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Our Primate Heritage, Our Primate Legacy

Oxford, UK, 8–11 September, 2019

Organisers: School of Anthropology and Museum Ethnography (University of Oxford), Department of Social Sciences (Oxford Brookes University)

Abstracts

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Plenary Sessions

OSMAN HILL MEDAL
Promoting Primate Welfare – Past, Present and Future

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Globally, approximately 100,000 non-human primates are used for experimental research and testing purposes each year. There are countless others held in captivity for breeding to become research subjects, housed in zoos and sanctuaries, or kept as 'pets'. Primatologists should be ambassadors for these animals. Our academic research, teaching and public engagement activities have the potential to positively impact the welfare of primates. I outline how our conceptualisation of the 3Rs (Replacement, Reduction and Refinement - the basic principles underpinning humane science) have evolved for the better since their inception in 1959. Concurrently, perceptions and methods of welfare assessment have changed from the five freedoms, which are concerned with the absence of suffering, to the promotion of positive affective states over a lifetime. Against this backdrop, I argue that what matters is how primates 'feel', and that the human community must work towards providing them with opportunities to thrive, optimising their wellbeing within research and financial constraints. Welfare must be considered 24/7 across the lifespan, especially given the critical effect of early life experiences on later resilience. The promotion of good welfare is the ethical responsibility of all who care for and study primates, whether in the wild or captivity; it is also fundamental for good science. My hope is that there will come a time, in the not so distant future, when primates are no longer used in regulated research and testing in laboratories.

The World's Primates: A Global Common Under Threat

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The world's primate fauna, distributed in the Neotropics, Africa and in South and Southeast Asia, represents an important global component of the Earth´s terrestrial biodiversity. The presence and activities of primates support a range of tropical community-wide ecological functions and services that provide vital resources to human populations. Alarmingly, ~60% of extant primate species are now threatened with extinction and ~75% have declining populations as a result of escalating anthropogenic pressures. In my talk, I focus on land use changes resulting from growing global market demands for food and non-food forest-risk commodities that have driven the extensive loss and degradation of primate habitats in the four primate range regions. Due to human activities, primates are losing their forest habitat at a rate of ca 10 million ha per year and half or more of this loss is commodity driven. Developed nations are the major consumers of these commodities. While revenues from exports of natural-resource commodities have increased significantly over the past two decades, primate range nations continue to lag well

behind importing nations in gross domestic product per capita (GDPPC) and in food security. Given that global commodity resource extraction is predicted to more than double, from 85 bn tons today to 186 bn by the year 2050, reversing the current trend of primate population decline and extinction due to habitat loss will require a stronger global resolve to reduce the world's per capita demand for forest-risk food and non-food commodities from primate-range regions. Changing consumer food habits (e.g. use less oil seed, eat less meat, diminish use of tropical timber, fossil fuels, metals, minerals and gemstones from the tropics) and implementing sustainable land use practices that improve the standard of living of human communities, protect the local biodiversity and mitigate climate change are actions needed to protect the world's primates.

Opportunities for Asian Conservation in the Anthropocene

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Asia stands out in the world for many reasons. Economic and political power is rapidly shifting back to this part of the world, which also houses more people than anywhere else, while the region also has high levels of biological diversity and endemism. That this creates tensions has been well demonstrated, but that this offers opportunities much less so. Through discussion of several examples, I will demonstrate that in conservation we have no choice but to innovate, and seek new solutions. This requires that we have a close look at everything we think we know about species such as primates and review this knowledge in the understanding that much of Asia's megafauna was fundamentally altered when modern human first walked onto the Asian scene some 75,000 years ago. It also requires that we question our long-held beliefs about what works and what doesn't in conservation. Orangutans, for example, are ecologically a lot more versatile than many of us would have thought. By closing our eyes to ecological realities and by not recognising the most important threats to the species, we end up implementing conservation management for the species that perhaps unintentionally, but fundamentally, undermines the likelihood of the species' survival. This points to the role of critical scientific thinking and the willingness to innovate, without which the conservation struggle in Asia will be just that much harder.

Plants of the Apes. Towards an Archaeology of the Perishable

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While hominin stone tool use dates back to at least 3.3 million years ago, plant-based tools probably have a much deeper history – just that they don't preserve as well. Clues about the evolutionary role of plant-derived implements can be gleaned from observing extant primates. For this, I researched the dynamics of tool-aided extraction and consumption of termites by wild chimpanzees living in environments similar to early human habitats in west Tanzania (Gombe, Mahale, Issa). A pioneering application of traditional archaeological methods found that the extraction of raw materials leaves scars on source plants which can provide rich information about past behaviour. The cross-site comparison revealed that (i) chimpanzees select specific plants and materials

to manufacture tools; (ii) chimpanzees at all sites exploit some identical source species, perhaps because of especially suited physical properties; (iii) chimpanzees in a drier, more open landscape travel almost double the distance to source raw material and utilise sources more intensively; (e) tool use features in neighbouring communities differ, suggesting cultural preferences. The study highlights how archaeological methods can reveal "invisible" aspects of technological behaviours. Albeit the "archaeology of the perishable" is still in its infancy, it may ultimately improve reconstructions of organic-based tool use in our ancestors.

Lab Cognition Going Wild: Field Experiments on Vervet Monkeys

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The social brain hypothesis proposes that complex social environments selected for advanced cognitive abilities in certain classes of vertebrates, including primates. Advances in testing and refining the hypothesis will depend crucially on our ability to link the ecology of species to social decision making and underlying cognitive processes. Therefore, we need to study animals in their natural habitat. I will present field experiments on vervet monkeys testing physical and social cognition, with a focus on social learning. The understanding of the emergence of these cultural behaviours in animals has advanced significantly with contributions from complementary approaches: natural observations and controlled field experiments. Experiments with wild vervet monkeys highlight that monkeys are selective about 'who' they learn from socially and that they will abandon personal foraging preferences in favour of group norms new to them. Theoretical studies predict preferential copying of higher payoff-gaining conspecifics, a bias demonstrated in primates only in captivity. In the wild, research has shown selective attention towards the philopatric sex, a group's stable core. Here we report the first rigorous experimental test of the existence of a payoff-bias in wild primates and its interaction with the sex of the model. We also report the temporal dynamics of participants' choices over three experimental sessions where age and experimental context seems to influence when individuals rely on their individual knowledge. These results demonstrate behavioural flexibility in the dispersing sex in these primates and suggest that the philopatric sex can afford to be more conservative in their social learning. Our findings show that multiple social learning biases can coexist and interact within the same species. The reported findings on social learning strategies highlight the feasibility of studying cognition under field conditions.

Genomic Data Reveal Surprising Patterns of Lineage Diversification in Madagascar's Mouse Lemurs (Genus, *Microcebus*)

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Evolutionary genetics has transformed our view of the diversity of life on earth and Madagascar's mouse lemurs are an iconic example of this increased appreciation of endangered biodiversity. As recently as 1992, primatologists recognised only two species of mouse

lemur, *M. murinus* from the west and *M. rufus* from the east. Today, the number of named species hovers around 25. This is a remarkable example of taxonomic "splitting," and it is entirely reasonable to ask whether this number is artificially inflated. Conversely, it is also worth asking whether the level of evolutionary diversity within this clade is as yet fully appreciated. Mouse lemurs occur across all habitats throughout Madagascar, and though genetic data reveal deep evolutionary divergence among the named species, they are morphologically cryptic. At present, the ecological and geographic forces driving this species radiation are unknown. My talk will provide a critical review of the literature that has led to our current understanding of mouse lemur species diversity and also present data from new and ongoing studies of lineage diversification across an ecological and geographic spectrum in Madagascar. Using a combination of whole-genome sequencing and RADseq analysis we have found that patterns of speciation in mouse lemurs range from cases of complete reproductive isolation in sympatry, on one end of the speciation spectrum, to incipient population divergence within a single species on the other. We have also identified examples of intermediate levels of lineage diversification, finding that effective population size, both past and present, can have enormous impacts on inferred patterns of gene flow and incomplete lineage sorting. In summary, there is no question that mouse lemurs are extraordinarily diverse and, with the benefit of genomic data and powerful statistical tools, we are entering a new phase of increased understanding of the patterns and processes that are shaping mouse lemur species' diversity.

Podium Presentations

The Experimental Investigation of Primate Emotions: Disentangling Valence and Arousal

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Understanding another's emotional state is critical for facilitating adaptive behaviour in complex social groups. Though it has been suggested that emotions may serve as a conserved mechanism of primate social behaviour, empirically we are still facing the challenging questions of what primate and other non-human animal emotions are and how we measure them. Moreover, previous studies have proposed that emotional contagion, an essential component of empathy, aids primates in rapid information sharing and establishing positive affiliative bonds such as long-term friendships. Yet, the current paradigms to study emotional contagion do not irrevocably demonstrate its occurrence. For example, previous studies have suggested that yawn contagion may reflect empathy, yet yawn contagion in itself does not necessarily imply affective sharing. For this reason, the systematic quantification of an animal's affective state, including both behavioural and physiological arousal as well as emotional valence, will substantially enhance emotion research. This will broaden our understanding of primate behaviour and the potential role emotions have in directing this behaviour. We will elaborate on the multi-componential

approach to study animal emotions and discuss the well-established cognitive bias paradigm to study emotional contagion comparatively in primates and other social animals. This paradigm may allow us to investigate both the arousal and affective valence element of an emotion, and thus further capture the affective valence of emotional contagion. To demonstrate the utility of this paradigm, we present empirical data demonstrating its successful application in common ravens (*Corvus corax*) and common marmosets (*Callithrix jacchus*). Additionally, we present preliminary data of an ongoing emotion study assessing reward satisfaction and frustration in capuchin monkeys (*Cebus apella*).

Fossils, Satellites and Drones: Developing a Geospatial Palaeontology across the Paleocene-Eocene Boundary in Southwestern Wyoming

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Palaeoanthropology has long been an interdisciplinary science whose practitioners rely on analytical methods and conceptual approaches developed in related scientific fields including chemistry, geology and systematics. Increasingly, the location, collection and analysis of fossils in different field settings have benefitted from the ongoing revolution in the geospatial sciences. Our fieldwork across the Paleocene-Eocene boundary in Wyoming's Great Divide Basin has utilised a series of such methods to develop a new, geospatially informed vertebrate palaeontology. We discuss these tools, data sets and analytical methods and demonstrate how they have improved our ability to locate fossils in a remote and spacious (ca. 25,000 km^2) sedimentary basin. We fly both helicopter and fixed wing design unmanned aerial vehicles (UAVs) to obtain high-resolution imagery in still and HD video formats for both individual fossil localities and entire palaeontological landscapes. We use several different photogrammetric software packages (Agisoft Photoscan and Pix4D) to create three-dimensional digital models of individual localities and landscapes, which – in combination with geological study in the field - allow *in silico* analysis of aspects of stratigraphy, taphonomy and geomorphology. We analysed medium (LANDSAT 7 and 8) and high-resolution (Quickbird) satellite imagery using pixel and object-based supervised image classification approaches in order to develop predictive models to guide our search for early primate and other mammal fossils. Ground truthing of these various methods over the past few field seasons in the Great Divide Basin shows significant improvement in our team's ability to locate fossil-bearing deposits compared to traditional surveying approaches, which often rely on serendipity. These and related machine learning based approaches are increasingly being utilised by other research teams and hold great promise for a truly geospatially-informed palaeontology.

The Impact of Socio-Ecology on Lethal Aggression in a Community of East African Chimpanzees (*Pan troglodytes schweinfurthii*)

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Killing of conspecifics has been reported in many species. Yet, the nature of these lethal aggressions varies between species. Ranging from intense mate competition to maternal infanticide, killing conspecifics appears an adaptive strategy for many animals. Primates are not an

exception. Many primate species, including all great apes, have been reported or suspected to employ lethal aggression. Chimpanzees and humans have the highest reported killing rates among apes, but the adaptive value of this behaviour is poorly understood. We use long-term data over 25 years of observations to explore how the socio-ecology of one East African chimpanzee (*Pan troglodytes schweinfurthii*) community (Sonso, Budongo) influences patterns of lethal aggression both within the Sonso community and between Sonso and their neighbouring communities. Behavioural data on aggression, dominance interactions, grooming, party composition and ranging were collected during focal follows together with 15-minute party scans. Data on fruit availability, rainfall and temperature were also collected. During the study period, the Sonso community were involved in 30 lethal events. Of these, 8 were intercommunity infanticides (Sonso victims = 1, Sonso as attackers = 7); 3 were intercommunity killings of mature Sonso members; 16 were intracommunity infanticides; and 3 were intracommunity attacks on mature victims. The rate of these events ranged from 0 to 2 events per month and from 0 to 5 events per year. We use multivariate models to explore how monthly variation in community socio-ecology (including: community size and demographics, sex ratio, hierarchy stability, home range size, food availability, seasonality) influences the occurrence of lethal events. Furthermore, we use social network analysis to investigate how the position of attackers within the community changes before and after a lethal event.

Saying Goodbye to the Methodological Conundrum of Studying Leave-Taking

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Humans typically greet when they meet one another, and have rituals of leave-taking when they part. These every day rituals are so ingrained in our social exchanges that they have been termed "bookends of interaction". Greeting rituals have been well-studied across human societies as well as across the animal kingdom. However, studies of leave-taking are sparse in humans and almost entirely absent in other species. One of the reasons for this gap in our knowledge could be the assumption that leave-taking does not exist in non-human species, or the perceived difficulty of studying a priori behaviours that occur before the noticeable parting event. Our preliminary study, focusing on 11 wild chimpanzees (*Pan troglodytes verus*) in Bossou, Guinea, showed an increased frequency of self-scratching (n=70, p<0.001) and fixed gaze in the direction of parting (n=70, p<0.001) in the six minutes prior to separation, over 30 hours of video footage. We assess the merits of using pre-recorded footage to collect detailed behavioural data for the study of leave-taking, i.e. high-resolution data, inter-observer controls and a priori data collection. We then propose a refined methodological approach to determine whether candidate behaviours are truly markers of social separation. In doing so, we compare dyad separation at the end of joint activities (e.g. play, allo-grooming), with dyad separation after solo activities in close proximity (e.g. foraging, self-grooming), and a control group (single individuals stopping solo activities and moving away). This study represents the first step of an investigation into one of our most common social rituals, allowing us to test hypotheses about why leave-taking has evolved in humans, and whether it might have adaptive social functions.

Ontogeny of Locomotion in Mouse Lemurs: Behaviour and Performance

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The environment of primate juveniles is very challenging, especially when parents do not carry infants. They have to forage and move on the same substrates as adults and escape the same predators, despite their immature state. In this study, we aim to highlight adaptive strategies during their development that may have evolved, allowing them effective locomotor abilities early in life. We have thus conducted an ontogenetic study of 36 arboreal grey mouse lemurs (*Microcebus murinus*) from birth to adulthood (6 months). The investigated parameters are, for both limbs, 1) grasping behaviour during locomotion (i.e. grip postures), 2) grasping performance (i.e. pull strength) and 3) motor coordination (i.e. RotaRod® test). Our results show that as early as 8 days old, infants are able to climb substrates of various slopes and diameters outside of their nest. Although juveniles can not successfully complete a motor coordination test before 30 days old, younger individuals display relative pull strengths that are very high or even as strong as in adults, guaranteeing strong stability. Moreover, individuals of all ages use pedal secure grasp on all substrates; however, the use of manual secure grasps decreases across development. These results highlight physiological and behavioural adaptations during development. From an evolutionary point of view, they show the importance of the grasping function in arboreal locomotion and suggest different functional roles of the hands and feet, with the hindlimbs ensuring body balance on the substrates. The research adhered to the legal requirements of the European Union (Directive 2010/63/EU).

Using Thermography to Understand Third-Party Social Evaluation in Cooperatively Breeding Common Marmosets

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Keeping track of good cooperation partners is essential for group-living species especially if individuals are interdependent like cooperatively breeding common marmosets (*Callithrix jacchus*). Experiments with human actors have shown that marmosets are able to evaluate social interactions between humans but experimental evidence for social evaluation of conspecifics is lacking. Additionally, behavioural reactions during social evaluation can be very subtle and not all social evaluation necessarily leads to punishment or reward of these conspecifics. Measuring body surface temperatures with infrared thermography has recently gained importance as a non-invasive measure for emotional reactions. In particular, nasal temperature changes indicate changes in arousal. We assed marmosets' (n = 21) changes in arousal during playbacks of opposite sex outgroup individuals. We used two different types of playback-stimuli either simulating (1) a social interaction between an adult and an immature (interaction playback), which could be positive (combination of begging calls of the immature followed by food calls of the adult) or a negative (begging calls followed by antagonistic chatter calls), or (2) a single individual being present (non-interaction control playback) by playbacks of food, chatter or begging vocalisations. After the playbacks simulating an interaction, (1) marmosets were allowed access to an additional compartment with a mirror thus simulating the conspecific whose interaction individuals just witnessed. Our results show that marmosets' changes in emotional arousal differ after having

witnessed the interaction vs. the control playback. Importantly, the reactions to the interaction playbacks cannot be explained as an additive effect of reactions to the control playbacks, indicating an understanding of the call combination. We validate the thermal reactions with simultaneously collected behavioural data and the behavioural reactions marmosets exhibit when exposed to the mirror.

Double Jeopardy: The Effects of Resource Availability and Predation Pressure on Cortisol and Activity Budgets in Captive Marmosets

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Resource availability and predation pressure are key determinants for primate behaviour and perhaps cognition. This is typically studied in wild populations that come with a set of limitations: evidence is correlative rather than causal, resource availability and predation pressure are often difficult to quantify, and cognitive experiments difficult to implement. Our goal was to investigate how experimentally induced variation in predation pressure and resource availability affects captive marmosets (*Callithrix jacchus*). We tested five family groups (n=28) in their outdoor enclosures in four counterbalanced conditions (resource high/predation high vs low; resource low/predation high vs low), each lasting for three weeks. Low predation risk corresponded to standard housing, whereas during the high predation condition, aerial predator models were presented at irregular intervals. Resource conditions differed in the availability of high-quality food; in both conditions, gum and monkey pellets were available ad-libitum but in high resource conditions, twice as much fruit and three times as many insects were provided. We measured faecal cortisol and collected behavioural data on foraging, vigilance and play and used generalised linear mixed models (GLMMs) to analyse the data. Different classes of animals were differently affected by the conditions: during *increased risk*, cortisol increased in all classes of animals but most in adult males. Likewise, all animals increased vigilance, but adult males did so most, whereas we observed no change in playing, feeding or resting. Under *low resource* availability, cortisol increased only in juveniles, but all increased foraging, in particular female breeders. Furthermore, play significantly decreased in juveniles. Overall, we find that subtle variation of resource availability and predation pressure affects marmosets in predictable ways. In the future, this will allow a more precise estimate for how these factors may affect cognitive performance.

Lemur Hunting in South-East Madagascar: Perspectives of the Hunter and Hunted

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Hunting by humans is increasingly recognised as a threat to lemur populations. To date it has received little scientific attention and is particularly understudied in southern Madagascar. We used an ethnoprimatological approach to investigate lemur hunting from the perspectives of people and lemurs living in the Tsitongambarika Protected Area, south-east Madagascar. Our objective was to investigate the drivers of hunting in rural communities and its effect on the

behaviour and demography of the two locally most targeted species – the collared brown lemur *Eulemur collaris* and southern bamboo lemur *Hapalemur meridionalis*. We worked at two sites, one that experienced high and one that experienced low hunting pressure, to enable a comparative approach. We used participant observation and semi-structured interviews in eight villages to explore the importance of lemur hunting in people's lives. Between 2017-2019, we conducted surveys of lemur abundance, group composition and lemur snare frequency over 110 km of line transects. Each time we encountered a lemur group (during transect walks and opportunistically) we used instantaneous scan sampling to record their reactions to human observers (in particular anti-predator behaviours including vigilance, crypsis, flight, vocalisations and aggressive signalling), together with individuals' sex and age class, position and group cohesion. We found that: a) the economic and social importance of lemur hunting differs between people living in the coastal and interior zones of Tsitongambarika; b) lemur group sizes and sex ratios were affected by hunting, and c) both species exhibited more cryptic behaviours at the high hunting pressure site, suggesting that they adjust their behaviours towards humans in areas of high hunting pressure. Our findings provide the basis for modelling indicators of hunting pressures on lemurids and developing effective conservation strategies.

A Global Analysis of Exposure Risk of Primates to Climate and Land Use Changes

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Globally, primates are facing an impending extinction crisis, driven by extensive habitat loss and land use change, hunting and unsustainable trade. Climate change is an additional threat, which alone or in combination with other drivers may severely impact species unable to track suitable environmental conditions. For 426 primate species, we investigated the extent of exposure risk to future climate and land use changes for 2050 under a best- and a worst-case scenario. We also identified correlates of variation in exposure risk with regard to region, conservation status, range size and predominant habitat, and quantified the percentage of species range and primate hotspots likely to be exposed to extreme temperature rises. We found that, under the worst-case scenario, 74% of Neotropical forest-dwelling primates, and most of African and Asian primates are likely to be exposed to temperature increases up to 7°C. About 25% of Asian and African primates will face extensive crop expansion under both scenarios. Primary vegetation is expected to disappear or considerably shrink across most species' ranges regardless of the scenario, particularly where primates are confined to forests and where less threatened species are presently found, whereas secondary vegetation will increase by up to 60% under the worst-case

scenario. Species with greater range sizes are generally more prone to be affected by environmental changes. With 86% of primate ranges likely to be exposed to temperature increases >3°C, the Neotropics is the region likely to suffer the greatest losses in terms of primate hotspots. Our study highlights the fundamental exposure risk of a large percentage of primates and their ranges to predicted climate and land use changes. Importantly, it underscores the urgency with which climate change mitigation measures need to be implemented to avert primate extinctions and loss of their vital ecosystem services on an unprecedented scale.

Longitudinal Analysis of Empathy Development in Sanctuary-Living Bonobos (*Pan paniscus*)

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Empathy – the sharing and understanding others' emotions and thoughts – is a defining feature of what it means to be human. Although comparative research suggests that empathy has deep evolutionary roots and may be more widespread than first assumed, we lack knowledge about how empathy develops, including in primates, with most studies focussing on adults. Here, we address this by presenting a longitudinal analysis of the development of empathy and socio-emotional competence in sanctuary-living bonobos with different rearing backgrounds. We compared the socio-emotional skills of 12 semi-free ranging bonobos (n = 6 orphaned, n =6 mother-reared) housed at Lola ya Bonobo Sanctuary, DR Congo during periods of juvenility (2011-2012) and adolescence (2016) using observational approaches. We also tracked the empathic responses of a second cohort of n = 13 mother-reared and orphaned juveniles during the second phase (2016) to examine whether variation in empathic responsiveness demonstrated in the first cohort as juveniles were replicable. We found notable consistency in the empathic tendencies of mother-reared versus orphaned juveniles in both cohorts: mother-reared juveniles showed significantly greater empathy and socio-emotional competence than orphans, including greater capacity to console distressed others and better emotion regulation. Crucially however, our subsequent analyses of cohort 1 as adolescents, using the same set of measures, revealed that most of these rearing effects had largely disappeared or had become strongly individually-differentiated. These results provide encouraging insights into the apparent resilience of great apes facing adverse circumstances when placed in a rehabilitative environment. The apparent amelioration of socio-emotional functioning in orphaned bonobos supports the potential for plasticity in great ape socio-emotional development and the apparently positive role that sanctuaries play in their rehabilitation.

Guenons in Islands: Species Occurrence and Baseline Genetic Assessment of Insular Populations of the Western Spot-Nosed Guenon in the Bijagós Archipelago, Guinea-Bissau

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The western lesser spot-nosed guenon (*Cercopithecus petaurista buettikoferi*) is globally declining across Africa. The species' northernmost point of distribution is Guinea-Bissau, where only the insular populations of the Bijagós archipelago (BA) are thought to persist. Here, the species is threatened by increasing hunting for bushmeat and by habitat loss. We sampled 6 of the 23 largest and human-inhabited islands of BA to update the distribution from the latest (20-year-old) reports and to assess, for the first time, the genetic diversity and gene flow dynamics between islands. DNA was extracted from 134 geo-referenced faecal, blood and tissue samples and assigned to the species level using DNA barcoding. Genetic diversity and gene flow were estimated using the mitochondrial DNA control region and 10 autosomal microsatellite loci. Fifty-two unique genotypes and mitochondrial sequences were obtained. We confirmed the occurrence of the species in 5 of the 6 islands. Contrary to what is usually found in insular populations, genetic diversity was relatively high for both types of genetic markers (mtDNA: $0.35 \leq Hd \leq 0.93$; $0.37\% \leq p \leq 1.65\%$ and nuclear: $0.44 \leq uHE \leq 0.68$). Results from individual Bayesian clustering suggest strong population substructure according to each of the sampled islands, not linked to the presence of highly related individuals in the dataset. However, we found individuals with admixed ancestry at Canhabaque and migrants with unknown origin on Uno island. Naturally occurring dispersal between islands is unlikely and limited gene flow may be explained by human-mediated translocations for a currently unstudied socio-cultural purpose. Our results highlight that special conservation efforts should be employed in BA since human-mediated disturbances are likely to increase the extinction risk of these naturally isolated populations. The work has been funded by Foundation for Science and Technology, The Born Free Foundation and Chester Zoo.

Filling Gaps in Primate Evolution: Machine Learning Approaches for Automated Fossil Site Discovery in Gorongosa, Mozambique

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Computer-assisted search for fossiliferous deposits has the potential to ground truth current hypothesis on ranging patterns, as well as processes of speciation and extinction of extinct primates. These methods are being developed and tested at the southernmost tip of the Rift Valley, in Gorongosa, Mozambique, a corridor between South and East African sites containing the

majority of the known African hominins. We cropped an atmospherically corrected LANDSAT8 satellite image to a 120 km^2 area in Gorongosa containing Late Miocene deposits. From this satellite image we extracted seven different variables of colour brightness at specific spectral bands (ultraviolet, blue, green, red, near-infrared, shortwave infrared 1 and 2). Additionally, we superimposed a SRTM digital elevation model, from which we extracted the following variables: elevation, slope, aspect, terrain roughness and flow direction. We also calculated NDVI – a vegetation index – from the spectral bands, to evaluate the influence of vegetation in surveying efforts at the miombo forests of Gorongosa. We modelled this dataset with the MaxEnt algorithm using coordinates of georeferenced fossils found during three short field seasons of the Paleo-Primate Project Gorongosa (2016-2018). Every time that a pixel (30x30m res.) contained fossils it counted as a single occurrence. The model performed exceptionally well, with an AUC = 94.6% under a 10-fold cross-validation scheme. An analysis of variable contributions shows that elevation (45.9 %) is the most important factor to model the distribution of fossiliferous deposits in Gorongosa, followed by vegetation (32.4%), roughness (7.1%), slope (5.4%) and the blue spectrum (5.1%). Using a very conservative predictive threshold (=0.95) we can effectively reduce the total surveying area to only 0.3744 km^2. We expect that the discovery of new fossil sites in Gorongosa will directly contribute to enlarge the virtually non-existent sample of late Miocene African hominoids.

A Holistic Multi-Biomarker Approach to Studying Long-Term Effects of Ageing and Stress: Allostatic Load in Western Lowland Gorillas

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Developed in human clinical research in 1997, allostatic load indices (ALIs) may be beneficial to researchers interested in better understanding the long-term effects of stress and ageing in non-human primates. Combining biomarkers from multiple somatic systems, ALIs estimate accumulated physiological dysregulation, or allostatic load (AL). Higher AL in humans is associated with increased risk of disease (e.g. heart disease, diabetes) and mortality, and factors explaining differences in AL have been identified (e.g. early life adversity, social position). We applied a 7-biomarker ALI to zoo-housed western lowland gorillas (*Gorilla g. gorilla*; n = 63, aged 6-52 years) and analysed associations with potential predictors and outcomes of higher AL using t-test, ANOVA, linear regression and odds ratios. Results from one of two pooling strategies and methods are presented here. AL ranged from 0-6 (= 1.84, SD = 1.71). Predictors: Males and females had similar AL (p = 0.972). Older age predicted higher AL (p = 0.003). Total stressful events did not significantly predict AL (p = 0.228). Parous females had higher AL than nulliparous females (p = 0.009). AL was significantly higher in wild-caught than zoo-born gorillas (p = 0.009). Outcomes: Gorillas with at least one chronic disease had two-fold higher AL (p = 0.003) and differences between gorillas with and without heart disease, the leading cause of death in captive great apes, neared significance (p = 0.076). Each unit increase in AL was associated with a 44% increase in mortality risk (p = 0.029, OR = 1.438). While research is ongoing to determine which combination of biomarkers is best suited for measuring AL in great apes, this research demonstrates that ALIs may identify physiological differences between individuals based on experiences as well as predict differential health outcomes, making it well-suited for addressing questions of both theoretical and practical interest in studies of captive and wild primates.

Population Density of the Northern Lesser Galago, *Galago senegalensis*, in Fongoli, Senegal and Lolldaiga Hills Ranch, Kenya

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Estimates of primate population density are vital for monitoring population change, assessing the importance of different habitats for primate conservation and classifying the conservation status of species. Distance sampling is widely used for estimating population densities, including some nocturnal primates, but few studies have used distance sampling to estimate galago population density. The northern lesser galago (*Galago senegalensis*) is the most widely distributed of the galagos and is therefore a perfect model species for comparing the density of different populations using distance sampling. We estimated the population density and abundance of *G. s. senegalensis* in an 86 km^2 mosaic of savanna, mixed woodland, forest and bamboo woodland at Fongoli in Senegal, and of *G. s. braccatus* in a 200 km^2 area of high elevation savannah, *Acacia* woodland and mixed woodland in Lolldaiga Hills Ranch in Kenya. We carried out 20 line transects on foot and 15 by motorbike (mean length = 2.29 ± SD 1.04 km) in Senegal and 15 line transects by car in Kenya (mean length = 6.66 ± SD 2.24 km). We walked at a pace of approximately 2–5 km/h and travelled at a speed of 5–10 km/h by motorbike and car. We used the 'Distance' package in R to estimate the density and abundance of individuals and groups at both sites. Our models predict that at Fongoli there are 1,892 galagos with 22.0 individuals per km^2 (CV = 18.54 %) and at Lolldaiga Hills Ranch there are 2,984 galagos with 14.9 individuals per km^2 (CV = 34.82 %). We discuss our population density results relative to those of other nocturnal primates and explore the effect of habitat type on galago density. In order to promote effective conservation, it is essential that more populations of this and other galago species are surveyed and monitored. If restricted by time constraints in the field, our research suggests that surveying by motorbike can enable researchers to cover a large area in a shorter time without compromising species detection. Our research complies with the International Primatological Society Guidelines for the Use of Nonhuman Primates in Research and was approved by the Ethics Committee at Manchester Metropolitan University.

Social Network Response to Severe Perturbation: a Barbary Macaque Case Study

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In wild living primates, the loss of group members is a natural occurrence, as individuals emigrate or die. Such disappearances of individuals will have knock-on effects on social relationships in the group, especially if a large number of individuals disappears in a short space of time. Little is known, however, about the extent to which the loss of a large proportion of a social group

affects the overall structure of the group's social network. Here, we use data from a population of wild Barbary macaques (*Macaca sylvanus)* that was exposed to an exceptionally harsh winter, culminating in the death of 65% of the adults from two social groups. We analyse how the structure of grooming and aggression networks was affected by this natural loss of individuals. In addition, we also assess if the relationships between survivors differed from that of non-survivors and how these pre-decline relationships are preserved in the post-decline networks. Our results show that the structure of the affiliative networks is remarkably resilient against disturbance: we found that post-decline grooming networks were not different from same-size pre-decline networks. However, agonistic networks were found to be a lot more plastic and deviated from the predicted network structure, suggesting that agonistic relationships are more responsive to environmental change than affiliative relationships. Furthermore, we found that social relationships between survivors before the decline in group size played an important role in their survival and in shaping the post-decline network structure. This adds further evidence to the importance of social network position for individual survival/fitness and demonstrates that although social networks are flexible, some structural elements, especially in affiliative networks, are maintained even during times of major perturbation.

Do Early Rearing Experiences Influence Physical Problem-Solving Skills in Chimpanzees and Bonobos?

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Children's initial rearing environment is influential on their skill development. Likely, not only the social interactions but also the interplay with the physical environment help form our cognitive skills during this time. So far, studies on non-human primates have suggested that individuals with different rearing histories also vary in their socio-cognitive skills. Less research is available on whether differences in rearing backgrounds also affect their physical cognition. We tested physical cognitive skills in problem-solving tasks in 54 captive chimpanzees (*Pan troglodytes*) and 21 bonobos (*Pan paniscus*) that differed in their experiences during the early years of their lives. To generate a heterogenous sample we included individuals from five different facilities belonging to the following categories of early rearing experiences during the first two years of life: orphan-sanctuary reared; orphan-human contact; mother-reared zoo environment; human-hand reared zoo environment and unknown background. Our results show that rearing categories affected the apes' physical cognitive abilities. Apes that have experienced close human contact were more likely to solve our tasks than apes who had been mother-reared. Also, we found species differences in inhibitory control and tool use. Bonobos were better than chimpanzees at an inhibitory control task and at a tool task (fishing for honey using a rope tool). Furthermore, within the chimpanzee sample we found a significant effect of facility and human orientation on performance in the inhibitory control task. As in humans, our results support the notion that the early social environment and the variation in human contact during early years also contributes to physical skill development in other apes. Our results stress the importance of studying intraspecific plasticity and developmental effects on cognitive skills in apes. Accordingly, we should be careful when considering test populations for assessing primate cognition in general.

