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### Social dynamics in a basal primate with facultative sociality

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The origins of sociality remain widely debated in both vertebrates and invertebrates. Among suggestions for advancing our understanding in this matter, the study of facultatively social species is key. We investigate social dynamics in a wild population of a facultatively social primate species, the grey mouse lemur (Microcebus murinus). In this nocturnal solitary forager, nest sharing corresponds with communal breeding, allocare and predator mobbing. We monitored sleeping associations of 250 individuals for two consecutive years in 120 nests. Preliminary analyses indicate the presence of at least three different social strategies in both males and females. Some individuals were never observed sleeping in the company of others, a second type appears to show stability in associations and a low number of partners, while a third type shows high connectivity with other third type individuals. In further analyses, we implement social network metrics to explore associations dynamics for that subset of the population showing high connectivity and flexibility in partner choice. Our study may offer a glimpse into the characteristics of initial stages of primate sociality and contribute to unravelling the mechanisms and ecological contexts that contributed to its spread and maintenance.

#### Parallel evolution of termite tunneling with differentiated behavioral rules

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Collective behaviors by grouping animals form various spatial patterns, including coordinated motion and nest structures. These patterns often vary within or among species, where a key question is how different group-level patterns emerge from individual responses and their interactions. In termites, tunneling through the soil by collective excavation has evolved several times; however little is known about the behavioral mechanisms underlying the pattern formation. Here we show convergent evolution of tunneling behaviors in termites accompanied by differentiation of behavioral rules for collective excavation. We found novel digging behavior in *Paraneotermes simplicicornis (Kalotermitidae*), who use their legs to kick back sand particles, contrasting with well-known behavior of *Reticulitermes tibialis* or *Heterotermes aureus* (*Rhinotermitidae*) who carry sand with their jaws. In spite of this variation, *P. simplicicornis* and *R. tibialis* showed less branching of tunnels, while *H. aureus* built more branched tunnels. We attribute this to the higher frequency of behavior by *H. aureus* in which they excavate side walls inside clogged tunnels, which we confirmed by data-based simulations. These results suggest that different behavioral repertoires can produce similar tunneling structures, where small modification of the behavioral parameter is important to determine the patterns. Based on these data and ongoing studies of basal species, we discuss the evolutionary process of termite collective building.

## Phenotypic behavioural variation at different hierarchical levels during rapid adaptation from fluctuating to stable environments

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Understanding phenotypic variation in the wild has been a central topic of biology since Darwin recognized it as a fundamental prerequisite for evolution by natural selection. However, explaining mechanisms responsible for within-population maintenance of phenotypic variation in fitness-related traits is still a major challenge. Much of previous work examined whether temporally and spatially fluctuating selection arising from heterogeneous environments increases phenotypic variation. The complementary perspective postulating that stabilizing selection decreases phenotypic variation when organisms adapt to homogeneous environments has received surprisingly little attention. We propose cave and surface environments as an ideal comparative model system to test this hypothesis, as variation of most environmental factors is strongly diminished in caves compared to the surface. Additionally, labile quantitative behaviours seem promising traits to investigate the evolution of phenotypic variation as they can be inspected across different hierarchical levels including the within-individual level. We applied this logic and repeatedly measured individual's behaviour in familiar (6x) and unfamiliar (2x) environments in four cave-surface population pairs representing independent cave colonisations of the freshwater crustacean Asellus aquaticus, an emerging model organism for rapid evolutionary adaptation. To control for sex and light regime induced variation, we collected 30 males and females per population and randomly assigned them into two groups that were alternatingly acclimatized to darkness and diurnal light cycle prior video-recording their behaviour in the same light conditions. Preliminary analyses suggest changes at different levels of phenotypic behavioural variation associated with cave adaptation. We expect our study will provide novel insights on an old question.

