

Abstracts

Day 1 - 23rd August 2021

PLENARY

The value of long-term data in gaining insight into the dynamics of cooperative behaviour

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The occurrence of cooperation is a well-researched topic that has produced both varied and fascinating findings. However, evidence for the assumption that cooperation will occur when the benefits outweigh the costs is at times equivocal, and the ability to directly measure such costs and benefits can often be logistically challenging. Climatic extremes (such as heatwaves) can add considerable noise to biological data, making it even more difficult to understand the factors promoting cooperation. In addition, long-lived animals – a characteristic typical of many cooperative species – make it considerably challenging to assess the benefits of cooperation an individual may receive over its lifespan. After collecting continuous and detailed life history data on cooperative species for over 18 years and combining it with short-term experiments, I highlight the incredible value of long-term research to help understand (a) whether cooperation can buffer individuals from climatic variation and (c) the relationship between cooperation, conflict and cognition.

Sensitivity to audience in chimpanzee complex vocal displays

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In many social species, the presence and type of audience has a substantial effect on vocal production and the function of calls. The presence of multiple receivers entails both costs and benefits for signallers. Long-distance calls in socially risky situations such as agonistic events can be especially informative when investigating how audience composition potentially affects signal production. Although extensive work has been conducted on chimpanzee behaviour in both aggressive and affiliative contexts, little is known about how vocalisations are used during agonistic interactions, and how this relates to the composition of audience. In this study, we examine the vocal behaviour of wild male chimpanzees during displays and investigate the effect of size and composition of audience as well as other social factors on call production and structure in the Sonso community of chimpanzees (*Pan troglodytes schweinfurthii*) in Uganda. Males were more likely to call during displays in the absence of affiliated individuals and in the presence of more dominant individuals. Males were less likely to call and drum in the presence

of large numbers of females and males, respectively. Furthermore, the production of specific components of pant hoot calls (the low-pitched introduction and let-down, and the high-pitched climax) was differently affected by audience composition, dominance, age, chorusing, and directed or non-directed displays. Our results suggest that displaying individuals flexibly adjust both call production and call structure depending on features of the social context. Our study adds to the growing body of literature on the effect of audience and social factors on animal vocal production and shows that even fine structural details of a sophisticated vocal sequence, previously thought to be inflexible, can be modulated by such effects. This likely enhances the communicative capacity in species with a limited vocal repertoire such as chimpanzees.

Need and quality in parent-offspring communication in pied flycatcher broods

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In the context of parent-offspring communication, three hypotheses have been suggested to explain the nature of the information encoded by begging behavior: the Signal of Need (SoN), the Signal of Quality (SoQ) and the Signal of Hunger (SoH) hypotheses. Compared with the SoN/SoH hypotheses, the SoQ has received less empirical support given the difficulty in teasing apart cryptic and non-cryptic (e.g. chick size) components of nestling quality. In this study, we experimentally induced variations in nestling cryptic quality by supplementing pied flycatcher (*Ficedula hypoleuca*) nestlings with either an antioxidant (Vitamin E, VitE) or coconut oil vehicle (controls). We measured nestling behavior and appearance and parental feeding responses at natural nests. VitE enhanced nestling growth but had no effect on mouth coloration or begging behavior (probability of gaping, latency to beg, postural intensity and rates of changing of spatial positions), but it increased the probability that a nestling positioned itself in a favourable nest location. The main predictor of begging performance was time of food deprivation, consistent with the SoN/SoH hypothesis. Male and female parents followed different feeding rules. Males fed nestlings according to spatial location and begging latency, apparently following a time-saving, passive allocation mechanism. Females also relied on these cues, but they were also affected by an interaction between treatment and postural intensity: they favored VitE over control nestlings when both begged at high postural intensities. These results fit reasonably well with a SoN scenario where parents maximize their fitness returns by responding to nestling signals and cues conveying information about offspring prospective fitness, integrating signals of need (hunger) and nestling cryptic quality.

Gestural communication as a tool for solving conflict and cooperation problem in wild chimpanzee society

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Competition and cooperation are key aspects of social life in group living primate species. The ability to solve the problem of competition and cooperation is especially cognitively demanding and may have contributed to evolution of increasingly large brains in primates. One key and greatly under-researched aspect of how animals solve these problems of group living is the way animals communicate. Many animals, and especially chimpanzees use gestures that show a high degree of voluntary control and these signals may play an important role in maintaining and coordinating cooperative and competitive interactions between group members. In this context, social complexity is defined as the network where individuals interact with many different individuals across many different social contexts, whilst communicative complexity is defined as systems which contain a larger number of functionally distinct elements, or in which a large number of bits of information are contained within signals. However, the specific role that cognitive skills play in this complex communication, and how in turn this relates to sociality, is still unclear. This presentation will address this question and examine the types of cognitive skills involved in solving problems of competition and cooperation in wild chimpanzees.

Competitive Scent Signalling in Female Voles

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Intrasexual competition for reproductive opportunities leads to the evolution of secondary sexual signals that indicate competitive ability and individual quality. Factors influencing the evolution of such signals vary between the sexes due to different costs of reproduction for males and females. Chemical signals are widely used for competitive and reproductive signalling across taxa and have been well studied in males. However, signalling among females has been largely overlooked. Here, we investigate female scent signalling in two species of voles with typically overlapping (*Microtus agrestis*) or exclusive (*Myodes glareolus*) home ranges during the breeding season. Adult females were established in home enclosures each linked to a neighbour enclosure that housed a familiar littermate or an unfamiliar and unrelated conspecific. Investment in urinary scent marking and protein components of scents was measured before and after controlled interactions between neighbours. Female competitive behaviours and space use were measured as indicators of female competitive strategy. As predicted, female *M. agrestis* invested more in urinary scent signalling than *M. glareolus*. By contrast, female *M. glareolus* tended to spend more time in direct aggression, consistent with different female competitive strategies in the two species. We found little evidence that scent investment was directly related to individual differences in competitive behaviour, suggesting that the factors driving female competitive signalling may differ from those studied in males. Relatedness and/or familiarity between

neighbours also influenced female space use differently in the two species, with unrelated neighbours invading more among *M. agrestis* but less among *M. glareolus*. Overall our findings suggest that patterns of female signalling differ between closely related species according to competitive strategies and that competitive scent signals may function differently in females and males.

Information use in foraging flocks of songbirds - no evidence for social transmission of patch quality

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Foraging animals regularly use social information to find food, and studies across a range of taxa found that information about the location of food patches can spread through a population via social connections. However, it is not clear whether information about the quality of potential food sources is used and transmitted similarly. We studied foraging behaviour in a population of wild songbirds with known social associations, and compared the order in which birds discovered artificial patches (bird feeders) that varied in their profitability (either stocked with food, or empty) with simulations under different information transmission scenarios. If information about patch profitability spreads via social connections, we predicted that empty feeders would only be sampled by individuals that are less connected to each other than expected by chance. In contrast, we found that individuals recorded at empty feeders were more closely associated with each other than predicted by a null model simulating random arrival of individuals, mirroring pattern of increased connectedness among individuals recorded at full feeders. The observed pattern at both full and empty feeders matched predictions derived from simulated arrival under network-based diffusion of information. Thus, our results suggest that foraging songbirds only use social cues about the location of potential food sources, but not their profitability. These findings agree with the hypothesis that individuals balance the relative economic costs of using different information, where the costs of personally sampling a patch upon arrival is low relative to the cost of searching for patches. This study extends previous work on information spread through animal social networks, by suggesting important links between how individuals use information at different stages of the acquisition process and the emerging population-level patterns of patch use.