Ecological and Reproductive Correlates of Energy Balance in Wild Moor Macaques (*Macaca maura*) Using C-Peptide Measurements

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Energy is a key factor for wild animal survival. Reproduction and energy balance might be affected by seasonal variation in food availability and reproductive costs in both sexes. This is relatively well established for seasonally breeding primates living in highly predictable environments and showing intense male competition, yet little is known about factors affecting energy balance in species with weaker ecological and reproductive seasonality. Here, we investigated the ecological and reproductive correlates of energy balance in adult individuals of the moderately seasonal, polygynandrous and tolerant moor macaques, *Macaca maura*. We studied one social group living in the karst forests of south Sulawesi (Indonesia), which provide relatively stable food supply. Urine samples (n=120; 11 males, 13 females) were collected for 11 months across 2 field seasons (each covering both dry and wet season) and analysed for urinary C-peptide (UCP), a biomarker of energy balance. We tested the effect of fruit availability on the energy balance of males and females of different reproductive states (each likely related to different energetic costs). We also tested male UCP in response to the presence of potentially fertile females. Both male and female UCP levels positively responded to fruit availability increase, and the strength of this relationship was similar in males and in cycling and lactating females. Pregnant females, however, responded more strongly than other groups, suggesting that they are more sensitive to ecological variation. Finally, the presence of potentially fertile females did not influence male UCP levels. Although based on a small sample size, these results challenge the applicability of classical socio-ecological theories to tolerant primates inhabiting a relatively steady environment since, in these species, competition for access to food resources might be as important in males as in females and male energetic investment in mating competition might be relatively low.

Chimpanzees Outperform Bonobos at an Experimental Cooperative Task in the Wild: Information Transfer Around a Stationary Danger

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The interdependence hypothesis posits that the cognitive dimension underlying unique human cooperation abilities evolved in contexts where several individuals needed to collaborate with each other to achieve a common goal. Alternatively, the social tolerance hypothesis

proposes that higher social tolerance allows conspecifics to cooperate more efficiently and with a wider range of partners. To understand the leap forward in human cooperative abilities in an evolutionary context, experimental evaluation of both hypotheses in our closest living relatives in the wild is essential, with chimpanzees expressing greater interdependence (due to territoriality) and lower tolerance than bonobos. We compared each species' performance during an in-group cooperative task: informing conspecifics about a potentially deadly threat. We presented Gaboon viper models to 82 individuals from five groups of wild chimpanzees and bonobos. Chimpanzees arriving late at the snake were significantly more likely to have heard a call and less likely to startle, indicating that chimpanzees were better informed about the presence of the danger than bonobos. This stems from clear species differences in how individuals adjusted their calling decisions to the level of information already available. Chimpanzees were more likely to call and produced more alarm calls when they had not yet heard a call, whereas bonobos did so when they had already heard a call. Finally, we found that both species tended to consider audience knowledge in their decision to call. Our results support the interdependence hypothesis and also inform theories on the evolution of human cooperation, linking inter-group competition pressure and in-group cooperative capability.

Comparative Thanatology of Primates: Exploring the Form and Function of Interactions Towards Dead Conspecifics

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Together with language, culture and art, awareness of death has been considered a defining trait of our species. In attempting to answer how and when ritualised treatment towards the dead began, we look towards our primate cousins and how they interact with their deceased. For two centuries, non-human primates have been reported to inspect, protect, retrieve, carry or drag the dead bodies of their conspecifics, although little scientific interest has been paid to such behaviours. We review recent evidence of thanatological responses and organise it into distinct terminologies: direct interactions (physical contact with the corpse) and secondary interactions (guarding the corpse, vigils and visitations). Although thanatological interactions imply these are a by-product of attachment relationships and operate on the expectation that the dead individual could recover, assuming primates learn valuable information from corpses, these interactions may serve an evolutionary purpose by: gathering information on the conspecific's state, promoting a faster re-categorisation from living to dead, reducing costly vigilant/caregiving behaviours, being crucial to the management of grieving responses, updating ranks in the group's hierarchy and accelerating the formation of new social bonds. The concept of death in humans is often composed of 4 subcomponents (Irreversibility, Universality, Cessation and Causality). Because research on human acquisition of the concept of death relies on verbal communication and is, therefore, inadequate for non-human animals, we propose an integrated model of life-death awareness that not only supports a gradual acquisition of such concepts, but also suggests a few underlying processes governing it. While reports from the field continue to shed light on this elusive phenomenon with regards to non-human primates, developing experimental procedures within ethical standards will prove critical in moving this field forward.

Information Transmission in Common Marmosets (*Callithrix jacchus*): Do Vocalisations Produced in Predator or Food Contexts Influence the Behavioural and Physiological State of Naïve Individuals?

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Life in a social group may bring several advantages, for example relying on information provided by other group members. Acoustic sources of information (e.g. alarm calls in the presence of predators), may allow individuals to respond appropriately without witnessing the situation themselves. Common marmosets (*Callithrix jacchus*) are highly social, cooperatively breeding Neotropical primates with a broad array of vocalisations. In this study, we experimentally simulated the visual separation of individual monkeys from their family groups in two different contexts: a) food condition, in which the group was presented with preferred food sources and b) predator condition, in which the group was presented with predator models. We measured behavioural responses of both the separated individual and the group, and we took salivary cortisol samples to measure the physiological changes in the separated individual. We found that separated individuals significantly differ in their physiological responses between conditions: as expected, separated monkeys showed lower delta cortisol levels in the food condition than in the predator condition. Unexpectedly, we found that the number of vigilance calls correlated with the delta cortisol levels in the food condition. In the predator condition, however, the number of contact vocalisations correlated with the number of stress behaviours. We will discuss possible reasons for the current unclarity in the link between the group vocalisations and individual's behavioural and physiological responses.

The Effect of Ecotourism on a Nocturnal Primate

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The primary goal of conservation is to maintain biological diversity. The biggest impediment faced by conservationists is insufficient financial resources to protect biodiversity. In response to the shortage of funds, conservationists have developed the concept of "sustainable ecotourism" as a means to fund conservation activities. Sustainable ecotourism involves people paying to visit fragile, pristine and relatively undisturbed natural areas. These trips are intended to be low-impact and are supposed to be small-scale in comparison to standard commercial mass tourism. As ecotourism is used and advocated more widely in conservation, quantifying its effects on the animals it is designed to protect has become correspondingly urgent. The goal of this research project was to explore the effect of tourism on the behaviour of Gursky's spectral tarsier (*Tarsius spectrum gurskyae*). This research was conducted between June – Dec 2018 at Tangkoko Nature Reserve on the northern arm of the island of Sulawesi, Indonesia. Four tarsier groups were located from the early morning audible vocalisations each individual tarsier emits upon returning to its sleeping site. Two groups were exposed to tourists regularly and two groups had no tourist visits. To minimise the effect of the PI and her assistants on the tarsiers' behaviour, blinds were created near the sleeping sites of the four groups behind which the PI and her assistants remained while observing behaviour. We found that the tarsier groups that were visited by tourists left their sleeping site significantly later than did the tarsier groups that were not visited by tourists. Likewise, the groups that were visited by tourists departed their sleeping trees at

significantly greater heights, emitted significantly more alarm calls and were much more likely to not return to the same sleeping site the following day. Clearly, tourism affects the behaviour of this nocturnal primate. Future research using larger sample sizes are necessary to determine whether the effects on the tarsiers' behaviour are positive, negative or neutral.

Dynamic Landscapes of Fear: Effects of Habitat-Heterogeneity, Seasonality and Predator Diversity on a Population of Chacma Baboons (*Papio ursinus*)

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"Evolutionary arms races" between predators and prey shape complex morphological and behavioural adaptations across the animal kingdom, with the risk of predation imposing two types of costs on prey. These include direct and severe cost of mortality, which alters prey survival rates, population sizes and demographics, and the chronic indirect costs of balancing predation-avoidance with biological requirements. These trade-offs create "landscapes of fear" within which species operate, influencing their movements and behaviours along both geographic and temporal dimensions. We explore the dynamics of such landscapes; we document the features and effects of different types of predation pressure on primate movement and behaviour in a heterogeneous and seasonal environment. Gorongosa National Park, Mozambique, is an area occupied by an abundant chacma baboon (*Papio ursinus*) population, which had previously low, but now monitored and increasing, predation pressure from several carnivorous species. Over 200 baboon troops are spread across Gorongosa's mosaic of landscapes, resulting in varied exposure to habitat-type, water availability, inter- and intra-specific competition and predation pressure. Within this natural laboratory, longitudinal data from a 300 km^2 camera trap grid and GPS-collared carnivores are used to map baboons' seasonal and diel use of the landscape in relation to habitat variation, the presence and movements of lions (*Panthera leo*) and the recent reintroduction of wild dogs (*Lycaon pictus*) to the ecosystem. Using preliminary results, we suggest that in such an environment, proximity to water is a strong predictor of animal activity, with seasonal consequences for primate-predator dynamics.

Are Monkeys Able to Discriminate Appearance from Reality?

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The ability to discriminate appearance from reality underlies the understanding that the perceptual appearance of the environment can differ in several ways from the reality. Being able to realise when a misperception can lead us to behave in inappropriate ways confers an evolutionary advantage, and may be a prerequisite to develop a Theory of Mind. Understanding that our own perception can differ from reality seems necessary to attribute to others perceptions or beliefs different from ours. This appearance-reality discrimination ability has recently

been demonstrated in great apes, but no information is currently available regarding this ability in other non-human species. In a comparative study, we tested Tonkean macaques (*Macaca tonkeana*), an Old World primate species, and brown capuchins (*Sapajus apella*), a New World primate species. We provided monkeys with two experiments using visual illusions of size and quantity to test their ability to discriminate appearance from reality, with an experimental setup similar to the one developed by Krachun and colleagues (2016) on chimpanzees. A large number of brown capuchins, of different ages and both sexes, as well as two Tonkean macaques succeeded in the two experiments. By ruling out all alternative explanations (i.e. visual tracking or associative learning), our study brings the first evidence that some Old World and New World monkeys are able to discriminate appearance from reality. Our results suggest moving the evolutionary apparition of this cognitive ability to earlier in time. Finally, it assumes that humans could share more Theory of Mind components with more non-human species than we previously thought.

Understanding the Impacts of Deforestation and Road Infrastructure Development on Chimpanzees Outside Protected Areas

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The majority of the Critically Endangered western chimpanzees (*Pan troglodytes verus*) occur outside protected areas. Ensuring their long-term survival in such areas implies addressing people-chimpanzee coexistence challenges. Using origin data of confiscated chimpanzees from two chimpanzee sanctuaries in West Africa, i.e. the Chimpanzee Conservation Centre (CCC), Guinea and the Tacugama Chimpanzee Sanctuary, Sierra Leone, and forest loss data from 2001 to 2015, we highlight how deforestation exacerbates interactions between people and chimpanzees and acts as a driver for the killing and capture of chimpanzees in the region. Finally, we present results from a systematic camera trapping survey (24 camera traps deployed across 27 1.25x1.25 km grids) conducted in the Moyamba district in south-western Sierra Leone in an area dominated by subsistence agricultural activities and practically devoid of forest. We employed a hierarchical Bayesian framework accounting for spatial autocorrelation to explore ecological and anthropogenic factors influencing chimpanzee relative abundance across the landscape. Our findings revealed that chimpanzees in such landscapes, where people are relatively tolerant of their presence, tend to avoid roads, including untarmacked secondary roads, and prefer to range in close proximity to more intact habitats such as swamps. Unexpectedly, they showed no preference for abandoned settlements where fruit orchard persist. Finally, although chimpanzees in this area did not avoid human settlements or areas frequented by people, areas of spatial overlap between the two species revealed temporal divergence in utilisation. Altogether, these studies emphasise the urgent need to understand better the factors that influence chimpanzee abundance and distribution outside protected areas, especially in the context of the rate of forest loss, and for aligning land use planning and infrastructure development to serve the needs of both people and chimpanzees.

Interactions with Humans Reduce Resting and Grooming Time in Commensal Rhesus Macaques (*Macaca mulatta*)

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Time is a valuable, but limited resource. Given that animals' survival is strongly contingent on their ability to navigate throughout their different daily activities, understanding the socio-ecological factors affecting animals' activity budgets has been a central topic in behavioural ecology. To date, the impact of human presence and behaviour on animals' time budgets has received comparatively little attention. In order to fill this gap, our study aims to investigate whether interactions with humans significantly affect time spent resting and in social interactions among three groups of urban-dwelling rhesus macaques (*Macaca mulatta*) living in Northern India. We tested two hypotheses: (1) the time constraints hypothesis, which predicts that interactions with people and monitoring human activity should reduce macaques' resting and social time; and (2) the free time hypothesis, which, instead, predicts that, under the premise that anthropogenic food is more calorific and therefore requires less foraging time, macaques who forage more frequently on anthropogenic food should spend more time resting and grooming. We collected a total of 1459 hours of observation from 124 adult male and female rhesus macaques, via focal animal sampling. Our analysis showed that macaques who interacted more frequently with people spent significantly less time resting and grooming, providing support for the time constraints but not free time hypothesis. Interestingly, we did not find evidence of human-induced time constraints for social grooming among subordinate females. We suggest that given that subordinates might use grooming to access services that dominants can provide, such as agonistic support, they might not be willing to give up grooming in order to interact with people. Future work will need to examine how these human-induced time constraints can affect species' long-term social relationships, health and fitness.

Canopy Camera Traps as an Efficient Tool to Advance Neotropical Primate Monitoring and Conservation

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Camera traps have been proven to be an efficient method to accurately assess and monitor terrestrial mammals, including a variety of primate species. However, this method has rarely

been used for arboreal species. We evaluated the detection efficiency of camera traps to survey arboreal primates in the Atlantic Forest of Brazil compared to traditional line transect sampling. We also assessed the influence of the study design on the detection probability by comparing different numbers of camera traps (2-8) placed at different distances (~ 250m to 2000m) in an array. Both camera trap and transect census methods detected three primate species that range in body sizes: *Callithrix flaviceps*, *Sapajus nigritus* and *Brachyteles hypoxanthus*. Detection probability by each method varied between species. Arboreal cameras traps provided higher detection efficiency than the traditional transect census for the small- and medium-sized species, but provided a similar detection efficiency for the larger northern muriqui. Comparing the sampling 'effort' necessary to reach a detection probability of ≥0.95 for each method, we found that 5-8 weeks of arboreal camera trapping corresponded to ≥12 survey events of single day transect censuses, or to ≥5 week-long transect censuses, depending on the species. Overall the detection probability increases with the number of cameras used and with a decrease of distance between them, but small and medium size primates benefited most from an array with multiple cameras. The use of canopy camera traps represents an exciting and promising tool for a non-invasive arboreal primate monitoring, providing great detection efficiency for different species. Its use may improve future studies and be valuable for conservation of aboreal primates, and it has great potential to be applied in remote areas and at large temporal and spatial scales.

Another Dimension to Primate Conservation: Human Impact Reduces Behavioural Diversity in Wild Chimpanzees

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We often measure the relative value of wildlife populations using metrics such as the number of individuals, genetic diversity or demographic viability yet the importance of behavioural variation or even socially transmitted traits, in other words culture, has traditionally been overlooked. I and colleagues from the Pan African Programme: the Cultured Chimpanzee, recently investigated the effect of a cumulative measure of human impact, or 'footprint', on the distribution of up to 31 chimpanzee behaviours, of which more than half have been argued by previous scholars to show cultural variation. We compiled presence data from both the PanAf and published literature to obtain information about these behaviours for 144 chimpanzee communities. Acknowledging that these data were limited, since they combine surveys and observations on wild chimpanzees from a multitude of sources and have been collected using both direct and indirect methods, we ran our analyses using various subsets to ensure results were not contingent upon particular datasets. These results were recently published and showed a consistent pattern: chimpanzee behaviours were less likely to occur in areas with high human impact. We found an average reduction of 88% across all behaviours for chimpanzees living in areas with the highest human impact compared to areas with the lowest human impact. Whilst interpreting our results, we also uncovered evidence for a 'protective effect' of long-term research sites, supporting the importance of research for conservation. We are currently working to keep our published dataset updated for future work. More importantly, we are engaging with the wider conservation community to discuss ways in which species behavioural diversity can contribute to conservation actions, such as designating species cultural heritage sites. For more information please visit our poster 'Primate Culture and Conservation' presented in collaboration with other animal culture specialists.

Dominance Style and Vocal Communication in Primates

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Empirical tests of major theories such as the social brain hypothesis tend to rely on group size as a measure of social complexity. Although group size is clearly important, other aspects of social structure may have played an equally important role in shaping behaviour and have to date been overlooked. Dominance style (the degree to which a dominance hierarchy is enforced; ranging from strict or 'despotic', to relaxed or 'tolerant') is a potentially important factor, but it is rarely quantified systematically outside of the macaque genus. We hypothesise that more tolerant primates will display more frequent and complex communication due to the increased uncertainty in social interactions, a greater need to use negotiation or persuasion, and a reduced risk associated with misunderstandings. Increasingly, primatologists are acknowledging that large-scale collaborative comparative projects are required to adequately test hypotheses relevant to the entire primate order. We present observational behavioural data from 109 wild, habituated, unprovisioned groups of 25 primate species. We tested the hypotheses that a) more tolerant individuals will vocalise more frequently, and more tolerant species will have b) larger vocal repertoires overall, c) more social vocalisations and d) fewer appeasement/dominance vocalisations

in their repertoires. From our dataset we extracted vocal rate and five measures of dominance style (Counteraggression, Aggression Intensity, Feeding Proximity, and Directional Inconsistency Index for Aggression and Grooming) at the individual and species level. We extracted vocal repertoire data from published literature. Using Bayesian Markov chain Monte Carlo (MCMC) generalised linear mixed models (GLMMs) controlling for group size, we found support for hypotheses a) and d) with some but not all dominance style measures. We discuss our results in light of the social complexity hypothesis for communication and the power asymmetry hypothesis.

The Primate Genome Sequencing Initiative: Assessing Primate Genomic Diversity at a Global Scale

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About 60% of the world's primate species are currently threatened with extinction. The majority have declining population sizes, mainly because of anthropogenic factors. While several species of primates have been studied in depth, mainly to understand better our own evolutionary trajectories, there is still a lack of data to understand primate evolution and genomic diversity at a global scale. We produced whole genome shotgun sequences to an average coverage of at least 30X for several hundred primates, and currently cover 136 different species. Our samples span 52 different genera and currently include around 30% of all described species of primates in Africa, Asia and the Neotropics. More than half of these samples are from species threatened with extinction and the majority are from wild born individuals. We explore how genomic variation within different primate lineages has been shaped across the globe and find New World monkeys and Asian Old World monkeys to have much lower degrees of genomic diversity than African Old World monkeys. Furthermore, we study how the IUCN extinction risk categories correlate with estimates of genomic diversity in several groups. Our dataset provides the most extensive and complete catalogue of primate genomic variation to date and we aim to use it to help guide future conservation efforts.

Chimpanzee Biogeography Inferred from Genetic Diversity and Effective Migration

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Understanding the demographic history of a species can elucidate patterns of behavioural and genetic diversity as well as provide context to guide conservation efforts for endangered species. Although many species display a general pattern of isolation by distance (IBD), geographic barriers can lead to differentiation that is greater than expected from geographical distance. Chimpanzees (*Pan troglodytes*) have a trans-continental distribution with four recognised subspecies demarcated by geographic barriers. However, this taxonomy is controversial: while several studies have found evidence to support these subspecies designations, others suggest they are artefacts of biased sampling. The Pan African Programme: The Cultured Chimpanzee (PanAf) comprises genetic, ecological, demographic and behavioural data collected throughout the entire geographic range of chimpanzees. Here we present the most comprehensive study to date on chimpanzee population demography based on microsatellite analyses of over 5000 geo-referenced, non-invasively collected faecal samples spanning 57 locations across the ranges of all four subspecies. We aimed to test for the presence of genetic structure, estimate effective migration rates and map the distribution of genetic diversity across the species. The broad pattern of genetic variation in our dataset is characterised by IBD with some local substructure, possibly due to recent isolation of several populations. Western populations have considerably lower diversity and higher effective migration rates relative to the rest of the species. We identified signals of longitudinal gene flow in the eastern populations as expected, but contrary to expectations, evidence of latitudinal gene flow was also present. Together, these results highlight the high degree of geographic mobility in this endangered species, indicating that conservation approaches should intensify efforts to improve and protect connectivity among populations to ensure their survival.

Effect of Group Size and Individual Characteristics on Between-Group Encounters in Primates

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Between-group encounters are common in primates and sometimes characterised by aggressive interactions between members of the opposing groups. We extracted data from the literature to test: 1) whether group size difference between the opposing groups affects the outcome of the encounter; and 2) what individual characteristic (sex, age or dominance rank) affects the likelihood that an animal would take part in an aggressive encounter. Our dataset comprised 58 studies on 31 primate species (3 lemur species, 5 New World monkeys, 19 Old World monkeys and 4 apes). We found support for the hypothesis that, for encounters where there is numerical disparity between the two opposing groups (based on total number of adults and sub-adults of both sexes in each group), the larger group is more likely to win an encounter against a smaller group than vice-versa. Contrary to our prediction, we did not find evidence that, in the primate species included in our analyses, males are more aggressive towards out-group members during between-group encounters than females. Finally, we found little support for the hypothesis that dominance rank and age affect how frequently animals engage in aggressive between-group encounters. Our analyses reveal that group size is an important factor shaping between-group interactions. Conversely, sex, age and dominance rank appear to have limited effects on aggressive participation in between-group encounters in primates and their role may differ across species.

Female Dispersal Patterns in Western Lowland Gorillas

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Evaluating the factors influencing the patterns of female dispersal in mammals is critical to understanding its importance for male and female reproductive strategies and the evolution of social systems. In western lowland gorillas, *Gorilla gorilla gorilla,* females leave their natal group (natal dispersal) but also move between reproductive groups multiple times in their life (secondary dispersal), an interesting strategy that is believed to represent female choice for the protective abilities of the male. In this study, we assess factors of feeding competition, mate competition and male competitive ability potentially influencing female secondary dispersal in western gorillas using a 20-year observation period at the Mbeli clearing in the north of the Republic of Congo. We found that females are more likely to stay with young males in the beginning of their tenure than transfer and more likely to disperse away from older males that reach the end of their tenure or are closer to their death. Female secondary transfer was not influenced by the size of the group nor the number of adult females. These results are consistent with similar reported effects on female reproductive success in the same population and suggest that female dispersal strategies are influenced by male competitive ability and not by feeding or mate competition.

Utilising Drone Technology in Primatology for 3D Mapping

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Emergent Unmanned Aerial System (or drone) technology allows the 3-dimensional mapping of forest landscapes, allowing a new perspective of arboreal primate habitat use. Utilising UASs in primatological studies enables the assessment of habitat quality for different arboreal primate species, the identification of discreet forms of anthropogenic disturbance (such as historical selective logging), and detailed investigation of canopy use by arboreal primate species. Combining 3D canopy structure with microclimate measurements, we can see how canopy structure buffers solar radiation and how arboreal species may be affected by future climate change. We present data on a study of the arboreal primate community in a lowland section of the Gunung Leuser Ecosystem in northern Sumatra, focusing on how 3D canopy structure effects ranging (siamang, *Symphalangus syndactylus*), different primate species' population densities (lar gibbon, *Hylobates lar,* siamang and Thomas langur, *Presbytis thomasi*) and habitat selection (orang-utan, *Pongo abelii* and siamang) and how UAS technology can be utilised in other future studies; the potential opportunities, challenges and pitfalls.

Underground Food Excavation in Captive Chimpanzees: Behavioural Repertoire and Tool Characteristics

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Foraging for underground storage organs of plants (USOs) has been hypothesised to have played an important role in human evolution during the colonisation of dry habitats. Indirect evidence from Ugalla (Tanzania) and Bandafassi (Senegal) suggest that chimpanzees use tools to excavate for USOs. Wild chimpanzees have never been directly observed performing tool-assisted USO excavation. We presented two groups of captive chimpanzees with the opportunity to use tools to excavate artificially-placed underground foods in their naturally forested outdoor exhibit. We gave no guidance or demonstration to the chimpanzees at any time – subjects were naïve to tool-assisted digging at test. We found that the naïve chimpanzees spontaneously used tools to obtain buried food, and that they displayed a variety of excavating behaviours in doing so. The spontaneous chimpanzee behavioural repertoire proved similar to that described for wild chimpanzees foraging for other underground food sources. Chimpanzees were also selective in their choice of tools - they preferred longer tools for excavation over shorter ones. Our results contribute to the growing body of research suggesting the existence of a shared behavioural repertoire in chimpanzees and provide new insights into early hominin foraging behaviour.

Cracking the Puzzle: Reconstructing Nut-Cracking Sites of Western Chimpanzees Using Phytolith Analyses

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Phytoliths are taxonomically diagnostic silica bodies that select plants deposit in different parts of their structure. After plant decomposition, they are usually deposited in sediments, potentially for millions of years. Phytoliths in sediments have been identified to reconstruct modern and past environments. This opal silica microfossil has also been detected in primate faeces and has expanded dietary interpretation in extant apes. Palms (Arecacae) produce a high abundance of phytoliths, including globular echinates. Productivity of this phytolith decreases during deposition in modern soils but, due to its robusticity, it has been found at Plio-Pleistocene hominin sites. Globular echinates are found in various parts of *Elaeis guineensis*, including the nut which is processed and eaten by West African chimpanzees (*Pan troglodytes verus*) using hammers and anvils. This study investigates the efficacy and limitations of phytolith work to reveal components

of localised nut-cracking sites used by chimpanzees in Bossou Forest, Guinea. We evaluated the relationship between globular echinate deposition (productivity) and distribution (soil-depth) in sediments and prevalence of nut-cracking activity. We systematically collected soil samples at various depths from: 1) active nut-cracking sites; 2) nut-cracking sites that have been dormant for 10 years; and 3) trees where nut-cracking has never been observed. Preliminary findings indicate that sediments (≤5cm depth) in the immediate vicinity of tools and processed nuts at active nut-cracking sites have greater productivity of globular echinates, but distribution generally decreases with greater soil depth across sites. This work contributes to primate archaeology and palaeoecology; phytoliths detected provide insight into the accumulation of non-visible organic residues at nut-cracking sites. Continued exploration of palm phytolith deposition in modern sediments also helps to refine palaeoenvironmental reconstruction efforts.

Investigating the Impact of Forest Fires on The Population of Müller's Gibbons (*Hylobates muelleri*) in Sungai Wain Protection Forest, East Kalimantan, Indonesia

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Increasingly, vast areas of Borneo's tropical forests are being affected by large-scale fire events. Gibbon species endemic to Borneo, such as the Müller's gibbon (*Hylobates muelleri*), have been found to be highly adaptable to habitat disturbance, able to persist in forests long after other primate species have disappeared. However, previous research has shown that as habitat characteristics such as canopy cover, fruit availability and number of emergent trees decrease due to fires, the population size and density of gibbons also follows this trend. With the frequency and severity of forest fires forecasted to increase in the face of a changing climate and increasing population, there is an urgent need for more research on the impact that fires can have on the long-term viability of gibbon populations. We investigated the effect of two large-scale fire events on the population size and density of Müller's gibbon in Sungai Wain Protection Forest, East Kalimantan. We carried out acoustic triangulation surveys in three forest types – once-burnt, twice-burnt and pristine – from March to August 2018, with a total of 14 arrays of listening posts surveyed throughout the forest. These data were used to: 1) calculate estimates of current population sizes and densities across the three different forest types; and to 2) compare current values with estimates from 2012. Our estimates for the whole forest showed a population size of 709.69 ± SD 293.59 individuals and a population density of 2.69 ± SD 1.11 groups per km^2. These values

represent a decrease of 0.42 groups per km^2 compared to estimates in 2012 across all forest types. Furthermore, we estimate density to be 2.45 ± SD 0.87, 1.7 ± SD 0.49 and 1.07 ± SD 0.34 groups per km^2 in the pristine, once-burnt and twice-burnt forest, respectively. Our results suggest that the forest fires of 2015 have led to a decrease in gibbon population size and density in Sungai Wain Protection Forest. The findings of this study suggest that further forest fires at this site could lead to a drop in the population below viable levels.

Social, Ecological and Abiotic Factors Influence Movement in a Nocturnal Primate

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Animal movement is initiated by the need to secure resources including food items, mates and shelter, but animals also move to avoid predators and to interact with conspecifics beyond seeking mating opportunities. Abiotic factors can also impact ranging behaviour, especially in species that are more impacted by strong winds (i.e. small-bodied terminal branch users), or display known behavioural changes due to lunar phases (lunarphobic or lunarphilic nocturnal species). To investigate how variations in the nightly activity and climatic variables influence movement in the Javan slow loris (*Nycticebus javanicus*), we used data collected between 2016 and 2018 at the Little Fireface field station in West Java, Indonesia. We calculated the nightly path length for 15 individuals and quantified the ratio of insect vs. gum feeding, the proportion of social behaviours and climatic variables (i.e. cloud cover, luminosity and wind) for each night. We found that in the Javan slow loris, nightly movement is modulated by social interactions, foraging bouts and variations in abiotic factors. Examples of these changes include increased nightly path lengths when individuals were feeding primarily on gums compared to insects and less travel on brighter evenings compared to darker ones. Our results shed light on the various ways that a nocturnal primate structures its nightly movement. Advances in technology and forest access have improved our ability to collect more robust data on nocturnal animals, facilitating an increased research emphasis on movement ecology and spatial cognition. As we look to simulate animal movement, it is crucial that we understand the factors that initiate and minimise travel in a wild context.

A Macro-Evolutionary Perspective on Papionini Craniofacial Diversification

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The Tribe Papionini (Order Primates; Family Cercopithecidae; Subfamily Cercopithecinae) is a highly successful group of medium to large-sized cercopithecines including the extant

mandrills and drills (*Mandrillus*), geladas (*Theropithecus*), baboons (*Papio*), kipunjis (R*ungwecebus*), mangabeys (*Lophocebus*, *Cercocebus*) and macaques (*Macaca*). As striking evidence of their adaptability, papionins are geographically spread throughout the Old World, with most of them being distributed throughout sub-Saharan Africa, while macaques occupy Asia and North Africa. Despite their evolutionary success, the factors underlying their radiation are still not well understood. This is particularly relevant because understanding the origin of diversity is a central evolutionary question. Among the morphological traits potentially involved in the adaptive diversification of papionins, craniofacial morphology is of particular relevance, as ecologically critical functions are linked to this anatomical structure (e.g. feeding, respiration, phonation, among others). In this study, we use geometric morphometrics and phylogenetic comparative methods to study the evolutionary process of cranial diversification in the large-scale radiation of papionins. A sample of 34 species was compiled from online databases to generate a representative sample with enough taxonomic coverage (~77%). First, we investigated the tempo and mode of craniofacial diversification, to then assess several alternative evolutionary scenarios that could explain the morphological evolution of this clade. The results show that no single explored factor (e.g. allometric or ecological) can be invoked as a unique explanation for the observed phenotypic diversity patterns in this tribe. When taken together, the present results indicate the evident complexity behind large-scale evolutionary radiations and the need to apply more sophisticated analytical tools.

Read My Lips: Does Women's Lip Colouration Contain Information About the Timing of Ovulation?

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Across human cultures, red is often associated with fertility. Men, from different populations, find women wearing or surrounded by red more attractive, and women are also more likely to wear red ornaments around ovulation. Studies of non-human primates showed that variation in female skin colouration (i.e. luminance: how dark or light the skin appears, redness: partially reflecting the colour of the blood itself) is influenced by sex hormones and can contain information about reproductive status. The link between red colour and fertility could thus have roots in human biological heritage and have emerged in a shared primate ancestor. While a few studies have tested whether women's cheek colouration varies according to the probability of ovulation, no studies have yet investigated whether the most colourful part of a woman's face, the lips, also contain such information. My study aimed at determining if women's lip colouration varies in relation to the probability of ovulation. I predicted that lips will become darker and redder (i.e. stronger signal) around the timing of ovulation. I collected 173 (mean per participant = 11.5 ± 1.4, range = 8-14) digital images of the face and saliva samples of 15 cycling women (mean age = 28.0 ± 4.1 years old, mean cycle length = 28.3 ± 2.5 days) at the Kyoto University Primate Research Institute, Japan. Samples were collected every second day from the onset of menstruation until the next menstruation (1 menstrual cycle per participant) between September 2018 and April 2019. I used digital images to measure lips' redness and luminance as perceived by the human eye and assessed ovulation period from salivary oestrogens and progesterone profiles. I will present results about variation in lip colouration according to the timing of ovulation and concentrations of sex hormones and I will discuss the possible inherited role of women's lip colouration as a sexual signal of ovulation.

Modelling Prehistoric Hunter-Gatherer Networks for the Study of Cultural Evolution

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Over the past decades, there has been a heated debate on the underpinnings of cultural evolution in prehistoric societies. The demographic-hypothesis predicts that cultural complexity depends on population size and the degree of social interaction within and among populations. While the influence of population size has been widely discussed, much less is known about the interplay between social structure (i.e. who interacts with whom and how frequently they interact) and cultural complexity in ancient foragers. In this study, we propose a network-based framework to formally assess how different aspects of the social structure can influence cultural transmission dynamics and, ultimately, cumulative culture. We apply this methodology within the context of the PALEODEM long-term project (ERC-CoG-2015 Ref. 683018), which aims to study cultural transmission processes during the Last Glacial and Post-Glacial periods in the Iberian Peninsula. We demonstrate how archaeological records, such as ornaments and lithic projectiles, can be used to estimate socio-spatial networks and to model cultural transmission dynamics in hunter-gatherer societies. We argue that a greater resolution of hunter-gatherer social structure might contribute to a better understanding of the contexts of cultural changes during prehistory.

Decision-Making Under Risk and Regret-Like Emotions in Tufted Capuchin Monkeys (*Sapajus* spp.)

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Although it is widely recognised that emotions have a crucial influence on decision-making in humans, little is known about the patterns of behavioural emotional responses shown by non-human animals as a consequence of an individual's decision, or about how emotions influence choice. We assessed whether tufted capuchin monkeys showed behavioural responses compatible with regret-like emotions in a risky decision-making task and whether these emotions affected their decisions. Twelve capuchins were presented with a series of choices between a safe and a risky option under three conditions: (i) Neutral: same probability of receiving either a 7-item or a 1-item outcome; (ii) Advantageous: 2/3 probability of receiving a 7-item outcome; (iii) Disadvantageous: 1/3 probability of receiving a 7-item outcome. We scored emotional and motivational responses before choices were made, and after (i) the outcome of choice was shown, and (ii) the alternative outcome was revealed. Capuchins performed risky choices according to the difference in the relative expected value between safe and risky options, and chose the risky

option more often after selecting a risky option, regardless of its outcome. In the trials immediately following the choice of a risky option with a 7-item outcome, as compared to the other two outcomes, they performed less scratching before choice although showing a higher latency to choose. Both scratching behaviour scored after the choice and the alternative outcome were revealed was not affected by those outcomes. In contrast, switching behaviour, i.e. the individual's attempt to change its initial choice, increased after the 1-item outcome was revealed and in potentially regret-inducing trials, where the alternative outcome was larger than the choice outcome. In conclusion, in a risky decision-making task capuchins showed a rich pattern of emotional behavioural responses compatible with regret-like emotions, although these did not directly affect their subsequent choices.