## Bet-hedging across generations can affect the evolution of variance-sensitive strategies within generations

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In order to understand how organisms cope with ongoing changes in environmental variability it is important to consider all types of adaptations to environmental uncertainty on different time-scales. Conservative bet-hedging represents a longterm genotype-level strategy that maximizes lineage geometric mean fitness in stochastic environments by decreasing individual fitness variance, despite also lowering arithmetic mean fitness. Meanwhile, variance-prone (aka risk-prone) strategies produce greater variance in short-term payoffs because this increases expected arithmetic mean fitness if the relationship between payoffs and fitness is accelerating. Using two evolutionary simulation models, we investigate whether selection for such variance-prone strategies are counteracted by selection for bethedging that works to adaptively reduce fitness variance. We predict that varianceprone strategies will be favored in scenarios with more decision events per lifetime and when fitness accumulates additively rather than multiplicatively. In our model variance-proneness evolved in fine-grained environments (with lower correlations among individuals in energetic state and/or in payoffs when choosing the variable decision), and with larger numbers of independent decision events over which resources accumulate prior to selection. In contrast, geometric fitness accumulation caused by coarser environmental grain and fewer decision events prior to selection favors conservative bet-hedging via greater variance-aversion. We discuss examples of variance-sensitive strategies in optimal foraging, migration, life histories and cooperative breeding in light of these results concerning bet-hedging. By linking disparate fields of research studying adaptations to variable environments we should be more able to understand the effects in nature of human-induced rapid environmental change.

# The role of the epigenome in plastic responses to rapidly changing social environments

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Social environments can be very dynamic and have important consequences for fitness. For example, males use social information to predict the amount of mating competition they will face and adjust investment in particular mating opportunities accordingly. To accurately match their reproductive strategy to this fluctuating environment requires plasticity that is fast acting and reversible. Whilst the role of the epigenome in responses to environmental change is becoming more understood, it has been suggested that it is not invoked in such flexible plasticity. We sought to test this using a *Drosophila melanogaster* fruit fly model. Male flies adjust their mating duration and ejaculate composition depending on the level of sperm competition signalled by exposure to rival males before mating. The behavioural component of this change occurs quickly (under 24h) and is entirely reversible. A previous transcriptome study showed that the expression of some epigenetic modifiers is sensitive to exposure to rival males. Here, we used chemical inhibitors and RNAi to test whether epigenetic remodelling is required to achieve this plastic response. We found histone deacetylation is crucial to a male's ability to plastically respond to increased sperm competition, but in a tissue specific manner. We are now investigating which loci are targeted by epigenetic remodelling in response to plasticity using ChIP-seq. Overall, this suggests epigenetic remodelling is an important mechanism in short-term, reversible plastic phenotypes, and must be considered when exploring adaptations to fluctuating environments.

#### Is there reciprocal cooperation in non-human primates?

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Reciprocal cooperation, i.e. helping those that were helpful before, is a ubiquitous and important trait of human sociality. Still, the evolutionary origin of this behaviour is largely unclear, mainly because it is believed that our closest living relatives, other primates, do not exchange help reciprocally. Consequently, reciprocity is suggested to have evolved in the human lineage only. However, recent findings challenge this view by demonstrating reciprocity in animals distantly related to us, such as rats and bats. Therefore, we systematically reviewed studies investigating reciprocity in non-human primates. Contrary to common belief, there are significantly more positive than negative findings in both experimental and observational studies. A thorough analysis of the findings showed that reciprocity is, for example, not confined to unrelated individuals, but that the choice of commodities can impact the likelihood of reciprocation. We conclude that reciprocal cooperation in non-human primates is present but largely neglected and not restricted to humans. In order to deepen our understanding of the evolutionary origins of reciprocity, future studies should investigate when and how reciprocity in non-human animals emerged and how it is maintained.