Collective behaviour and leader-follower dynamics of interspecific hunting between *Octopus cyanea* and multiple fish species

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In collective behaviour, complex coordination and individual/group decision-making can emerge from simple, localized rules of interaction, considering every individual as identical. However, in biological systems, variation amongst individuals can alter the “weight” of specific individual’s decision within a group, creating a dynamic network of attraction-repulsion forces driving individual and group movement. Parallely, sociality has the potential to drive brain evolution and cognition, but the role of individual cognition on collective movement and group decision-making constitutes a largely unexplored field. Using SCUBA, we recorded interspecific hunting events between *Octopus cyanea* and multiple partners (i.e. various fish species), and obtained animals tracks over a 3D reconstructed habitats, which enables multi-scale analyses gauging novel and key parameters in interspecific collectives, e.g. movement synchrony between *O. cyanea* and fish partners, leader-follower dynamics, habitat, social, and individual level factors influencing leadership, and presence/absence of social rules. From individuals to collective, understanding the underpinnings of these interspecific interactions can potentially deepen our knowledge on cephalopod cognition in a social context, mechanisms of intentional/unintentional communication, and the influence of higher order traits (morphological, behavioural, and cognitive) on collective movement and decision-making in naturally-occurring heterogenous groups.

Inter-group cooperation: how and why do ants share resources with other nests?

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Cooperation within groups is ubiquitous, whereas inter-group relationships are typically characterised by conflict or competition. Inter-group cooperation is very rare, but is seen in some primates, and also in certain ant species that form networks of socially connected nests. Here, each nest contains reproductives and a stable worker population, but, unusually for ants, aggression between nests is rare and resources are shared between nests, buffering against temporary local resource deficits. Wood ants are an ideal study system to investigate inter-group resource sharing, because they depend on discrete identifiable food resources (trees), and form large networks enabling tracking of resource sharing between socially connected nests. We have collected behavioural and genetic data on the social network dynamics of 13 large multi-nest networks of the wood ant *Formica lugubris* over 9 years, and manipulated resources to test the nature of inter-group cooperation. Our dynamic network analysis results show that nest survival is affected by access to resource sharing. Specifically, the flow of resources through a nest, a result of its position within the wider cooperative network, determines a nest's likelihood of

surviving. Combined with size-based nest foundation, this enables the network as a whole to track the resource environment, resulting in a network structure that is well-matched to the spatial pattern of resources. Using manipulations to prevent access to certain key resources, we show that losing an important food source causes a dramatic re-structure of cooperative networks, but without reducing growth or survival. Relatedness between nests does not predict the occurrence of resource sharing, but does predict the strength of these cooperative relationships. Taken together, these results show a dynamic social structure in which cooperation is influenced by both relatedness and the resource environment, resulting in context-specific alliances of convenience.

How feedback and feed-forward mechanisms link determinants of social dominance

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In many animal societies, individuals differ in their ability to win agonistic interactions, resulting in dominance hierarchies. These competitive differences are shaped by numerous factors, from genetically driven traits to individuals' recent interaction history. However, a general understanding of how such different factors work together to determine individuals' positions in hierarchies is still lacking. We first discuss how most research on dominance has focussed on five factors independently: intrinsic attributes, resource value asymmetry, winner-loser effects, dyadic interaction-outcome history or third-party support. We then propose that our understanding of social dominance would benefit from considering the interplay between these factors. Specifically, we propose that the outcomes of previous agonistic interactions, driven by one factor (e.g. winner-loser effects), impact factors that might be important in subsequent interactions (e.g. intrinsic attributes – for example body condition), producing feedback loops between interaction outcomes and their determinants. Considering such feedbacks allows us to generate a conceptual framework detailing how the factors affecting dominance interactions and their outcomes are intertwined. We further generalise our framework to include multi-generational processes, highlighting how dominance and its determinants may feed forward into subsequent generations via a range of parental effects. Thus, our general framework describes how interaction outcomes and the factors determining them are linked within generations via feedback loops, and between generations via feed-forward mechanisms. These feedback loops and dominance dynamics likely require novel analytical approaches and raise multiple interesting avenues for future research. Ultimately, by considering dominance interactions as part of a dynamic system, we will better understand the factors that structure dominance hierarchies in animal groups.

Does warfare promote helping in cooperative banded mongoose societies?

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Intergroup conflict has been proposed as a major force promoting the evolution of altruism in animals as diverse as insects and primates. A long-standing hypothesis is that individuals under attack from rival groups should become more altruistic towards fellow group members. Previous research has found evidence that intergroup conflict increases affiliative behaviour, like grooming, but no study has tested whether intergroup interactions affect helping behaviour in cooperative breeders – a form of cooperation with demonstrable fitness costs and benefits. Here we perform the first such test using 20 years of data on wild banded mongooses, a species that features intense intergroup fighting and conspicuous helping behaviour. Our results suggest that intergroup aggression promotes some forms of help but not others. Contributions by males to ‘escorting’, the care of pups after they emerge from the den, increased immediately following conflict with a rival group. By contrast, contributions to babysitting pups at the den remained unchanged after an intergroup fight. These different responses may reflect a fundamental difference in the fitness costs of these two forms of cooperation: babysitters take on personal risk by remaining behind at the den, whereas escorts can increase contributions to helping behaviour while enjoying the safety of the group. Our findings suggest that intergroup conflict may elevate or inhibit selection for helping, depending on the individual versus social costs of intergroup attack.

The effect of the physical environment on agonistic behaviours in the cooperatively breeding daffodil cichlid

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Group living offers significant advantages including protection from predators but may also increase competition for resources among group members. Such costs and benefits will depend upon the ecological conditions to which the group is exposed. The daffodil cichlid (*Neolamprologus pulcher*) is a cooperatively breeding fish that forms complex social groups, composed of a dominant breeding pair and up to 20 smaller subordinate fish (“helpers”). Collectively, daffodil cichlids defend small benthic territories, usually consisting of shelters excavated from sand among partially buried rocks, and they use these areas to forage, avoid predators, and reproduce. Within social groups, helpers may display submissive behaviours to avoid conflicts with dominant individuals, remain tolerated within the territory, and maintain their status in the group. However, little is known on the effect of the physical environment on agonistic behaviours in daffodil cichlids. Here, we investigated how ecological context may affect the expression of such behaviours in daffodil cichlids by manipulating, under controlled laboratory conditions, the environment in which they live. We predict that increasing the number of shelters will result in helpers displaying fewer submissive behaviours, as they may find

additional refuges to avoid aggression from dominant group members. Adding nesting sites may result in a rise in the helping behaviours among helpers, which could reduce the need for submission. Augmented territory quality may also make dominants more tolerant towards helpers, as they may need more help in maintaining their territory. Alternatively, increasing territory value may motivate helpers to retain their position within a group, as the territory would have more places to hide from predators and be more valuable upon ascension to a dominant position. Results of these experiments will contribute to our understanding of how the environment affect social behaviour in group living species.

Subordinate female baboons exhibit greater foraging specialisation

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Intraspecific variation in resource use occurs in a widespread range of taxa and often results in individuals using a particular subset of resources, termed individual foraging specialisation. This specialisation is often caused by competition between individuals, and can influence and their survival and reproduction. However, few studies have tested predictions about the causes of foraging specialisation in social, group-living species where competition is likely to be influenced by social structures such as dominance hierarchies. In this study we explored the effects of social rank and seasonality on foraging specialisation in wild chacma baboons (*Papio ursinus*) in Namibia. In particular, we tested competing hypotheses about the effects of competition which predict that more subordinate individuals should exhibit higher (optimal foraging theory) or lower (niche partitioning theory) levels of foraging specialisation. We used stable isotope analyses of 373 hair samples to estimate individual foraging niche in 40 individuals, combined with field observation of dominance interactions over six months. Subordinate baboons had smaller foraging niches – in support of the niche partitioning hypothesis – but only in females as males are predominantly high-ranking. Individual foraging niches were also smaller in the dry season when competition for food is more intense. Our study shows how, in addition to competition effects experienced by non-group living species, the competitive environment created by group-living can promote individual differences in behaviour such as foraging specialisation.