The Importance of Olfaction in Assessing Potential Feeding Items for a Nocturnal, Folivorous Lemur, *Avahi meridionalis*

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Olfaction is important for foraging primates in locating and assessing food items; it is important for captive and wild primates in distinguishing between ripe and unripe fruits and when assessing novel food items. Studies have largely focused on frugivorous species, although recent analyses showed no significant difference in sniffing frequency when foraging between frugivorous and folivorous New World primates. *Avahi* spp. are dedicated folivores and nocturnal, a rare niche within the primates, making them a good model to examine the importance of olfaction for folivorous primates. We conducted continuous focal animal follows on four pairs of *Avahi meridionalis* for ten months. We collected data on the sensory foraging methods used for finding tree species and plant part. To quantify leaf odour, we collected leaf samples from the top three feeding species (*Harungana madagascariensis*, *Canephora madagascariensis*, *Cynometra* sp.) and collected the volatile organic compound (VOC) content of the leaf samples using dynamic headspace sampling. We investigated the VOC content of the leaves using thermal desorption followed by gas chromatography-mass spectrometry. *Avahi meridionalis* was observed using olfactory foraging on 47% of feeding tree species and used olfaction in 44% of foraging attempts. We found significant differences in the diversity of VOCs in the odour bouquets of the top three feeding species (F (2,18)= 10.966, p=0.001), with *H. madagascariensis* (10.7 ± 4.5) showing the highest VOC diversity. Olfaction was only observed to be used in short distance foraging (≤0.5 m) by *A. meridionalis*, suggesting the main function of olfaction is in assessing the quality of feeding items, rather than locating feeding items. Olfactory cues (VOCs) may be important for *A. meridionalis* in interpreting information that can inform individual decisions on avoiding leaves that may contain large amounts of toxic compounds.

Longitudinal Chimpanzee Social Networks Using Deep Learning

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An increasing reliance on video recordings and remote camera traps for data collection in ethology and conservation has led to the accumulation of large archive and image datasets. A significant challenge facing researchers is the time and resources required to process manually such large volumes of data. Here we introduce a computational framework for the automated sampling of behaviour, using a deep convolutional neural network (CNN) pipeline for detection, tracking and recognition of wild species, and apply it to a longitudinal archive of wild chimpanzees (*Pan troglodytes verus*) from Bossou, Guinea. Our fully automated pipeline, trained on 10 million face images from a 14-year video dataset, spanning 23 individuals and 50 hours of footage, achieved accuracy of 92.5% for identity recognition and 96.2% for sex recognition. Our dataset features video footage from the Bossou Archive, systematically collected by Kyoto University Primate Research Institute since 1988 at the 'outdoor laboratory', where naturally occurring stone tools and nuts were provisioned in a forest clearing by researchers, which provides a unique opportunity to examine how individual and group behaviour changes over multiple generations. Using our face recognition pipeline, we automatically process ~250 hours of video footage by generating co-occurrence matrices from individuals (n=23) simultaneously detected in video frames, and examine how the group structure and individual social network positions change in response to a reduced and ageing population. This non-invasive, automated approach represents a paradigm shift in how researchers can harness the potential of large-scale and longitudinal archives to tackle key questions in behaviour and conservation.

The Development of Sex Differences in Diet Repertoires and Social Learning Biases in Wild Bornean Orangutans

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Sexual dimorphism in orangutans is very pronounced compared to other primates and goes hand in hand with sex differences in lifestyle. These sex differences are likely to result in different energetic demands and, thus, dietary needs in adults. We predict that, having to sustain pregnancy and lactation, females depend on more balanced and thus broader diets and go to greater lengths to obtain those than males, who mostly need to maximise their caloric intake to sustain their large bodies. Because wild orangutans learn their diets through a multi-year, socially guided learning process during infancy, we hypothesise that sex-specific adult dietary needs will be reflected in infants' diet repertoire development and social learning biases. We analysed 15 years of feeding data containing 60,687 observation hours of 13 immature, 10 adult female and seven flanged male Bornean orangutans (*Pongo pygmaeus wurmbii*), and 670 peering events, collected at Tuanan, Kalimantan, Indonesia. We found that compared to flanged males, adult

females have more variable and more complex daily diets as well as overall broader dietary repertoires. Immature females acquire broad diet repertoires faster and by the time of weaning have acquired larger diets that are overall more similar to the diets of their mothers than their male peers. We also found evidence that immature males avoid complex items. Furthermore, whereas immature females preferentially peer at their mothers, with increasing age, immature males show increasing interest in other role models. Our results confirm that differing dietary needs of adult orangutans are reflected in their foraging behaviour. Immatures seem to prepare for their sex-specific adult niches by adopting different learning schedules and social learning preferences. The detected social learning biases match with the species' dispersal patterns with philopatric females benefiting most from adopting the local diet and dispersing males from learning from a larger variety of role models.

Comparison of the *Pan* Social Brain: a Candidate Gene Approach

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The difference in cognition between humans and apes is not simply a greater degree of general intelligence, but rather a quantitative difference in social cognition. Social cognition comprises the ability to understand and respond to social responses of others. This concept includes social skills related to self-knowledge and theory of mind, which indicates the ability to understand the emotions and behaviour of a person from their perspective. In our project, we focus on our closest living evolutionary relatives: bonobos and chimpanzees. These two species diverged from the human lineage only 5-8 million years ago (mya). This makes them keystone species for investigating our own evolutionary past and identifying unique human traits. Although bonobos and chimpanzees diverged from each other only 1-2 mya, they show considerable differences in social cognition. Studies of bonobos suggest that they have higher social sensitivity and are better at tasks that require social tolerance and cooperation. However, to date very little is known about the mechanisms underlying these behavioural differences. To further our understanding of the evolutionary origins of human sociality, we study variation in candidate genes that are crucial in the regulation of the social brain. We report newly identified differences in the genes coding for the receptors for vasopressin (*AVPR1A*), oxytocin (*OXTR*), serotonin (*HTR1A*), dopamine (*DRD2*), oestrogen (*ER1* and *ER2*) and androgen (*AR*) based on high-resolution whole genome data for 20 unrelated bonobos and 57 chimpanzees. We examine the impact of non-synonymous nucleotide substitutions on protein function and structure and discuss their potential relevance for reported differences in social cognition between the two species.

Ability to Attend to Functionally Relevant Features of Objects in Gibbons (*Hylobatidae*)

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The use and manufacture of simple tools has been reported in a wide range of species. In particular, numerous reports describe the use of tools to extract food sources by non-human

primates, both in the wild and in captivity. Fewer reports have explored how non-human primates represent tools, and more specifically their level of understanding of which properties are relevant when considering the functionality of a potential tool. We assessed the ability of 23 gibbons (*Hoolock leuconedys*, *n* = 8, *Hylobates moloch*, *n* = 4, *Hylobates pileatus*, *n* = 5, *Nomascus leucogenys*, *n* = 4, *Symphalangus syndactylus*, *n* = 2) to attend to functionally relevant features of rakes, during a food retrieval task. Outside each of the subjects' enclosures on a platform, we presented one functional and one non-functional rake, both baited with food rewards. Gibbons were required to select the functional rake to draw in the out-of-reach reward. Performance was poor during an initial assessment of this ability, suggesting gibbons struggled to differentiate between the properties of rakes that made them useful for goal attainment. However, subjects reliably selected the functional rake across incremental training experiments presenting rakes with more distinctive perceptual variations. When re-tested with the original rake set, 10 subjects now performed at criterion level, with eight continuing to select a functional rake during a final experiment in which we presented a novel rake shape, suggesting they had learned to attend to the relevant functional properties of the rakes. Subjects reached criterion level performance faster during later experiments, providing some evidence of ability to generalise learning and transfer knowledge across rake sets, rather than learning being tied to specific perceptual features. Taken together, the findings support the proposal that typically non-tool using species may possess a mechanism for attending to functionally relevant features of objects, given sufficient experience.

Comparing Social Tolerance Between Wild and Captive Common Marmosets (*Callithrix jacchus*)

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According to the cooperative breeding hypothesis, reliance on allomaternal care played an important role during human evolution, among others by increasing social tolerance. It thus predicts higher social tolerance in cooperatively breeding species compared to independently breeding ones. Such a link has been reported for captive primates, but comparisons with wild populations are missing. We therefore compared social tolerance in different environments, predicting higher social tolerance in captive groups because of the higher food availability. We conducted 140 trials in six marmoset groups: two from the natural environment (caatinga, north-eastern Brazil, Assú-RN; 30 trials/group) and four from captivity (20 trials/group). We used a 1 m^2 arena and distributed banana pieces evenly within it (same number as non-infant subjects per group). The arena was placed in the absence of the subjects, 1 m above the ground, close to one of the resting trees in the natural environment and in the groups' outdoor enclosures in captivity. The experiment began when the first marmoset entered the arena and ended when no banana pieces were left. We measured time inside the arena for each subject and all social interactions; time inside the arena was analysed using LME and social interactions with GLMM. We controlled for infant presence, sex ratio and sex-status categories, and included individual nested in group as random effect. We found that wild groups were more tolerant than their captive counterparts (stay inside the arena: F=2.670; df=30.301; p=0.012; evade the arena: Z=-4.237; df=7; p=2.27e-05; cofeeding: Z=2.583; df=8; p=0.00981) while showing similarly low rates of agonistic behaviours (Z=-1.340; df=10; p=0.1801). Unlike our prediction, social tolerance was higher in wild groups. We suggest that the harsher conditions in the wild lead to stronger interdependence and social tolerance, thus corroborating the Cooperative Breeding Hypothesis.

An Introduction to the Great Ape Welfare Group (GAWg) and Consideration of How We Can Translate Our Research to Ensure Optimal Outcomes for the Wellbeing and Conservation of Captive and Wild Great Apes

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The Great Ape Welfare group (GAWg) was established in 2018 by Susannah Thorpe (University of Birmingham) and Kirsten Pullen (CEO of the British and Irish Association of Zoos and Aquariums). GAWg's members include zoo practitioners, researchers of wild and captive great apes and representatives of great ape-related representative bodies, welfare charities and government organisations. Our aim is to combine expertise in great ape behaviour, welfare, ecology and management and relevant guidance and legislation which apply to them, to generate evidence-based improvements in welfare, husbandry and policy that are interlinked with conservation and research. From an academic perspective, GAWg fits within the increasing realisation that we should work more closely with end users of our research to maximise its impact. This talk will outline the aims and rationale of the group and some of the key activities that we have already undertaken, including the formulation of great ape-specific guidelines to be included as a chapter within the Secretary of State's Standards for Modern Zoo Practice, the regulatory document that sits alongside The Zoo Licensing Act 1981 (England and Wales) as amended, providing guidance to the licencing and regulation of UK zoos. The presentation will also seek to initiate consideration of a framework that will enable us, as primate researchers, to communicate our research in the most effective way for end users to make optimal use of the findings.

Mum's the Word: the Lasting Impacts of Maternal Loss on Offspring Survival, Growth and Reproductive Success in Wild Chimpanzees

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Childhood is a distinctive human life history adaptation characterised by a prolonged juvenile dependence on maternal care that is uncommon outside of our species. A long childhood has likely been adaptively selected to enable sustained somatic and brain development, as well as prolonged exposure to social learning opportunities, in turn leading to the extraordinary cognitive and cultural traits of the human species. In chimpanzees, immature individuals continue to preferentially associate with their mothers for years beyond weaning and often until sexually

mature. However, what clear fitness benefits may be gained from this sustained association have not been fully explored in this species. Drawing upon a combination of demographic, physiological and genetic data from the wild chimpanzees of the Taï Chimpanzee Project (Côte D'Ivoire), we demonstrate that maternal loss negatively affects growth, survival to adulthood and future reproductive success during adulthood. Using urinary creatinine (a by-product of metabolic activity in muscle tissue) as a non-invasive measure of growth, we demonstrate that orphaned chimpanzees grow slower than chimpanzees of the same age that still have their mother present. Using long-term survival data, we show that years spent with mothers has a positive association with survival probability. Finally, using genetic paternity data, we demonstrate that adult males that lose their mothers during early development are less likely to sire offspring, and when they do, they achieve their first paternity later in life compared to males that have their mother present throughout ontogeny. Taken together, these results demonstrate that chimpanzee mothers have a sustained influence on offspring phenotype and fitness hitherto undemonstrated outside of humans, suggesting that prolonged maternal association, at least until adulthood, is a life history adaptation with deep evolutionary roots.

Olfactory signals and fertility in olive baboons (*Papio anubis*)

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Female primates signal impending ovulation with a suite of sexual signals. Studies of these signals have focussed on visual and, to a lesser extent, acoustic signals, neglecting olfactory signals. We investigated the information content of female olfactory signals in captive olive baboons (*Papio anubis*) and relate these to the female sexual cycle and the fertile period. We studied five adult females living in three social groups at the CNRS Station de Primatologie, Rousset-sur-Arc, France. We used vaginal cytology to detect ovulation. We investigated the volatile component of odour signals using solid-phase microextraction and gas chromatography-mass spectrometry. We identified a total of 82 volatile compounds, including several volatile fatty acids and hydrocarbons that have also been identified in odour profiles for other primates, and we examined the relationship between these and the timing of ovulation. Our results show that the total amount of baboon vaginal odour differs with sexual receptivity, suggesting that odour plays a role in signalling the timing of the fertile period. We also discuss the potential relationship between vaginal odour and group composition, female age and parity. This study of olfactory signalling provides a crucial missing piece of the puzzle of how females advertise their sexual receptivity.

Mammalian Diversification at the Species and Subspecies Level: Do Primates Follow the Rules?

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The presence, absence, or state of specific intrinsic characters might predispose lineages to diversify regardless of extrinsic context. Several character-state culprits of increased

within-lineage diversification rates, captured in speciosity, have been identified in mammals, including small body size, faster life histories and ecological specialisation. An unexamined question that might provide new insights into the relationship between micro- and macroevolution is whether these patterns are scale-free: that is, whether characters associated with within-lineage speciosity are likewise associated with the number of distinct populations within species. Subspecies represent genetically and spatially distinct intraspecific populations and we ask, therefore, if correlations are evident between subspecies richness (number of subspecies) and (i) body mass, (ii) age at female maturity, and (iii) dietary diversity in 194 primate, carnivore, cetacean and artiodactyl sister species pairs (total number of species: 388). Here, we provide evidence that patterns at the species level hold at the subspecies level in these mammal groups. The relationships between the intrinsic characters of interest and subspecies richness in Primates mirror those found in Carnivora and Cetacea. We also show that in the Primate order as a whole, time since sister species diverged (TSD) has little bearing on their independent rates of subspecific divergence; in this, primates again resemble carnivores and cetaceans, but not artiodactyl species. Within the Primate order, however, we demonstrate a negative relationship between TSD and per-pair difference in subspecies richness in the Atelidae and Indriidae, and a positive relationship between TSD and per-pair difference in subspecies richness in the Hylobatidae, Cebidae, Pithecidae and Lemuridae.

Deforestation Projections Imply Range-Wide Population Decline for the Critically Endangered Bornean Orang-utan

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Deforestation is driving the deterioration of ecosystems and biodiversity in the tropics. To assess the effect of forest loss on species it is necessary to understand where the largest numbers of individuals are at risk from future habitat change. Bornean orang-utans occur in a biodiversity hotspot that experienced deforestation at one of the highest rates in the world in the last decades. Here, we applied an innovative and spatio-temporally explicit deforestation model to project forest cover change on Borneo until 2031. We combined the projections with range-wide density distribution estimates for orang-utans to assess potential impacts on the species. This approach helps to quantify population declines under different scenarios of habitat loss, and is a significant

improvement on past assessments based on species ranges alone. Our projections point to continued deforestation in all states on the island, which could lead to habitat loss directly affecting up to 10,400 Bornean orang-utans. Populations that currently persist in industrial plantation concessions and other unprotected forests are expected to account for the majority of these losses. In particular, unprotected lowland forests in West and Central Kalimantan with high orang-utan densities were identified to be under acute threat from future deforestation. In contrast, orang-utans remaining in protected areas and logging concessions are found in forests with low levels of projected deforestation. Effectively anticipating where action is most urgently needed is an important step in halting the dramatic loss of primate species such as the orang-utan in biodiversity-rich areas undergoing rapid and extensive forest cover change.

How to Be the New Guy? Strategies of Unflanged Sumatran Orangutans (*Pongo abelii*) to Cope with a New Environment after Dispersal

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Dispersal is the movement from one's natal area to one's breeding site and occurs in all great ape species. Dispersing individuals are expected to show behavioural strategies to cope with their new physical and social environments, especially in species with long-distance dispersal, such as the Sumatran orangutan. Orangutans show extensive geographic variation in behaviour – including variation in diet repertoires, and feeding and nest building techniques – which is the product of ecological differences and cultural processes. As the dispersing sex, unflanged males must adjust to the physical and social environment of their new neighbourhoods. Here, we investigated (i) the extent to which males learn from locally resident individuals by peering (attentive close range watching) and (ii) the social strategies that males use to establish themselves in their new neighbourhoods. We used 10 years of association data collected at Suaq Balimbing, South Aceh, Indonesia, including 1,240 hrs of behavioural data and 270 peering events by 40 unflanged males. Associations were mostly tolerant and included extended time at close proximity and many positive social interactions. Peering occurred mostly in learning intense contexts (such as feeding and nest building) and was mostly directed towards resident females. There were also significantly higher interaction rates with the same object as the peering target after a peering event and a positive correlation between peering rates and complexity of the observed activity. Unflanged males that had arrived only recently in the area peered more frequently than established males. Furthermore, unflanged males seemed to occupy positions of high connectivity in the population's social network. In summary, we found evidence that dispersing unflanged males adjust to the environment of their new neighbourhood by learning socially from resident females, and that they establish themselves socially via frequent and highly tolerant associations.

Hand-Eye Coordination? Weak Evidence that Manual Manipulation Favours Increased Binocular Vision in Primates

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Two derived traits of primates are grasping hands and relatively convergent eye orbits, the latter allowing for binocular vision and, in turn, improved depth perception. Most hypotheses for primate origins posit that these two features evolved together for a single adaptive purpose, for example to facilitate the manual capture of insect prey. Similarly, it has been proposed that variation in binocular vision among primates may be associated with variation in manual activity, although this remains largely untested. Further, orbital convergence increases with body size across primate taxa, but there is little reason to think that larger primates engage in more complex manual manipulation than do smaller primates. Increased predation pressure on small-relative to large-bodied primates may, however, favour divergent orbits because convergence decreases the size of the total visual field, likely limiting the ability to detect predators approaching from the side or back. Here we test the hypothesis that variation in orbital convergence among primates results from the conflicting pressures of 1) predation risk favouring divergent orbits and 2) the use of the hands for complex manipulation favouring convergent orbits. We measured manual manipulation complexity using food-related tasks with captive primates. From the literature we collected data on body size (as a proxy for predation risk) and orbital convergence (two independent data sets). We conducted a phylogenetically-controlled analyses with each of the two data sets (n=34 and n=40 species, respectively), reaffirming the significant relationship between body size and orbital convergence. However, the relationship between manipulation complexity and orbital convergence approached significance in only one of the two analyses. Although reduced predation risk may thus allow for increases in orbital convergence, the importance of manual manipulation in driving increases in binocular vision among primates requires further investigation.

Use of Automated Image Analysis to Monitor Primates in Captivity and in the Wild

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The last few years have seen a rapid increase in the use of automated analysis of image data to monitor animals both in the wild and in captivity. Many of the projects fall into one of two categories – monitoring of wild animals for conservation purposes and monitoring of captive animals for welfare and research purposes. At best, cameras can be a non-invasive way of identifying species, individuals within a species and behaviours. Collecting, storing and analysing photo and video data is becoming more affordable, leading to a large increase in the amount of

such data. Recent methods such as deep learning that require large amounts of data for training are rapidly expanding the feasibility of this approach and its application in the lab and the field. The use of such technology with primates (excepting humans) lags behind that of other animal species such as farm animals and rodents. We will review the reasons behind this lag and the specific issues that primates present. We highlight two of our current projects involving captive rhesus macaques (*Macaca mulatta*) and wild Zanzibar red colobus (*Piliocolobus kirkii*) to illustrate the strengths and limitations of this approach. In both cases, we use face recognition technology to identify individual monkeys in videos (macaques; success rate of 95%) and photos (colobus; success rate of 61-82%). We discuss the role of visual data quality and quantity and its effect on the rate of successful face recognition and identify best-practice guidelines for image-gathering. Finally, we provide recommendations for the future application of this method to new species that would make important contributions to primate research both in captivity and in the wild.

Intra-Group Behavioural Changes in Consequence of Inter-Group Encounters in Javan Gibbons (*Hylobates moloch*)

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Agonistic inter-group interactions can cause individuals costs such as physical injuries, increased physiological stress and disrupted intra-group social relationship. Therefore, individuals employ various behavioural strategies to minimise the cost associated with the aggressive inter-group encounters. However, studies on impacts of inter-group encounters on intra-group behaviours are generally lacking, especially in species that live in small groups. We investigated behavioural strategies of territorial and pair-living Javan gibbons in response to inter-group aggression such as I) affiliative behaviours among pair-partners, II) changes in activity patterns, and III) potential inter-group avoidance strategies, such as sleeping site selection. We observed 129 encounters among three habituated gibbon groups surrounded by four unhabituated groups in Gunung Halimun-Salak National Park from 2014 to 2016. Overall, we found no increase in the affiliative behaviours between pair-partners following the inter-group encounters. However, we found a decrease in grooming interactions after more aggressive encounters but not after lost encounters. During inter-group encounters, gibbons significantly altered their activity budgets: they foraged and socialised less but stayed inactive and called more often. We also found that gibbons avoided inter-group encounters by sleeping farther away from the inter-group encounter location on days with more aggressive interactions. Our study indicates that between-group conflicts do not promote affiliative behaviour in gibbon pairs, but provide evidence of changes in activities during encounter and inter-group avoidance through sleeping site selection in gibbons.

Tracing the Origins of Language: Syntactical Rules and Combined Contexts in Common Marmoset Vocalisations

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How did human language evolve? Investigating the linguistic abilities of non-human primates might provide important cues to the linguistic abilities of our ancestors. One feature considered uniquely human is complex syntax – rules governing the combination of call elements. Non-human primates show evidence for combinatorial syntax (calls combined into a sequence with a new meaning) but compositional syntax (calls combined into a sequence whose meaning is derived from the elements' meanings) lacks empirical support despite decades of research. Interestingly, a simple form of compositional syntax has been found in two highly social songbird species, one of them a cooperative breeder. Unlike apes and most other primates, common marmosets (*Callithrix jacchus*) share their cooperative breeding system with humans. This socioecological factor has been suggested as a driver of vocal complexity. We examined the syntactical rules and contexts of a call combination (tsik+egg) and its elements (tsik, egg) in free-living common marmosets. We asked (1) whether calls are acoustically different when they are given on their own or combined, (2) whether calls are always combined in the same order, (3) whether single and combined calls are used in the same contexts. Preliminary analyses did not reveal acoustic differences between calls on their own and in the combination but showed that calls are consistently combined in the same sequential order. Whereas tsik calls were given in the presence of a predator or directed at a human observer and egg calls were given during foraging and play, the combination of tsik+egg was given during intraspecific competition as well as directed at an unknown animal (domestic rabbit). The contexts of tsik and egg calls thus seem to be related to fear and excitement, respectively, while the contexts of tsik+egg seem intermediate and may therefore combine both fear and excitement. On-going analyses will determine if this holds true with bigger sample sizes.

Speed Presentations

Chimpanzee Cultural Behaviour in the Anthropogenic Landscape of Guinea-Bissau

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Chimpanzee culture is prolific, and varies at multiple levels, between subspecies, within subspecies, between neighbouring communities and within communities. While a considerable part

of the species' range across Africa has been explored, less is known about chimpanzees inhabiting the western-most part of their distribution. Ours is the first study to document cultural variation between unhabituated chimpanzee communities in Cantanhez (CNP) and Dulombi (DNP) National Parks, Guinea-Bissau. Over a period of two consecutive years (2017-2018) we studied a total of five neighbouring chimpanzee communities in CNP, inhabiting a habitat mosaic: secondary-forest, mangrove, savannah, agricultural fields and human settlements. As an additional comparison, we included data from a one-month pilot study in DNP (2015). Our study aimed to provide behavioural profiles for the studied communities, thus expanding our knowledge of the region; identify behavioural variation between neighbouring communities; and contribute to continental-level comparisons of the ever-growing chimpanzee behavioural repertoire. We employed a combination of direct and indirect methods, including reconnaissance walks, camera trapping and collection of indirect traces. We identified 22 putative cultural traits, present in at least one (but not all) of the six studied communities, including extractive and non-extractive tool use as well as the use of mangroves. We add to our limited knowledge of Guinea-Bissau's chimpanzees and confirm that despite being challenging, the study of behavioural variation in unhabituated chimpanzees inhabiting anthropogenic habitats is nonetheless possible and can yield important results. We hope to provide inspiration for behavioural studies of thus-far neglected chimpanzee communities, thus helping to expand our knowledge of chimpanzee culture and adaptation to changing environments.

Late Miocene Primates and the Biogeography of Hominin Origins: A Role for the Unknown South?

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The late Miocene was key in the emergence of human ancestors. Molecular and palaeontological data indicate that the last common ancestor of the African apes likely lived in the late Miocene of Africa. Likewise, the earliest Hominini first appeared in the late Miocene, during a time of profound climatic and environmental changes. Yet this time remains poorly sampled in Africa, with major chronological and geographical gaps in the distribution of fossil localities. These gaps severely limit our understanding of the origin of the African apes and hominins and of the ecological conditions in which these primates first evolved. The late Miocene gap is particularly acute south of the equator, with only one locality currently known to represent this massive region. Here we describe the fossil record of a new fossil site dated to the late Miocene of Africa: Gorongosa National Park at the southern end of the East African Rift System in Mozambique. At Gorongosa, our team has discovered several palaeontological localities in estuarine depositional environments. Abundant fossil wood at the western end of the exposures documents mesophytic species intolerant of water stress, while pedogenic carbonates reflect predominantly C_3 vegetation. Most of the localities have yielded a range of fossil mammals, including proboscideans, suids, hyracoids and a possible anthropoid. The mammalian fauna is dominated by brachydont species, and stable isotopes from dental enamel indicate a diet of C_3 vegetation. Gorongosa fills key gaps in our knowledge of the African late Miocene. It is the first site in the East African Rift System to sample estuarine environments, the first to document late Miocene coastal forests and woodlands, and it is one of the few sites south of the equator. Gorongosa is thus the first site that can be used to test key hypotheses about the importance of coastal forests in the origin and early evolution of the Hominini.

Distinguishing Variants of Primate Facial Expressions Using the Facial Action Coding System for Macaques (*MaqFACS*)

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Though it is widely believed that human facial expressions are derived from primate equivalents, there is inconsistency in the methods of analysis between expressions produced by humans and non-human primates. While it has been demonstrated that subtle variation in human facial expressions can lead to significant changes in the meaning of expressions, primate facial expressions have generally not been examined using similarly objective and rigorous analysis. Construction of primate facial expression repertoires, for example, is often subjective and oversimplified, with expressions often arbitrarily pooled and/or split into subjective pigeonholes. We aimed to analyse primate facial expressions in greater detail than has been attempted before, in order to assess whether there are discernible differences in the morphology of facial expressions that are reliably connected to their function. Using MaqFACS (Macaque Facial Action Coding System) to quantify bared-teeth expressions produced by wild crested macaques (*Macaca nigra*) engaging in spontaneous behaviour, we utilised discriminant analysis to look for morphological differences between bared-teeth produced in four different contexts, defined by the outcome of interactions: Affiliation, Copulation, Play, and Submission. We found that bared-teeth produced in these contexts could be distinguished at significantly above-chance rates, indicating that the expressions produced in these four contexts differ morphologically. We identified the specific facial movements that were typically used in each context, and found that the variability and intensity of facial movements also varied between contexts. These results indicate that non-human primates share the human ability to use subtle changes in facial expression to communicate different meanings, and that further work should examine non-human primate facial expressions in sufficient detail to capture this subtle variability.

From Extant Morphotypes to Extinct Morphotypes

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Primates' morphotypes are highly heterogeneous in size and shape (inertial properties). They also exhibit various posturo-locomotor capacities. From a biomechanical point of view, morphotypes are likely to reflect performance and, as a result, posturo-locomotor habits. In this context, a better understanding of the interaction between morphotypes and posturo-locomotor repertoires in extant species can help to model the locomotor habits of extinct species as well as their morphotype. With this aim, I have measured non-human primates for many years using a geometric model that estimates inertial properties of body segments. By collaborating with various zoological parks (e.g. Planckendael, Mulhouse, Besançon, Stuttgart), as well as the primatology station of the CNRS in Rousset (France), I have collected an important amount of morphological data on various species (e.g. *Cercopithecus lhoesti*, *Papio anubis*, *Nomascus gabriellae*, *Nomascus siki*, *Pan paniscus*). By combining these data with those available in the literature, I am able to investigate the variability of extant morphotypes as well as their relationships with the posturo-locomotor habits in living primates. Based on this knowledge, I will propose a phylogenetic meta-analysis in order to reconstruct morphotypes of possible primate ancestors.

Assessment of Welfare and Abnormal Behaviour of Rescued Spider Monkeys (*Ateles geoffroyi*) Under Different Housing Conditions

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Primate rehabilitation programmes aim to counteract the effects of the illegal pet and bushmeat trades on the welfare of rescued/confiscated individuals. In Mexico, several black-handed spider monkey (*Ateles geoffroyi*) rehabilitation centres have been established in recent years, but research comparing spider monkey behaviour and welfare between different facilities is lacking. The objective of this study was to assess and compare the welfare state of animals housed at two Mexican facilities; spider monkeys were either housed socially (four individuals in a pre-release enclosure) or in single-housing (eight individuals). All subjects were wild-born and originated from the illegal pet trade. Most subjects housed in the pre-release enclosure were confiscated as infants or juveniles and had been previously reared with other spider monkeys, whereas all single-housed individuals were received as adults and reared in unknown conditions. Individual spider monkey welfare state was assessed by (1) measuring behavioural indicators, (2) measuring physical welfare indicators (by two veterinarians), and (3) a primate welfare survey that was completed by two raters. Most of the indicators/survey items had acceptable levels of inter-rater reliability. There were significant differences in welfare state between the facilities: 75% of single-housed monkeys displayed abnormal behaviours, whilst monkeys housed in the pre-release enclosure were not observed to perform abnormal behaviours (motor stereotypies and self-injurious behaviours). Moreover, socially-housed monkeys were considered to have better social relationships and responses to stress, were more psychologically stimulated and displayed fewer negative welfare signs than single-housed individuals. We propose that a lack of environmental enrichment and deprived early rearing history had a greater impact on welfare than current housing.

Facial and Bodily Emotion Perception in Humans and Bonobos

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Recognising and properly responding to the emotions of others are vital skills for social species. Humans reliably recognise different emotions from both facial and bodily expressions. Observational studies in bonobos have suggested an ability to use facial and vocal signals for emotion communication in this species as well. However, no studies have yet systematically compared the species difference in perceiving emotions across different modalities and valences. The present study was designed to directly compare humans and bonobos in their attentional bias toward different emotions (positive/negative/neutral) expressed through face and body (with the face blurred). Viewing time was measured from 24 humans at Leiden University and

five bonobos at Apenheul Primate Park in the Netherlands. First, both humans and bonobos looked at non-scrambled pictures longer than at scrambled pictures, validating that content-related information, not the pixel based properties, captured their attention. Whereas humans looked at emotional expressions longer than at neutral expressions regardless of modalities (face/body), bonobos' looking time was significantly different in only the face condition, with neutral faces being looked at for longer than emotional faces. A similar study conducted in chimpanzees showed the opposite pattern to the bonobo, with this species looking at bodily expressions of negative emotions (agonistic interactions) longer than at neutral expressions. Potential biological and methodological differences will be discussed.

Baboon Survivorship and Group Demography Following Cyclone Idai

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In March 2019, Cyclone Idai devastated central Mozambique, creating inland oceans of water and killing at least 600 people and affecting almost 2 million more (OCHA). Also impacted in this extreme weather event was wildlife, including the animals of Gorongosa National Park (GNP), a 3,770km^2 area in this part of Mozambique. The park underwent severe flooding, with >8500 ha^2 more land inundated than in usual flood seasons. Since the cyclone, scientists in the park have been working to locate and assess study animals to understand the impact it may have had on their survival. However, primate adaptation to seasonal flooding has not yet been studied in GNP and there is little literature on primate adaptations to natural disasters in general, despite the fact that baboons are abundant and play a large role in the ecosystem as both grazers and opportunistic hunters. This study examines the survivorship and demography of a troop of baboons (*Papio ursinus*) known to be ranging in GNP's main floodplain when the cyclone struck. The group is semi-habituated and has been the target of a behavioural study since May 2018. As of November 2018, the group consisted of 8 adult males, 10 adult females, 1 sub-adult male, 4 sub-adult females, 10 juveniles and 4 infants, of which all adults and sub-adults and some juveniles were individually identifiable by sight. Researchers had observed the same troop on the floodplain in two previous years and thus we predict that the troop is accustomed to seasonal flooding inundating its normal home range. Here, we present preliminary data focusing on presence/absence in the study troop, demographic changes and ranging behaviour changes following displacement by the cyclone, and elucidate the wider impact on the population through comparisons of 2018 and 2019 encounters with neighbouring troops. From this, we hope to have a better understanding of the limits of primate adaptations in the face of extreme ecological change.