### Direct and indirect benefits as drivers of complex group structure

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Cooperative breeding, i.e. individuals helping others in their brood care, is among the most derived social behaviors. It can be explained by helpers gaining indirect fitness benefits through increasing the survival of related individuals. However, indirect fitness benefits cannot explain why unrelated individuals help others in raising offspring. Here, direct benefits are of importance. Protection from predators is such direct benefit and has been acknowledged as a major driving force of sociality. Still, how such risk related direct benefits interact with indirect fitness benefits in driving the evolution of complex cooperative societies is limited. We investigated this interplay in the cooperatively breeding cichlid *Neolamprologus pulcher*. We measured group structure, helping behavior, relatedness and reproductive success in eight populations, differing in predation risk. Group structure related to predation risk, with groups in high risk populations containing more large helpers that engage most in predator defense. In these populations the number of large helpers had a strong effect on the breeder's chance to reproduce. Microsatellite analyses revealed that the degree of within-group relatedness was generally low. Notably, smaller helpers, which invest least in defense, were more related to breeders in high risk populations. These results indicate that direct fitness benefits play a crucial role in the cooperative system of *N. pulcher*, which can be further modified by indirect fitness gains depending on the predatory environment. Our work highlights the importance to understand the interplay of direct and indirect benefits when aiming to comprehend the evolution of complex animal societies.

## Relatedness, social structure and helping behaviour in the cooperatively breeding cichlid *Neolamprologus savoryi*

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The evolutionary mechanisms underlying cooperative societies, where breeders and other individuals collaborate in raising offspring, pose an intriguing challenge. Kin selection is thought to play an important role in the development and stability of such cooperative groups, but many species exhibit a complex within-group relatedness structure, where indirect fitness benefits alone cannot explain helping behaviour. The Lake Tanganyika cichlid *Neolamprologus savoryi* has been shown to breed in cooperative harems, wherein up to four breeding females form subgroups and may be assisted by helpers. The relatedness structure of these groups is hitherto unknown, which precludes understanding of the selection mechanisms underlying apparently altruistic alloparental care. Here we present the genetic relatedness patterns of 43 groups from two populations containing 578 individuals, using 10 to 13 microsatellite DNA markers. Helpers were significantly more related to the breeding male than to the breeding female. Within subgroups, breeder to helper and helper-to-helper relatedness declined with increasing helper age. Comparison between sub-groups within a male harem revealed that helpers were more related to the breeding female they were assisting than to neighbouring females. Immigrants accounted for 16.5% of the group members, while patrilineal and matrilineal inheritance were common due to rapid breeder turnover. Interestingly, female inheritance was more likely in large than in small harems. Breeder and helper workload significantly increased with the number of young produced within the harem. Our results highlight the importance of both direct and indirect fitness benefits in a cooperative society comprising complex social and relatedness structures.

# Isotocin receptor expression and social experiences in the Trinidadian guppy (*Poecilia reticulata*)

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Across taxa individuals cooperate, paying costs so others can benefit. While research has focused on the behavioural strategies underlying the emergence and maintenance of cooperation, little is known about the proximate mechanisms underpinning it. Nonapeptides, such as oxytocin, and their associated receptors are thought to be important regulators of prosocial behaviours, including cooperation. Here, we use the Trinidadian guppy (*Poecilia reticulata*), to explore the neuroregulatory response of experiencing cooperation or defection from the social environment, by examining gene expression for the isotocin receptor (itr = homologous to the mammalian oxytocin receptor). We tested females from a High Predation (HP) and a Low Predation (LP) site of the Guanapo river on the island of Trinidad in a predator inspection paradigm, manipulating whether social partners ostensibly cooperated or defected during inspection. HP fish originate from a habitat abundant in predators and are therefore experienced in predator exposure, compared to fish originating from LP habitats. The relative expression of the itr gene in brain midsection was then quantified. We found that in HP fish exposed to a predator, ostensibly experiencing defection from the social environment led to 1.5\*10-1-fold higher itr midsection relative expression than experiencing cooperation. In the absence of a predator, ostensibly experiencing defection led to 1.3\*10-1-fold lower itr relative expression compared to cooperation. We found no difference in itr relative expression in the inexperienced population (LP). Our findings demonstrate the effects of cooperative experiences on brain nonapeptide receptor gene expression patterns, and provide insight into the neuromodulatory mechanisms underlying cooperative behaviour.