Archerfish shooting success does not vary across two group sizes, despite changes in shooting behaviour

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Group living brings competition for resources and can lead to aggressive contests or the active theft of resources by competitors. Foragers are expected to alter their behaviour to minimise the risk of competition, such as by increasing the distance between themselves and their neighbours, however, it is unclear how such changes impact the performance of hunting behaviour.

Archerfish (*Toxotes* spp.) are a good model for investigating the behavioural responses to kleptoparasitism, as their method of hunting (shooting jets of water at insects above the water) leaves them vulnerable to theft. They must successfully hit the target prey while using enough force to knock it from its position amongst vegetation, thus the prey always lands away from the shooter. Previous studies have shown that kleptoparasitism rates increase with group size and that archerfish are aware of their neighbours and alter their behaviour in the presence of conspecifics. We investigated whether group size affected shooting performance, using seven-spot archerfish *T. chatareus*. We considered a shot to be successful if a fly, placed on a transparent platform suspended above the tank was knocked into the water by a spitting fish, and modelled the probability of success in shooting down prey as a function of group size, aiming duration, nearest neighbour distance and position, and trial number. We analysed a total of 169 trials, finding that there was no effect of group size, aiming duration, or nearest neighbour distance and position on shooting success. Shooting success did increase as trials progressed, likely due to the fish becoming more familiar with the shooting task. A post-hoc analysis found that aiming duration was shorter in the larger groups, which could be a response to perceived competition. Overall, we showed that even though archerfish appear to adjust their behaviour based on the perceived threat of kleptoparasitism, these changes do not affect their shooting success.

Do ravens follow large carnivores?

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Scavengers rely on food sources often unpredictable in space and time. Some species developed kleptoparasitic strategies stealing food from predators. It remains however unclear to which extent scavengers adjust their movements to those of predators. We studied this question in common ravens (*Corvus corax*), a facultative scavenger known to frequently associate with wolves (*Canis lupus*). We tested whether ravens followed wolf packs and/or other predators like cougars (*Puma concolor*) by equipping more than 60 ravens in Yellowstone National Park with GPS-tags. We compared the GPS-tracks of the ravens with the movements of 5 wolf packs (one GPS-collared individual per pack), 11 GPS-collared cougars, as well as with their respective kill sites. We found that ravens covered areas many times larger than those of wolves or cougars. During a period of 14 months GPS-tagged ravens exploited 43% of the 201 known wolf kills and 25% of the 91 known cougar kills. For their first visit, ravens approached the kill sites on average from 15 km distance to their previous night roost, in some cases even from up to 155 km on a highly directional trajectory. Such distances are likely far beyond ravens' perception range and challenge current hypotheses for the transfer of information about the location of food sources. Surprisingly, however, the Yellowstone ravens used primarily anthropogenic food sources often 50-100 km away from their territory or trapping site. We discuss effects of anthropogenic food sources on this predator-scavenger system and how ravens might use their spatial memory for larger scales and perception as well as social information transfer on smaller scales.

Partitioning variance in a signaling trade-off under sexual selection reveals among-individual covariance in trait allocation, but no repeatable plasticity

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Understanding the evolution of traits subject to trade-offs is challenging because there are multiple levels at which traits can vary and covary, each with particular consequences for evolution. Among-individual covariation indicates consistent, possibly genetic, differences in how individuals resolve the trade-off. Within-individual covariation indicates a plastic response of the traits involved, and here things get even more complicated because there may be among-individual variation in plasticity, although these sources of variance have not all been investigated for multiple traits involved in a trade-off. We studied the sources of variance and covariance in two characteristics of an acoustic advertisement signal that are subject to an energetic trade-off and are under sexual selection in gray treefrogs, *Hyla chrysoscelis*: the number of pulses per call and call repetition rate. We recorded males on multiple nights calling spontaneously and in response to two playback stimuli simulating different levels of competition. Pulse number was significantly repeatable, but call rate was not. These two traits covaried negatively, and there was significant covariance at both the among- and within-individual level, indicating that although males were highly plastic in response to competition, some males consistently allocated more calling energy to pulse number over call rate than others. There was no evidence that the multivariate plastic response to competition was repeatable. The among-individual covariance in trait values is perpendicular to the major axis of sexual selection in this species, indicating potential limits on the response to sexual selection. However, the lack of repeatable covariance in trait plasticity indicates that males can be relatively flexible in how they allocate calling energy among these traits for short-term responses to competition, which likely weakens the strength of sexual selection for particular values of male signal characteristics.

EARLY CAREER RESEARCHER

The Visual Ecology of Cleaner Shrimp-Client Fish Mutualisms

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Cleaner shrimp clean their reef fish clients by removing ectoparasites. Although a large portion of client visits are by fish that eat crustaceans, cleaner shrimp are rarely eaten during cleaning interactions. One hypothesis for how cleaners and clients come to cooperate is that they each use visual signals to identify themselves as beneficial partners. Here, I present data on the visual systems of each party, both cleaners and clients. We used electrophysiology and behavioral assays to show that cleaner shrimp vision is both colorblind and very coarse. Client fish, however, tend to have tri- or tetra-chromatic color vision and acuity an order of magnitude

higher than that of cleaner shrimp. We applied these measures of visual capability to in situ interactions between the cleaner shrimp *Ancylomenes pedersoni* and their client fish to examine how they may appear to their mutualistic partners, and used network analysis approaches to show that certain cleaner and client behaviors function as signals. Overall, we found that signaling by both parties, but primarily the cleaner, is necessary to initiate cleaning. Lastly, I discuss how studying the signals that mediate cleaner-client interactions can help us gain insight into how these intriguing interactions remain stable over time. In particular, I discuss how the cleaner shrimp *Lysmata amboinensis* strategically adjusts its signaling and cleaning behaviors when interacting with predatory versus non-predatory clients, in a way that minimizes potential risks.

EARLY CAREER RESEARCHER

Animal contests from individuals to groups

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Animals compete over access to crucial and limited resources. Understanding what factors predict competitive success, and how animals gather and use information to make decisions during contests, can reveal how animals have evolved under the selective pressure of competition. These concepts can be studied across at least two scales of animal contests: individual animals compete in dyadic contests, and groups of social-living animals compete in intergroup contests. I discuss studies of dyadic and intergroup contests, revealing shared principles of the role contests play in organismal evolution. First, I describe how the Caribbean mantis shrimp (*Neogonodactylus bredini*) resolves dyadic conflicts safely despite using weaponized, high-speed striking appendages that produce some of the most powerful movements in biology. Through the use of a ritualized behavior—exchanging appendage strikes onto each other's armored tailplates—competing mantis shrimp communicate relative competitive ability instead of solely inflicting damage. I then extend concepts from dyadic contests like those of mantis shrimp to the intergroup case. Banded mongooses (*Mungos mungo*) live in social groups of ~20 individuals, and neighboring groups engage in often-violent contests over territory. Using data on over 20 years of contest observations, I show that groups with more male members than their rivals, and those with an older oldest male than their rivals, are more likely to win contests. The advantage of these “senior males” declines for very old males, suggesting that male competitive ability senesces. Banded mongooses care more for male than female pups and rarely evict males from the group until those males are very old, consistent with the idea that group member decisions account for the competitive benefit gained by raising and retaining male warriors. Combined, these studies at the dyadic and intergroup levels reveal how contests exert selection on animal behavior and morphology.