Prosociality Enhances Cooperation in Common Marmosets (*Callithrix jacchus*)

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Prosocial motivation has been hypothesised to facilitate the initiation and maintenance of cooperative interactions. For this reason, prosociality has also been suggested to be a central target of selection within social systems reliant on costly forms of helping behaviour and social coordination, such as the societies that are characteristic of recent human ancestors and other cooperatively breeding primates. While many studies have investigated prosociality in animals, its potential effects on cooperation remain unclear. Currently, mixed findings across taxa are difficult to interpret due to a reliance on interspecific comparisons, as well as the absence of directly comparable measures of prosociality and cooperative behaviour among the same individuals. To our knowledge, no prior animal experiments have utilised intraspecific variation in these traits to directly examine the proposed sociocognitive effects of prosociality on cooperation. In the present study, we therefore examined intraspecific variation in prosociality and cooperative tendencies among a captive colony of group living, cooperatively breeding common marmosets (*Callithrix jacchus*; *n*=23) to provide a direct experimental test of these hypothesised benefits. As predicted, we found that cooperative success, measured in a loose-string coordinated pulling paradigm, depended strongly on whether a dyad contained a prosocially motivated individual, which was measured separately in a group-service food provisioning paradigm. This effect was independent of partner choice across experimental sessions, as well as age, sex and personality, demonstrating that prosociality has generalised benefits for behavioural coordination among social partners. Our results thus suggest that prosocial motivation is a plausible target of selection for cooperative social interactions, such as those central to human sociality and various other primate societies.

Comparing Relationship Indices

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Many studies in animal behaviour, and especially primatology, use relationship indices as predictors or outcome variables in an attempt to capture social preferences, integration and affiliation among group members. A growing number of different measures have been proposed and are applied, often in parallel, but they all come with different assumptions, properties, strengths and limitations that are rarely explored. For instance, we usually assume that the index we choose correctly represents the underlying relationships within communities, but as we work with incomplete datasets, it is impossible to test how well these indices solve this task. Here, using simulated datasets, we test how well some commonly used relationship indices deal with small or imbalanced datasets, changes in interaction preferences over time, differences in interaction

frequencies of different behaviours, changes in group sizes and the inclusion of both socio-positive and socio-negative behaviours. We give guidance on how to decide which index is appropriate for which dataset and questions.

Is Certifying the Trade of Captive-Bred Primates an Effective Strategy to Prevent the Illegal Trade in Brazil?

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Trade in primates is a major threat for their conservation. A common supply-side intervention to reduce or prevent illegal wildlife trade is to flood the market with legal captive-bred individuals. In 1997, Brazil certified marmoset and capuchin breeders. However, it remains unknown whether captive-bred primates are successfully substituting wild-collected or illegally-bred primates in the domestic market. We aimed to compare the current legal and illegal trade in primates in Brazil. We monitored the trade of primates on Brazilian social media between 2017 and 2019, visited three open fairs in Rio de Janeiro state in 2019 and sampled certified breeders. We recorded 139 individuals of two genera being illegally traded online, 37 (26.6%) common marmosets *Callithrix jacchus*, 34 (24.5%) black-pencilled marmosets *C. penicillata*, 42 (30.2%) unidentified marmosets *Callithrix* sp. and 26 (18.7%) capuchins *Cebus* sp. We recorded four capuchins and three marmosets in the open fair and the legal breeders sell only eight capuchins yearly. Legal breeders sell capuchins for ~$17,000, 20-fold more than individuals illegally sold online ($823), and 10-fold more than those illegally sold in open fairs ($1,950). A similar pattern was observed for marmosets ($1,300 vs $155 vs $74). A fifth of the online sellers (n=8) consisted of fake profiles dedicated only to wildlife trade. The majority used their own personal profiles to sell those individuals (n=29). Our outcomes indicate that, despite the existence of legal sources, the illegal trade in primates still prevails. The lack of awareness, an unbalanced supply-demand rate and the difference in prices may be reasons driving people to buy from illegal sources. The number of traded specimens recorded surpassed the annual quota authorised by the government, indicating that the strategy of certifying breeders is still ineffective to curb the illegal trade.

Old Age Primates (Oaps): Locomotion and Musculoskeletal Disease in Ageing Populations of Chimpanzees

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Continuous improvements in zoo animal welfare have led to extended lifespans compared to wild conspecifics, particularly for the great apes. With ageing in humans, we commonly see slower more unsteady movement, increased risk and fear of falling and musculoskeletal disease, namely osteoarthritis. Given the challenging environment that wild apes must move around in, if present, these age-related impacts ought to be more salient. Osteoarthritis in particular is thought

to be a disease of sedentary lifestyles, where inactive joints are poorly maintained and cartilage breaks down. Evidence comparing wild and zoo chimpanzee activity is limited, but suggests captive chimpanzees are more sedentary, ergo prone to osteoarthritis. With this research, we seek to quantify how chimpanzee positional behaviour and locomotor ecology (movement and posture in a given environmental context) are impacted by ageing, and whether a potentially more sedentary lifestyle has adverse risks to joint and bone health. We aim to inform future captive animal welfare decisions as well as enclosure design and modification considerations.

Animals as Natural Resources? Primatological Research and the Responsibility for Human Communities

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Field researchers' responsibility towards human communities and ecosystems surrounding their study subjects is a growing topic in the wider dominion of ethics of behavioural research. Very roughly speaking, a consolidated idea is that researchers working in the field should act in order to not exploit local communities, but - on the contrary - to "compensate" and benefit them for the "scientific use" of the animals and the environments where they live. This seems to be a sound principle for a fair scientific practice, but such a principle also seems to rely on a questionable basis. Animals and environments are regarded as natural resources on which surrounding human communities have some kind of property rights. As a matter of fact, the legal status of animals and natural environments all around the world still justify such a view. Nonetheless, it is worth discussing whether ethical principles of behavioural field research should move forward from such a principle. Is it possible to ground responsibility for human communities on a different basis from the view of animals as natural resources? Primatological research seems to be an excellent case study for such a possibility, both for the nature of the research subjects (non-human primates are generally regarded to have a special moral status) and for the tradition of primatological research in establishing non-instrumental bonds with local communities. The authors will try to develop an analysis of such a question, relying on some experiences of interaction with local communities during field research in Madagascar.

The Importance of Local Ecological Knowledge for Species Conservation: A Case Study of the Lemur Community in Southeast Madagascar

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The success of wildlife conservation efforts is closely tied to species' significance to the local human population. Studies of wildlife ecology and behaviour, however, still

considerably outnumber those focused on people-wildlife relationships. The littoral forests of southeast Madagascar are no exception; while they are home to a diverse array of species, many of which are well-studied, few efforts have been made to document their relationship with and relevance to the local people. In this project, we focus on people's local ecological knowledge of the lemur species that inhabit these littoral forests. We based our study in two protected areas - Sainte Luce and Mandena Conservation Zone. Between July and October 2018, we conducted semi-structured interviews with 60 adults (30 men and 30 women) from six villages located in the two areas. All interviews were conducted in Malagasy, with the help of a local translator. We asked a series of questions about what people knew about the lemur community (i.e. the species' diets and activity patterns), how they viewed them (i.e. positively or negatively, and why), and whether they were hunted locally. The best known species in both areas was the red-collared brown lemur, *Eulemur collaris*, likely due to its daytime activity and the troops living near the villages being well-habituated. We found a positive relationship between knowledge about species and positive attitudes towards them, but in many cases, positive attitudes were associated largely with participants perceiving the animals as food. All surveyed lemur species have previously been hunted for food, but respondents report this has greatly reduced since the protected areas were established. Our study contrasts the ecological knowledge against the culturally embedded perceptions of species, which persist even after the related practices have receded. This highlights the complexity of long-term species protection, for which ecological, economic and cultural factors must be considered.

Social Antecedents and Consequences of Rhythmic Behaviours in Chimpanzees (*Pan troglodytes*)

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Recently there has been a growing interest in the rhythmic abilities of non-human animals, as a way of tracking the evolutionary origins of human musicality. Emerging evidence suggests that a handful of avian and mammalian species can (be trained to) align rhythmic actions to an auditory rhythm. This evidence has spurred an effervescence of speculations and debates regarding the origins of musicality. These are currently divided between theories that postulate the emergence of rhythmic abilities as the result of audio-motor neural adaptations that enabled flexible vocal learning and language evolution, and theories that view their evolutionary emergence as an essentially social phenomenon, primarily expressed in social bonding contexts, where it enabled individuals to move together in time, thereby allowing precisely timed cooperation. Extant empirical evidence from non-human species, however, is insufficient to substantiate any of these theories. In particular, there is a scarcity of data from our closest genetic relatives - the chimpanzees (*Pan troglodytes*) - and a lack of studies tracking the presence and potential functions of rhythmic behaviours in the (social) contexts in which they occur. To address this limitation, we conducted an observational study in which we documented the range of rhythmic behaviours exhibited by chimpanzees across solitary activities and social interactions. We collected data at two sites - Furuvik Zoo in Sweden (n=6 individuals) and MONA Foundation in Spain (n=14) - totalling 120 hours. Preliminary results show that rhythmic behaviours are frequent in a variety of social contexts (initiation of social interaction, play, grooming, courtship, display) and relatively absent in solitary contexts, with the exception of object play. Given their

high frequency in social contexts, it is plausible that rhythmic behaviours accomplish a communicative function, which in turn corroborates social theories on the evolutionary origins of rhythmic abilities.

Densities of Bornean Orang-utans (*Pongo pygmaeus morio*) in Heavily Degraded Forest and Oil Palm Plantations in Sabah, Borneo

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With over 75% of the current orang-utan populations living outside protected areas, habitat loss and fragmentation continues to be a primary threat to the species. Yet, there are still few published estimates of orang-utan densities in these heavily modified landscapes to inform range-wide population assessments and conservation strategies. We implemented nest surveys of the Northeast Bornean orang-utan (*Pongo pygmaeus morio*) across degraded forest and remnant forest fragments and riparian reserves in oil palm estates in Sabah, Malaysian Borneo. We then assessed the influence of landscape features and forest structural metrics obtained from LiDAR data on estimates of orang-utan density. Orang-utans were present in remnant forest patches in oil palm plantations, but at significantly lower density than in degraded forests. Densities were strongly influenced by variation in canopy height but, interestingly, were not associated with other potential covariates, such as distance to large forested areas. Our findings suggest that orang-utans can persist, at least in the short-term, within human-modified landscapes and highlight the need for further research and greater recognition that these degraded habitats can have a role in supporting orang-utan populations.

Investigating *Papio* sp. Genetic Variation and Gene Flow in Gorongosa, Mozambique, to Improve the Understanding of Introgression or Admixture Processes Between Baboons Species in the Top End of the Great Rift Valley

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Several cases of hybridisation and introgression between the six species of baboons (genus *Papio*) have been described. Molecular research in contact zones between baboon species has improved our understanding of the evolutionary history, speciation processes and determinants of gene flow in primates. Additionally, such studies may contribute to our understanding of hominin biogeography given that *Papio sp.* is considered a suitable model to investigate human evolution. Gorongosa National Park (GNP) is located near a predicted boundary area between two baboon species - *Papio ursinus griseipes* (grey-footed chacma) and *Papio cynocephalus* (yellow). GNP baboons have morphological features common to both chacma and yellow baboons and are intermediate between the two species concerning cranial diversity. These observations suggest introgression and/or recent events of admixture in the region. Our team is analysing more than 300 samples (faeces and tissue) collected from social groups within GNP limits and at locations outside the park, aiming to provide the first comprehensive description of the genetic diversity and population sub-structure of baboons in Mozambique. We amplified DNA for the first half of the mitochondrial DNA cytb gene and for 15 human-derived microsatellites loci. We found high levels of genetic diversity and gene flow from within and outside GNP. We discuss our results, highlighting the potential of baboon genetics as a proxy to investigate hominin demographic dynamics and gene flow in this region of Mozambique.

Testing Cognitive Aspects of 'Group Personality' in Common Marmosets (*Callithrix jacchus*): Does Social Environment Affect Individual Variation in Learning?

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Animal personality has recently been described in common marmosets (*Callithrix jacchus*) using a set of personality tests and observations. In particular, consistent inter-individual behavioural variation in exploration-avoidance and boldness-shyness was found to be smaller between individuals of the same group as compared to the variation among individuals of different groups. Marmosets are apt learners and they have also been reported to display substantial inter-individual variation in the learning tasks. However, no study to date asked whether and how inter-individual variation in exploration and boldness-shyness affects marmosets' propensity for individual learning, and whether this is also dependent on their social environment. In this study,

we tested 27 common marmosets in standard personality tests (general activity, novel food, novel object, foraging under risk, predator) and a series of cognitive tasks, divided into simple motor tasks (novel room, scale, target) and discrimination learning tasks (feature discrimination, size discrimination). We found that i) marmosets show individual consistency in learning across different tasks, but that the speed of learning differs between the family groups, and ii) marmoset personality affects the speed of individually mediated learning. In sum, it seems that both personality and the social environment of an individual are important factors linked to the individual variation in information processing, possibly also influencing the likelihood of subsequent social information transmission in the group.

Listen to the People, Hear the Gibbons Sing

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It has become widely recognised that acknowledging and understanding local people's perceptions about the environment is imperative for developing successful and effective conservation programmes. The perceptions local people have about a conservation project or the wildlife within their immediate area can be fundamental to the project's success. Conservation attitudes and knowledge may be influenced and guided by variables such as gender, education level, overlapping ecological and geographical spaces and socio-cultural values and beliefs. The goal of our research was to explore how communities living on the border of Gunung Gede-Pangrango National Park in West Java perceive the natural environment and the wildlife with which they share the forest. Specifically, we sought to gain a better understanding of how people feel about local conservation activities, determine their depth of knowledge about Javan gibbons (*Hylobates moloch*) and to assess their knowledge about threats to Javan gibbons in the wild. We conducted semi-structured interviews with 101 people during the months of June through August, 2016. Overall, 44% of women under the age of 40 reported they valued forest preservation over agricultural expansion, compared to just 27% of men. Both women and men over the age of 40 valued agricultural expansion over forest preservation. The majority of respondents (57%) reported knowing that Javan gibbons are a protected species, and 69% knew it was illegal to keep them as pets. Many people were uncertain as to the objectives of the Javan Gibbon Centre and felt 'left out' of conservation initiatives and expressed a desire to be involved. We must listen to the people and ensure their thoughts and beliefs about the natural world are acknowledged and valued, and woven into local conservation efforts. Developing inclusive conservation programmes and increasing awareness in local communities is one way to ensure the success of conservation efforts for Javan gibbons.

Free Vocal Expressivity in Young Chimpanzees

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Communication in primates closely related to humans, such as chimpanzees, provide crucial insights into the evolution of language. However, major differences exist between vocal production in humans and other primates. By three months of age, human infants have a vocal repertoire characterised by a mixture of affectively-biased vocalisations (e.g. screams, cries and laughter – which mostly occur in the presence of a specific affective state) and 'freely expressed' vocalisations, which are produced across a range of affective states. Free vocal expressivity is an essential foundation for language development and is a key component of the pragmatic character of language. In the present study, we examined the relationship between affect and vocal production in young chimpanzees. We observed semi-wild infant (n=19) and juvenile (n=12) chimpanzees aged 0-4 and 5-8 years, respectively, at Chimfunshi Wildlife Orphanage Zambia. A range of call-types were found, including grunts, whimpers, screams and laughs. Affective state during vocal production was characterised as positive, neutral or negative based on concurrent facial and behavioural cues. Laughter occurred significantly more often in positive affective states, $\chi^2(2)=15.00$, $p<0.001$, while screams, $\chi^2(2)=19.54$, $p<0.001$, and whimpers, $\chi^2(2)=16.63$, $p<0.001$, were significantly associated with negative affective states. By contrast, grunts were not significantly associated with any particular affective state, $\chi^2(2)=0.21$, $p=0.90$. The results indicate that, much like human infants, the vocal repertoire of young chimpanzees is characterised by a mixture of affectively biased and freely expressed vocalisations. Since free vocal expressivity is an important precondition for language development in humans, our results imply chimpanzee grunts may follow different developmental patterns compared to other call types and ultimately suggest one of the key developmental foundations for language is rooted in our primate ancestry.

The Human Factor in Primate Research

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Across the various fields and contexts of primate research (field observation, behavioural captive research, neuroscience, etc.) human beings interact in different ways with primate species of choice in a scientific context. Such interactions are somehow affected by the "human factor", that is, for example, character, attitude, expectations of the scientists carrying out their research, specific moral values endorsed by them, technical skills or particular traces of past education and training. In particular, we will highlight three questions: (1) What counts as a "human factor" in primatological research? (2) Is the role of subjectivity more influential in primate research than in research on other species, i.e. are primates a "special case" in this regard? (3) Is the attitude towards study subjects different in different research with primates, e.g. is there a difference between research on monkeys and research on apes? The authors will not aim to answer these questions, but rather to present some working hypotheses to propose possible research lines of enquiry to contribute to the ongoing debate on the objectivity of animal research, using primatology as a special case study.

Translocation Experiments Reveal that Vocal Dialects in Common Marmosets are Most Likely the Result of Vocal Learning

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Vocal dialects can result from vocal learning, but there are also alternative explanations, such as genetic or environmental differences between populations. In this study, we performed a series of translocation experiments to establish the most likely explanation for vocal dialects previously found between three captive populations of common marmosets (*Callithrix jacchus*). In a first experiment, we translocated 10 animals between different physical environments, specifically between different buildings with a different physical structure, and compared their vocalisations both before and immediately after translocation as well as after 5 – 6 weeks after translocation. We did not find any long-lasting changes in the call structure of the translocated animals due to the different physical environment in any of the three call types analysed. We corroborated this result in four additional animals that were translocated from their home colony to a quarantine facility and did not show any change in vocal structure. These four individuals were later translocated into a new colony with a different dialect, and thus also into a new social environment. We compared the vocal distance between them and four individuals from the new colony before translocation as well as over a time of 16 weeks after translocation. We could show that the vocal distance decreased significantly over time in two out of three analysed call types (phee- and trill calls, but not in food calls). As the translocated animals were only in acoustic, but not direct social contact with the new colony, these results indicate that common marmosets can modify their vocalisations due to passive exposure to a new dialect, so called crowd vocal learning. To our knowledge, this is the first study able to distinguish between different explanations for vocal dialects as well as to show crowd vocal learning in a primate species.

Symposia

Symposium
Technological Origins: Primate Perspectives and Early Tool Use in Africa

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Tool use is found in multiple animal lineages yet is a rare behaviour within the animal kingdom. Only half a dozen extant primates evolved tool use as an adaption. From these,

only *Pan* and *Homo* display tool use as a 'generalised' trait, i.e. documented in all populations. This raises the possibility that chimpanzees, like humans, may be dependent on technology. But how does tool use become an obligatory behaviour? Recent reviews suggest tool-aided extractive foraging as a pervasive part of some primate adaptations. Past scenarios depicted the hominin lineage as the pinnacle of tool use. Data from primatology and archaeology over the last 20 years renders this perspective obsolete. The presumed evolutionary interconnected relationships between brain size, bipedalism, meat consumption and tool use are not supported by current data. The state of the art proposes technology as undeniably 'Older than the Oldowan", reframing our expectations for the origin of tool use in hominins. An in-depth debate focused on the expectations of the archaeological record given this renewed perspective has yet to be realised. Inspired by the visionary approaches of Glynn Isaac, this symposium brings together an exceptionally interdisciplinary group of scientists conducting research at the heart of the origins of technology. Archaeologists examine the earliest hominin tool kits, primatologists report on precursor behaviours in the emergence of tool use, palaeoanthropologists discuss tool use in the LCA of *Pan*/*Homo*. We recommend avenues for future investigation and address essential questions: How much older than the Oldowan should hominin technology be? How pervasive could non-human primate tool use be in the past records? Were all hominins tool users? What ecological and social factors elicit tool use? Answers to these questions will need to build on the ecological and social context that can be observed in modern primates and explored in the deep past.

Primate Bifocals: Evolutionary Frames, Etho-Archaeological Lenses

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Palaeoanthropologists have a long tradition of using heuristic analogies with living human and non-human primates to develop evolutionary models of human origins. Now researchers are increasingly analysing the site-specific tool use and resource exploitation behaviours of wild primates, like chimpanzees, with fine-grained methods that can facilitate archaeological comparisons. One benefit of these studies is they have the potential to help discern and evaluate archaeological records of the cultural variation of chimpanzee populations. Such comparative methodology is also critical because it can be used to develop testable hypotheses to account for the formation of early archaeological sites – time-consuming, but much more potent than the "primate models" of an earlier generation. For example, these ethological-archaeology studies can help discern how processes of chimpanzee behaviour, which vary across the landscapes and lifetimes of living animals, could potentially produce patterns of behaviour that are cumulative. But under what frameworks and spatial or temporal scales is it appropriate to extrapolate from such inter- and intra-site patterns? As ethnoarchaeologists and experimental archaeologists often remind us, we must cope with the challenges of equifinality; even simple processes can independently produce convergent patterns in a cumulative archaeological record. To avoid having behavioural studies of the material records of chimpanzees become cautionary tales without tails, we should develop frameworks to facilitate the comparison of data from expanded and repeated observations at multiple sites, with similar methodologies and comparative purpose, while fully recognising the complex differences in socio-ecological histories of different populations that contextualise the work.

How Much Older Than the Oldowan? Tool Use and Manufacture in the Last Common Ancestor of *Pan* and *Homo*

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Complex forms of tool use and manufacture are often seen as a defining feature of hominins, but the manufacture and use of tools is not restricted to humans and their ancestors. Although tool use is a rare behavioural strategy in the animal kingdom, the use of tools for both subsistence purposes (i.e. extractive foraging tasks) and aggressive display is well documented in other primates. Chimpanzees have been the focus of numerous studies reporting on the regional variation, sometimes labelled cultural, in the behavioural repertoires of different groups. After humans, chimpanzees *(Pan troglodytes)* have the largest repertoires of tool use and manufacture known among primates. Bonobos *(P. paniscus)* have been the focus of less research and appear to be infrequent tool users in natural contexts. Because chimpanzees and bonobos are both our sister species and, notwithstanding their different degrees of reliance on technology, both are known to use tools, a comparative study of tool behavioural variation, but also of the morphological and cognitive correlates of tool use (e.g. hand morphology) between *Homo* and *Pan* may be useful in making inferences on the tools and tool-making behaviours of our last common ancestor, the LCA. Here, we address two questions pertaining to tool use and manufacture in the LCA. Was the LCA able to use and/ or manufacture tools? And if so, what type of tools likely composed the tool kit of this Miocene ape and in which ecological contexts was it more likely to use tools to solve problems? To answer these questions, we will explore four complementary lines of evidence: (1) comparative tool use in extant apes and other primates, (2) comparative anatomy and biomechanics of primate hands, (3) comparative cognition in hominoids, and (4) evidence from the fossil and archaeological records of early hominins.

Tool Use in the African Apes and Human Hunter-Gatherers: Comparative Human and Ape Technology (CHAT) Project

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Complex technology is a defining feature of modern humans. Despite its enormous significance to the success of our species, the evolutionary origin of complex tool use is not well understood. Comparative research in a natural setting is crucial to determining the evolutionary forces which prompted differences in technological skill to emerge and diverge among humans and other species. The *Comparative Human and Ape Technology (CHAT) Project* aims to construct

a comprehensive framework for understanding the evolution of technology that integrates the development of tool use with ecological and socio-cognitive factors across African apes and humans. The project involves a multi-site study of BaYaka Mbendjele hunter-gatherers, chimpanzees, gorillas and bonobos residing in the contiguous forest of the Congo Basin. In this comparative developmental study, we assess the ecological factors influencing tool use, as well as the relative importance of exploratory tendencies and learning mechanisms in the acquisition of tool use skills. This study is the first to explicitly examine the link between object manipulation and the emergence of tool use within individuals, as well as the factors promoting variation in tool use capabilities among species. We compare developmental trajectories of different types of tool use across humans and African apes, with information on the accompanying ecological and social contexts, to elucidate factors prompting technological skill in each of these species. This research advances our understanding of the adaptive qualities of tool use and the selective pressures associated with the origins and evolution of technology.

On the Pliocene Origins of Stone Tool Use

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Nearly a decade ago, the publication of two fossil bones from Dikika, Ethiopia, with surface modifications attributable to the use of stone tools and dated to some 800,000 years before the, then, earliest stone tools caused some disruption in debates over the origins of tool use in the hominin lineage. For some, the Dikika finds fit perfectly with analyses of early Oldowan assemblages that suggested still older examples of stone tool use and production would eventually be found. It has also been suggested that there was likely a long period of experimentation with stone tool use and production prior to 2.6 ma, after which stone tool technologies rapidly became an essential component of hominin adaptation. Others challenged the interpretations of the marks on the Dikika bones, attributing them instead to carnivores or to trampling. This challenge launched a vigorous debate, not only over the interpretation of the Dikika marks themselves but more generally over how surface modifications should be described, analysed and interpreted. A consensus view has not yet emerged. More recently, a stone tool assemblage of similar age to the Dikika bones was reported from Lomekwi 3, Kenya. The stone tool technology described from Lomekwi 3 is distinct from 2.6 ma assemblages in that it emphasises heavy, percussive activities rather than systematic flaking. Here again, for many the Lomekwi 3 finds fit well with expectations for what pre-Oldowan technologies might look like, drawing especially on a phylogenetic model that predicts percussive activities to have been a part of the behavioural repertoire of the last common ancestor with the apes. Others have challenged the Lomekwi 3 finds, arguing in part that it has not been satisfactorily demonstrated that the artifacts come from Pliocene deposits. Here, we review these two important data points, Dikika and Lomekwi 3, with an update on the most recent analyses of the Dikika marks and with new observations on the context of the Lomekwi 3 finds, and we attempt to evaluate models for early stone tool use and production in light of the relative uncertainties of these two data points.

Teaching and Prosocial Helping in the Tool Use of Wild Chimpanzees (*Pan troglodytes*)

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High-fidelity social learning and prosocial helping are hypothesised to help promote cumulative culture. We examined teaching and prosociality during tool use in wild chimpanzees by assessing the transfer of tools from skilled to novice tool users. We hypothesised that tool transfers comprise a functional form of teaching among chimpanzees in the Goualougo Triangle, Republic of Congo. In this population, termite gathering is a complex task involving two tool sets, selectivity for tool raw materials, and modification of tools to improve their efficiency. We scored chimpanzees' rates of tool use and feeding before versus after transfers. Tool donors experienced significant decreases in tool use and feeding after relinquishing tools, while tool recipients increased their rates of tool use and feeding after receiving tools. Transfers thus satisfied functional criteria for teaching: they occurred in the presence of a learner, were costly for the teacher, and conferred benefits on the learner. In a subsequent study, we compared tool transfers among Goualougo chimpanzees to those in Gombe, Tanzania. We hypothesised that prosocial helping would be greater at Goualougo than at Gombe, where termite gathering is a simpler task. Multiple measures indicated population differences in prosociality: the rate as well as the probability of tool transfer after request were higher at Goualougo, while the probability of resistance to tool transfer was higher at Gombe. Active transfers, in which tool possessors moved to donate their tools, occurred only at Goualougo. Together, these findings demonstrate that high fidelity social learning and prosocial helping intersect to promote the transmission of complex tool skills in chimpanzees, supporting the hypothesis that these factors may have contributed to the flourishing of technology during human evolution.

Variability in Core Rotation Strategies Among the Earliest Stone Tool Makers

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Human tool production is unique in its combination of high amounts of force, extremely accurate applications of that force and the sequential organisation of force application strategies. These three features are exemplified in flaked stone artefacts, and particularly in the ability of hominin knappers to implement a sequence of flake removals while shifting focus between different surfaces of a core. This shifting focus in flake production is sometimes called core rotation, and may have been a key step in the evolution of hominin technological behaviour. Systematic and repeated core rotation implicates both (1) a clear understanding of fracture mechanics, and

(2) the fine motor capacities needed to produce a number of flakes systematically. The refitted tools of some Early Stone Age (ESA) contexts, like Lokalalei 2C (West Turkana, Kenya), indicate hominins had a relatively advanced understanding of core rotation. In contrast, low numbers of sequential removals and emphasis on percussion rather than sharp-edged flake production at the much older Lomekwi 3 locality implies, potentially, a more limited understanding of, or need for, the benefits of core rotation. We therefore predict some diachronic variability in the efficiency of these tool production strategies through the Early Stone Age, as resources that required sharp edged flakes became more central and as selective pressures on knapping skill became more acute. Here we investigate tool production by characterising flake removals on cores using configurations of three-dimensional vectors. These vectors approximate the relative orientations and sizes of the flake removals on each core. We then use simulations to develop a set of predictions for what patterns in these vectors might reflect about core rotation decisions. We apply our model to assemblages of cores from multiple sites to assess tool manufacture across the first two million years of hominin artefact production. We will present and discuss preliminary results of these analyses.

Earliest Known Oldowan Artifacts at >2.58 Ma from Ledi-Geraru, Ethiopia, Highlight Early Technological Diversity

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The manufacture of flaked stone artefacts represents a technological milestone in the human lineage. Although the earliest production of primitive stone tools has been reported at 3.3 Ma from Lomekwi, the systematic production of sharp-edged stone tools is unknown prior to the 2.58-2.55 Ma Oldowan assemblages from Gona. The organised production of Oldowan stone artefacts is part of a suite of characteristics associated with the adaptive grade shift linked to the genus *Homo* and has been shown to significantly increase processing efficiency of high-quality food items. Recent discoveries from Ledi-Geraru, Ethiopia, place the first occurrence of *Homo* ~250,000 years earlier than the Oldowan at Gona. Here, we describe an assemblage of systematically flaked stone tools excavated *in situ* from a stratigraphically constrained context

(Bokol Dora 1, BD 1 hereafter) at Ledi-Geraru dated 2.61-2.58 Ma. The BD 1 assemblage represents the earliest evidence of hominin understanding of sequential flake removal and systematic production that is characteristic of the Oldowan. Technological analyses of the BD 1 artefacts indicate that hominins had not yet mastered the skills that experimental studies have shown to be critical in the systematic production of sharp edges. The technological pattern of BD 1 most closely aligns with the earliest Oldowan rather than with the earlier Lomekwian or with stone tools produced by non-human primates. This reinforces the evidence that hominin flaked technology is distinct from generalised tool use which may be a shared feature of the primate lineage. The earliest tool use likely enhanced the extractive foraging abilities of *Australopithecus* or *Kenyanthropus*, as it does in living primates, but the ability to produce sharp-edged flakes at BD 1 is a derived trait related to new foraging strategies. The BD 1 assemblage, near the origin of our genus, links behavioural adaptations and the biological evolution of our ancestors.

Object Manipulation and Play Behaviour by Wild Chacma Baboons (*Papio ursinus*) in Gorongosa National Park: Comparisons with Apes and Implications for the Evolution of Primate Tool Use

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The distribution of tool use across the animal kingdom presents an enduring puzzle. Elucidating which ecological, social and cognitive factors influence its presence or absence across multiple species is key to understanding its emergence and current taxonomic breadth. Comparative studies focusing on behaviours considered precursors to tool use in closely related species that differ in tool-using propensity can offer significant insights into this puzzle. Previous work comparing object manipulation and play by immature bonobos (limited tool users under natural conditions) and chimpanzees (prolific tool users in the wild) has suggested that variation in intrinsic predispositions may contribute to interspecific differences in tool use within the primate lineage. Adding data from other, more distantly related species to such research would represent valuable additional points of comparison. In the present study, we document object manipulation rates and repertoires, as well as components of play behaviour that are object-directed, in wild chacma baboons (*Papio ursinus*) in Gorongosa National Park, Mozambique. Wild baboons display limited tool use, and hence we predicted that their patterns of object manipulation and play would be more bonobo-like than chimpanzee-like. Our findings offer partial support towards this prediction: while chimpanzees did exhibit higher levels of object-directed play than either baboons or bonobos, baboons in fact showed the highest rates of object manipulation and we did not find clear differences in the object manipulation repertoires of the three species. Further, analysis of age-related effects in the baboon data showed immatures exhibited a more diverse target object repertoire than adults, but not a higher probability of object play or rate of manipulation. We explore the relevance of our results to understanding the role of precursor behaviours in the emergence of tool use in primates.

Symposium
Human Understanding of Primate Signals

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In a series of now classic experiments, researchers studying the evolution of language attempted to teach human language to non-human primates, with limited success. More recently, researchers have explored primate species' own signal repertoires. These have included the function of vocalisations, facial expressions and gestures, with a particular focus on signal use by our closest relatives: other great apes. In addition to understanding primate communication, these studies have investigated patterns of similarity and distinction across species, including humans, in order to inform theories on the evolution of human language. Nevertheless, a common drawback of these studies is that they rely on highly trained specialists who spend countless hours analysing primate signals, blurring our ability to detect a potential primate heritage that naïve human primates may share with their non-human primate relatives. Several recent studies have tried to address this gap, asking whether human participants can understand other primate species' signals without training. In this symposium, we present the findings of these studies and aim to evaluate them critically in light of what they bring to the scientific debate on the origins of language and, more broadly, on the evolution of communication. Participants will present experiments relying on a wide array of techniques including: large-scale computerised tasks, and behavioural, physiological and neural analyses. If any phylogenetic effect is at work, we expect lay participant recognition or understanding to be significantly above chance. It is necessary to consider alternative explanations unconnected to phylogeny, e.g. common acoustic properties. We must critically consider what is being explored in experiments that place participants in atypical socio-ecological contexts. All these questions will be addressed by the speakers, who come from disciplines including primatology, affective sciences and philosophy.

The Great Ape Gesture Dictionary

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Great apes deploy a gestural repertoire that is largely shared across all species (chimpanzees, bonobos, gorillas and orang-utans). The extent to which humans retain this repertoire is difficult to assess because humans additionally deploy co-speech gestures and learn large repertoires of conventionalised gestures. Rather than observing whether humans *produce* gestures from the great ape repertoire, we tested whether humans can *understand* the gestures produced by chimpanzees and bonobos. We conducted an online experiment hosted by Gorilla.sc, where participants watched videos of 10 chimpanzee and bonobo gesture types (for which the meaning was known, determined by the Apparently Satisfactory Outcome) and were asked to select the correct meaning from a choice of four. The order of videos and answers were randomised, and participants were randomly assigned so that half would see the video only, and half would see the video with a short text description of the context. After data exclusions, we analysed n=112,648 responses (Video only, n=59,001; Context, n= 53,647) from n=5,656 adult participants (Video only, n=2,962; Context, n= 2,694). Participants were able to interpret correctly the meanings of chimpanzee and bonobo gestures with or without additional contextual information (Video only: Success rate mean=52.1 ±11.0%; binomial, n=59,001, p<0.0001; Context: Success rate mean=57.3

±11.9%; binomial, n=53,647, p<0.0001). Humans are able to understand the meanings of chimpanzee and bonobo gestures better than would be expected by chance, suggesting that we have (to some extent) retained the great ape gestural repertoire.