## Ant activity-rest rhythms vary with age and interaction frequencies of workers

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Social insect colonies are highly organized systems, where communication among nestmates (i.e. social interactions) has a pivotal function for colonial organization. In order to further the understanding of social organization, the chronobiological system of social insect species, particularly their circadian rhythm, has recently attracted much attention. However, gaps still remain in our understanding of how individual active/rest rhythms are governed in various social contexts. In this study, we investigate the effects of worker-worker interactions on circadian activity rhythms, using the monomorphic ant, *Diacamma sp*.

Continuous tracking of solitary ants elucidated circadian activity rhythms, both in young and old workers. The color-tag based automatic tracking of multiple workers revealed that young old interactions reduced circadian rhythmic activities in both young and old workers, whereas young workers retained active/rest rhythms under young-young worker interactions. Together with the analyses of worker-worker interaction frequencies, we conclude that interactions between workers in different age-groups (i.e. workers with different tasks) function as different cues to alter worker active/rest patterns. We discuss the potential roles of worker-worker interactions on the chronobiological organization of the ant society.

### Flapping for migrating: energy expenditure quantification

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Modern high-resolution technology allows tracking migrating birds over long distances, Depending on species, duration of displacement, environmental conditions, social organization, etc., different flock topology and flight dynamics arise. Two main flying styles are typically used: soaring/gliding and flapping flight. The former's performance has been studied in details for single birds as it is achieved with fixed wings, whose modelling relies on the aeronautic tradition. Soaring/gliding is cheap, as it harvests all the energy from upwards 'thermals'. Social implications for the flock have recently been pointed out. Nevertheless, a range of circumstances makes the choice of flapping flight a preferable or unavoidable option: absence of near thermals, size of the animal, and strict time requirements, e.g. seasonal availability of food at destination. Our current work focuses on flapping flight. In particular, we intend to unveil observed flock spatiotemporal synchronization through the quantification of the mechanical power required for flying in group - and related disparity in energy consumption between leader and follower. For this purpose, we developed a novel aerodynamic model that achieves a trade-off between computational affordability for a large number of birds and essential features of collective flapping flight: 3D motion, bird-wake interaction and unsteadiness. Stable configurations, representative of formation flight, and transient ones predicting the cost of maneuver are analysed. Where available, comparison with field-data are reported. Finally, application of our cheap computational technique in light of decision-making strategies implementation are prospected. Acknowledgements: This work has received funding from the Belgian Joint Research Activity RevealFlight.

#### Individual tracking reveals consistent headings in migrating hawkmoths

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Insects are the most diverse and abundant group of terrestrial migrants. However, in comparison to vertebrates, the migratory pathways of insects and behaviour en route are relatively poorly understood. While individual tracking can allow for insects to be monitored during migration, this technique has rarely been applied, primarily due to most insect species being too small to carry radio-transmitters. Here we present the first study to individually track nocturnal migrating insects, to identify migratory routes and understand factors affecting flight behaviour. Using a Cessna 172 aeroplane, we tracked individual hawkmoths (*Acherontia atropos, Sphingidae*), fitted with 0.25 g radio-transmitters. During tracking, all moths maintained a consistent heading, which persisted across days in some individuals. However, there was variation in headings among individuals. Furthermore, we analysed wind data to determine if moths compensated for wind drift in order to maintain consistent headings.

# Closer-to-home' strategy benefits juvenile survival in a long-distance migratory bird

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Human-induced changes in climate and environment are challenging the existence of migratory species. Species with diverse and flexible migratory behaviour suffer less from population decline, as they are more capable to response by altering migratory behaviour. At the individual-level, variations in migratory behaviour may lead to differences in fitness and subsequently influence demographic dynamics. Using lifetime GPS bio-logging data from 169 white storks (Ciconia ciconia), we answer whether their recently shortened migration has survival benefit during the juvenile stage, the riskiest life period for many migrants. We also explore how other variations in migratory decisions (i.e. time, destination), movement activity (measured by the overall body dynamic acceleration), and early life conditions influence juveniles' survival. We observed that first autumn migration was the riskiest period for juvenile white storks. Individuals that migrated shorter distances and fledged earlier experienced lower mortality risk. In addition, higher movement activity and overwintering 'closer-to-home' in Europe and North Africa (84.21% of tracked individuals adopted this new strategy) were associated with higher survival. Our study shows how quickly avian migrants can change life history decisions linked to fitness and thus helps us to understand and predict how migrants respond to the changing world.

