001), indicating that reward location affected asocial RRT learning. Children with a Near demonstration (88%) were more likely to use the demonstrated RRT than children with a Far demonstration (63%, FET, p < .01) although two-year-olds showing a much greater Near-Far difference than older children. Reward location can have a major impact on RRT attention, success and social learning in both young human and non-human primates.

Paper **Emotion intermodal matching task in dogs, orangutans, and human infants**

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My present study investigates whether domestic dogs and orangutans can match emotional faces to voices in an intermodal matching task or whether they show preferences for looking at certain emotional facial expressions over others, similar to human infants. We presented 52 domestic dogs, and 24 7-month-old human infants with two different human emotional facial expressions of same gender simultaneously, while listening to a human voice expressing an emotion that matched one of them. The 7 orangutans were presented with the same stimuli but in a modified setup. Consistent with most matching studies, neither dogs nor infants looked longer at the matching emotional stimuli, yet dogs and humans demonstrated an identical pattern of looking less at sad faces when paired with happy or angry faces (irrespective of the vocal stimulus), with no preference for happy versus angry faces. Preliminary findings for the orangutans showed a similar trend to the dogs. Discussion focuses on why the subjects might have an aversion to sad faces, or alternatively, heightened interest in angry and happy faces.

Paper **Evidence for vocal learning in common marmosets?**

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Most primates show only limited evidence for vocal production learning, even though they strongly rely on vocal communication. This is even more surprising considering the vocal learning skills of humans. The cooperatively breeding Callitrichid monkeys might be an exception amongst non-human primates and could provide important insight into the evolution of language. Here, we report evidence suggestive of vocal production learning, by showing that (i) different captive populations of C. jacchus show marked differences in the structure of a variety of calls and (ii) that family signatures in these calls can also be distinguished. To investigate if these differences are indeed the result of vocal production learning, we paired animals with a new breeding partner either from the same or from a different colony. We recorded their calls before, during, and after the pair formation process to measure whether the pairs converged in their call structures. At the same time, we collected behavioral data in order to quantify the influence of relationship quality on vocal assimilation. Assimilation to a partner can provide strong evidence for vocal production learning and the importance of relation quality during the process can reveal similarities and differences in vocal accommodation in humans and marmoset monkeys.