A Gestural Repertoire of 1- to 2-Year-Old Human Children: In Search of the Ape Gestures

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When we compare human gestures to those of other apes, it looks at first as if there is nothing much to compare at all. In adult humans, gestures are thought to be a window into the thought processes accompanying language, and sign languages are equal to spoken language with all of its features. Some research firmly emphasises the differences between human gestures and those of other apes; the question about whether there are any commonalities is rarely investigated and has mostly been confined to pointing gestures. The gestural repertoires of non-human ape species have been carefully studied and described with regard to their form and function – but similar approaches are much rarer in the study of human gestures. Studies on human and non-human apes tend to rely on different methodologies and definitions, as well as conceptualisations of gesture and communication. In this study, we make a first attempt at classifying the natural gestural repertoire of human infants in their second year of life with the same methodology that has been applied to other ape species, allowing for a direct comparison. Applying this methodology to the study of human infant gesture is worthwhile and can tell us more about the development of human communication, but also supplement what we know about similarities and differences to the communication systems of other apes. We recorded (n = 13) children's gestures in natural settings with peers and caregivers in Germany and Uganda. We found that children employed 52 distinct gestures, 50 of which (96%) are shared between children and other apes, and 46 (89%) are present in the chimpanzee repertoire. Like chimpanzees, children used them both singly and in sequences, and employed individual gestures flexibly towards different goals. Many of the gestures we documented may be part of a universal repertoire of available gestures, shared across human and non-human ape species.

Emotion Processing in *Homo* and *Pan*

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Evolutionary processes selected group-living species, human and non-human primates included, to recognise and adequately respond quickly to conspecifics' emotional expressions. Different theories propose that mimicry of emotional expressions facilitates these swift adaptive reactions. When species unconsciously mimic their companions' expressions of emotion, they feel reflections of their emotions which inform social decisions. The majority of emotion research has focused on full-blown facial expressions of emotion in humans. Facial muscles can

sometimes be controlled; humans know when to smile and when not to. In this research, I therefore argue for a broader exploration of emotion signals from sources beyond the face or face muscles that are more difficult to control. More specifically, I show that implicit sources including the whole body and subtle autonomic responses including pupil-dilation are picked up by observers and influence subsequent behaviour. In my research, I take a comparative approach and investigate similarities and differences in the perception of emotions between humans and great apes. I will here discuss new, recently collected data and suggest avenues for future research that will hopefully eventually lead to a better comprehension of emotional expressions and how we come to understand each other's emotions.

What Can Chimpanzee Vocalisations Tell Human Listeners?

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Vocal signals, like laughter and screams, that are linked to emotional states are in part conserved among genetically related species. Such phylogenetic continuity of emotional vocalisations may yield not only similarities in production of vocalisations but also cross-species recognition of affective information from them. We draw on two main approaches to phylogenetic continuity in emotional expressions, and test whether human listeners can identify from chimpanzee vocalisations 1) the context in which vocalisations were produced, and 2) core affective dimensions (arousal and valence). In a laboratory experiment, participants (n = 310) listened to 155 chimpanzee vocalisations produced in 10 different behavioural contexts. Listeners judged the context in which they thought each vocalisation was produced in a ten-way forced choice task, and indicated the extent to which they thought the individual who produced the vocalisation was feeling negative/positive and aroused using Likert rating scales. The results show that human listeners were able to accurately infer levels of arousal (high, medium, low) and valence (positive, negative), but not the specific production context. Moreover, judgments were more accurate for negative than for positive vocalisations. Acoustic analyses reveal that acoustic features of chimpanzee vocalisations vary systematically across different behavioural contexts, as well as across arousal levels and valence. Overall, these findings highlight that different behavioural contexts in which the chimpanzee vocalisations were produced elicit a different affective state in the producer and provide key insights on how human listeners infer animals' affective states from vocalisations.

A Comparative Approach to Human Recognition of Emotions Using Acoustic Properties of Human and Non-Human Primate Vocalisations

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Humans are able to extract emotional information and meanings from both their own and other animals' vocalisations. It remains unclear whether the human ability to recognise affective

cues in vocal stimuli from other species is due to cross-taxa similarities in acoustic parameters, to the phylogenetic distances between species, or a combination of both. The present study investigated human affective recognition abilities in vocalisations in four primate species: humans, chimpanzees, bonobos and rhesus macaques. Sixty-eight human participants listened to a total of 864 primate vocalisations and were asked to evaluate their emotional affiliative, aggressive, or distress content. We found that species identity, task (categorisation 'A vs B' or discrimination 'A vs non-A'), and affective content all impacted participants' accuracy and reaction time in evaluating stimuli. Furthermore, 88 acoustic parameters that defined the various calls were subject to principal component analysis revealing specific factors that could best describe the vocalisations according to both species and affective content. Using general(ised) linear mixed models, we investigated whether these factors were related to the participants' accuracy and reaction time. We found significant interactions between species, task and acoustical factors (both related to species and to the affective content of the vocalisation) influencing both accuracy and reaction time of participants. Overall, this study showed that human participants can both categorise and discriminate affective cues in other primate vocalisations and that such abilities are strongly related to the acoustic characteristics of the calls. These findings support the hypothesis of a pre-human origin of affective recognition mechanisms inherited from our common ancestor with other primates. Furthermore, our results highlight the importance of both phylogenetic and acoustic parameters levels in these crucial mechanisms.

Neural Correlates and Comparative Approach to Affective Primate Vocalisations

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Findings connecting the Hominidae phylogenetic tree present an extraordinary opportunity to improve knowledge on human evolutionary history. For instance, Darwin, in *The Expression of the Emotions in Man and Animals* (1872), highlighted the importance of an evolutionary approach to understand affective signals expressed in human voices. The studies presented here aimed at investigating how human participants process affective primate vocalisations at the brain level using functional near infrared spectroscopy (fNIRS) and functional magnetic resonance imaging (fMRI). In both studies, two different participant samples were asked to categorise affective vocalisations produced by humans, chimpanzees (*Pan trolglodytes*), bonobos (*P. paniscus*) and rhesus macaques (*Macaca mulatta)* related to threatening, distressful and affiliative situations. Whole brain fMRI analysis revealed that a subregion of the voice sensitive areas, the right middle superior temporal gyrus (right mid STG), was enhanced for correctly categorising both human and chimpanzee as opposed to bonobo and macaque vocalisations. This study thus shows a common network in the voice sensitive areas between human and chimpanzee affective vocalisations. Furthermore, the fNIRS study, specifically aimed at recording frontal activations, showed that the triangularis part of the bilateral inferior frontal gyrus was activated differently depending on the evaluation task (categorisation or discrimination), a difference found for all four species and all three affective contents. This study thus suggests that some brain regions seem implicated in the evaluation task regardless of the species or even of the affective content of the vocalisations, while others are specific to some species and the kinds of affective vocalisations. Combined, these

results highlight the importance of an evolutionary approach to understand affective processing in the human brain, as well as the different methodological approaches that can be applied to improve our understanding of this issue.

The Importance of Context and Interaction for the Extraction of Information from Unknown Signals

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Research projects like the *Great Ape Dictionary,* testing the comprehension of great ape signals by untrained human subjects, provide an opportunity to test whether there is a phylogenetic connection to what information a signal provides. If untrained subjects were to grasp the signals' meaning correctly, it may be the case that we are not required to display complex cognitive processes and an understanding of a potential convention involved in the use of the signal. Instead, part of understanding signals may involve an innate understanding of the information provided. In turn, signals we use to convey certain messages may not be fully conventional, and, with that, may be arbitrary in their use but involve some innate preference for certain signals to convey certain information. The aim of this talk is to discuss the scientific value of research projects of this kind for the study of language evolution and their issues. In particular, studies designed to show only brief footage of a gesture or vocalisation collide with the generally accepted hypothesis that humans grasp unknown signals' information through context. That is, we take into account relevant contextual cues to *infer* the meaning. A second hypothesis is the comprehension of unknown signals through interaction, be it observing interactions of others or being part of the interaction themselves. Both hypotheses collide with the research protocols of the above studies. Following from this, their design may not be most suited to provide evidence linked to the evolution of language and signal comprehension. Human subjects will fail to comprehend the signals, given the lack of assessable context and the lack of options of interaction. This questions the usefulness of the research paradigm in itself. In conclusion, it will be argued that the discussed research projects need to clarify which hypothesis regarding the evolution of language they aim to test and, following from that, how to modify research protocols.

Symposium
Primate Archaeology, Developments of a New Research Field

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Primate archaeology is a relatively new and emerging field of research. Since the early 2000s it has transformed the way we view and study primate technology and our understanding of the evolutionary, socio-ecological and cognitive contexts of primate tool use. It combines archaeological methods, such as excavation techniques, use-wear analysis and raw material selection, with behavioural, ecological and cognitive research in the study of technological non-human primates.

This holistic approach, in turn, has also provided a unique opportunity to draw parallels with early hominins to better infer the potential origin and evolution of technology in our own clade. Originally focussing on stone tool use of western chimpanzees (*Pan troglodytes verus*), bearded capuchin monkeys (*Sapajus libidinosus*) and Burmese long-tailed macaques (*Macaca fascicularis aurea*), research has extended to plant tool use, as well as other tool-using primates, such as the white-faced capuchins (*Cebus capucinus*). Gradually, these are building on the rich technological and cultural heritage of the Primate order and shedding light on our collective technological histories. This symposium provides an update on the latest findings and perspectives of this field by bringing together experts specialised in different aspects of tool use in different technological species: from the archaeology of the recently discovered stone tool use of white-faced capuchins, the ecological contexts of tool-site selection in chimpanzee nut-cracking, and the technical and inter-population variations in macaque shellfish foraging, to archaeological excavations and use-wear analysis of bearded capuchin stone tools, capuchin plant tool use, and the social contexts of cultural and technological evolution. Together we address the underlying circumstances that allowed tool use to emerge and develop in living primates, which may inform our understanding of the early archaeological record of ancestral humans.

The Archaeology of White-Faced Capuchins (*Cebus capucinus*) Stone Tool Use

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We recently reported the first case of habitual stone tool use in gracile capuchin monkeys – a population of white-faced capuchins (*Cebus capuchinus imitator*) on Jicaron, Coiba National Park, Panama. They use hammerstones and anvils to open a variety of enclosed food items: seeds of the sea almond (*Terminalia catappa*), hermit crabs, Halloween crabs and, less frequently, marine snails and coconuts. Here, we will present some preliminary results of archaeological work that focuses on 1) techniques and methods of hammer and anvil food processing and 2) site formation processes. Based on camera trap video footage, capuchins use a percussion technique, holding a hammer with two hands, rather than free hand percussion. We explore the association of hammer size and morphology with the type of grip and extrapolate this prediction to the early archaeological record. We further examine hammer selection based on biomechanical constraints of hand morphology. Additionally, since capuchins use both stone and wood anvils and hammers, we look into the potential selection of tools depending on the toughness of the

food item being processed. Sites we observed at Jicaron are defined by a clustered accumulation of processed food and tools and can be further grouped based on the size of the accumulation. The latter could indicate settlement patterns with temporary tool use, medium-size occupations and larger accumulations, but could also indicate preservation biases. In archaeology, the latter frequently affects site visibility and, thereby, our understanding of foraging behaviours. Tide and seasonal streams might remove food debris and create a biased archaeological record. We test the hypothesis that the amount of accumulation at a site is correlated with its location, in particular, with its proximity to water. This work bears great relevance for our ability to interpret the fossil record of early hominin occupations.

A Home Range Approach to the Ecology of Site Selection in Wild Chimpanzee Nut-Cracking

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As with many aspects of non-human primate behaviour, ecology plays a key part in shaping primate technological activity: from whether it emerges in a population, where and how often it occurs, to the distance and frequencies of tool transport. Previous studies on tool site selection have addressed the relevance of the immediate 'facilitators' of tool use (i.e. availability and location of target resources and raw materials for tools), but few have investigated the impact of the broader foraging landscape. Extractive foraging in non-human primates, whether to access primary or fall-back foods, is part of a broader daily, and seasonal, foraging strategy that also involves procurement of resources that do not require tools, as well as access to shelter and water. We predict that the 'ecologies' of non-tool related activities have an effect on where tool use takes place. Using a primate archaeology approach, we test different ecological factors of tool site selection in wild chimpanzee (*Pan troglodytes verus*) nut-cracking in Bossou (Guinea), within their home range. We conducted extensive quadrat surveys (5-metre radius) of the Bossou forest, documenting tool-site presence, vegetation composition, nest count, watercourses, and raw material availability for nut-cracking. All features were spatially recorded using an Arrow Gold GPS/GNSS Receiver. Initial results suggest that, in addition to nut trees and raw materials, the number of food bearing trees that are known to be part of the chimpanzee diet is also a significant predictor of whether nut-cracking occurs in a given location. Ongoing investigations with additional ecological and spatial dimensions will add to the picture of the ecological determinants of tool site formation, while also informing questions about the patterns of landscape use and resource exploitation associated with the tool assemblages of our earliest ancestors.

Diversity of Stone Tools Between Long-Tailed Macaque Populations

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Difference in tool selection between populations of wild primates has been used to detect underling cultural diversity. So far, this method has been applied to chimpanzees and capuchin monkeys. Long-tailed macaques have been known to use stone tools to forage for different species of shellfish along the ocean shore, which leave very distinct damage patterns (use wear) on the hammerstones. These damage patterns are not universal across macaque populations. Here we applied primate archaeological methods to study the tool selection of two long-tailed macaque (*Macaca fascicularis*) populations in the Ao Phang Nga National Park in Southern Thailand, Boi Yai Island and Lobi Bay. Comparisons of potential variation in ecological and environmental conditions between the two populations, such as the size of prey species as well as the available stone material in their landscape, did not reveal any differences in their environment. Macaques on the two islands, however, consistently showed differences in their tool selection preferences when foraging for the same marine prey species. We found pronounced differences in use wear intensity and damage pattern of stone tools between the islands, which develop through intense reuse of stone tools on one island. Within populations that showed increased tool reuse, we additionally found multi-use tools that were used for more than one prey species. Our results show that wild long-tailed macaques create an archaeological record that is different between populations. This provides the first empirical evidence for potential cultural variation in tool using behaviours between neighbouring populations of Old-World monkeys. This study additionally highlights the fact that material culture can differ within the same timeframe across small geographic scales.

3000 Years of Wild Capuchin Stone Tool Use

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It is well understood that the human lithic archaeological record changes over time and understanding this chronological variation has been a focus of numerous palaeolithic archaeological studies. Finding such diachronic change in other primates requires similar evidence, namely, a long-term sequence of material culture. It has been argued that chimpanzees possess a long-term archaeological record, however, the associated lithic material remains static, seemingly solely representative of nut cracking. Here, we report on archaeological excavations, dating and primate lithic analysis of a wild capuchin monkey (*Sapajus libidinosus*) site in Serra da Capivara National Park, Brazil. We identify primate stone tools throughout the excavation, including at the lowest levels. Based on the metric and damage patterns on these tools, we suggest that capuchin food processing may have changed over a substantial period of time; this represents the first example of long-term tool use variation outside of the human lineage.

The Effect of Raw Material Quality on Primate Anvils

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Capuchin monkeys (*Sapajus libidinosus*) have been recognised as the primate species with the widest variety of stone tool uses, including nut-cracking, stone digging, seed and fruit processing and stone-on-stone percussion. In this presentation, we will focus on a series of nut-cracking experiments performed at the Tiete National Park (Sao Paulo, Brazil) in which the subjects used anvils of different raw materials ranging from low to high quality. Our aims were three: i) investigate how different raw materials behave when nut-cracking is performed by the same primate species; ii) compare the tools using a combination of analytical approaches, including technological and refit analysis, microwear, and spatial distribution analysis of percussive marks using GIS techniques; iii) study the mechanics and the motion of the nut-cracking. This approach will allow us to perform further comparisons with other primate tools, gain a better understanding of hominin pounding activities and give us the basis to track down these percussive behaviours in the early archaeological record.

Probe Tool Use in Capuchin Monkeys

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Primate archaeology usually takes lithic artefacts as the object of its analysis. Rocks are long lasting and can retain marks of use even after thousands of years. However, primate archaeology studies primates that are still displaying tool use behaviour today, so we have the opportunity to observe other types of tool use, such as the use of more perishable stick tools. Capuchin monkeys are one of the few primates that use stick tools in the wild. However, the use of sticks as probes by capuchin monkeys is only known, to date, to be customary at one population, in Serra da Capivara National Park (Brazil). Probe tools are mostly used to dislodge prey from hiding places and dip for honey or wax, but also to threaten dangerous animals, such as snakes, and for self-care. This behaviour also presents a strong sexual bias towards males. Although there are no physical constraints, only the males in that population use probes to get food. This difference appears to be a male motivation bias, rather than a learning opportunity bias. The three groups studied in the area show a highly consistent probe tool average size, showing that probe tool use is strongly conservative in the population. Although a perishable tool is likely to be invisible in the archaeological record, observing wild primates can be a way to understand the factors involved in the appearance and development of perishable tools in the evolutionary history of the primate lineage.

Experimental Field Investigations of Cultural Capacities in Tool Using Bearded Capuchins

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Experimental studies of captive capuchin monkeys and wild observational data indicate that these primates are 'cultural', yet direct experimental evidence of social learning in wild individuals is sparse. The populations of bearded capuchins (*Sapajus libidinosus)* inhabiting the caatinga of the Serra da Capivara National Park (SCNP), in Brazil, are ideal for acquiring such evidence as they possess the largest toolkit described for monkeys. We present social network analysis and several open-diffusion experiments, involving posing novel foraging tasks to two wild groups of capuchins. Using network-based diffusion analysis we find, across tasks, that observation from close range, versus a distance, better predicts learning by naïve individuals, indicating observational learning rather than local/stimulus enhancement. We thus empirically support the argument that inter-population variability of toolkits in wild bearded capuchins is underpinned by cultural behaviour patterns. In addition, we present evidence for various biases in the cultural transmission of information in this species and briefly discuss how these biases compare to those seen in other species, including humans. For example, grooming networks outside the experimental context robustly predicted the diffusion of one task's solution, highlighting the importance of considering the role of social interaction, as well as association, networks in cultural transmission studies. We also find evidence for a bias towards observing the most successful individuals, moderated by sex. Finally, we discuss findings from a study using a cumulative problem-solving task, indicating that the capuchins are able to use social information to switch flexibly to higher payoff behaviour, a requirement for cumulative cultural evolution. Understanding the social context of tool use in New World monkeys provides comparative insight, beyond great apes, regarding the cultural evolution of technology.

Symposium
What Works and What Doesn't Work? The Challenge of Creating Effective Applied Conservation Research in Human-Modified Habitats

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Considering no primate habitat is "pristine" and free from anthropogenic influences, the field of conservation biology is emerging in its importance. One of the main goals of research on non-human primates in human-modified landscapes is to improve conservation outcomes. As researchers, we intend that our work will be useful for targeted conservation strategies, but how often do our results actually feed into effective strategies? In this symposium, we present research on primate responses to human-modified habitats as well as research exploring human perspectives on sharing landscapes with primates, all of which aim to feed into conservation strategies. We will discuss the need to factor in local knowledge, as well as potential issues in translating our findings into conservation strategies. These include a lack of data in unprotected areas, practical difficulties of influencing people to change their behaviour, the need to increase the economic value of forest habitats for people and the importance of creating systematic methods for cross-site and species comparisons. We will examine the success of specific conservation initiatives, including the use of exotic and crop species to improve landscape connectivity, and consider the

data and infrastructure required to make initiatives successful, or not. We will explore a wide range of evidence-based conservation studies and, crucially, whether and how their results were translated into conservation strategies. With talks from established academics and conservation practitioners to early career researchers, we aim at further facilitating the dialogue to improve applicability of our research in the roundtable that follows the symposium.

Developing an Evidence-Based Conservation Strategy for Cantanhez National Park, Guinea-Bissau

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Understanding the capacity for humans to share space and resources with large-bodied wildlife is vital for biodiversity conservation and human well-being in shared landscapes. It also requires comprehensive understanding of human and wildlife dimensions of interactions over both fine spatial scales and at the landscape level. The Cantanhez National Park in Guinea-Bissau, IUCN Category V National Park (Protected Landscape), is 1067 km^2 and is inhabited by approximately 28,000 people. It comprises a mosaic of sub-humid forest, secondary forest, mangrove, savanna, human settlements and agricultural fields, and is the country's most biodiverse protected area. It is home to numerous threatened primate taxa, including the western chimpanzee (*Pan troglodytes verus*) and red colobus monkey (*Piliocolobus temminckii*). We demonstrate how our biological and social research is assisting in the development of an evidence-based conservation strategy for Cantanhez NP through integrating data on wildlife behaviour, abundance and distribution with local people's knowledge and perceptions of nature and the environment. In shared landscapes, biodiversity conservation requires a flexible and transparent approach that safeguards key wildlife habitat. At the same time, such approaches should respect indigenous knowledge and management systems, and ensure that local populations are integrated into the development and implementation of conservation activities.

Orangutans in the Anthropocene

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Orangutans are the only great ape taxon in Asia and all three species are classified as Critically Endangered. Although they occurred on mainland Asia in the past, they are now confined to the islands of Borneo and Sumatra. I will present an overview of recent research that has indicated that orangutans are more flexible than previously thought and what the conservation implications of this are. In particular, I will review research that shows that orangutans can survive, at least in the short-term, in mosaics of different land uses and in well-managed logging concessions, albeit often at lower densities. This realisation means we need to rethink our conservation strategies and perhaps move away from the well-established protected area vs non-protected area divide for our conservation efforts. It also means that we need to find ways to

provide recommendations that are informed by our research for the managers of non-protected area land uses about how they can potentially manage orangutans in their concessions as well as collaborate with local communities to manage orangutans on their lands. This is particularly challenging in the context of killing of orangutans for food or during human-orangutan conflict. Such issues also highlight the gaps in our knowledge such as requirements for corridors and wildlife bridges that orangutans would need to move between forest patches. This lack of knowledge is worrying since it might impact our effectiveness to provide solid recommendations for such connections to industry. The latter is relevant because due to changes in the International Finance Cooperation's (IFC) performance standards there now is a requirement for companies to consult with the IUCN in case IFC loans impact great apes. This provides a unique opportunity to try to mitigate and/or offset the impact of projects or argue for projects not to go ahead on the basis of solid scientific advice. This means that we need to conduct more research on how orangutans behave in human-altered landscapes.

Using Utilitarian Plants for Lemur Conservation

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Many protected areas in Madagascar are too small for long-term conservation of viable lemur populations, and are subject to exploitation for a variety of natural resources, such as fire and construction wood, food and medicinal plants. Trying to exclude people from the utilisation of these resources has not been successful whenever needs increased (such as during economic and natural crises or due to excessive human population growth that outruns any development effort), or during political crises. People need economic benefits and conservation measures have to account for these needs. We have analysed the utilisation of native forest and introduced trees and shrubs by people and lemurs across the island. Degradation of natural forests results in gaps in phenological patterns such as the availability of flowers and fruits. By complementary phenological traits, introduced plants can compensate for the loss and add valuable species for flower and honey production, fruit production and fuel wood. A combination of exotic and native tree and shrub species could thus increase the economic value of forest habitats for people. These plantations of mixed utilitarian trees and shrubs could be integrated into agricultural landscapes and could be supplemented by individual, village-based tree plantations. Lemurs could use these mixed tree plantations as buffer zones, corridors or stepping stones to move between suitable forest habitats. This type of connectivity represents parts of the structures for habitat connectivity in Europe under the concept of NATURA 2000 and seems to be a suitable model for Madagascar also. While the core of Madagascar's conservation problems cannot be solved with these approaches, they might contribute to a successful array of biodiversity conservation measures in anthropogenic landscapes.

Does Conservation Need or Want Habitat Suitability Research?

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Over the past few years we have concentrated research efforts, as part of LEAP - the Landscape Ecology and Primatology Programme - on understanding how animals' habitat requirements shape their distribution patterns, and how climate and landscape changes will influence their future distributions and survival. Much of the work shows how species will struggle in the future and shows the areas that remain suitable for these species. However, we remain sceptical about how much of this information will be used effectively to support the conservation of these species. In so many cases, primate conservation actions are focused on saving the animals and their habitats on the ground through forest protection and anti-poaching activities. In this short discussion-based presentation we will address the question: With such urgent actions needed on the ground to conserve species, is there really a place for the use of science that predicts long-term effects and future distributions? We will show examples of situations in which long-term planning effectively uses scientific studies on distribution patterns and examples in which we feel there is no use for long-term projection studies in ensuring species-conservation. This presentation is aimed at promoting discussion on this general subject in order to find ways to improve how long-term planning is used effectively in conservation strategies.

Coffee for Conservation: Promotion of Organic and Wildlife Friendly Practices Among Farmers at Cipaganti, Java, to Protect Local Biodiversity

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There is an urgent need for a global transition to sustainable farming systems that provide social and economic equity and protect ecosystem services on which agriculture depends. Java is home to 60% of Indonesia's population and harbours many endemic species, thus managing agriculture alongside human well-being and biodiversity is vital. We implemented a project meant to integrate the needs of local farmers and to protect and increase biodiversity. Within a community of ~200 coffee farmers in Cipaganti, Java, we started promoting organic and Wildlife Friendly (WF) practices in February 2019 with the aim of developing a long-term sustainable relationship between farmers and biodiversity. We firstly investigated, via interviews, the issues encountered by 28 farmers who had converted to organic production in 2016. We used this information to establish a problem-solving plan for transition to community-wide organic practices. Informants identified three main issues: a decrease in productivity, solutions for removing grass without herbicides and high costs of materials at the beginning of production. We uncovered additional issues which needed solving to meet the standards for organic and WF certifications, including banning hunting activities and increasing coffee quality for international export. We worked alongside the heads of the coffee farming community to establish an action plan to meet WF and organic certifications. We are providing equipment, shade trees to increase coffee and soil quality and training to farmers, as well as financial help to have a supply chain of organic

fertilisers for the community. We developed a community law banning hunting activities with the aid of the heads of the villages. We aim at obtaining certifications to help farmers exporting their product within three years. During this process, plantations will be monitored in terms of biodiversity (mainly bioindicators and pollinators), coffee productivity, hunting activities and the use of organic materials by farmers.

Including People in Primate Conservation: How Ethnography Makes a Difference

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The support and involvement of local people is fundamental to the success of any primate conservation initiative. Conservationists have a responsibility and a need to acknowledge that local communities may view primates in a different way to how conservationists view them. We use a case study from Bouhachem forest, Morocco in the context of a Barbary macaque (*Macaca sylvanus*) conservation project where we collected and analysed ethnographic data to understand better human-macaque relations. Our aim was to develop a culturally and socially meaningful and inclusive conservation strategy. We used participant observation and conducted open-ended interviews with 50 male shepherds aged 14-84 from 10 villages. We found that the marginalisation of villagers by the occupying power, the state and urban society is demonstrated by their past and present exclusion from resource and conservation management and planning by outside agencies. In addition, the shepherds' relationship with the macaque is complicated, with the species occupying an anomalous position in shepherd ontologies that is reflected in the shepherds' behaviour towards wild macaques. We continue to engage positively with shepherds, sharing general information about the macaques and developing community health activities in their villages. These inclusive efforts encouraged some shepherds to become conservation actors, persuading their peers to abstain from killing and torturing Barbary macaques or capturing them for the illegal pet trade. Using an ethnographic approach can enable conservationists to gain a greater understanding of how communities perceive and behave towards the primates with which they coexist.

Effects of Anthropogenic Noise on Pygmy Marmosets (*Cebuella pygmaea*) in the Peruvian Amazon

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Ecotourism can be used to support primate conservation by raising awareness and funding. Tourist visitation to wild primates can have negative impacts on visited groups, and minimising these negative effects can increase the efficacy of this conservation strategy. The effects of tourist-generated noise on free-ranging wild primates is relatively understudied. Using an experimental playback study using recorded human speech, we show that pygmy marmosets (*Cebuella pygmaea*) within the Tamshiyacu-Tahuayo Reserve, Peru are significantly less visible, and often

move completely out of sight after louder playbacks. Playbacks of human speech also tended to increase the amount of time individuals were alert and decrease feeding and resting behaviours. Additional studies in the same system have investigated the impact of other anthropogenic noises generated by ecotourism, such as motorboats. Our results demonstrate that noises associated with ecotourism can alter the behaviour of visited primates. As responses were not observed (nor was any other consistent behaviour change) in control trials where the marmosets were exposed to human presence but not to noise, this suggests that negative tourism impacts can be reduced by encouraging tourists to reduce noise and refrain from speaking in the presence of visited primate groups. This structure represents a potential win-win for ecotourism, as anthropogenic noise causes changes in pygmy marmoset behaviour in a way that may be detrimental to both primate welfare and tourist enjoyment. The efficacy of this strategy depends on both tourists and tourism operators changing their behaviour to generate less noise.

The Application of Behavioural Studies for the Effective Management of Cape Peninsula Baboons in a Human-Changed Habitat

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Despite a strong theory and support for applying behavioural studies to the effective management and conservation of wild populations, we argue that behavioural ecology has had limited impact in the field of conservation biology and wildlife management. In many sites in the Cape Peninsula, South Africa, chacma baboons (*Papio ursinus*) forage on anthropogenic food sources found in public, residential and commercial properties and spaces (e.g. agricultural crops, food waste). This baboon foraging behaviour creates conflicts with people, and the City Council of Cape Town and private landowners hire 'rangers' to keep baboons out of urban and agricultural areas. Here, we present details of systematic behavioural studies conducted using novel bio-logging technologies to investigate baboon and human behaviour and space use. We consider how these studies inform and improve efficacy of ranger management strategies, and discuss the challenges of communicating this work to the public.

Symposium
Battery Tests of Primate Cognition: A Counter Reply from Field Primatology

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To understand the evolution of human cognition, we need to broaden our understanding of cognitive skills of a large variety of animal species and populations. Within the field of comparative psychology, battery tests have been developed to compare cognitive abilities of a limited set of primate species in captivity. We envision that field primatologists can contribute importantly to this endeavour, particularly because datasets of ranging patterns, behavioural data and food distribution exist – and continue to grow – for a large number of primate species in the wild. These create much potential for promising comparative phylogenetic analyses of spatial cognitive abilities that have the power to include the natural contexts in which such skills are employed. In addition, the unprecedented rapid pace of habitat loss faced by wild primate populations increases the urgency to examine the ecological and social drivers of the evolution and nature of spatial cognition in primates. In this symposium, we present a variety of methods that enable us to draw inferences about foraging cognition (e.g. use of a spatio-temporal memory, route planning) by focusing on analyses of long-term observational data on ranging patterns and food distribution. We aim to initiate the development of battery tests to measure foraging cognition that can be applied to a wide variety of primate species and populations, in similar way as is currently done with captive primates. We believe that such development can eventually help comparisons of cognitive abilities between primates in the wild and captivity, but more importantly can provide crucial insights into the adaptive value of cognition. Lastly, we aim to map the current availability of long-term ranging datasets in wild primates and the willingness among primatologists to share these data.

Methodologies in Primate Spatial Cognition: Where Do We Stand?

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Primate habitat is characterised by ephemeral patterns of food availability where primates daily face the challenge to decide what, where and when to eat. Given that efficiently locating food resources, while minimising competition and predation, can have important effects on an individual's fitness, a premium is placed on primates that have evolved spatio-temporal cognitive

abilities. These abilities enable individuals to internally represent their environment, which can then allow them to make efficient movement decisions. Data on ranging behaviour of individuals or social groups are thus central to our abilities to infer cognitive processes underlying primate movements and foraging strategies. In this study, we provide an overview of the various methodological approaches using ranging data to examine primate cognitive abilities related to foraging decision making, which will be discussed in more detail in the symposium. These methods include movement linearity indices, cognitive maps, directional change points, revisits of feeding sites and habitual travel routes, as well as comparisons of observed patterns with predictions derived from null models of random movements. For each of these methods, we explore which aspect of cognition (e.g. spatio-temporal memory, intentionality, route planning) can be inferred and which confounding factors need to be considered when employed in comparative analyses. The ever-growing datasets on ranging behaviour available for many primate species at numerous field sites provide a unique opportunity to develop comparative phylogenetic analyses of spatial cognitive abilities in primates. As such, we conducted a survey across field primatologists to map the current availability of long-term ranging datasets in wild primates and the willingness among primatologists to share these data.

When Less is More: Strategies to Reduce Cognitive Load in Black Howler Monkeys (*Alouatta pigra*)

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Information acquisition and processing are fundamental aspects of animal navigation. Animals differ in their capacity to store, process and integrate information. The capacity of an animal to cope with cognitive load (number of operative elements involved in cognitive processes) has been argued to act as a selective pressure in the evolution of navigation strategies. As such, travelling through habitual routes is thought to reduce the number of locations to remember and simplifies the process of movement decision making. In addition, selecting routes that maximise the number of potential food resources within visual range reduces the number of locations that need to be remembered. The use of nodes at the intersection of habitual routes enhances visual access over the terrain, which can minimise an animal's cognitive load and help by redirecting movements to facilitate successful food localisation. Here, we explore whether a small-brained Neotropical primate, the black howler monkey (*Alouatta pigra*), evolved mechanisms to minimise their cognitive load associated with movement decisions. From September 2016 through August 2017, we collected data on five adjacent groups in Palenque National Park, Mexico, and georeferenced all the potential food resources of their preferred tree species within the study area (n = 931 trees). We found that howlers travelled through habitual routes that visually intercepted a high number of potential food resources. Directional changes were detected at the intersection of habitual routes and associated with large trees, which enhanced the visual access of howlers over the landscape. Overall, black howler monkeys display navigation strategies that minimise their cognitive load and simplify the process of food localisation and movement decision making. We argue that the accumulation of information within cohesive social units in group-living primates helps to select optimal routes to navigate through their home range.