Day 2 - 24th August 2021

PLENARY

Cooperation, conflict and competition within the family

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Family groups arise as a consequence of parents caring for their dependent offspring after hatching or birth. Here I will provide a brief overview over our current understanding of cooperation, conflict and competition among family members, focusing on insights from recent studies on the burying beetle *Nicrophorus vespilloides*. Firstly, I will discuss the tension between cooperation and conflict between caring male and female parents. I highlight that the mechanisms that mediate the resolution of sexual conflict might be more complex than traditionally recognized, often involving multiple mechanisms such as negotiation and direct assessment of the partner's state. Secondly, I will discuss the scope for competition between caring parents, especially in systems where parents share access to a limited resource that may aid an individual's future reproduction. Finally, I will discuss recent evidence for cooperation between offspring dependent on their parents for food, which has challenged the long-held position that siblings are under selection to compete for access to resources controlled by their parents. In general, I suggest that, in order to expand our understanding of cooperation, conflict and competition between family members, we now need to extend empirical work in this field to a wider range of taxa, develop new experimental designs for detecting alternative mechanisms of cooperation, conflict resolution and competition, and use multiple experimental designs across taxa.

What explains the prevalence of male-only parental care in fish?

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Among animals with parental care, fish are unusual for the high prevalence of male-only care. In other taxa, lower investment in parental care by males than females is usually explained by sexual selection acting more strongly on males to increase re-mating rates, yet in many fish with male-only care, males are also under stronger sexual selection. Here, we seek to explain the occurrence of male-only care in fish using a phylogenetic meta-analysis to quantify the costs and benefits of paternal care across 46 teleost species. We find that, on average, offspring care imposes little cost on males in terms of loss of condition. Surprisingly, we also find a limited effect of care on offspring growth and survival. Instead, our results suggest that paternal care in fish is driven by sexual selection, with females showing a preference for mating with males in possession of a brood. In many species, fathers commonly cannibalize a proportion of their brood. Additional analyses suggest that this cannibalism represents a selfish investment in future reproduction by males, and, that by spawning with males that are already caring for broods, a female can dilute the risk that her own offspring will be eaten. In fish, therefore, investment in

offspring care does not constrain a male's mating success but rather augments it, suggesting that the relatively high prevalence of male-only care in fish may be in part explained by female preference for caring males.

Begging and feeding responses vary with relatedness and sex of provisioners in a cooperatively breeding bird

Rita Fortuna

CIBIO-InBIO

Begging behavior can provide information on offspring hunger levels and be used by parents to adjust food provisioning efforts. In cooperative breeders, helpers also provide care by feeding the young. However, how helpers of different sex and relatedness to the offspring respond to begging behavior has rarely been studied, which limits our understanding of the indirect and/or direct benefits that helpers may obtain by responding to offspring needs. Here, we used a cooperatively breeding bird, the sociable weaver (*Philetairus socius*), to investigate how inter-visit intervals of breeders and different types of helpers, distinguished by sex and relatedness, varied with acoustic begging and whether these different classes of provisioners experienced distinct levels of begging. We found that breeding males returned faster to the nest after experiencing more begging calls. However, there was no evidence for such relationship for breeding females or for helpers, independently of their sex or relatedness to the nestlings. This apparent difference in responses to begging was statistically supported when comparing breeding males and breeding females. Surprisingly, the class of helpers that included half siblings of the brood experienced more begging calls than the other classes of more related helpers and breeders. Our results show that there can be differences in how provisioners respond to increasing begging levels and suggest that the benefits and costs of adjusting feeding efforts differ with sex and life-history stage. Experimental and more detailed investigations on begging-feeding interactions in cooperatively breeding systems are necessary to understand the origin and prevalence of these differences.

Access to resources shifts the balance of cooperation and conflict between caring parents

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The evolution of biparental care has attracted much interest as it involves a complex balance between cooperation and conflict between male and female parents caring for their joint offspring. Changing environmental conditions, such as ambient temperature, predation risk and density of interspecific competitors, are thought to play a major role in driving shifts in this balance between cooperation and conflict. Here we investigate the impact of one such environmental variable – resource availability – on the balance between cooperation and conflict between caring parents in the burying beetle *Nicrophorus vespilloides*. This species breeds on the carcasses of small vertebrates, which are the sole food source for parents and offspring during

breeding. We manipulate the access to resources by providing breeding pairs with mouse carcasses from a broad range of sizes (3.65–26.15g). We then monitored subsequent effects on the duration and amount of male and female parental care, male and female food consumption and weight change during breeding, and larval traits related to offspring performance. We found that the duration of biparental care increased with carcass mass, which was mainly the result of males adjusting care to carcass mass, while females showed little response. Further, lower access to resources led to more pronounced sex differences in parental care. We also found that parents gained more weight and produced more offspring on larger carcasses. Overall our findings show that greater access to resources can shift the balance towards more cooperation between caring parents by extending the duration of biparental care.

It takes two: Evidence for cooperative parental care in the Manx shearwater

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In species where offspring care is shared between multiple individuals, coordinating parental behaviour can be an effective way to ensure investment is delivered efficiently. However, while many multi-carer species exhibit apparently coordinated care, it is often unclear to what degree this is an active behavioural process and what mechanisms may underlie it. Seabirds care for their offspring in remote breeding colonies, which are often long distances from ephemeral foraging sites. During this time, offspring may be unaccompanied for extended periods of time when their parents depart to sea to feed, leaving them vulnerable to predation and exposure. Seabirds should consequently be selected to coordinate their care with their partner to minimise the time offspring are left alone. We investigated whether and how incubation is coordinated in the Manx shearwater *Puffinus puffinus*, a biparentally caring species in which parents alternate 5-7 day shifts on the nest while the other feeds. We temporarily handicapped parents to reduce their foraging efficiency, forcing them to choose between an extended foraging trip or to return to the nest before they have fully recovered their body mass. We found that handicapped parents embarked on trips that were twice as long as normal, and that their partners compensated for this reduction in effort by continuing to incubate. We further found that the length of time the foraging bird spent at sea was mediated by the condition of its incubating partner: birds that departed the nest when their partners were in good condition spent longer at sea and returned at a higher mass than those whose partners were in poor condition. These findings support a cooperative mechanism of providing care, whereby foraging birds consider both their own and their partner's condition when deciding how long to spend at sea: spending longer away from the nest (if needed) when their partners are in good condition, and returning earlier if they are not.

Social recognition in Damaraland mole-rats

Amy Leedale, Jack Thorley & Tim Clutton-Brock

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The ability to discriminate between conspecifics functions in mate choice, kin-selected cooperation and territory defence. In mammals, olfaction plays a key role in such social interactions. Olfactory cues may be particularly important for subterranean mammals, for which visual and acoustic cues are less effective. Damaraland mole-rats *Fukomys damarensis* live in groups comprising a breeding pair and their non-breeding offspring, and independent dispersal represents the usual route to reproduction for both sexes. As yet, little is known about how dispersing individuals locate mates. Using a series of behavioural experiments, we reveal that mole-rats discriminate between unfamiliar breeding groups and solitary, non-breeders of the opposite sex using odour cues. Our experimental subjects spent more time investigating sand taken from other mole-rat groups than control sand, indicating an ability to recognize substrate-borne conspecific odours. Mole-rats also spent more time moving sand taken from the tunnels of unfamiliar, solitary animals of the opposite sex than sand taken from unfamiliar breeding groups, and removed a higher volume of this sand during the experiments. Together, these results suggest an olfactory preference for solitary, opposite-sex animals over breeding groups. Our results are supported by observations from the field that immigration into breeding groups is rare, with dispersing females typically establishing new groups, where they are subsequently joined by unfamiliar males. This study supports olfaction as a potential recognition cue which may facilitate adaptive dispersal.