# Seasonal contrasts in individual consistency of oriental honey buzzards' migration

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Individual consistency, or how repeatable individuals are, in migration can help us understand the mechanisms of migration. Most studies reported that birds are more consistent in the timing than in the routes or stopover sites during migration, but some specialist species showed the opposite patterns, being more consistent in spatial than temporal aspects of migration. One possible explanation for this contrast is that specialists rely on particular food or habitat resources, which restrict the migratory routes they can take, leading to high spatial consistency. If this is the case, the effect of specialist foraging should become apparent only when birds forage, instead of fasting and flying continuously. To test this effect, we analysed individual consistency in migration of the oriental honey buzzard (Pernis ptilorhynchus), a specialist raptor that feeds on honeybees and wasps, using a longterm tracking data set. As honey buzzards make extended stopovers during which they forage in spring but not in autumn, the spatial consistency should be higher in spring than in autumn. Honey buzzards were highly consistent in both their migratory routes and stopover sites in Southeast Asia, but only during spring migration. While birds showed significant repeatability in timing of migration both in autumn and spring, the seasonal difference was less conspicuous compared to that in routes. Our results highlight an important link between species' migratory consistency and foraging ecology.

# Differential use of energy available in the landscape by two soaring bird species

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Soaring birds use the energy available in the environment in the form of atmospheric uplifts, to subsidize their flight and move across the landscape. Their movement pattern is therefore shaped by the spatial and temporal availability of uplifts, resulting from an interaction of local atmospheric conditions with the underlying landscape structure. So far, the energy available in the landscape and the cost of transport of soaring birds have been related to atmospheric information only. Here we compared the accuracy of static landscape features (topography, land cover) and commonly used uplift estimators (based on atmospheric information) in predicting the flight behaviour of two obligate soaring species, the white stork *Ciconia ciconia* and the griffon vulture *Gyps fulvus*. We used soaring and flapping flight locations of 67 individuals as indicative of the presence and absence of uplifts. We found that static landscape features alone can predict and map the uplifts available to the two species across Europe. Both species strongly rely on the availability of uplifts. However, the uplift availability maps suggested speciesspecific differences in the use of the landscape and the available energy. These uplift availability maps highlight the importance of considering inter-specific differences, even in species with similar flight behaviour, when generalizing the complex relationship between environment and movement patterns. These maps provide a base to explore the effects that changes in the landscape structure have on the energy expenditure for different soaring species, allow identifying low-cost movement corridors and can ultimately inform the planning of anthropogenic developments.

### Life-long repeatability and heritability of sexual display behavior in captivebred African houbara bustards

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Between-individual variation in behaviour (i.e. personality) has been described in a wide range of animal taxa. However, personalities have been mostly investigated along a few behavioural axes, typically involving activity, exploration, boldness and sociability, while other behavioural domains have been largely neglected. Notably, despite the documented existence of discrete alternative mating strategies across several species, typically either condition-dependent or under simple Mendelian genetic control, few studies have investigated continuous individual differences in sexual behaviour and its degree of quantitative polygenic control. We therefore assessed between-individual variation in sexual behaviour, and its underlaying genetic versus environmental components, in a captive-bred population of the North African houbara bustard (*Chlamydotis undulata undulata*), a promiscuous long-lived species, wherein males display in exploded leks to attract females. Using a large sample of more than 1 000 000 behavioural observations across more than 3 000 captive males, and spanning a period of 15 years, we found long-term individual repeatability in the extent of sexual displaying in isolation and in the occurrence of precopulatory display behaviour towards a dummy female, together with individual differences in the seasonal expression of these behaviours, and agedependent individual trajectories, including variation in senescence patterns. We further highlight associations between behaviour, body size and condition. Amongindividual variation in these traits was underlaid by significant genetic components. We discuss factors that may have generated and maintained heritable variation in sexual behaviour, and the relevance of these findings for the fields of animal personality and sexual selection.