Cognitive Insights from Large-Scale Ranging Patterns: Male Dispersal Can Affect Dynamics of Home-Range Overlap Between Neighbours in Baboons

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In many solitary and group-living animals, neighbours partially segregate within their respective home ranges. Theory suggests home ranges could mainly arise from the use of spatial memory by individuals. In groups, some individuals may have a disproportionate influence on the overall group's ranging behaviour. When such individuals disperse from one group to another, their memory of the neighbouring ranging area may be in direct opposition to the ecological determinants of neighbour's segregation, such as conflict avoidance. To date, there are virtually no empirical data describing how wild animal groups solve this paradox. Here we investigate how the transfer of male chacma baboons (*Papio ursinus*) between troops affects patterns of range avoidance and overlap between neighbours. We used ranging, demographic and environmental data collected on two wild troops over seven years. We found that troops with relatively more fertile females overlapped less with a neighbours' "traditional" home range when the alpha male had immigrated from that neighbouring troop. In contrast, troops with relatively more fertile females overlapped more with a neighbouring "traditional" home range when the alpha male had not immigrated from there. These findings suggest that "informed" alpha males influence troops to minimise the reproductive competition with males from their natal area; but in the absence of such "informed" males the ranging patterns of troops may reflect the reproductive interests of fertile females. We hypothesise this pattern may be widespread in societies where influential individuals have privileged access to environmental resources such as food. This could limit spatial information transfer between groups in the wild. The fine-scale mechanisms through which such war of influence could be mediated within groups remain to be investigated; as well as the fine-scale spatial behaviour (e.g. route-following) of troops when they do intrude within the neighbour's home range.

Comparison of Large-Scale Spatial Performances of Human Foragers and Chimpanzees in Tropical Rainforests

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To understand the evolution of human spatial cognition, researchers have compared spatial abilities of humans and those of one of our closest living relatives, the chimpanzee (*Pan troglodytes*). Spatial abilities of humans and chimpanzees have been compared mainly in small-scale laboratory settings, as measuring such abilities in natural environments is challenging due to many confounding factors. Here we propose a 'post-hoc quasi-experiment' to control for main confounds, which allows a direct comparison of large-scale spatial performance of the Mbendjele BaYaka people in the Republic of Congo and Taï chimpanzees in Côte d'Ivoire in forests. As proxies for spatial knowledge, we measured linearity and speed during off-trail travels toward out-of-sight locations, and compared how linearly and rapidly these two populations moved towards food locations. We tested their reaction on group composition and the level of familiarity with an area with the foraging areas (the sum of time spent in the area). Mbendjele foragers and Taï chimpanzees exhibited similarly high levels of linearity. We found a clear species difference in the effect of familiarity and group composition on linearity and speed. Mbendjele people increased travel linearity with increasing familiarity and group size, without obvious changes in speed. This pattern was reversed in Taï chimpanzees. We suggest that these differences resulted from different foraging styles of Mbendjele people and Taï chimpanzees, such as life-time range size and trail use. Our study is the first to investigate how humans and chimpanzees compare in solving spatial tasks during real-world foraging, and thus provides a first step toward comparing the long-range spatial performance of two closely-related species in their natural environments.

HRAM and the Spatial Mapping in Wild Primate Navigation

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Travelling across known landscapes may not require costly investment in the learning process once an individual's brain has associated the paths that are regularly used to revisit the desired location. Humans choose their repeated paths by acquiring information about the lengths of the paths and configure them in a network manner. Such paths typically contain key locations along a route where individuals then make network decisions. A large body of literature states that non-human primates in the wild are efficient travellers, navigating mainly via the route network system as do humans. The analysis of route networks used by primates is challenging to replicate on a case-by-case bases since it depends on human visual interpretation; that is, two experts rarely develop the same output network from the same input animal movement data. We develop an automated process known as the habitual route analysis method (HRAM), which detects the use of habitual routes by wild animals. The main goals of the HRAM are to; (i) analyse the daily vector of navigation in animal movement, (ii) allow for comparison across differing studies, or the same study with many routes, by developing a standard network map from animal movement

data, (iii) limit human error, (iv) automate the time-consuming network creation process, and (v) remove the issues of scale from the network creation process. When comparing 58 days of black capuchins' (*Sapajus nigritus*) travel, HRAM detected 351 repeated segments (mean = 410 metres) while the human method detected 91 repeated segments (mean = 516 metres). Additionally, HRAM detected 248 network intersections as opposed to 122 via the human detection method. The positional accuracy of human-defined intersections was two metres whereas HRAM has essentially no error as the manual interpretation of intersection location is not required. The manual method was found to be highly scale dependant with differing outcomes dependent on the scale used whereas HRAM is scale independent.

Modelling Encounter-Conditional Search Using Annotated GPS Tracking Data

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We develop a generative, Bayesian model of encounter-conditional search dynamics that includes Brownian walks, Lévy flights and area-restricted search models as special cases. Using this model, we first evaluate the search dynamics of Colombian blowgun hunters, finding that movement patterns are better explained by encounter-conditional, area-restricted search models than by Lévy flight models. We then conduct a wider cross-cultural examination of movement patterns, showing consistent support for encounter-conditional, area-restricted search models. Finally, we connect our model of search dynamics to Charnov's marginal value theorem (MVT), to test whether Mexican mushroom foragers shift between intra-patch and inter-patch search styles as predicted by the MVT. We find near numerical correspondence between the predicted and empirical time-spans of intra-patch search duration. We conclude by discussing the role of our generative modelling frame-work for cross-population and cross-species comparisons of search dynamics, with a focus on the importance of longitudinal, individual-level databases in testing the relative importance of individual and social learning in acquisition of optimal search dynamics.

Don't Let it Be Too Observational - How Inference from Observational Studies Can Benefit from Careful Planning of the Data Collection and/or Analysis

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Studies of free-living animals are frequently observational, for instance, because experiments are impossible for ethical or practical reasons. The analysis of such observational data can be challenging because of the multitude of factors to be controlled for, potentially leading to

very complex data structures and statistical models. Consequently, researchers frequently employ mixed models in the analysis of observational data since they provide an unprecedented flexibility with regard to the data structures they can handle. Their flexibility is not unlimited, and fitting complex mixed models may provide challenges unanticipated during the planning of the project. In extreme cases, it might even not be possible at all to analyse the data appropriately. In my talk, I shall give examples of such challenges and how they can be avoided by a careful planning of the observations to be made and/or included in the analysis. In particular, I shall argue that limiting the observations to be made or the data to be analysed can be beneficial. In fact, decisions about which data to collect or include into a dataset can have a profound impact on model complexity. Consequently, limiting the observations to be made or used can help to reduce model complexity. Such a limitation comes at costs in terms of sample size and scope of the study. Hence, I shall point out aspects to consider when making such trade-offs between model complexity and sample size and scope of the study.

Symposium
Human-Primate Interactions in the Anthropocene

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The rapid expansion of human populations and the consequent diminution of non-human primate (afterwards primate) habitats mean that people and primates come into contact as never before. Such interactions are often (but not always) to the detriment of the primates. Human-primate interactions are extremely diverse, and people's perception of primates is key in understanding such complex interspecies interfaces. For instance, primates are deified, Disneyfied, commoditised or reviled in some cultures and eaten in others. In August 2018, the IUCN SSC Primate Specialist Group approved the creation of a new Section for Human-Primate Interactions, which is the focus of this symposium. Many of the presentations cross disciplinary boundaries of the natural and social sciences and the humanities. Participants will discuss human-primate relations in various contexts such as primates in agroecosystems, trade and tourism, and how ethnography provides a method to study the human dimension of our relations with primates in the Anthropocene.

Factors Influencing the Perception of Monkey Crop Foraging by Farmers

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Non-human primates are geographically widespread, with many taxa living or foraging within agroecosystems. Many genera of primates are also widely regarded as pest species.

Farmers' attitudes towards primates often differ from those towards other crop foraging mammals, as primates occupy a liminal position between the human and animal worlds in many cultures. Primates are also intelligent and can learn to avoid common mitigation strategies, making them a particularly difficult group for farmers to manage. Despite these challenges, farmers' perceptions of primate crop feeders vary widely, with some taxa being well tolerated in agricultural lands and others actively persecuted for crop foraging events. We reviewed the literature on crop foraging and farmer perceptions for monkeys living in agroecosystems. Our review shows that monkeys are generally better tolerated by landowners in the Neotropics than in the Old World, but that the reasons for variable attitudes are complex. Attitudes are influenced by perceived economic loss, political and cultural factors, historical influences of conservation efforts in the region and the monkeys' conformity with human behavioural expectations. When local attitudes allow, however, many primates thrive in agroecosystems and land-sharing conservation strategies have much potential for primate conservation. These findings highlight the complexity of human-animal interactions and demonstrate that understanding local peoples' world view is a vital tool for designing successful conservation efforts.

Where Have All the Monkeys Gone? Surveying and Reassessing the Long-tailed Macaque (*Macaca fascicularis*)

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In 2008, Ardith Eudey raised concerns regarding the declining populations of and increasing threats to long-tailed macaques (LTM) (*Macaca fascicularis*) at the IPS presentation of the "World's 25 Most Endangered Primates" and in her paper entitled "The crab-eating macaque (*Macaca fascicularis*): widespread and rapidly declining". Following up on her work, we conclude that LTM are still heavily harvested from the wild, yet are still listed as Least Concern on the IUCN Red List and in CITES as Appendix II. Intensive extraction of LTM for bio-medical research began in the early 2000s. From 2008-2017, at least 450,000 live LTM and over 7.5 milion "specimens" from an unknown number of individuals were part of this trade, with over 360,000 wild-caught. These official trade numbers exclude laundering of wild-caught individuals as captive bred, harvesting for breeding centre upkeep, pet trade, hunting for consumption and culling due to human-macaque conflicts. With Fooden's population estimate of 3 milion LTM in Southeast Asia in 2006, this offtake is not sustainable. In some areas, they are already extirpated, as a survey of 200 km through suitable habitats in Cambodia in 2008 showed. The behavioural plasticity of LTM is immense and they are one of the most widely dispersed and adaptable primate species. Flexibility draws them to edges of anthropogenic habitats, where visibility results in assumptions of over-abundance, as was demonstrated in surveys of Java in 2009 and 2017. LTM are facing many threats and there is an urgent need for systematic surveys across Southeast Asia, as well as an investigation of the perceptions of LTM. Current conservation foci should not only be on globally threatened species. Focusing on dynamic, widespread, commensal species, which are targets of intensive trade and other threats, may offer critical insights for conservation and management for the 21st century. We advocate for reassessment of LTM conservation and trade status by the IUCN SSC Primate Specialist Group and CITES.

Conservation Across Boundaries - Co-Existence of Wild Orangutans and Oil Palm

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The traditional paradigm of farming practice and government wildlife department policy is one of segregation between wild animals and human agricultural production landscapes. The traditional paradigm of conservation agencies and industry is one of polar opposition and "redlines". In this presentation, we will share how a new initiative uses an integrated cross-disciplinary, mixed-method approach to facilitate multiple paradigm shifts "to make resilient landscapes for orangutans, (*Pongo pygmaeus morio*), and people a reality" in the Kinabatangan River floodplain of eastern Sabah, Malaysia. The foundation of this new work is the presenter's MSc and PhD study in collaboration with a 20-year community conservation programme to quantify density variation, behavioural and feeding ecology of wild orangutans living in degraded and highly fragmented habitat. These results revealed, contrary to prior assumptions, that forests exploited for timber but then left to natural restoration in a floodplain ecosystem remain prime habitat for orangutans. In fact, these degraded, but still florally diverse floodplains, may be even more suitable for this species today than nearby primary habitat. Our work also shows orangutan males are attempting to move throughout the wider landscape as expected, but not without negative consequences. Currently, there are enough wild orangutans left to still be viable. But, without industry cooperation to retain females still living in private lands and allow male access across plantations and between forest fragments, long-term meta-population survival cannot be assured. Our scientific objective is to characterise patterns of use and key habitat requirements in degraded forest "islands" within agricultural landscapes. The essential social science component is active ongoing collaborative engagement of agricultural practitioners as equal partners to address misperceptions and resolve true conflict to facilitate a human-transformed landscape that includes rather than excludes Asia's emblematic great ape species. In this presentation, we will share results from the first six months of work.

The Impact of Social Media on the Trafficking of the Small Apes

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Asia is Facebook's largest region with almost 400 million users actively accessing the site daily. Since 2016, the photo-sharing app Instagram gained significant momentum reaching over 700 million monthly active accounts, most of which are in Southeast Asia. Wildlife traders may take advantage of the rapid growth and widespread use of social media to facilitate the wildlife trade, a practice that often goes undetected. Evidence points to Indonesia and Malaysia as the main two primate range countries with the most prolific trade in wildlife, predominantly of very young gibbons servicing the illegal pet trade. The questions become 1) how can we reduce demand from buyers through novel educational narratives; 2) what can legally be done about the use of such platforms that are facilitating illegal wildlife trade; 3) what do we do with the rescued gibbons and 4) can we effectively stop the trade at source? Much trade occurs on inaccessible

closed groups on social media sites. The 'back-end' of social media sites, for security and privacy reasons, are strictly controlled by the companies. These companies are technically not 'publishers' and have no requirement to 'edit' content, even if illegal. We present an overview of the situation and the current and future plans to reduce demand and how to reach and counter the activities of vendors and potential buyers of gibbons.

First Impressions Matter in Human-Macaque Interactions

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Human-primate interactions, such as close encounters during wildlife selfie taking, is a growing tourist activity raising serious concerns for both human safety and animal welfare. In this research we aimed to test the "first impression hypothesis" in Barbary macaques (*Macaca sylvanus*), and explore whether social traits perceived in macaques' faces influence human's willingness to approach them to take a selfie. A total of 227 participants were asked to assess 17 different images of neutral macaque faces on the perceived facial characteristics of dominance and cuteness, and to estimate how close they were willing to approach each macaque to take a selfie with it. For each macaque, their real-life dominance rank, sex and facial measurements (i.e. facial weight-to-height ratio (fWHR) and baby schema) were collected to act as possible predictors for the two facial characteristics dominance and cuteness. We found that fWHR was an accurate predictor of perceived dominance ($r_s = 0.510$, $p = 0.037$) whilst baby schema was an accurate predictor of macaque real-life dominance ($r_s = -0.669$, $p = 0.003$), but not perceived dominance ($r_s = -0.022$, $p = 0.933$) or cuteness ($r_s = -0.039$, $p = 0.881$). Participants could accurately perceive dominance ranks in male macaques ($r_s = 0.738$, $p = 0.037$), suggesting the possibility of a shared signalling system in humans and these primates, but not in females ($r_s = -0.150$, $p = 0.700$). Participants were more willing to approach the macaques they perceived to be cuter ($\beta = 0.509$, $p = 0.002$) and less dominant ($\beta = -0.373$, $p = 0.009$) to take a selfie, therefore indicating that first impressions matter in tourist-macaque interactions. This finding can be used to inform regulations targeted to reduce the risks related to wildlife selfie taking in both humans and macaques.

Using Ethnography in Primatology: Learning from Current Research

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Non-human primates (hereafter, primates) possess human-like characteristics that can make them difficult to categorise, thus adding complexity and nuance to the human-primate interface. This nuance is difficult to examine using quantitative methods and has traditionally been overlooked in conservation and primatology research. The idea that an understanding of human-primate relations is important in the development of effective conservation initiatives is starting to reach more primatology researchers and conservation practitioners, but, particularly for those trained primarily in biological and ecological methods, the process of applying

ethnographic methods to a research question or conservation problem can be daunting. Having undertaken a literature review of 12 studies by contemporary researchers in primatology and primate conservation, I discuss the ways in which primatologists can use ethnography to elucidate complex aspects of the human-primate interface. With examples ranging from the use of discourse analysis to study human-macaque interactions in Gibraltar to the use of multiple ethnographic techniques to look at human-orangutan relationships at a rehabilitation centre, I explore the methodologies used for and the diversity of research questions influenced by ethnographic research. I also offer some perspective on what the use of ethnographic methods means for the practice of conservation and primatology and discuss how much of a focus there should be on teaching these methods to early-career researchers.

Applying an Interdisciplinary-Multispecies Lens to Advocate Conservation that Benefits People and Primates

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It is widely recognised that interdisciplinary research about people and their interactions with wildlife, specifically non-human primates (hereafter primates) in this case, provides unique and significant contributions that enhance the conservation of landscapes under threat. The successful integration of social science with biological science methods of inquiry to address environmental problems requires accurately defining the underlying beliefs and drivers that guide people's interactions with primates. Studying human-primate associations also involves examining the hemispheric identities of local people, as well as the impact of religion and social and cultural diversity on people's associations with wildlife. I present arguments based on an extensive literature review and supported by two case studies, including data from my research at two sites – the Colombian Amazon and rural Guinea-Bissau. Firstly, I demonstrate how indigenous people living in regions of environmental degradation adopt transcultural belief systems, show innovation and resilience in the face of change, and how these processes generate opposition towards or long-term interest in conservation goals. Secondly, I consider the historical shift which has encouraged social scientists to look beyond 'speciesism' and the human-centred nature narrative, and suggest how viewing landscapes through an 'interdisciplinary-multispecies lens' (where humans interact with non-humans to shape and create environments) can help identify solutions to socioecological problems, where the needs of people and primates are met simultaneously. Finally, I discuss how Western ideals of conservation can be made complementary to existing indigenous belief systems, sometimes resulting in unique and insightful outcomes. I conclude that acknowledging indigenous populations as changing groups with dynamic, practical understandings of primates is a vital step towards identifying solutions to pressing conservation issues, whilst advocating the amalgamation of perspectives from ethnoprimatology with those from multispecies ethnography to advance the study of human-primate interactions and aid productive discourse which may enhance future interdisciplinary research.

Workshop

What Works And What Doesn't Work? The Challenge of Creating Effective Applied Conservation Research in Human-Modified Habitats

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This roundtable will follow the symposium "What works and what doesn't work? The challenge of creating effective applied conservation research in human-modified habitats." The session is designed to reflect on the issues raised in the symposium and open a discussion on how best to move forward when planning applied conservation research. By addressing the question "what works and what doesn't work?" the aim of the session is to trigger an open and honest dialogue to find ways to bridge the gap between academic studies and conservation practise. The roundtable will be opened with an introduction from Professor Catherine Hill, who will co-chair the session together with the symposium organisers. We will not only share successful experiences that could translate into conservation strategies but explore failures, obstacles and gaps that often do not emerge from standard presentations. The point of the discussion will range from biases in our research design or in data collection to the infrastructure needed to implement action on the ground. The room will be open for contributions from all participants in addition to speakers from the symposium to consider the needs and priorities for conservation practitioners and the limits and possibilities of our research.

Posters

Population Status, Threats and Conservation of the Bengal Slow Loris *Nycticebus bengalensis* in Northeast Bangladesh

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The Bengal slow loris (*Nycticebus bengalensis*) is the only nocturnal primate in Bangladesh. This species is categorised as Vulnerable on the global IUCN Red List but in Bangladesh it is Endangered. Due to its cryptic and nocturnal behaviour very little is known about this species in Bangladesh except its distribution. From June 2017 to August 2018, we conducted a survey in five

protected areas in north-east Bangladesh by using recce transects to estimate encounter rates of the Bengal slow loris. A team of 2-5 persons conducted night surveys (18.00–03.00), using head lamps with red filters. We walked very slowly in the forest (1-1.5 km per hour) and covered a total of 127 km over 58 night surveys. We encountered Bengal slow lorises a total of 74 times in four protected areas. We did not encounter any slow loris in Juri Reserved Forest. Encounter rate was highest in Satchari National Park (1.78/km) and lowest in Rajkhandhi Reserve Forest (0.17/km). Different types of threats were recorded in the four protected areas. Habitat destruction, hunting and light pollution are the main threats to the slow loris. Beside these threats, road kills and electrocutions are direct causes of mortality of the Bengal slow loris in these forest patches of Bangladesh. During the study period we recorded three cases of electrocution of Bengal slow lorises in Lawachara National Park and one road-kill in Satchari National Park. This study presents information on population and threats to the slow loris in Bangladesh for the first time. A precautionary approach is needed to conserve this cryptic and least studied nocturnal primate species in its natural habitat. Our research complied with the International Primatological Society (IPS) Guidelines for the Use of Nonhuman Primates in Research.

Effect of Age and Sex on Play in Javan Slow Lorises (*Nycticebus javanicus*)

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A critical understanding of animals' life history and behaviour is crucial to conservation efforts. Currently, the development of slow lorises in the wild is little understood. Our aim in this study was to examine the importance of play in the development of the Critically Endangered Javan slow loris (*Nycticebus javanicus*) up until the age of dispersal. Play is thought to be of significant importance to growing youngsters to facilitate the acquisition of adult behaviours. We analysed eight years of focal observational play data on individuals at the Little Fireface Project in West Java, Indonesia to determine if age and/or sex influenced the frequency of play; if frequency of play was dependent on age difference between participants; which partners (mother-daughter/son; father-daughter/son; siblings; mated pair; unrelated pair) engaged in play most frequently. We ran Generalised Linear Mixed Models that showed that although the frequency of play decreased as individual age increased, the relationship was not significant. Males played significantly less than females ($p = 0.028$) and female juveniles and subadults engaged in significantly more play ($p = 0.010$; $p = 0.003$ respectively) than infants and adults. There was not a significant effect between play and the difference in play partners' ages. The beta values of father-daughter ($\beta = 2.749$) and mother-daughter ($\beta = 2.427$) pairs were statistically significant ($p = 0.016$; $p = 0.030$ respectively). No other relationship pairs were significant. These results suggest that young females may benefit from play more than males. Conversely, females may be more spatially cohesive and therefore have more opportunities to engage in play. Slow lorises are venomous and highly territorial, especially among adult females, with both sexes engaging in dispersal. Play behaviour in slow lorises resembles venomous displays used against conspecifics. Thus, play may allow for the learning of vital social skills for territorial interactions in later life.

Vervet Vocal Flexibility in a Landscape of (Little) Fear at Gorongosa National Park

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The emergence of language is regarded as a major transition in human evolution. In order to shed light on how/why such a trait evolved, researchers have adopted the comparative approach and studied the communication of non-human primates, searching for pre-existing neural mechanisms which may have been co-opted for the development of language. Vocal flexibility is an essential component of the faculty of language; however, studies have found the acoustic structure of non-human primate vocalisations to be largely genetically fixed, with general call types being relatively consistent at the population and species levels. Despite this, appreciable differences in call structure have previously been documented, and it has been suggested that further flexibility may be found in call usage. Here, we present preliminary results of a quasi-experimental study investigating variability in the structure and usage of vervet monkey (*Chlorocebus pygerythrus*) alarm calls in Gorongosa National Park, following large, well-recorded, shifts in predation pressure. During the Mozambican Civil War (1977-1992), 90% of mammal populations in Gorongosa disappeared, leading to the local extirpation of multiple apex predators, such as the once ubiquitous leopard (*Panthera pardus*). Since 2006, the Gorongosa Restoration Project has restored 80% of the wildlife, but leopards, hyenas and other once prominent carnivore species are still absent. Another major shift in ecology is expected in 2020, when leopards will be reintroduced to the park. Through the collection of a combination of behavioural, acoustic and experimental data from two vervet troops in Gorongosa, we discuss the variability of alarm call structure and usage and the vocal flexibility in response to a real-time shift in a landscape of (little but increasing) fear.

Monkey Sick: An Example of Village to Village Knowledge Variance on Zoonotic Diseases and its Implications for Disease Control and Education

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In 2018, a new species of Ebola virus in free-tailed bats and a previously unknown occurrence of Marburg virus in Egyptian rousette fruit bats were found in northern Sierra Leone. Focus group style interviews were conducted in 21 of the 23 villages within the Outamba Section of the Outamba Kilimi National Park where 256 individuals participated. When asked about zoonotic diseases, 61% of participating villages stated that monkeys (various species) could transmit 'monkey sick,' the symptoms of which are consistent with those of epilepsy. Of the 13 villages that cited 'monkey sick' as a zoonotic disease, there were four different species/combination of species attributed to spreading the 'sick' and three different beliefs in how the sickness could be transmitted. These variations were not consistent among tribal groups, location within the park, proximity to each other, or religious belief. Additionally, at least one village held the belief that the monkeys which are responsible for spreading this sickness were safe to eat, as long as you did not step in the footprints of the species. This presents complications for disseminating information about zoonotic diseases in an effective manner. The transmission of illnesses from animals to

humans is not completely unknown in this area, however only two villages stated that you could get sick from eating primates, but only specifically the primates which could spread 'monkey sick'. Additionally, because there is no consistency, apart from the name and symptoms, it is unlikely that reliance on village to village communication about zoonoses would prove effective, though this strategy was employed in this region during the 2014-2016 Ebola outbreak. Understanding the historic reliance on hunting of wildlife that can spread zoonotic diseases and the cultural beliefs relating to wildlife is essential to disseminating information in a culturally sensitive and more understandable way.

Do Common Marmosets (*Callithrix jacchus*) Take the Other's Needs into Account When Making a Decision? A Prosociality Game to Assess Fairness Concerns in Primates

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Proactive prosociality has been documented in several primate species, but in many tests, prosocial and fairness concerns are confounded. When choosing to behave prosocially, agents can base their decision about the recipient of the prosocial act on different criteria. Our goal was to develop a new experimental paradigm that allows us to isolate the fairness concerns involved in this decision, especially the one based on the recipient's need. We ran this experiment on captive common marmosets (*Callithrix jaccus*), a cooperatively breeding primate that routinely behaves prosocially. We tested the subjects in trios, with a donor individual in a middle compartment and two potential recipients in adjacent compartments to the left and the right of the donor. We selected the two recipients from the donor's family group in order to minimise the differences in social bond strengths between the donor and each receiver. The donor could choose to provide food to one or the other recipent, by the means of a tray pulling apparatus. In the two experimental conditions, one of the receivers is either eating while conducting the test, or was eating in the two minutes prior to the beginning of the test. We hypothesised that the giver would consider the receiver's need for food when making their decision. Our results will help us to understand better how other-regarding preferences and fairness concerns interact.

Ultrastructure of Common Chimpanzee (*Pan troglodytes*) Glabrous Skin Sensory Formations

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The two recognised species of chimpanzee, the common chimpanzee (*Pan troglodytes*) and the bonobo (*P. paniscus*), are the primate species genetically closest to humans. Primates relate to their environment through the five senses, one of which is the somatosensory system present in the skin. The skin is structured in two layers, epidermis (the outermost and of ectodermic origin) and the dermis (the innermost and of mesodermal origin). The skin's thickness and pigmentation

shows great regional changes and depending on the presence or absence of hair, it is classified into hairy skin and glabrous skin. The intention of this work is to show high resolution images of several aspects showing sensory formations in chimpanzee's glabrous skin. We use optic and electronic (transmisión and scanning) microscopy. The digital glabrous skin samples came from chimpanzees that had died of natural causes and were donated by Spanish zoos to the Anatomical Museum of the University of Valladolid. This study was carried out by SINPOS group (University of Oviedo) dedicated to the study of the Periferic Nervous System and Sense Organs in several species in collaboration with the Osteology and Compared Anatomy research group (University of Valladolid) that host a large collection of primate specimens.

Activity Patterns, Diet, Ranging and Strata Use of *Cercopithecus mitis* on a Small Island

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Samango monkeys (*Cercopithecus mitis*) exhibit a highly flexible behaviour that allows them to occupy different habitats and to be widely distributed in Africa. To contribute to understanding this species' behavioural flexibility, we studied a habituated group of samango monkeys living in a small and seasonal island in Mozambique. To our knowledge, this is the first study of the species on a small island (14 km^2). We collected data on the group's activity patterns, diet, ranging and strata or vertical habitat use from October 2018 to February 2019, covering 2.5 months of the dry and 2.5 months of the rainy season. We found that in the dry season the group spent significantly more time feeding and drinking while in the rainy season it spent significantly more time resting, moving, playing and grooming. We recorded a total of 52 different plant and animal species being consumed by the samagos during our study. We found significant differences in plant part consumption between seasons, with more seeds being eaten in the dry and more fruit being eaten in the wet season. We did not find significant differences in home range size or daily path length between seasons. Finally, we found that the ground stratum was used significantly more during the dry than during the rainy season. Our data suggest that the samangos are able to inhabit this small island because of their high behavioural flexibility that allows them to deal with the seasonal changes in the availability of water and fruit. However, our study lasted only five months and it is necessary to extend it to at least one annual cycle to understand better how the behaviour of the samagos differs between seasons on the island.

Touch Supports Visual Recognition of Objects in Capuchin Monkeys (*Sapajus* spp.)

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Primates rely strongly on vision and touch to perceive and identify objects in the environment. Thus, visuo-tactile interaction is a crucial ability for survival, but to what extent it promotes object recognition still remains to be clarified. Previous evidence indicates that non-human primates use the sense of touch to support vision during foraging and that their perceptual and/or attentional processes in the visual modality are influenced by tactile information. We tested capuchin monkeys (n = 14, *Sapajus* spp.), highly manipulative New World primates, with a recognition memory task aimed at assessing whether haptic cues enhanced the following visual discrimination of objects. The stimulus set included 12 different rotatable objects, six of which contained food rewards. In the preliminary *Exploration phase*, capuchins manipulated the objects one at a time to identify which of them contained a reward. Half of the objects were explored in the Sight & Touch condition that allowed the acquisition of both visual and haptic cues during manipulation; the other half were explored in the Sight condition, which prevented the acquisition of haptic cues about the objects. In the following *Recognition phase*, the objects previously explored individually were presented as pairs, and capuchins had to visually identify the rewarded object within each pair. Objects within a pair differed in size, shape or surface structure. We found that when capuchins had the chance to acquire both visual and haptic cues, they recognised the rewarded objects in significantly fewer trials than when the acquisition of haptic cues was prevented. Overall, our findings demonstrate that gaining haptic cues can affect visual memory for valuable and non-valuable objects, which is a fundamental faculty in primate ecology and evolution. We also evaluated hand movements for manipulating objects and compared these with data from humans.

Does Energy Budget Manipulation Affect Risk Preferences in Tufted Capuchin Monkeys (*Sapajus* spp.)?

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Plenty of research has shown that human and non-human animals are far from being rational when they deal with decisions under risk (where risk is defined as variability in the rate of gain). At an ultimate level, it has been hypothesised that risk preferences vary across species as a result of the different environments in which they evolved. At the proximate level, it has been proposed that risk preferences depend on an individual's energy budget. In particular, according to the Risk Sensitivity Theory, when in a positive energetic state individuals should prefer a constant option, whereas when in a negative energetic state they should prefer a variable, risky option. However, Risk Sensitivity Theory nicely predicts the risk preferences of small-bodied animals, for which a low energy budget is critical for survival, but it is unclear whether it works for

larger-bodied species as well. Here, we aimed to test the Risky Sensitivity Theory by individually presenting 12 captive capuchin monkeys with a risky decision-making task under two conditions: (i) *Low-energy state* and (ii) *High-energy state*, whose order of presentation was counterbalanced across subjects. In each session of the risky decision-making task, capuchins were presented with 10 choices between a constant option, yielding a constant amount of food (four food units), and a risky option, yielding either one or seven food units with a 50% probability. We performed 10 sessions for each condition. In the *Low-energy state* condition, capuchins were tested before receiving their main meal, whereas in the *High-energy state* conditions, they were tested 20 minutes after receiving a high-caloric meal yielding 65% of their average daily energy expenditure. Our findings will be discussed within the framework of the Risky Sensitivity Theory and will contribute to the currently on-going debate on this topic.

UAV Technology as an Effective Tool to Assess Chimpanzee Abundance in Degraded Landscapes

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Estimating population size and density of a population of a species are essential to inform conservation management strategies and land-use planning. Some landscapes dominated by fallow areas pose great challenges when it comes to traditional transect surveys. Unmanned aerial vehicle (UAV) and camera trapping technologies have demonstrated great potential when it comes to surveying wildlife. In this study, we employed camera trapping in combination with spatially explicit capture-recapture (SECR) models for estimating chimpanzee (*Pan troglodytes verus*) numbers in a non-protected area in the Moyamba district in south-western Sierra Leone, ca. 90 km^2. We estimated trapping rate per 1.25 km square grids across the target area based on a systematic layout of camera traps (n = 30). In this environment practically devoid of forest, chimpanzees nest only in semi-domesticated oil palms (*Elaeis guineensis*) that are prevalent in the landscape. Due to the nesting specificity of the chimpanzees in this area, we were readily able to estimate nest density per grid and across the entire target area using drone imagery based on a sampling regime of 3 missions (each 200 m^2) within each sample grid. We compared these abundance estimates with those generated from the SERC model and individual chimpanzee identification. With our study we reveal that drone imagery data yield equivalent results and can effectively estimate chimpanzee population parameters across such degraded landscapes. The application of UAV technology in such environments can serve to inform conservation and land-use planning for chimpanzees, especially in areas prone to infrastructure and industrialised agricultural development.

Understanding Connection: Effects of Prior Task-Relevant Experience on Understanding Connectivity in Gibbons

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Progress towards understanding how experience impacts cognition has been almost undetectable in the study of humans. Those working with non-human animals have fared better, although results have confused, rather than clarified. We evaluated how prior object exposure influenced problem-solving in an evolutionarily important group – the gibbons. We presented eighteen hylobatids with a raking-in task where they had to choose between a tool that was 'broken' and therefore useless for goal attainment, or 'continuous' and therefore functional. We presented broken rakes in two or three pieces, with a gap in the handle perceivable at the time of choice, or with the broken pieces aligned when the response was made. Approximately half of the gibbons received 12 hours exposure to the rakes (broken and continuous) prior to testing, with the remaining half exposed to the rakes for the first time on test. Seventeen gibbons progressed to the test phase after successful completion of a series of familiarisation tasks. Of these, nine completed all trials in the test phase (120 trials per subject), with a further three completing 60 test trials. Overall, the gibbons had difficulty in understanding the concept of connection. Performance was significantly better when presented with three-piece handles compared to two. However, whether the gap was visible at the time of choice had no effect, and prior exposure seemed detrimental to learning.