Cleaners & Clowns: Cooperative and antagonistic interactions in a world of noise, bleaching and habitat degradation

Isla Keesje Davidson, Shamyi Lanjouw, Suzanne C. Mills, Ricardo Beldade, Steve Simpson, Andrew Radford

University of Bristol

Understanding how organisms are impacted by, and adapt to, the stressors they face is fundamental to predicting the global consequences of environmental change. Coral reef ecosystems can shift to alternative environmental states, and research is urgently needed to assess the resilience of reef organisms to rapidly changing environments. When experienced concurrently, multiple stressors can amplify changes in animal behaviour, influencing the likelihood of survival. Anthropogenic stressors can degrade habitats and reduce the capacity of fish to interact appropriately, affecting their ability to sense, feed, breed and survive. Here, we present new findings on the effects of motorboat noise, coral bleaching and habitat degradation on fish behaviour in both cooperative and antagonistic interspecific interactions. By exploring shifts from behavioural baselines, we investigated how the synchronicity of signals in cooperative interactions, or the balance in perception and evasion between predator and prey, are altered in the context of multiple stressors. The blue-streaked cleaner wrasse (*Labroides dimidiatus*) is an

ideal model species for understanding cooperative dynamics due to the interspecific interactions with their “clients”. We monitored behavioural changes in *L. dimidiatus* in a field-based multi-stressor context when exposed to boat noise and/or habitat degradation. On the same reefs, orange-fin anemonefish (*Amphiprion chrysopterus*) depend on symbiotic host anemones for protection, but these are increasingly subject to bleaching events. This provides an ideal model for testing how motorboat noise and bleaching can affect anti-predator behaviour. In the context of predator-prey dynamics, behavioural resilience to such stressors can have direct benefits for survival. We used model fish predators and stereo cameras in a field experiment to explore anti-predator behaviour at anemones with and without bleaching and boat noise.

Associative learning of (non-)nestmate templates in ants

Volker Nehring, Melanie Bey, Rebecca Endermann, Christina Maria Raudies

Freiburg University

Cooperation within groups depends on the ability to close off groups to outsiders. In eusocial insects, discrimination against intruders is typically based on colony-specific blends of cuticular chemicals. These are “labels” that are evaluated by e.g. guards at a nest entrance, in what is often described as a label-template-matching process. The template, some sort of neural representation of the nest-specific chemical profile, is not yet well understood. While the variation in labels typically does have a genetic component, ecological influences can change the colony label in a matter of days. Thus, the templates need to be updated regularly and cannot be genetically determined. Theoretical models for plastic template formation range from simplistic ones that propose nestmate recognition to be a mere filter in the neural periphery, to models that favour complex templates in the brain that are learned by experience. We conducted a set of experiments testing the latter hypothesis in *Lasius* ants and found that (non)-nestmate recognition templates are learned associatively, which explains much of the inter-individual variation that has been observed in nestmate recognition behaviour.

The ability to delay gratification in non-human animals: A systematic review

Claudia A.F. Wascher, Irene Susini, Alexandra Safryghin, Friederike Hillemann

Anglia Ruskin University

The ability to withhold an immediate action in pursuit of a more preferred but delayed outcome is important for adaptive decision-making and in the context of cooperation. Responses to delay in gratification have been investigated in a range of species using a variety of experimental paradigms. We here attempt a first systematic evaluation of data from non-human animals. Responses to delay of gratification tasks were analysed for 21 species, spanning across different taxonomic groups (e.g., 9 Primates, 5 Passeriformes, 3 Psittaciformes). Mean percentage of successful waiting trials ranged from 19 % in Passeriformes to 82 % in Psittaciformes. In most orders with multiple species tested under different paradigms, performance is very variable (delay choice tasks: mean $\pm$ SD = 54 ± 23 %, delay maintenance tasks: 41 ± 33 %). We conclude

that, at present, cross-species comparisons of delay of gratification abilities are hindered by a lack of consistency in experimental designs and low number of species tested across taxonomic orders. We hope to stimulate research on a more diverse set of species, and future considerations of potential social and ecological factors causing variation in test performances.

General intelligence declines with age in females but not males in a cooperative breeder

Camilla Soravia, Benjamin James Ashton & Amanda Ruth Ridley

University of Western Australia

Identifying the causes and consequences of intraspecific variation in cognitive performance is essential to understand how cognition evolves. In social species, interactions with conspecifics are hypothesised to be the main drivers of intraspecific variation in cognitive performance. Pied babblers (*Turdoides bicolor*) are cooperative breeding birds endemic to the Kalahari region in Southern Africa. Individual rank, sex, age, and social group size are major determinants of within-group interactions in this species, but it is currently unknown whether these individual attributes are associated with differences in cognitive performance. We carried out a cognitive test battery consisting of associative learning, reversal learning, inhibitory control, and spatial memory in 31 wild pied babblers belonging to 11 groups (2-7 individuals), and examined the link between cognitive performance and individual rank, sex, age, and group size. A single factor explained 58% of variation in cognitive performance across tasks, supporting the existence of general intelligence (G) in this species. G was not predicted by confounding factors such as neophobia, interval between trials, weight, and foraging efficiency. We found that G declined with age in females but not males. Female competition for breeding is frequent in pied babblers and negatively impacts female fitness, whereas the same has not been observed in males. Our finding suggests that female competition for breeding not only carries a cost in terms of reduced breeding output, but also cognitive senescence.

Complex Strategies: A comprehensive characterisation of contest behaviour

Kyriacos Kareklas, Hansjoerg P. Kunc & Gareth Arnott

Instituto Gulbenkian de Ciência

Strategic decisions during contests can be used to manage injury and energetic costs. The most common prediction is that disadvantaged contestants decide to retreat and, thus, research has almost exclusively been framed by contest outcome. However, strategic decisions are primarily the adjustment of individual phenotype with changes in contest related information, independently of outcome. This suggests that strategic decisions can be applied throughout a fight to adjust different behavioural outputs, which could address outstanding questions regarding the assessment of fighting ability and underlying motivational states. We demonstrate this in an appropriate model with a well-described behavioural repertoire, the territorial contests of male Siamese fighting fish. Our findings show that discrete behaviours during contests exhibit sequential organisation, enabling individuals to integrate information from ongoing behaviour.

Notably, this implicates progressive effects on motivational state and different types of assessment, which include information about own ability, the opponent's and their interaction. Finally, we reveal that contest phenotypes are structured by highly related behaviours in either of two components, cost mitigation (display and retreat) and fight escalation (initiation and attack tendency), which exhibit differences in their relationship to motivational state and the assessment of resources and fighting ability. This evidence reveals that strategic decisions are complex and employed throughout a contest with variable effects on behaviour, which contrasts the dominant view of fixed decisions and the use of one particular type of assessment.

PLENARY

Vervet “Thermology”: Uncovering the Hidden Costs and Benefits of Social Life

Louise Barrett

University of Lethbridge

Social relationships have been shown to have fitness-related benefits in a number of primate species, but the mechanisms by which these effects operate remains an open question. In many cases, the mechanisms are suggested to be psychosocial in nature—that is, those animals better able to navigate their social landscapes via the formation and maintenance of relationships will experience reduced levels of resource competition and stress, which then translates into higher survival and reproductive success. Here, using data from a long-term collaborative project on vervet monkey behavioural ecology and thermal physiology, I offer evidence for some ‘hidden’ physiological mechanisms that influence the costs and benefits of sociality, relating to behavioural thermoregulation, sickness behaviour and the social costs of fever, and factors that affect birth timing. These findings add extra nuance to Tinbergen’s famous characterization of ethology as “physiology without breaking the skin”. What I hope to show here is that, sometimes, knowledge of what’s going on under the skin can help sharpen our understanding of behavioural processes and give deeper insights into the ways that ecology and sociality intersect.