It's Tough at The Top: Sex, Fertility and Stress in Colony Female Olive Baboons

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We investigated the relationship between social status, hormones and behaviour in 10 colony-living female olive baboons (*Papio anubis*) in their second post-partum cycle. Faecal samples were collected non-invasively on alternate days for reproductive energetics. Faecal glucocortisol (fGC) metabolite assays acted as potential stress indicators (previously validated using ACTH challenge). Interactions with infants, females and males were scored during 30-min focal samples over the day. Each female was observed eight times per day on alternate days throughout her cycle. Dominance rank was classed as High ($n = 2$), Mid ($n = 5$) and Low ($n = 3$) from long-term observations of approach-retreat interactions. E total (total oestrogen), PdG (pregnanediol glucuronide) and cortisol (faecal glucocorticoid metabolites) were determined for each sample day in five cycle states (menses, inflate, full, deflate, flat); ovulation was determined using the rise in faecal PdG levels above a threshold of mean+2SD in five preceding baseline values, backdated by two for excretion. Faecal glucocortisol levels varied with anogenital swelling state, and with male attention to females peaking at mid cycle. Females of high rank had higher fGC levels throughout their cycles than did Mid- or Low-ranking females, and the rates of some maternal-infant interactions were also significantly related to fGC. Disruption of the infant-mother relationship tended to be associated with higher fGC, while maintenance activities and rates of female-female or female-male grooming were unrelated to fGC. The reactivity of the High-ranking females in this colony suggests that they were using a variety of social strategies associated with

managing increased energetic or stress costs during reproduction to cope with their relatively confined but rich environment. Ethical permission was from the Comité Regional d'Ethique sur l'Expérimentation Animale (Marseille, France) and followed European Science Foundation observation guidelines. There was no physical disturbance to or manipulation of individuals during this study.

Testing for the Contagion of Play in Orangutans and Chimpanzees

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Positive emotional contagion has been linked with social-emotional and cognitive development, social bonding and empathy in humans. The present work examined if such contagion is present within play environments in 24 rehabilitant orangutans and 58 sanctuary-living chimpanzees. To specifically test for this phenomenon in these species, we examined in socially uninvolved subjects, who were in a relaxed (neutral) state, whether an emotional state change followed positive play actions of nearby conspecifics (i.e. congruent behaviours) or not (incongruent behaviours). Our results revealed that significantly more orangutans and chimpanzees showed congruent behaviours than incongruent behaviours in such situations (one-tailed McNemar, $n = 82$ subjects, $p < 0.001$). Thus, social play of nearby conspecifics most likely induced play actions in the subjects. The subjects also seemed to show purposeful movement toward the potential playmates, results that were similar for both ape species. We therefore argue that the examined orangutans and chimpanzees must have been motivated to play, and underwent an emotional state change from neutral to positive prior to producing the play action. Our findings provide evidence that positive emotional contagion, in accordance with the use of this term in human research, is present in great apes and that emotional contagion may underpin some of their social motivations.

Chimp See, Chimp Do: The Transmission of a Novel Skill across Two Groups of Chimpanzees

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Social learning is necessary for the development of many aspects of typical primate behaviour. Observational and experimental studies with chimpanzees in captivity as well as in the wild have demonstrated that novel behaviours are acquired and transmitted via social learning. Researchers have identified social tolerance as an important prerequisite for social learning and have proposed differences in group-level social tolerance to be responsible for observed

differences in socially learned skills among orangutans. In our study, we investigated the transmission of a novel skill across two groups of sanctuary chimpanzees that differed in their group-level social tolerance, as measured with a co-feeding paradigm (median proportion of group co-feeding: Group 1 = 0.42; Group 2 = 0.49, Wilcoxon rank-sum: $p = 0.0037$). We trained one mid-ranking female in each group to operate a food-dispensing device and subsequently ran 38 two-hour sessions in which the whole group had access to the dispenser and were able to observe their conspecifics demonstrate the novel skill. A total of 14 individuals learned the new behaviour across the two groups. None of these individuals had learned the behaviour in a previous control condition without a demonstrator. The number of observations and learning success were significantly correlated (Pearson product-moment correlation = 0.43; $p < 0.001$), providing additional support for the role of social learning in individuals' skill acquisition. Preliminary results also suggest a differential effect of kinship on the transmission of the behaviour: maternal kin were more likely to acquire the skill in the group with lower levels of social tolerance than in the group with higher levels of social tolerance. Future social network analyses will further investigate the role of social learning in the transmission of the novel skill as well as the extent to which kinship and affiliation facilitate individuals' learning opportunities.

Seasonal Variation in Pair-Bond Maintenance Behaviour in the Bolivian Gray Titi Monkey, *Plecturocebus donacophilus*

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Titi monkey are the only primates strictly conforming to the standard monogamous profile, being monomorphic and territorial with a high level of paternal investment. Tightly bonded male and female pairs are known to experience strong physiological and behavioural responses to separation. Titi pairs maintain and reinforce these bonds through a suite of affiliative behaviours (e.g. grooming) and conspicuous vocal and visual displays (e.g. duetting and tail-twinning). Little is known, however, of the relative contributions of the male and female to pair bond maintenance and whether investment varies with the reproductive cycle. Pair bond maintenance behaviour (grooming, approach/follow interactions, contact and tail-twinning) was recorded for four habituated groups of wild Bolivian gray titi monkeys (*Plecturocebus donacophilus*) at Yvaga Guazu, Santa Cruz, Bolivia from February 2010 to December 2011. Pair bond maintenance behaviour was found to be significantly higher and the male invested more in the relationship after the birth of an infant and for the duration of its dependency. Affiliative behaviour declined significantly during the mating season, March through May, and male and female investment was reciprocal with a marginally greater investment by the female.

Development of Social Interest in Orangutans over Age and Sex

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Wild orangutan infants have been shown to acquire their skill sets through socially induced practice. Optimal learning theory predicts that young immatures should learn most of their skills

from their mothers, whereas older immatures should widen their pool of role models, but be more selective about what skills they show interest in. Because they will have to cope with a change of environment, dispersing individuals are expected to be more attentive to a broader array of role models. In this study, we investigated the development of social interest in infant Sumatran orangutans (*Pongo abelii*) by looking at peering behaviour (sustained, attentive, close range watching) and patterns of associations. Our data consisted of 3,254 peering events by 22 infants (aged 0 – 8 years) and association data collected from 2007 to 2018 at Suaq Balimbing, Sumatra, Indonesia. We found that infants preferentially peered at rare and complex skills, becoming increasingly selective with age. Young infants of both sexes mostly peered at their mother. In males, the interest in other role models increased throughout infancy. In females, however, the interest in others peaked around mid infancy. These sex-specific patterns were reflected in the proportion of association time spent in close proximity to others. In terms of role model identity, we found that when excluding the mothers, males preferentially peered at and associated with juveniles and unflanged males. Females additionally preferred adult females. All in all, the development of social interest in orangutan infants roughly followed the age-specific patterns predicted by optimal learning theory. The sex-specific peering preferences can be explained by the species' dispersal pattern where, upon reaching adulthood, females settle close to their mother's range and should thus be most interested in acquiring the skills of local residents, while males disperse and thus benefit from learning from a larger number of role models.

Using Scents to Improve the Welfare of Primates in Zoos

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Many of the world's populations of primate species are declining as they face a number of ongoing threats in the wild. Many zoos in the UK and across the world house endangered primates and play an important role in their conservation through ex situ breeding programmes and reintroductions. Modern zoos employ a variety of enrichment techniques to promote natural species-specific behaviours and to help prevent the onset of abnormal stress behaviours. Enrichment aims to improve both psychological and physiological wellbeing of captive animals by providing a stimulating environment. There are currently a number of studies on using enrichment as a tool to increase welfare in captive primates, but these usually focus on feeding and cognitive puzzles, with less emphasis placed on sensory stimulation. Olfactory enrichment programmes are still understudied and the majority of published works focus on big cats. Furthermore, the effects of enrichment and welfare on breeding programmes have received little attention. This project aims to investigate the effects of an olfactory enrichment programme on an endangered captive primate species to improve welfare and encourage breeding. Scents will be collected from individuals, analysed and then used as the basis for a new sensory enrichment that can be placed into enclosures. This project involves the use of widely-used behavioural observations paired with faecal endocrinology to test whether olfactory enrichment can help to improve captive primate welfare. It will provide zoos with a new way to enrich primates and will have findings that will help to inform on best practices for captive primate management in the UK and Europe. There is a potential for it to also improve reproductive success which will have a positive effect on conservation efforts for endangered primate species.

Brief and Rare: Geophagy in Yellow-Tailed Woolly Monkeys (*Lagothrix flavicauda*), Peru

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Geophagy, i.e. the deliberate ingestion of earth, is documented in all groups of primates – prosimians, New and Old World monkeys and apes. Although its exact function remains unclear, it is suggested to aid in mineral supplementation, gastrointestinal tract protection, or in self-medication. Geophagy was recently observed in a free-ranging group of yellow-tailed woolly monkeys (*Lagothrix flavicauda*), a Critically Endangered primate species endemic to Peru. We collected data during 14 months of field surveys (2016 – 2018) on a habituated group of 24 individuals at La Esperanza study site – a montane cloud forest area where altitude varies between 1,800 and 2,400 m. Geophagy events were recorded through camera traps and direct observations during animal follows. We also collected data on daily activities and food items consumed. We found that geophagy was a brief and rare behaviour. Events lasted ~15 seconds and were recorded during only 0.001% of the 2,239 camera trap days. Geophagy was a mostly solitary behaviour performed evenly across all age/sex classes, and occurred significantly more in dry seasons. Individuals often took earth prior to leaving the site, maximising the benefits of geophagy against the risks this arboreal primate faces when descending to the forest floor. Adults used their hands while juveniles mostly used their mouth to retrieve earth. Geophagy sites were small cavities between tree roots located on slopes. Earth consumed was reddish, soft, bare, richer in clay and poorer in minerals than the more common black earth around. Even though the feeding activity rate was similar between the dry and wet seasons (~25%), individuals ate significantly less ripe fruits, more leaves and earth during the dry season. Our results suggest that geophagy in *Lagothrix flavicauda* may serve the function of detoxification of secondary plant compounds – commonly found in leaves and they are more concentrated during the dry season – and so could improve digestion.

Sleeping Site Selection in Yellow Baboons (*Papio cynocephalus*) in a Savanna Woodland: Issa Valley, Tanzania

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Sleeping site selection in baboons (*Papio* spp.) has been investigated in several study sites across Africa. To our knowledge, it has never been studied in savanna woodland, a habitat underrepresented for this genus. We thus investigated sleeping site selection in a troop of yellow

baboons in the Issa Valley, western Tanzania. From June to September 2016, we observed the troop at its sleeping sites 30 minutes after the baboons settled for the night and the next morning before they departed, using night vision equipment. We compared environmental attributes (vegetation type, topography, presence of rocks and distance to water) of sleeping sites to those of plots randomly located within the troop's home range to investigate whether the baboons would select and reuse sites for sleeping based on such attributes and, if so, which of these would be selected. We also investigated if frequency of use of a sleeping site (revisits) could be explained by the physical characteristics of trees (tree species, DBH, total height, height to the first branch, crown height, crown length, crown width, number of escape routes, leaf size, leaf canopy density) at the site. Our results revealed that elevation and distance to water were significant explanatory variables of sleeping site selection: the probability of being used as a sleeping site decreased as elevation increased (suggesting a preference for elevations below 1500 m.a.s.l.) and as distance to water increased. Our results also revealed variation in the frequency at which sleeping sites were reused, but we were not able to identify the drivers of this behaviour. We found that environmental factors influenced baboon sleeping site selection in our study. Our data are preliminary and a longer study is needed to more accurately identify such factors in savanna woodland baboons and thus better contribute to understand sleeping site selection patterns in the highly flexible genus *Papio*.

How Do Chimpanzees and Children Perceive Other Species' Bodies

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We investigated how chimpanzees and children process bodies of other species and which kinds of cues they use, including embodied and visual experience. Previous research has found that human adults show the inversion effect to bodies of conspecifics and other species that they have visual or embodied expertise with, that is, they are better at recognising the bodies when they are upright than inverted. The inversion effect is not found for other objects. Chimpanzees also show the inversion effect to bodies of conspecifics, but little is known about the processing for other species' bodies. In this study, we tested the inversion effect in 7 chimpanzees and 33 children (43-75 months old). For chimpanzees, we used stimuli of crawling humans, horses (they had no visual experience with them but they share the quadrupedal postures) and bipedal humans with visually familiar and unfamiliar postures. For children, we used stimuli of humans (conspecific), chimpanzees (not familiar), horses (familiar) and houses (other objects). They did recognition tasks with upright and inverted stimuli on touch screen computers. Chimpanzees showed the inversion effect to crawling humans, horses, and bipedal humans with familiar postures, suggesting that they use both embodied and visual experience when processing other species' bodies. Children showed the inversion effect to humans, chimpanzees and horses, suggesting that children are more sensitive to visual experience cues than chimpanzees, because they have limited visual experience with chimpanzees but still showed the expert-only inversion effect. We observed no change in the inversion effect with age, suggesting that children's use of visual experience is stable at the pre-school stage. This study complied with the IPS Guidelines for the Use of Nonhuman Primates in Research. The proposals were approved by the ethical committee of Primate Research Institute, Kyoto University (2018-125 and 2018-10).

Ground vs. Drone: A Comparison of Methods to Survey the Bornean Orangutan (*Pongo pygmaeus wurmbii*) Population within Eight Distinct Habitat Types in Gunung Palung National Park, West Kalimantan, Indonesia

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Recent reports indicate that orangutan populations have decreased by over 100,000 in the last 16 years. However, the methodology from some of these reports, which did not account for habitat type, has been called into question. Thus, a rapid, reliable survey method that can be used across all orangutan habitat types is needed to track orangutan population numbers. Orangutan populations have historically been evaluated through systematic, ground-based nest surveys. These were done in Gunung Palung National Park (GPNP) in 2001, 2002, 2010 and 2016. Surveys should ideally be conducted annually, but they are costly and time-consuming, require some degradation of the forest and are restricted to areas accessible to ground teams. In 2017, we pilot-tested the use of drones to survey orangutan populations, determining that nests can be spotted and counted from the imagery collected. We are now further validating the effectiveness of drones as a survey tool across the different habitat types on a larger scale by conducting ground censuses at the same time as drone surveys, paving the way for widespread application. As orangutans live in a range of habitat types, habitat-specific nest densities are critical for accurate determination of population density. GPNP is unique with eight different habitats, making this the ideal place to test this technology as it can be applied throughout the orangutan range. Our results reveal the need for habitat specific conversion factors when using drones to estimate orangutan population densities. Density was determined using a formula taking into account the number of nests observed, length of the transect, width of the habitat surveyed, proportion of nest-builders in the population, number of nests made per orangutan per day and the nest decay rate. We compare the density values using these two methods and demonstrate the validity of using drones as an effective technique for estimating orangutan population size.

Considerable Overlap Between a Hybrid Macaque Group (*Macaca fascicularis* x *M. nemestrina*) and Tourist Infrastructure at Sepilok Orangutan Rehabilitation Centre

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Primate tourism has been heralded as a conservation tool that can provide reliable employment for residents of primate habitat countries. An important drawback, however, is that human-primate contact increases the risk of disease transmission. Anthropogenic activity can also impact wild primates negatively by reducing appropriate habitat and increasing physiological stress. Several macaque species (*Macaca* spp.) have been studied at popular tourist locations where provisioning and physical contact are common, which leads to aggression towards tourists. This study aimed to understand better how to improve primate tourism by examining human-macaque interactions and macaque ecology in an anthropogenically-altered environment: the

Sepilok Orangutan Rehabilitation Centre in Sabah, Malaysia. We hypothesised that: i) the group's home range would include significant overlap with tourism infrastructure; ii) the macaques' use of provisioned food would fluctuate with tourist attendance; and iii) the macaques would spend more time on anthropogenic structures (e.g. railings) during the low tourist season. We tracked macaque movement by recording GPS points from the centre of the group every fifteen minutes from 0700 – 1800h. We assessed activity patterns, feeding behaviour and strata use at 1-minute intervals during 10-minute focal follows. We examined the spatial overlap between the macaques' home range and tourist infrastructure using univariate selection ratios. The macaques spent a significant amount of time within a 20 m buffer of the tourist area, even during peak visitor hours. They rested more on days where they fed on provisions, which made up ~35% of their diet year-round. Their use of different strata did not appear to be influenced by tourists. These results demonstrate that the group is not avoiding tourists, and the macaques' frequent use of provisioned food and tourist structures for locomotion could have implications for immune function and exposure to environmental pathogens.

Preliminary Results on Behavioural Variation Following Tubectomy Sterilisations in Free-Ranging Female Long-Tailed Macaques (*Macaca fascicularis*) in Bali, Indonesia

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Nowadays, primates and humans are increasingly forced to share space, often resulting in conflict when primates proliferate in anthropogenic environments such as cities. Developing means of population control and strategies for coexistence is urgently needed. Reproductive control by chemical or surgical means is increasingly used to limit population growth as an ethical alternative to culling and translocation. However, the impact of birth control on sociosexual behaviours of free-ranging primates remains poorly documented. A long-term monitoring of potential implications is crucial to assess efficiency and suitability of such programmes. Our study investigates behavioural changes in sterilised female long-tailed macaques (*Macaca fascicularis*) at the Ubud Monkey Forest in Bali, Indonesia, where sterilisations using endoscopic tubectomy have been conducted since 2017. Tubectomy preserves the ovarian cycle and, therefore, does not induce direct sexual steroid hormonal modifications. Whether the absence of progeny over the years will or will not affect females' life is a question left open, especially given the attention females show towards new-born infants. First, we monitored the potential changes in sexual behaviours, sexual motivation and intrasexual competition by comparing sterilised and unsterlised (control) females. Second, we investigated the consequences of the absence of new infants for the sterilised females through a long-term follow-up before and after their sterilisation. We present preliminary results based on 1073 hours of focal sampling on 129 females over 3 years. We found that sterilised females kept their sexual motivation high. Compared to control females, they were more active and engaged in sexual interactions, probably because they were experiencing repeated non-conceptive cycles. Further monitoring is necessary to evaluate the temporal variation in social dynamics. Ultimately, this information might help to design optimal birth control programmes for wild macaques.

Age and Sex Differences in the Early Social Environment of Crested Macaque Infants

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Different social behaviour can be beneficial for male and female primates because of sex specific selective pressures. From an early age we see sex differences in primate social behaviour. As well as genetics, experience can impact the development of behaviours. There is evidence in chimpanzees that mothers socialise their infants differently depending on infant sex. Barbary, Japanese and rhesus macaques alter some of their parenting behaviour depending on their infant's sex. We characterise the early social environment of wild crested macaques (*Macaca nigra*) and investigate if sex differences in their early life environment may be controlled by the mother. We characterised the early social environment for male and female infants in the first six months of life. We conducted focal scan follows at 15-minute intervals on 15 mother-infant dyads (10 male infants and five female) from birth to six months. We examined mother-infant distance, nearest neighbours, social partners and if infants could see their mother. Preliminary results show that crested macaques become increasingly independent from their mother during the first six months of life. Infants spent an average of 86% of the time in body contact with their mother in the first and second month of life compared to 54% in the fifth and sixth months. Conversely, infants spent more time further than 10 m from their mother in their fifth and sixth month compared to their first four months. Female infants interacted less with non-mothers than male infants did during the first two months of life. On average, females interacted with their mothers in 74% of social interactions whereas only 34% of male infant social interactions were with the mother. We show that sex differences seen in crested macaques may begin to emerge because mothers provide differential mothering behaviour towards male and female offspring before they start to become independent.

Long-Term Monitoring of Nocturnal Lemur Populations in the Littoral Forests of Sainte Luce, Southeast Madagascar

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Approximately one-fifth of the world's 504 recognised primate species are endemic to the island of Madagascar. Of these, 87 species are considered globally threatened as defined by the IUCN and 100 are reported as undergoing population declines. Understanding the factors driving these declines and estimating the rate of loss is critical for lemur conservation. Here we summarise results from a longitudinal study spanning 8 years in the littoral forests of Sainte Luce, southeast Madagascar. Littoral forests represent a useful model for monitoring population dynamics, as they are relatively well studied and their highly fragmented nature allows for the effect of forest size and human impacts to be explored. We focussed our study on the nocturnal species, *Avahi meridionalis* (EN), *Cheirogaleus thomasi* (CR*) and *Microcebus tanosi* (EN*) (*draft assessment, C. Schwitzer pers.comm), across three study forests of different size and anthropogenic resource usage histories. Surveys were conducted between January 2011 and December 2018, based on a line transect methodology using perpendicular and exact distances. Analysis was completed using DISTANCE v7.3 and SPSS 24. Our results indicate that each species responds non-uniformly to

forest patch size and to levels of forest degradation, forming a complex picture. The largest species, *Avahi meridionalis,* shows declines in density and encounter rate over time in the three study forests, and one sub-population now stands on the brink of extirpation in an unprotected fragment with heavy resource extraction. *Cheirogaleus thomasi* populations appear stable in all three fragments, with densities increasing in the most degraded forest. *Microcebus tanosi* encounter rates are extremely low across all fragments, but are lowest in the heavily degraded and unprotected forest. Careful monitoring of key population dynamics can provide an early warning signal to conservationists ahead of species loss and enables crucial interventions to be made.

Sleeping Site Selection and Diurnal Activity in the Southern Woolly Lemur (*Avahi meridionalis*)

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Many lemuriforms exhibit activity throughout the 24-hour cycle, known as cathemerality. The number of species showing this activity pattern and its evolution in primates is still uncertain. Studies exploring the temporal niche of woolly lemurs (*Avahi*) provide evidence of diurnal activity within this nocturnal group, suggesting some degree of cathemerality. In this study, we investigated the degree of diurnality in the southern woolly lemur, *A. meridionalis*, and explore the link between activity bouts and sleeping site selection. From May to July 2018, we conducted systematic surveys in the lowland rainforest of Tsitongambarika in southeastern Madagascar within the home ranges of three pairs of *A. meridionalis* to locate day-time sleeping trees. At the sleeping trees, we conducted continuous behavioural observations from dawn to dusk until the animals left the tree for their nocturnal activity. We measured the characteristics of the sleeping trees to identify the driving factors of sleeping site selection and to investigate whether the micro-habitat architecture influences diurnal activity. We found that the nocturnal *A. meridionalis* exhibited opportunistic diurnal activity: being active for 28% of their time within or around the sleeping site. While active, individuals displayed vigilance, grooming and feeding behaviours. The study animals demonstrated a selection for tree-height within pristine areas as opposed to selecting for vegetation density in edge areas. Similarly, our behavioural analyses revealed that *A. meridionalis* exhibited more diurnal activity in disturbed edge habitats. We suggest that an anti-predatory strategy may be a driving factor in both sleeping site selection and diurnal activity. With our results, we confirm that the secondary nocturnal genus *Avahi* exhibits cathemerality and add support to the idea that activity patterns in lemurs are more diversified than traditionally thought.

The ManyPrimates Project: A Multinational, Multi-Institutional, Multi-Species Collaborative Effort to Study Primate Cognition

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Understanding how cognitive abilities evolved within the primate clade requires large and diverse samples. Primatologists are often able to test only a small number of subjects

and/or species, mostly hosted in one institution, which prevents them from systematically answering questions from a phylogenetic perspective. Current open science projects in other fields, like the ManyBabies project, established platforms for large-scale collaborative research that a single research group could not study alone. So, the idea emerged to gather researchers interested in the evolution of cognitive abilities, and the ManyPrimates project was created for researchers to collaborate on a large scale and run research in primate cognition across sites. We report here the first ManyPrimates study, a case study of short-term memory, to demonstrate the viability of the project. We successfully tested 176 subjects from 12 species housed at 11 sites located in Africa, Asia, Europe and North America. All subjects were tested in a delayed-response task using consistent methodology across sites. Individuals could access food rewards by remembering the position of the hidden reward after a 0, 15, or 30-second delay. In each trial, subjects were shown three opaque cups, a reward was put under one and the cups were inverted. The subject was then asked to choose the baited cup after the determined delay. Our phylogenetic analysis showed a strong phylogenetic signal for short-term memory abilities. However, with only 12 species, the validity of this analysis remains limited. Our initial results demonstrate the feasibility of a large, collaborative open-science project, and we present the ManyPrimates project as an exciting opportunity to address open questions in primate cognition and behaviour with large, diverse datasets. Having demonstrated the efficacy of ManyPrimates, we look forward to answering new challenging questions and welcome new collaborators.

The Occurrence and Potential Explanatory Factors of Abnormal Behaviours in Zoo-Living Bonobos

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Behaviours of captive great apes that are atypical for their wild conspecifics are often considered abnormal and are used as indicator of poor welfare. While abnormal behaviours are well-reported in chimpanzees (*Pan troglodytes*), comparable studies in the closely-related bonobo (*P. paniscus*) are currently lacking. Despite reports on individual abnormal behaviours, we are unaware of the scope of the occurrence of abnormal behaviours in general across the captive population of bonobos. As such, we studied the demographics of abnormal behaviours (i.e. prevalence, diversity and proportion of time spent) and identified what factors contribute to the presence of abnormal behaviours in bonobos. We report data from 25 female and 17 male bonobos, all older than 6 years of age, living across six European zoos. We studied each bonobo by focal animal sampling, totalling between 12 h and 22 h of focal observation per individual. We recorded all behaviours of the focal subject, but analysed only behaviours here that have been listed as "abnormal" in the literature. We tested for consistency of abnormal behaviours between years and used factor analyses to identify dimensions of abnormal behaviours. Subsequently, we used these dimensions as dependent variables to examine factors, such as sex, rearing background, location and personality factors, which may contribute to the occurrence of these behaviours. Through reporting the extent of abnormal behaviours in zoo-housed bonobos and by identifying factors that explain the variation in their occurrence, this study contributes to our understanding of the aetiologies of abnormal behaviours in these populations, which ultimately aids in improving their welfare.

A Study Using the Animal Welfare Assessment Grid (AWAG) to Measure Quality of Life of Captive Breeding Rhesus Macaques at the Medical Research Council Centre for Macaques facility

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The Home Office recorded a total of 2,960 scientific procedures using rhesus macaques in 2017, highlighting the extent of animal testing in the UK. Whilst research using animals parallels the development of medicine, it is our responsibility to ensure their best quality of life; from the animals' perspective, rather than our anthropogenic view. The Animal Welfare Assessment Grid (AWAG) is designed to revolutionise animal welfare by offering an objective, quantitative measure; using the harm: benefit ratio to justify the use of animals in research. The AWAG is based on four parameters (environmental, psychological, physical and procedural). Results are presented as an ethogram and cumulative welfare graph, a technique that is not currently in use, which appears to be an effective way to highlight short-term events or interventions that impact welfare. The AWAG tool can measure positive emotions, as well as the absence of pain and suffering, which is important for promoting positive welfare states in animals. A pilot study was conducted before the actual research project where we aimed to validate the AWAG whilst developing practical factors that score and assess the quality of life of breeding rhesus macaques and encourage improvements in their welfare. The research was undertaken at the Centre for Macaques, in Salisbury. Results from the pilot study validated the software. We show the impact of novel enrichment techniques on the AWAG score and consequently welfare of the rhesus macaques. The intention is to disseminate these results to other centres for macaques to suggest ways in which they can improve welfare.

Social Tolerance and Inhibitory Control Skills in Macaque Species

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Living in a complex social environment requires primates to manage their emotions and inhibit impulsive behaviours in order to maintain group cohesion and survival. Such cognitive processes are defined as inhibitory control. Inhibitory control is a multi-dimensional construct comprised of separable processes: 1) inhibition of emotions, the ability to focus on a goal in the presence of distractors; 2) inhibition of actions, the ability to suppress reflexive actions; 3) inhibition of a cognitive set, the ability to flexibly adjust behaviours. While various paradigms have been designed in order to measure inhibitory control, common tasks used to measure this cognitive process yield unreliable results and inconsistencies between tasks, possibly because inhibitory control is not one phenomenon but is, instead, composed of multiple processes. Hence, the aim of this project was to develop, test and compare a battery of four different inhibitory control tasks to validate measures of the inhibitory process in primates. We tested 21 rhesus macaques (*Macaca mulatta*, 11 males, 10 females) in a battery of four different touchscreen tasks assessing the main components of inhibitory control: a goal-oriented task, a go/no-go task, a reverse

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learning task and a reaction time task with distractor. To assess the reliability of these tasks, the macaques were tested 3 times, across 3 different time points. We evaluated consistencies in the individual performances among the 4 tasks. To assess performance in the tasks, we used a GLMM with social status, time point, task, sex and age as predictors while controlling for the identity of individuals. Results are examined to determine whether inhibitory control is best conceptualised as composed of separable processes that do not necessarily correlate within individuals. This project will help to develop a valid assessment of inhibitory control in primates, which would lead to a better understanding of the evolutionary underpinnings of this ability.

Individuals in Urban Dwelling Primates Face Unequal Costs and Benefits Associated With Living in an Anthropogenic Environment

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Living in an anthropogenic environment is inevitably linked to certain benefits but also entails social costs for group-living primates. Benefits for individuals can be summarised by access to anthropogenic food resources that are often more abundant, spatiotemporally predictable and have higher calorific value than natural foods. Yet, close proximity to humans and provisioning also often increases aggressions between group members, potentially impacting an individual's health, wellbeing and, ultimately, fitness. Here we investigated inter-individual differences in benefits (access to anthropogenic food resources) and costs (aggression received from conspecifics) in an anthropogenic environment. We determined whether such differences in costs and benefits are sex- or rank biased and how they are affected by an anthropogenic environment. We included more than 300 individuals living in nine urban groups across three macaque species in this study. We found that males and high-ranking individuals have a higher proportion of anthropogenic food in their diet, thus better access to such food resources. At the same time, low-ranking individuals and females are more subject to aggressions. These aggressions are increased in an anthropogenic environment through provisioning. We conclude that living in an anthropogenic environment may increase the advantages of high-ranking individuals beyond the patterns observed in the wild. Our results will contribute to a better understanding of the drivers and mechanisms of selection pressures on urban primates.

Camera Traps Offer a Robust Means for Social Network Analysis in Wild Chimpanzees

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Camera traps are an increasingly valued tool for studying behaviour and demography in primates. Nonetheless, little is known about the robustness of camera trap data for social network construction. Chimpanzees (*Pan troglodytes*) live in stable communities with fission-fusion dynamics; their fluid associations offer the opportunity to test the efficacy of camera traps for studying social variation. Here we used camera traps and observational data, collected concurrently over nine months on habituated western chimpanzees (*P. t. verus*), to construct social networks, assess their similarity and compare their robustness. Networks constructed using both methods were stable at adequate sample sizes, with similar structures, patterns of sex assortment and individual network positions. Group density and dyadic association strengths were lower while modularity was slightly higher in the camera trap network compared to the observational network, highlighting the caution warranted when comparing social networks derived using different methods. Next we applied this method to camera trap data from unhabituated eastern chimpanzees (*P. t. schweinfurthii*), demonstrating that a robust social network can be constructed even without extensive prior knowledge of the study subjects. Differences between the eastern and western chimpanzee social networks followed patterns that would be predicted based on known social differences between these populations, illustrating the potential of this method for comparative studies of social variation. Although direct observations of long-term study groups will continue to provide valuable social data in many primate species, camera traps offer a robust alternative to study social dynamics, particularly in elusive or unhabituated primates. This method can also extend beyond fission-fusion primates to explore relative proximity and behaviour coordination even in cohesive social groups, making it broadly applicable across many species.

Thermal Constraints on Habitat Use in Forest- and Savanna Mosaic-Dwelling Red-tailed Monkeys (*Cercopithecus ascanius*)

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While most guenon species are forest-dwelling, others are also distributed across other habitats, including drier, hotter savanna mosaics. These latter, more heterogeneous environments should exhibit greater temperature ranges and steeper thermal gradients between vegetation types. As such, we expect high intra-specific variation in how savanna mosaic-dwelling monkeys exploit hotter, open canopy and cooler, closed canopy vegetation types compared to their forest-dwelling conspecifics. We investigated strategies of open and closed vegetation use in two populations of red-tailed monkeys (*Cercopithecus ascanius*), a primarily forest-dwelling species that also lives in savanna-woodland mosaics. Specifically, we evaluated ranging patterns of eight groups at Ngogo (Uganda), a mosaic of predominantly closed primary forest and small proportions of open colonising forest, and three groups at the Issa Valley (Tanzania), an open miombo woodland-dominated mosaic with minimal closed forest (4% cover). We predicted that (1) higher temperatures would have a stronger negative effect on travel speeds at Issa compared to Ngogo and (2) open vegetation use would be constrained more strongly by temperature at Ngogo, given the greater availability of resource-rich forest compared to Issa. We used Garmin GPS units to collect high-resolution ranging data on each group and HOBO and Kestrel weather stations to record temperature at 20- to 30-minute intervals in each vegetation class. By modelling habitat-specific patterns of vegetation use against temperature, our results have implications for establishing intra-specific variation in optimal ranging and foraging strategies exhibited by a forest guenon living in two contrasting mosaic landscapes. These methods complied with the International Primatological Society Guidelines for the Use of Nonhuman Primates in Research.

Distribution of Nocturnal Primates in Disturbed and Non-Disturbed Areas in Peninsula Malaysia and Brunei Darussalam

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Anthropogenically disturbed areas may sometimes be as diverse as non-disturbed areas. We studied the distribution of nocturnal primates in Peninsula Malaysia and Brunei Darussalam. We focused on three species; the Sunda slow loris (*Nycticebus coucang*), the Philippine slow loris (*Nycticebus menagensis*) and the Horsfield's tarsier (*Cephalophacus bancanus borneanus*). We also gathered information on a number of other mammal species during our survey, including the cryptic Sunda colugo. We conducted transect surveys following set paths to assess their presence/absence and population density. We surveyed three areas in Peninsula Malaysia (Penang Island, Langkawi Island and Segari Melintang) and two areas (Temburong and Bandar) in Brunei, comprising a minimum of 15 transects per 500 m in each area, including non-disturbed virgin rain forests and rural (disturbed) areas. We used a red head torch and a Flir thermal device to enhance

detection rates of the animals. Using this technology, animals like slow lorises or colugos are easily visible even when they are sleeping. We compared the use of different lights and detection of animals in different habitats to exclude detection bias. Our results indicate that the slow loris is easily recorded with this method but the tarsier is more difficult, as the use of trails might not be the best way to see them. There is great variation depending on the area but we found a density of slow loris of 0.12 ind/km in Penang Island, 0.24 ind/km in Langkawi Island, 0.58 ind/km in Segari Melintang and 0.6 ind/km in Brunei Darussalam. This survey increases knowledge of the habitat preferences of slow lorises, which will be vital for future conservation efforts.