Day 3 - 25th August 2021

EARLY CAREER RESEARCHER

Stress and survival in vertebrates: transgenerational effects of stress, environmental context, and why it matters

Kirsty MacLeod

Lunds Universitet

Ecological stressors such as predation can shape ecosystems, driving prey population and community dynamics through indirect, non-consumptive effects that may cascade across generations through parental effects. I show that predation risk in a wild mammal (the snowshoe

hare) can have lethal inter-generational effects. I explore potential hormonal mechanisms for such effects using a different system, the eastern fence lizard, and demonstrate that short term elevations of glucocorticoid hormones at the level of a predator encounter can induce similar effects on adult survival and reproductive success. I will also discuss the importance of considering the ecological context in which maternal effects occur for determining their evolutionary importance across species and taxa.

EARLY CAREER RESEARCHER

The role of skill in animal contests: Insights from hermit crab fights

Sarah Lane

University of Plymouth

Fighting ability is traditionally viewed as a product of fixed morphological traits which offer a physical advantage, such as body size and weapon size. However, throughout a fight, individuals perform a range of repeated agonistic behaviours, and mounting evidence indicates that victory is dependent not only on physical prowess but also on the performance of these behaviours. One aspect of fighting performance which has received little attention to date, is skill, the ability to perform a challenging behaviour well. Skill has long been recognised as an important determinant of success in human sports and animal courtship, but we are only just beginning to understand the role it plays in animal contests. In this talk, I will present the results of the first major study into skill, conducted over the past three years. These results provide insights into how skill can be quantified, the influence of skill on fighting success and the underlying determinants of variation in skill.

Environmental correlates of sexual signalling in the Heteroptera

Eleanor Gourevitch & David Shuker

University of St Andrews

Sexual selection is a major evolutionary process, shaping organisms in terms of success in competition for access to mates and their gametes. The study of sexual selection has provided a rich empirical and theoretical literature addressing the ecological and evolutionary causes and consequences of competition of gametes. However, there remains a bias towards individual, species-specific studies, whilst broader, cross-species comparisons looking for wider-ranging patterns in sexual selection remain uncommon. For instance, we are still some ways from understanding why particular kinds of traits tend to evolve under sexual selection, and under what circumstances. Here we consider sexual selection in the Heteroptera, a sub-order of the Hemiptera, or true bugs. The latter is the largest of the hemimetabolous insect orders, whilst the Heteroptera itself comprises some 40,000-plus described species. We focus on four key sexual signalling modes found in the Heteroptera: chemical signals, acoustic signalling via stridulation, and vibrational (substrate) signalling, and finally tactile signalling (antennation). We compare how these modes vary across broad habitat types and provide a review of each type of signal. We

ask how we might move towards a more predictive theory of sexual selection, that links mechanisms and targets of sexual selection to various ecologies

Pheromones that correlate with reproductive success in competitive conditions

Ken Luzynski, Doris Nicolakis, Maria Adelaide Marconi, Sarah M. Zala, Jae Kwak, Dustin J. Penn

Konrad Lorenz Institute of Ethology

In a previous study on house mice (*Mus musculus musculus*) living in seminatural conditions, we found that after males acquire a territory and become socially dominant, they increase their output of urinary protein (mainly composed of major urinary proteins or MUPs), and two pheromones, *Mup20* and HMH. In this study, we tested whether these or other pheromones influence male reproductive success (RS). Over a 16-week period, we observed the behavior of mice living in large seminatural enclosures and collected urine for conducting protein and gas chromatography-mass spectrometry analyses. We conducted genetic paternity analyses on the offspring to measure RS. We found that excretion of urinary protein and HMH both correlated with male RS. Unexpectedly, high levels of urinary trimethylamine was negatively correlated with male RS. Dominant and subordinate males excreted different intensities of many urinary volatiles. Male social status was correlated with reproductive success, urinary protein excretion, and several urinary volatiles. Female reproductive success also depended upon social status but we found no urinary compounds that correlated with their RS. These findings support our previous results showing how territorial males increase the production of urinary protein and pheromones. Moreover, to our knowledge, these results provide the first evidence of male pheromones that correlate with RS in naturalistic conditions for any mammal.

Dispersal and mating system interact to determine sex differences in aggression across vertebrates

Eleanor Bath, Jonathan P Green, Jennifer C Perry, Joan Ferrier Obiol

University of Oxford

The animal kingdom teems with examples of intense intraspecific aggression. In many species, aggression is a key determinant of fitness, establishing an individual's social dominance, access to mates, food, territory, and vulnerability to predation. Although studies of aggression have focused largely on males, it is increasingly clear that female aggression is pervasive and has significant consequences for female fitness. Across species, there is remarkable variation in the extent to which aggression differs between the sexes, but to date there is little understanding of the selection pressures that give rise to this variation. We report the results of comparative analyses of sex-specific aggression across 107 vertebrate species that test key predictions from sexual selection and social evolution theory. Our results show that the intensity of sexual selection interacts with local relatedness to shape sex-specific aggression. Specifically, we find that in polygynous species, the sex that disperses further – for which local relatedness to

competitors is lower – is more likely to show greater aggression, while sex differences in dispersal have no effect in monogamous species. We also find that cross-species variation in the magnitude of sex difference in aggression is driven more by variation in female aggression than male aggression. Across species, male aggression rates varied little with mating system. However, among birds with female-biased dispersal, male aggression declined with increasing investment in paternal care, again consistent with predictions from inclusive fitness theory. For females, however, species differences in aggression were unrelated to either mating system or sociality. Together, our results demonstrate the important and interacting effects of sexual competition and relatedness in the evolution of sex-specific aggression, and raise new questions about the evolutionary forces shaping competitive strategies in females.

The reproductive consequences of female competition in a harem-breeding cichlid

Rebecca Goldberg & Jonathan Green

University of Oxford

Intrasexual competition has been studied extensively in males competing for access to females. Increasingly it is becoming evident that competition between females for breeding resources is also common. Although female success in competition can have benefits for reproduction, the expression of competitive traits may be limited by females' need to invest more in gamete production and parental care than males. Despite increasing interest in female competition, understanding of the fitness consequences of competitive investment in females remains limited. The shell dwelling cichlid *Lamprologus ocellatus* requires empty snail shells in which to spawn and guard their young. Males compete for territories with multiple shells to create a harem of females but competition between females within these harems is intense and females must invest in competitive displays to keep ownership of their shell. Using a laboratory population of *L. ocellatus*, we investigated how females respond to different competitive environments and the outcomes for reproductive success. We altered the intensity of competition experienced by females by manipulating the number of females in a harem and the distances between territories. By observing female parental behaviour and reproductive investment through multiple brood cycles, we assess the costs and benefits to females of investment into competition.

Effects of resource competition and relatedness of competitors on female social behaviour and reproductive success

Stefan Fischer, Callum Duffield, Amanda Davidson, Rhiannon Bolton, Jane Hurst, Paula Stockley

University of Veterinary Medicine Vienna

Female reproductive success is often limited by access to resources. This can lead to competition both within and between kin groups. Theory predicts that both resource availability and relatedness should influence the nature and fitness consequences of social interactions. However, testing key predictions requires differentiating the effects of these two factors. Here we achieve

this experimentally by manipulating the social environment of wild house mice, a facultative communal breeding species with known kin discrimination ability. This allows us to test if: 1) reproductive success is constrained by costs of social competition, 2) social competition leads to increased competitive signalling, 3) relatedness of competitors affects the propensity of kin to cooperate, and 4) competition between non-kin is more costly than between kin. Our results support the hypothesis that resource competition has fitness costs. Offspring weaning weights were lower when competition for nest sites was more intense, and subjects responded more strongly to simulated territory intrusions via competitive signalling. However, we found no evidence that the propensity for kin to cooperate was influenced by relatedness of rivals. Communal breeding between sisters was similarly common in groups with related and unrelated competitors. In contrast to our predictions, communal litters were smaller when breeding females competed with unrelated rivals, regardless of resource availability, indicating that competition with non-kin is more costly overall. By revealing independent effects of resource availability and relatedness of competitors on female reproductive success, our study demonstrates that: 1) resource competition is costly for breeding females, and 2) associating with kin is beneficial to avoid negative fitness consequences of competing with non-kin. These findings have broad implications for understanding the selective pressures resulting from social competition in vertebrate animals.

Calf-conspecific interactions in the Kabini Asian elephant population, southern India

Revathe T & Vidya T.N.C

Jawaharlal Nehru Centre for Advanced Scientific Research

Allomaternal care is defined as caretaking behaviours shown by individuals other than the mother towards conspecific young ones (Hrdy 1976). To check if allomaternal care exists in the study population of Asian elephants, we looked at spatial proximity and behavioural interactions between calves (? 1 year old) and conspecific females (? 5 years old). We found that calves spent most of their time near their mothers and one other female, which we call as an escort—usually 5-15 years old. The interaction rates of calves with mothers and escorts were high and were five and seven times less than that with other females in the group. A high proportion of calf interactions were feeding related and were mainly with mothers and escorts. Social interactions and resting-related interactions such as calf leaning on a conspecific, conspecifics guarding calves while calves rested, etc., were also mainly with and by mothers and escorts. The proportion of positive and negative responses shown by mothers and escorts towards calves were similar, but other females showed a higher proportion of negative and a lower proportion of positive responses towards calves than mothers and escorts. Since the nature of mother-calf and escort-calf behaviours are comparable and more positive than that between other female-calf pairs, we conclude that allomaternal care exists in the study population, but not all females show it.

Sex-differential social aging in macaques – an effect of contrasting competitive strategies?

Julia Ostner, Nadine Müller-Klein, Roger Mundry, Oliver Schülke

University of Göttingen

In adult humans, social activity decreases with increasing age, and older individuals become increasingly selective in their partner choice biasing social interactions towards more valuable partners. This socio-emotional selectivity has been attributed to the human awareness of a decreasing lifetime. Studies on nonhuman primates that lack an awareness of limited lifetime provide comparative insights into social aging. Indeed, also in nonhuman primates overall social activity and the number of social partners decline with increasing age. It remains largely unknown, however, whether this declining sociality is due a general decrease in social activity and an associated decline in network size or a selective loss of less valuable partners. Here, we asked how the frequency and duration of affiliative behaviors (close proximity, body contact, grooming) varied with age, the extent to which individuals concentrated their social interactions on a reduced number of recipients with increasing age, and how these effects varied with the sex of the dyad. We used focal animal data (3,245 focal hours) collected on 77 male and female Barbary macaques (*Macaca sylvanus*) at a free-ranging population in Germany and ranging in age from 5 to 29 years. Across a number of models, we found lifetime trajectories of social behaviour to vary with sex and behaviour. Females showed the expected pattern of an early peak in social activity followed by a steady decline, yet seemed to be less selective at old age compared to earlier life phases. Males showed strikingly different patterns, with a general lower degree of social activity, a more u-shaped pattern of body contact and grooming interactions with highest levels at young and old age, and more differentiation to preferred partners during these – young and old - life stages. While these patterns do not conclusively speak to social selectivity, they can be explained by the sex differential trajectories of reproductive strategies.

Collective defence and behavioural homogeneity during simulated territorial intrusions in banded mongooses (*Mungos mungo*).

Megan Nicholl, Patrick Green, Elizabeth Preston, Darren Croft, Faye Thompson, Michael Cant

University of Exeter

Intergroup conflicts, whereby social groups compete for limited resources, are widespread and may favour the evolution of within-group cooperation. One way in which this cooperation can be exhibited during intergroup conflicts is through collective defence. Collective defence can be exhibited by, but is not limited to, all members of one group displaying identical behaviours in response to the threat of another group. This behavioural homogeneity may increase a group's competitive ability or success, while reducing the costs associated with conflict. We tested how intergroup conflicts influence collective defence and behavioural homogeneity in banded mongooses (*Mungos mungo*) using simulated territorial intrusions. We compared the behavioural responses of groups when they were presented with three types of stimuli (scents, calls and live intruders) from a rival group to when they were presented with the same three stimuli from their

own (control) group. Consistent with collective defence, a greater proportion of group members approached and exhibited defensive behaviours in response to rival stimuli, as compared to controls. However, contrary to our prediction, groups showed fewer homogenous behaviours when presented with rival stimuli. This response was due to group members increasing their use, and diversity of, defensive behaviours. Our results show that collective defence can increase during an immediate threat of intergroup conflict. However, collective defence can be achieved without all group members needing to behave in the same way.

Collective foraging: experimentally-increased competition decreases group performance exploiting a permanently available resource

Patrícia Beltrão, Ana Cristina R. Gomes, Gonçalo C. Cardoso

CIBIO/InBIO - Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto

Foraging collectively offers advantages such as access to social information on food locations, but it may also intensify competition for local resources. Social information should be most advantageous during ecologically challenging conditions, such as when food sources are scarce or unpredictable, which predicts more collective foraging during such conditions. Alternatively, higher within-group competition when resources are scarce might destabilize social groups and reduce collective foraging. To evaluate these effects, we experimentally decreased the number and predictability of food sources (feeders with ad libitum seeds) available to common waxbills (*Estrilda astrild*) in a large open-air mesocosm. Compared to control periods, competitive aggressiveness at feeders increased in the treatment with few food sources, the social network became more fragmented, with on average weaker associations between individuals, and foraging groups became smaller. Foraging groups also spent less time per visit to the feeding area, had to make more visits to the feeding area per day, and individuals spent less time at the feeders per group visit, all of which indicate less efficient exploitation of the food sources. Several of these effects were also observed when the number of food sources was unpredictable (oscillating between normal and few), by comparison to a period with medium number of feeders. Even though the collective behaviour of waxbills appeared to exacerbate, rather than mitigate, the ecological challenges of reduced or unpredictable food sources, we suggest that, in natural conditions, this increased aggressiveness and fragmentation of the social network may function adaptively as an early trigger to explore alternative foraging locations before local food sources are severely depleted.

The consequences of stress in social groups of zebra finches

Hanja Brandl & Damien Farine

University of Konstanz/Max-Planck-Institute of Animal Behavior

What happens in social groups if some of its members are stressed? As humans, we have all experienced situations where interacting with stressed friends or observing a colleague nervously

delivering a presentation has made us feel stressed ourselves. Decades of research in humans have established that the process of stress transmission might be as evolutionarily deeply rooted as the stress response itself, but its function and consequences in animal groups remains almost completely unexplored. Zebra finches are colonial breeders with stable bonds and socially synchronized reproduction that helps them survive and breed in a harsh ecosystem. We explored how experimentally induced mid-term chronic stress affected the dynamics and performance of social groups, and how this changed with the proportion of the breeding pairs that were stressed. We found that body condition, breeding latency and movement patterns of both manipulated and unmanipulated birds were affected by the number of stressed individuals in the colony. Our study reveals a largely understudied process with the potential for severe consequences in animal groups.