Action Co-Representation as a Primate Universal? The Joint Simon Effect in Tonkean Macaques

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The Joint Simon task allows assessing action co-representation in partners engaged in behavioural coordination. It critically builds on the individual Simon effect (SE), which describes an interference effect that typically manifests in a higher probability of making mistakes when choosing between two response options. The SE describes that an initially learned discrimination (e.g. between two sound stimuli to choose either a left- or a right-hand response option) is more difficult when an interfering cue (e.g. the sound indicating to choose the right-hand option is played back from the left-hand side) is present. While the effect disappears when the subject only has to solve one half of the task, it reappears when the second half of the task is solved by a social partner (Joint Simon Effect, JSE). The JSE is described in humans and common marmosets, both cooperative breeders who routinely interact in coordinated actions. To better understand the evolutionary origin of co-representation, we therefore need to test independently breeding non-human primates who do not extensively engage in cooperative activities. In this study, we tested semi-free ranging Tonkean macaques, *Macaca tonkeana,* (two subadult males, three adult males and two adult females) with an auditory Simon task, using a comparable testing paradigm to the one developed for common marmosets. As in marmosets, the Tonkean macaques made more mistakes in the experimental conditions, i.e. full & joint task, compared to the control conditions, i.e. half & joint-control task, consistent with a SE and JSE. The subjects' sex, age, and the identity of the co-action partner, had no influence on the size of the effect. We analysed additional variables (first heading directions, reorientation, gaze behaviour). Our results suggest that co-representation describes a primate universal, given that a dyad is socially tolerant enough to engage in a joint task, and not a convergent trait in cooperative breeders.

Past and Present Populations of the Western Lowland Gorilla: A Multidisciplinary Approach to Conserving a Critically Endangered Primate

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The Western lowland gorilla (*Gorilla gorilla gorilla*) was listed as Vulnerable in 1986 according to the IUCN (International Union for Conservation of Nature) Red List of Threatened Species. Ten years later, its status was ranked as Endangered and in 2007 it was uplisted to Critically Endangered. Despite being the most numerous and widespread of all gorilla subspecies, genetic studies are still relatively few. Here, combining population genetics, phylogeography and historical geographic distribution data from museum archives, we aim to identify regional variation in the Western lowland gorilla for conservation biology purposes. Microsatellite genotyping and preliminary analyses across 10 loci, using 94 historical samples from the Powell-Cotton Museum (PCM) and 64 contemporary samples (54 FTA cards and 7 tissue samples) from the captive population held by The Aspinall Foundation, allowed us to identify patterns of genetic diversity and structure. Moreover, mitochondrial (mt) DNA diversity was studied using 62 historical and 53 contemporary samples; however, the presence of nuclear inserts of mtDNA (NUMTS) somewhat limited the phylogeographic analysis. Using Geographical Information Systems (GIS) of historical museum catalogue data (PCM) of Western lowland gorillas collected by Major Percy Powell-Cotton and Fred Merfield between 1927 and 1936, revealed 30 geographical locations forming three distinct groupings in North West Congo, South West and South East Cameroon. The museum archives represented a unique and valuable resource for the study of the geographic distribution of this Critically Endangered subspecies. The results of this multidisciplinary study provide reliable information for conservation managers implementing captive breeding and reintroduction programmes.

Could it be Culture? An Inter-Troop Comparison of Baboon Behaviour in Gorongosa National Park, Mozambique

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Despite the large existing body of research on baboons, a thorough large-scale study of inter-troop behavioural variation has yet to be conducted. Cultural inter-group variation has been suggested for a range of other primates including apes, macaques and capuchins. Here we present preliminary results from a two month pilot study in 2019 in addition to limited 2018 field season data on inter-troop behavioural variation in two types of resource attainment and consumption (i.e. hunting and bark stripping) in baboons of Gorongosa National Park, Mozambique. The park

is particularly well-suited for this study, being home to over 200 baboon troops, predicted to be chacma-yellow baboon hybrids, spread across a mosaic ecosystem. Hunting instances and carcass processing by baboons is recorded for three troops, all residing in a floodplain habitat (n = ca. 35 to 100 individuals per troop). We additionally monitor bark stripping across a closed-habitat region of the park, comparing presence and absence of stripped trees between home ranges of several unhabituated troops. We build upon previous work completed during 2018, which indicates regional variation exists in acacia tree bark stripping. Following the 'method of exclusion' approach, we assess ecological differences between home ranges using phenological transects and ongoing genetic research in the park that will provide further insight into potential genetic correlates. In future fieldwork, we will study a total of six troops, targeting candidate behaviours including hunting, grooming, sleeping site choice and environmental modification. We will improve our understanding of baboons as an analogous model for aspects of human evolution and extend our knowledge of culture in primates. We will also lay the foundation for valuable future research at the site, allowing for investigation of the interaction of culture, genetics and environment, as well as the presence of cumulative culture in non-human primates.

Phylogeography and Population Genomics of the Sanje Mangabey (*Cercocebus sanjei*)

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The Sanje mangabey (*Cercocebus sanjei*) is an Endangered primate, endemic to the Udzungwa Mountains, Tanzania, that is found in only two isolated forest blocks, Mwanihana in the Udzungwa Mountains National Park and the Udzungwa Scarp Nature Reserve. These forests are separated by 120 km of agricultural land and it is unknown when they became isolated, preventing dispersal and gene flow between forests. This fragmentation is cause for concern with the isolated populations being at more risk to negative genetic processes such as genetic drift, inbreeding depression and loss of rare alleles and, as a result, adaptive potential. Therefore, the investigation of the genetic diversity and structure of the species is invaluable for informing conservation management. This study has been conducting the first genomic characterisation of the Sanje mangabey, investigating the phylogeographic structure, phylogenetic history and genome-wide diversity at neutral and adaptive loci. DNA was extracted from faecal samples collected from both forests in 2017. A fragment of the mitochondrial control region was amplified with newly designed primers. Early results suggest that the populations are highly divergent and have been isolated for a longer time than previously expected, suggesting this is a more ancient structure, rather than one resulting directly from recent human impact. A method to enrich host DNA in extracts from faecal samples was used to capture host DNA for sequencing with ddRADseq. Ongoing work is identifying SNPs to elucidate nuclear genomic structure and diversity. These results combined with previously collected demographic data will be used to model population and habitat viability using the VORTEX modelling suite. The impact of no intervention and a range of conservation actions will be modelled to best inform conservation actions for the species. Recommendations will be included in the Sanje mangabey entry for the *Cercocebus* and *Mandrillus* Conservation Action Plan.

Ranging Behaviours and Activity Budgets of Rehabilitated and Reintroduced Howler Monkeys

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The Yucatán black howler monkey (*Alouatta pigra*) ranges from Mexico's Yucatán peninsula, throughout Belize and into Northern Guatamala. This species is listed as Endangered by the IUCN Red List. The forests that these howler monkeys inhabit are threatened by habitat loss and fragmentation. Hunting also poses a significant threat to howler monkeys. Howler monkeys exhibit behavioural flexibility regarding feeding ecology and are often considered coliniser species. Howler monkeys fill an important ecological role as seed dispersers because of their large body size and resilience to persist in degraded habitats, making them crucial for ecosystem health. Our study worked in conjunction with local wildlife rehabilitators and the NGO Wildtracks, who have been reintroducing howler monkeys since 2011, into a protected area in Northern Belize. Wildtracks has a 75% success rate of their reintroduced howler monkeys that often are confiscated from the illegal pet trade. Five troops were investigated during this study. We investigated daily range length to evaluate rehabilitated howler monkeys' effectiveness as seed dispersers and observed what plant species they were consuming as well as what part of the plant. Home range size was also investigated. We recorded ranging behaviours using a GPS as well as activity budgets using instantaneous focal sampling. Daily ranging behaviour observed from reintroduced troops was consistent with findings from other studies, as was home range size. We found the most frequently observed behaviours being resting and feeding and only a small part of their days are engaged in social behaviours. This is also consistent with previous findings. Through the dissemination of the results via Wildtracks connections, this study aims to provide similar projects with information on howler monkey reintroductions, increase effectiveness of rehabilitation projects, and improve survival rates of reintroductions.

Anterolateral Ligament of the Knee in Chimpanzees (*Pan troglodytes*)

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In 1879, the French surgeon Segond described in humans an anatomical structure proposed as a new ligament. This structure is placed on the outer side of the knee and extends from the femoral external condyle to the tibial external condyle, in front of the head of the fibula. Since then, scientific controversy surrounds the existence of this particular ligament. There are authors who find it in a small percentage of cases, others who deny its presence or consider it a reinforcement of the joint capsule and, finally, some authors who consider it as a constant ligament present both in adults and foetuses, giving it the function of a brake for knee internal rotation and collaborating with the anterior cruciate ligament. In 2015, Inhgam and collaborators searched for it in animals. This ligament was absent in all of the 58 species studied (including four humans, two bonobos and eight gorillas). In our work, we studied six knees of three common chimpanzees (*Pan troglodytes*). The specimens were dissected after being frozen, without application of any preservation methods. We did not observe the ligament in any of the six knees. Human and

chimpanzee locomotion differs ostensibly, in that the displacement is carried out on both extremities only. The chimpanzee does not perform a full extension of the knee joint and therefore does not need to prevent the internal rotation of the knee completely.

Manipulative Abilities in Great Apes and 5-6 Year Old Children for the Same Tool Use Task: Exploring the Prerequisites of Handwriting

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Among primate manipulative abilities, one of the most conspicuous grasping skill specificity is human handwriting. Learning to handwrite is a process requiring several neuromotor prerequisites (e.g. motor control, neurological maturation, muscular maturation). The study of prerequisites for handwriting should help us to gain a better understanding of human unique grasping abilities, sometimes not easy to demonstrate. The aim of our study was to compare grasping and manipulative capacities during a complex tool use task in 13 adult great apes (6 gorillas and 7 orangutans) and 20 human children, aged 5 to 6 years, before they started to learn how to write. The task required the use of a tool to recover a walnut in a wooden maze and all subjects of all species were in the same experimental conditions. We quantified the grip postures applied by the individuals on the tool and other manipulation parameters (e.g. unimanual or bimanual grasping and in-hand manipulations). Our results showed that whereas great apes and children shared some abilities (e.g. a large number of grip postures, and intraspecific variability), they also differed (e.g. great apes used unimanual whereas children were using bimanual grasping). To conclude, we need to further explore the motor control of great apes and children but also the underlying learning processes of writing. Thus, we will be able to discuss if these prerequisites have evolved in non-human and human primates or are a human specificity. This study complies with the ethical guidelines by the CNRS and French governmental animal care committees and with the IPS Guidelines for the Use of Nonhuman Primates in Research.

Environmental Factors and Homeostatic Need Regulate Sleep Patterns of a Nocturnal Primate (*Nycticebus javanicus*)

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Sleep is a fundamental requirement for many animals in maintaining cognitive performance and physiological functions. Researchers have suggested that sleep evolved as a process to deal with immediate intrinsic homeostatic needs and as a response to predictable and unpredictable environmental conditions. While research on the evolution of primate sleep has increased in the

last decade, information is still lacking for the sleep architecture of wild populations. We present the first-ever study to measure sleep of a wild nocturnal primate. We studied a population of Javan slow lorises, *Nycticebus javanicus,* in West Java, Indonesia. We measured locomotor activity of seven slow loris individuals over 321 days using accelerometer devices. To test for environmental influences on resting patterns, we measured ambient temperatures and light environment across the 24h period. Slow lorises performed nocturnal activity patterns with a synchronisation of onset and end of activity in relation to sunset and sunrise. All individuals displayed an average total sleep time of eleven hours during monophasic daytime rest, as well as least locomotor activity clustered in the beginning and end of the light period. Additionally, all individuals displayed sleep rebound by displaying 'naps' during the dark period. Observed influence of lighting conditions on rest and activity suggest that the levels of illumination are an intrinsic determinant of the circadian rhythm in activity patterns in these animals. Patterns of consolidated rest may suggest increased 'sleep intensity', but were also inversely related to daily fluctuations of the ambient temperature. The distribution of naps may indicate that individuals get tired, as naps never occur in the first half of their activity period. This suggests that sleep intensity of *N. javanicus* is most regulated by their intrinsic circadian rhythms. Our data support hypotheses that primate sleep traits derived somewhere in the strepsirrhine clades.

Can Breeding Behaviour and Life History Details Predict the Captive Breeding Success of Aye-Ayes (*Daubentonia madagascariensis*)? A Novel Use for ZIMS Data

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Captive aye-aye (*Daubentonia madagascariensis*) breeding behaviour is understudied. With fifty captive individuals worldwide and just 1-2 births/year, sustainability of the captive population is low. Yet captive breeding success (occurrence of live births and survival of infants for the first year) is vital to the survival of the species due to poorly mitigated anthropogenic threats to wild populations. Our study aimed to identify predictors of breeding success in captive aye-ayes using ZIMS (Zoological Information Management Software) data on the life history and behaviour of successful and unsuccessful aye-aye pairings (n=38) from ZSL London Zoo, The Duke Lemur Centre and Bristol Zoo Gardens, spanning over 30 years of animal records. We scrutinised records for information using mixed qualitative approaches (semi-deductive thematic analysis and content analysis). We produced breeding pedigrees, showing how genetically narrow the captive population is. Generalised linear models found female age, difference in age between the male and female, oestrous stage and number of encounters as significant predictors of breeding success. Duration of interaction and duration of mountings were significantly greater in successful births, and parents' place of birth, wild versus captive, were also important factors in breeding. We found certain behaviours such as approaching, stress-call and scent marking to occur significantly more than expected in successful births. We found affiliative behaviours, often used as an indicator for breeding by keepers, significantly less than expected in successful births. For successful breeding, the aye-aye breeding pair should comprise a wild-born male, an older male though not greatly older than the female and a pair who are agreeable (tolerate each other well) outside of oestrus, also required is a long copulation, involving many mounting attempts and many successful mountings. Further research into wild and captive breeding behaviour is needed if we are to understand agreeableness and what leads to successful mounting.

Spatial Representations of Time in Chimpanzees: A STEARC-Like Effect

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In humans, it is well established that cognitive representations of time have spatial characteristics, as do representations of other stimuli such as numerals and pitch. There is evidence for a left-right 'mental time-line', whereby early time and short time periods are mapped to the left, and late time and long time periods are mapped to the right. These characteristics influence manual response time, in that stimuli facilitate faster responses when presented on the side of space congruent to their spatial mapping. This is termed a 'spatial-temporal association of response codes (STEARC) effect' in reference to time, and a 'SNARC effect' in reference to number. It has been shown that there is a SNARC-like effect in chimpanzees, gorillas and orangutans. Here, we explore whether chimpanzees also show evidence of a STEARC-like effect, by analysing seven chimpanzees' response times to an adapted matching-to-sample task. Each trial began with a brief video-clip of an event (e.g. a fruit being placed in a box), in order to generate an early/late time association with the start and end images. These images were then used as stimuli in the trial, and response times for when the answer was presented on the left vs right were analysed. A GLMM analysis did not find any significant STEARC-like effect at the group level. There were large individual differences, and so we then analysed individuals independently. Three chimpanzees showed some evidence for a left-right STEARC-like effect, and 2 showed some evidence for an effect in the opposite direction. This implies a time-space mapping is possible, but its existence and direction varies. The presence of a STEARC-like effect in chimpanzees holds implications for our understanding of the interconnected nature of space, time and number, and of innate vs cultural influences on the mental time-line. The methods used comply with the International Primatological Society Guidelines for the Use of Nonhuman Primates in Research.

Analysing the Trade and Welfare Status of Pigtailed Macaques (*Macaca nemestrina*) Used to Harvest Coconuts in Southern Thailand

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Pigtailed macaques represent one of the few primate species to perform agricultural labour for human economic gain by harvesting coconuts. This practise occurs in several Southeast Asian countries, where juvenile macaques are taken from the wild between the ages of one to two years to commence training. The impacts of this practise on the population status and individual welfare of wild pigtailed macaques remains largely unknown. We assessed the origins and breadth of the trade network involved in supplying macaques to the coconut harvest and evaluated the welfare status of working macaques in three Southern Thailand provinces using the 'five freedoms' approach. The practise of working with macaques is widespread in Southern Thailand and has not decreased in the past few years. Further, in recent years, the tourist draw to so-called monkey training schools that advocate the use of working macaques has created new economic incentives to perpetuate this practise. Extraction rates from the wild appear to be substantial and overall low macaque welfare scores indicate the necessity of improvements to minimise long-term negative

physical and psychological effects. Main improvements include altering the diet and promoting the expression of species-specific behaviours in working macaques. Through continued collaboration with farmers and trainers, we aim to improve the welfare of working macaques and reduce the need for new wild-caught macaques. We will also liase with the Department of National Parks and Conservation of Wildlife in Thailand to generate future plans that improve human and non-human primate welfare.

Conservation of Novaes' Bald-headed Uakari, *Cacajao calvus novaesi*, Amazon Rainforest, Brazil

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The predicted increase of deforestation rates in Brazilian Amazon rainforest will aggravate the impact of habitat loss for many primates. The assessment of the conservation status of Data Deficient species is key to planning effective strategies for their long-term protection under this scenario of habitat loss. Here we review the occurrence and distribution of the Data Deficient Novaes' uakari (*Cacajao calvus novaesi*), aiming to provide a framework to assess its conservation status. We present new data on the occurrence of this primate from multi-year surveys to delimitate its geographic range. We use predictive deforestation models to estimate forest loss within the subspecies' range under two deforestation scenarios. *Cacajao c. novaesi* is limited to an area of 17,862 km^2 in Gregório-Tarauacá interfluve and the major threats to populations are deforestation and hunting. The deforestation within the subspecies' range will reduce its habitat by 38.1% under the Governance scenario and by 65.9% under the Business-as-Usual scenario. Thus, considering its limited geographic range, the potential habitat loss under the worst case scenario of deforestation and the current scenario of uncertainty in the Brazilian environmental policies, we recommend that *C. c. novaesi* is listed as Endangered under criteria A3c, i.e. a projected population reduction to be met in the future (30 years, three generations) due to a decline in the species' extent of occurrence (EOO) of more than 50%. Other Amazonian primates currently categorised as Data Deficient or even as Least Concern can be reassessed using a similar approach.

Female Japanese macaques' personality and friendship in an atypical social environment

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Social bonds in primates influence cooperative interactions and, thereby, individual fitness. The determinants of close bonds include age, sex, rank and kinship. In addition, increasing evidence shows that personality, particularly similarity in personality characteristics among

partners, is an important factor in bond formation. In Japanese macaques, kinship and sex are the main determinants of close bonds, reflecting the social structure of this despotic, nepotistic macaque species. However, whether and how these socio-ecological factors may constrain the significance of personality in determining bonding is unstudied. We asked, whether dyadic personality similarity influences female relationships in a group of semi-wild Japanese macaques. The study group has a rather atypical social structure, as multiple adult males reside in their natal group. We assessed several social personality traits as well as an indicator of curiosity by the frequency of exploring enrichment and experimental devices. We collected 155h of focal data (5h/ind.) of 31 adult and adolescent semi-wild Japanese macaque females living in Affenberg Zoo, Landskron, Austria. We extracted several behavioural indices and tested their repeatability and personality trait structure. We calculated dyadic sociality index for each female dyad and tested whether it is predicted by dyadic personality similarity, sex or kinship. We will discuss the results in the light of comparative data on macaque and other primate personality and, more broadly, the influence of ecology on primate social bonds and individual differences in behaviour.

Thriving on Facebook: the Online Trade of Primates in Thailand

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Social media and increased Internet accessibility has changed the way wildlife are traded, shifting from traditional brick-and-mortar markets to virtual platforms. We systematically surveyed the online market of primates on Facebook in Thailand over a two-year period from April 2017 to March 2019. From eight public-accessible buy-sell groups, we recorded at least 424 individuals (n = 412 posts) from 24 species, with a combined identifiable market worth at least $US 95,000. An Anthropogenic Allee Effect was evident, where import premiums were put on exotics from South America and Africa. These rarer species were offered at significantly higher prices (US$ 1101 ± 328 vs US$ 110 ± 72). Primate species native to Thailand comprised 89% of the trade; these were more affordable and accessible to purchase as exotic pets. Legal and illegal wildlife trade was evident on the platform, however, 81% of individuals traded (284/412 posts) were either domestically protected, or CITES Appendix 1 listed species, reflecting the illicit nature of the trade. Furthermore, many of the macaques, langurs and slow lorises were too young to be identified to the species level. Over 63% of recorded posts were of primates listed as globally threatened by the IUCN, reflecting the impact of trade on species conservation. We found a statistically significance price difference between the IUCN Red list categories (Least Concern US$ 451 ± 508; Near Threatened US$ 126 ± 29; Vulnerable US$ 81 ± 34; Endangered US$ 275 ± 127). We urge for improved legislation to address online trade, continued monitoring of virtual market dynamics, and for stakeholders to be actively involved in regulating this thriving trade.

Learning With Lemurs: Evaluating a Forest-Based Conservation Education Programme

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Due to the significant threats to lemurs in Madagascar, policy makers have identified conservation education as an important component of a nation-wide conservation strategy. In this study, we conducted a forest-based conservation educational programme with children from local secondary and high schools in Northeast Madagascar. Fifty children in five groups were taken on three-day trips into Marojejy National Park to participate in exploratory educational activities focused on lemur ecology and rainforest biodiversity. Given that one of the most crucial, yet often overlooked, aspects of conservation education is evaluation, this programme emphasised not only empathetic and imaginative learning, but also thorough and reflective evaluation. Prior to each trip, we assessed children's knowledge and attitudes regarding lemurs and forest biodiversity via drawing—we asked students to draw a picture of a forest and a lemur that lives there. Two weeks after each trip, we again asked children to make these drawings. During each trip, we assessed students' opinions via evening focus groups during which children discussed the events of the day. From these drawings and conversations, we generated free lists and determined the presence of cultural domains. We hypothesised that children's drawings and opinions would demonstrate an increase in knowledge and awareness and would represent a domain shift over the course of the trip and immediately following it. Additionally, during each trip, we assessed children's engagement with various educational activities through behavioural observations. Over the course of these evaluations, social science methods allowed for thorough assessment of the educational programme.

Do Artificial Food Markets Modify Partner Value in Wild Black Capuchin Monkeys?

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In group-living primates, behavioural exchanges have been reported to occur according to market-driven patterns where grooming is used as a currency in exchange for different commodities such as agonistic support and feeding tolerance. As in a marketplace, the law of supply and demand plays a crucial role in determining not only the specific trading dynamic but also

the market value of trading partners. Primates pay more when partner value is higher (i.e. individuals groom longer those partners that exert higher control over resources). In this regard, a previous experimental study has showed that grooming received by two low-ranking females, trained to provide food to their group, shifted according to their artificially enhanced values, with the increase in grooming received by the first provider being reduced by the addition of a second provider. By adopting a similar experimental paradigm, this study tests whether the market value of experimentally induced food providers responds to variations in the supply/demand ratio in black capuchin monkeys (*Sapajus nigritus*). To do so, we created an artificial food market in a group of wild capuchins in Iguazú National Park, Argentina. In this market, a low-ranking female (provider 1) and a subadult male (provider 2) were trained to provide food to the entire group by opening two boxes containing banana pieces. Grooming interactions were collected across 3 phases: baseline (phase 0), only provider 1 (phase 1), and both providers (phase 2). We then analysed the duration of grooming received by the providers across the 3 phases, predicting that: i) grooming received will increase in favour of provider 1 from phase 0 to 1; and that ii) such an increase will be reduced by the addition of provider 2 in phase 2. Results indicate that grooming received by provider 1 significantly increased during phase 1, as predicted by the BM theory; however, such an increase was not reduced by the introduction of a second provider.

Primate Genome Analysis Reveals Two Possible Independent Origins for Trichromatic Colour Vision in Catarrhines

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Primates are unique among mammals in having a substantial diversity in the type of vision they possess. Catarrhine primates, the group that includes apes and Old World monkeys, are characterised by possessing routine trichromacy, as they have the short, medium and long wavelength sensitive opsin genes. It has been proposed that routine trichromacy was originated by a single gene duplication event in the last common ancestor of the group. An alternative hypothesis postulates that routine trichromacy originated in the common ancestor of anthropoid primates; however, in New World monkeys the medium wavelength sensitive opsin gene would have been removed from their genome. The aim of this study is to unravel the history of duplication of the X-linked opsin genes, in order to understand the origin of routine trichromacy in catarrhine primates. Our results do not match with any of the proposed hypotheses, and show that routine trichromacy in apes and Old World monkeys originated independently in the last common ancestors of each group, and not in the last common ancestor of catarrhines or anthropoid primates, as previously thought. Our data provide evidence that, in both groups, descendent copies of the same ancestral gene may have been independently neofunctionalised to originate the same phenotype in both lineages.

Keep Your Distance: Using Social Media to Evaluate the Risk of Disease Transmission in Gorilla Ecotourism

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Trekking with mountain gorillas (*Gorilla beringei beringei*) represents a substantial source of revenue to the areas where this subspecies occurs. However, this type of ecotourism also poses a threat to gorilla survival as disease transmission from human visitors can have disastrous effects on wild populations. Ways to mitigate this include maintaining a 7-metre distance to gorillas and wearing facemasks. We used a novel method to assess adherence to these practices by using publicly posted photographs of human-gorilla twoshots (selfies) on the online platform Instagram. We obtained 643 unique photographs and estimated human-gorilla distance, gorilla age class, sex of visitors, month of posting and trekking location. Overall, 96% of the sampled pictures showed visitors closer than the recommended 7 metres, most of which (84%) were within a critical distance of 4 metres. We recorded 20 incidents of physical contact between tourists and gorillas. Young gorillas were over represented in the sample and no effect of seasonality was found. Facemasks were only recorded in photographs from the Democratic Republic of Congo, where they are present in 65% of the photographs. Altogether, the results indicate that guidelines are not adhered to and suggest that more efforts have to be made to ensure a safer environment for both humans and gorillas during trekking holidays.

Bonobos React to Unequal Payoffs in a Token Exchange Paradigm

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Humans are typically regarded as the ultimate altruists, a species that cooperates like no other. A major aspect of the cooperative nature of humans is our sense of fairness and its aspect of inequity aversion, i.e. compare what we get relative to what others get and react to unequal outcomes. Studying our closest living relatives may help in understanding the evolution of inequity aversion. Most of the previous research focused on capuchin monkeys and chimpanzees as model species to solve fairness-related questions. However, studies focusing on our second closest living relative, bonobos (*Pan paniscus*), are scarce and often involve immature individuals. Bonobos are frequently described as being the more tolerant and egalitarian ape species when compared to chimpanzees, which would result in lower inequity aversion scores in experimental tasks. However, this tolerant and egalitarian image of bonobos has been disputed. In this study we implemented a traditional token exchange paradigm on six adult bonobos in Zoo Planckendael. Based on food preference tests, we used parsnip and grape as a low and high value reward, respectively. Individual performance and stress-related behaviours were compared between equity and inequity conditions. Preliminary results indicate that bonobos show comparable levels of aversion to inequity, i.e. refusals to return the token and refusals to accept the low value reward, when compared to chimpanzees. Unsurprisingly, sexual interactions were observed during several testing sessions, which at first sight may have altered the response to unequal payoffs. Further, different factors like relationship quality, relatedness and rank difference are taken into account to explain individual differences in responses to inequity. Our findings support the idea that the bonobo-chimpanzee dichotomy might not be so black and white, as is often suggested. This study also helps in gaining knowledge on how the response to inequity evolved.

Primate Culture and Conservation

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Evidence of social learning and culture in non-human primates and other animals has accumulated exponentially. Recognising potential implications for conservation, in 2018 UNEP invited experts in animal culture to a workshop under the auspices of the Convention on Migratory Species (CMS) to explore the opportunities that discoveries about animal culture present. The resulting 'Parma Report' is now proceeding up through several strata of UN committees for eventual consideration at the 2020 Conference of the Parties in India. To highlight these developments, the report's authors recently published a 'Policy Forum' article summarising their work and recommendations in Science (P. Brakes et al., vol. 363, March 2019). Coincidentally, in the same month, H. Kühl et al. published another article in Science reporting the erosion of chimpanzee behavioural and cultural diversity through human impacts, independently echoing core messages about culture and conservation in the Forum Policy article. This poster highlights the convergence in scope and messages of these recent high-profile articles and the emergence of the concerns they address. The two articles together propose a dozen key recommendations for linking our understanding of culture with conservation. Among these, we highlight proposals to: (i) go beyond traditional approaches focussed on species and genomes as the units for conservation, to seriously consider conserving culturally distinctive units, as illustrated in a case study of the nut-cracking culture of chimpanzees that is distinctive in West Africa but not the remainder of the species' distribution; (ii) take account of the importance of cultural knowledge in reintroduction programmes, illustrated by early massive mortality in the golden lion tamarin reintroductions, much reduced once learning from indigenous conspecifics was facilitated; and (iii) assemble databases of behavioural and cultural diversity for incorporation into IUCN and other Action Plans.

Exploring Attentional Bias Towards Threatening Faces in Chimpanzees Using the Dot Probe Task

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For primates, the ability to rapidly detect and respond to danger in their environment is essential for survival. Therefore, attentional priority is given to threatening stimuli (especially snakes and threatening faces) over neutral stimuli. The dot-probe task is a widely used experimental paradigm to investigate the mechanisms underlying attention to threatening stimuli in humans. However, few studies have been conducted in non-human primates. We investigated if the touchscreen dot-probe task can measure attentional biases towards threatening faces in eight adult chimpanzees at the Primate Research Institute, Kyoto University. On each trial, two stimuli appeared simultaneously on a screen for 150 ms, one of which was a conspecific threatening face (scream face or bared-teeth face) whilst the other was a non-threatening face (neutral face or scrambled face). The stimuli then disappeared and a black dot (probe) appeared randomly in place of either the threatening face or non-threatening face. Response times (RTs) (ms) to touch the dot were recorded. It is assumed that if attention is biased towards one stimulus

type (threatening faces or non-threatening faces), RTs to detect the dot located in the same spatial location as that stimulus type will be relatively faster. Forty-eight trials x 12 sessions were completed. We predicted faster RTs to touch the dot appearing after threatening faces than non-threatening faces. The chimpanzees were significantly faster to touch the dots replacing bared-teeth and scream faces versus scrambled faces, but not bared-teeth and scream faces versus neutral faces. Therefore, we found no evidence that the touchscreen dot-probe task can measure attentional biases specifically towards threatening faces. Methodological limitations of using the task to measure attentional biases will be discussed. The research complied with the International Primatological Society (IPS) Guidelines for the Use of Non-human Primates in Research.

Male Behaviour in Golden Monkeys (*Cercopithicus mitis kandti*) In and Out of the Mating Season in the Volcanoes National Park, Rwanda

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Most forest guenons live in polygynous groups. During the mating season, the resident adult male regularly faces reproductive competition from both solitary males and from males residing in adjacent groups. In the Volcanoes National Park (Rwanda), golden monkeys (*Cercopithecus mitis kandti*) occur in groups of 30 to over 100 individuals, larger than expected for a guenon species, and we know very little about their social system. In the first behavioural study of golden monkeys, a group of more than 100 individuals was observed for four hours a day, five days a week over a 12-month period. Data on spatial distribution, displacements and aggressive encounters were collected using focal and ad libitum observations to investigate the relationships between males that reside in the group all year and those who were present only during the mating season. We found that 11 resident males remained in the group all year and up to 24 males were observed to be in the group simultaneously during the mating season. Spatial data showed that resident males were more tolerant of each other outside the mating season. Non-contact aggression involving males within the group at any particular time, measured through aggressive chases, head bobbing and aggressive vocalisations (nasal screams), occurred more frequently during the mating season. Contact aggression (bite) between adult males was rarely observed, and only during the mating season. It is clear, therefore, that reproductive competition is evident in male golden monkeys in a similar way to other guenons during the mating season. However, the presence of several adult males during the rest of the year in golden monkeys is different from what occurs in other guenon social systems. It would seem that some aggression occurs between these resident males, but at a lower frequency and in a less intense manner than is seen when non-resident males are also present in the group during the mating season.

Characteristics of Food Items Consumed by Chimpanzees and Baboons in the Savanna Woodland of the Nguye Site, Ugalla Area, Tanzania

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We investigated food items consumed by chimpanzees (*Pan troglodytes*) and yellow/olive baboons (*Papio cynocephalus*/*Papio anubis*) in the savanna woodland of the Ugalla area, Tanzania (05°13.0′S, 30°27.5′E), by faecal analysis, together with direct and camera trap observations. We collected 465 faecal samples from chimpanzees and 196 from baboons and determined the frequency in these of each of the food items that we had identified during our previous research in the Ugalla area. Chimpanzees fed on 100 plant species (117 plant parts), three insect species, one bird species and one mammal species; baboons fed on 26 plant species (27 plant parts), two insect species and one mammal species. Among the food items, 25 species were common to baboons and chimpanzees. At the Nguye site in Ugalla, we analysed frequently consumed food items in terms of the number and total weight of fallen fruits per tree and the number of herbaceous plants per patch. The number and total weight of fallen fruits per tree were, respectively, 5–45 and 14–1,055 times larger for *Parinari curatellifolia* than for any other species. In the study area, chimpanzees and baboons are reported to forage in groups with mean size of 3.3 (range, 1–12) and 33.3, respectively. *Parinari curatellifolia*, which produces a large amount of fruit, and the herbaceous fruit of *Aframomum* spp., which grows in large patches, can provide sufficient food for large groups of primates. Compared with tropical rainforests, savanna woodlands have fewer tree species, and primates compete for food. However, while foraging, the primates are able to feed on certain plants that produce large amounts of fruit. Baboons fed on fewer food items in the study area than in other areas. This result may be due to the baboons using cheek pouches or to the small number of faecal samples, indicating a need for further research.

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