New Zealand giraffe weevils of both sexes suffer increasing fitness costs from large rivals as densities increase

David Fisher, Rebecca J Le Grice & Chrissie J Painting

University of Aberdeen

Social selection occurs when traits of interaction partners influence an individual's fitness and can alter total selection strength. However, we have little idea of what factors influence social selection's strength. Further, social selection only contributes to overall selection when there is phenotypic assortment, but simultaneous estimates of social selection and phenotypic assortment are rare. Here we estimated social selection on body size in a wild population of New Zealand giraffe weevils (*Lasiornychus barbicornis*), an enormous insect (up to 9 cm long) which use their elongated heads to fight each other on tree trunks for access to mates. We then tested whether social selection varied with sex-ratio, density, and interacted with the body size of the focal individual. As densities increased social selection became more negative, and this was true for both males and females. A cost of large rivals is consistent with size-based competitive interactions for access to mates, yet why this should be equally true for females is unclear. We also estimated phenotypic assortment, and found it was always close to zero, indicating negative social selection at high densities will not impede the evolution of larger body sizes. Despite its predicted importance, social selection may only influence evolutionary change in specific contexts, leaving direct selection to drive evolutionary change.

Sexual differences in phenotypical predictors of floating status in a secondary cavity nester.

Iraida Redondo, Lorenzo Pérez-Rodríguez, Raquel Monclús, Jaime Muriel, Diego Gil

Museo Nacional de Ciencias Naturales (CSIC)

Floater are non-territorial members of a population. Their elusive behaviour makes them difficult to detect and monitor, biasing research towards territorial individuals. The scarcity of true alternative strategies in birds suggests that floating status is more likely to be a conditional strategy and floaters have been typically considered individuals of lower quality that fail to

acquire breeding resources. In this work, we used long-term monitoring data (2012-2020) from a wild colony of spotless starlings (*Sturnus unicolor*) equipped with PIT-tags since birth. Our aim was to investigate if floaters and territorial individuals facing their first reproduction differed in a suite of phenotypical and behavioural traits commonly associated with resource acquisition. We examined if body condition, ornament size and distress behaviour during handling were related to male and female breeding status. As every individual in this study was monitored since birth, we also investigated if variables of early life (nestling condition, hatching date and brood size) were associated with breeding status. We found that the likelihood of breeding was strongly influenced by body condition in males, detecting a long-term effect of early life. This association was absent for females, suggesting a strong male intrasexual selection for reproductive resources. Neither ornamentation nor behaviour predicted reproductive status in either sex. In the case of females, reproductive status was only negatively associated with hatching date. The link between body condition and reproductive status supports the hypothesis that being a floater is not an alternative reproductive strategy in this species but the “best of a bad job”, in particular for males, which have a low probability of acquiring a nest site later in life. Our study also highlights the influence of early conditions on long-term life trajectories, underlining sex-specific effects that could be relevant to understand breeding decisions.

Phenology-mediated effects of phenotype on the probability of social polygyny in a migratory passerine

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Why females engage in social polygyny remains an unresolved question in species where the resources provided by males maximize female fitness. In these systems, the ability to gain access to females, the willingness to mate with an already mated male and the benefits of this choice may be constrained by the socio-ecological factors experienced locally, with subsequent effects on the incidence of social polygyny at the population level. Here, we use a 19-year dataset from a pied flycatcher (*Ficedula hypoleuca*) population to examine through local networks of breeding pairs whether the probability of becoming socially polygynous and of mating with an already mated male (thus becoming a secondary female) is influenced by morphological traits as proxies of individual quality relative to the neighbors. Then, we examined how the breeding contexts experienced by individuals shaped the spatiotemporal separation between polygynous males' broods. The phenotypic quality of individuals, by influencing their local breeding time, mediated the probability of being involved in a polygynous event. Middle-age individuals, with large wings and, in the case of males, with conspicuous sexual traits, breed earlier than their neighbors. By breeding locally early, males increased their chances of becoming polygynous, while females reduced those of becoming secondary. Further, the probability of polygyny decreased sharply with the distance between nests. Throughout the season, there was large variation in the temporal separation between primary and secondary broods, which was, in turn, related to the breeding time of the polygamous males (first nest) relative to the neighbors. Polygynous males that bred late relative to their neighbors had a short time window to attract a

second female. We emphasize the need of accounting for the local breeding settings (ecological, social, spatial, and temporal) and the phenotypic composition of the neighbors to understand individual mating decisions.

Sexual selection shapes variation in the innate immune Toll-like receptor 3 gene in a wild passerine population

Charli Davies, Jan Komdeur, Terry Burke, Hannah Dugdale, David S. Richardson

University of East Anglia

Sexual selection can be a powerful evolutionary force shaping genetic variation. However, very few studies have investigated the role sexual selection may take in shaping variation at genes involved in the innate immune system, despite evidence that pathogen-mediated balancing selection is acting at these loci. Previous work in a bottlenecked population of Seychelles warblers (*Acrocephalus sechellensis*) indicated that viability selection is driving contemporary evolution at one non-synonymous SNP in the viral-sensing Toll-like Receptor 3 (*TLR3*) gene. Here, we investigate whether pre- and post-copulatory sexual selection is also acting at this locus. Results show that *TLR3* genotype was not related to dominance gain, or extra-pair success, but *TLR3CC* males had reduced annual within-group paternity, potentially explaining their reduced reproductive success. Secondly, we found evidence of *TLR3*-based assortative social pairing, *TLR3AA* females were more likely - and *TLR3AC* females less likely - to pair with *TLR3AA* males, although *TLR3CC* females exhibited random pairing. Third, we found evidence of inheritance bias against paternal – but not maternal - *TLR3C* haplotypes (post-copulatory mechanism). The latter two results could explain the deficiency of *TLR3AC* heterozygote offspring found in this population. Thus, both pre- and post-copulatory sexual selection, as well as naturally selection, may act to shape *TLR3* evolution in the Seychelles warbler. However, as of yet, both the phenotypic cues that could mediate *TLR3*-dependent social mate choice, and the mechanistic basis behind the paternally inherited allelic bias in offspring are unknown and warrant further investigation.

PLENARY

Rui Oliveira

ISPA - Instituto Universitário

Social interactions play a major a major role in different functional domains relevant for Darwinian fitness, such as finding food, choosing mates, or avoiding predators. Therefore, it has been assumed that they are a major selective force in the evolution of brain and cognition, putatively leading to the evolution domain-specific social traits (e.g. social learning). In our lab we combine the study of proximate causes (gene modules, hormones, neural circuits, cognitive processes) and ultimate effects (evolutionary consequences) of social behavior using zebrafish as a model organism. In the first part of this talk, I will focus on the phenotypic architecture of sociality and its evolvability in zebrafish. For this purpose, I will characterize the phenotypic

correlations among cognitive and motivational social traits and analog non-social traits, and the genetic polymorphisms (SNPs) associated with them. I will then address the evolvability of sociality in zebrafish illustrated by an artificial selection experiment (currently in the F5). In the second part of the talk, I will focus on oxytocin, which can be seen as a genetic tool kit for sociality in vertebrates. I will show how oxytocin plays a critical role in the development of sociality in zebrafish and how it interacts with the developmental environment to shape the emergence of different aspects of adult social behavior. Finally, I will show how oxytocin is necessary and sufficient for complex social behavior in adult zebrafish, including social contagion of fear and emotion recognition. Together these results support a deep homology role of oxytocin in the regulation of social behavior across vertebrates.