# Experimentally flight-impaired females show higher levels of extra-pair paternity in a passerine bird

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There is yet no consensus on the reasons why females engage in extra-pair copulations (EPC) and although in some species they may accrue indirect benefits, these effects are by no means common. The sexual conflict hypothesis posits that extra-pair paternity (EPP) is the result of strong selection for male pursuit of EPC without real benefits for females. In order to test this hypothesis, we experimentally reduced wing area (reversibly tying together some primary feathers), thereby increasing wing loading (body mass/wing area), which is negatively associated with flying ability and thus, with capacity to escape from unwanted copulations, in a group of pied flycatcher females (*Ficedula hypoleuca*). We compared EPP in their broods with those in a group of control females. Our results showed a significant increase in EPP in nests of the experimental treatment compared with control nests. These results suggest that in our study population, EPP could be partly a product of female capacity to avoid EPCs.

#### On the evolution of monandrous mating strategy in moths

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In most sexual breeding species females are polyandrous and thus most females mate more than once, whereas in the minority of species female are monandrous, whereby most females in the species mate once only. Males in both mating systems typically mate more than once. During mating, male moths transfer to females a spermatophore full with nutrients and two types of sperm, eupyrene, the fertilizing sperm that is produced in limited amounts, and apyrene, a none fertilizing sperm, that is produced in high numbers and is assumed to have a role in sperm competition. Testing the costs and benefits of remating in the monandrous moth *Lobesia botrana*, we applied strong selectin for polyandry, producing 70% of remating females, vs 90% of monandrous females in the wild type. After a few generations we measured the sperm content in testes of virgin and mated males and found that sons of polyandrous females have had an increased amount of the apyrene sperm and they transferred to females more of the apyrene sperm than sons of monandrous females. Searching for a cost imposed on males and females in the polyandrous line we compared fitness parameters of females and males in the two selected lines and male preference to monadrous and polyandrous females.

### The role of male-male interactions in female reproductive decisions

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Conspicuous male advertisements signals play a key role in female choice of social and copulation partners. In species where males engage in male-male interactions, females may eavesdrop on such interactions and be able to directly compare competing males with little costs. However, little is known about what kind of information females may gather about males when eavesdropping, whether females change their behaviour in the long-term in response and whether reproductive decisions based on male performance in such interactions lead to benefits for females. Here we explore the role of eavesdropping on male song interactions in a population of wild great tits (*Parus major*) combining data from a recorder array, microsatellite genotyping. We present results on the long-term spatial responses of females to male interactions and male traits that may be honestly indicated by male performance during such contests, providing new insights into the role of male song interactions for female reproductive decisions.

#### Fitness consequences of female alternative reproductive tactits in house mice

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Alternative reproductive tactics (ARTs) are defined as discrete differences in morphological, physiological and/or behavioural traits associated with reproduction, which occur within the same sex and population. House mice (*Mus musculus domesticus*) provide a rare example for ARTs in females, which can either rear their young solitarily, or together with one or several other females in a communal nest. We assessed the fitness consequences of communal and solitary breeding in a wild population to understand how the two tactics can be evolutionarily stable. Females switched between the two tactics, pointing towards them being two tactics within a single strategy. Communal breeding resulted in reduced pup survival and negatively impacted female reproductive success. Older and likely heavier females more often reared their litters solitarily, indicating that females use a condition dependent strategy. Solitary breeding seems the more successful tactic and only younger and likely less competitive females might opt for communal nursing, even at the cost of increased pup mortality. This study emphasizes the importance of analysing phenotypic plasticity and its role in cooperation in the context of female ARTs.

### Causes and consequences of baboon (*Papio ursinus*) urban-foraging in Cape Town, South Africa

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Human-induced environmental changes present both opportunities and challenges for wildlife. While many individuals, populations and species are negatively affected by change, some modify their behaviours (within their morphological and physiological constraints) and take advantage of new opportunities presented in human-changed landscapes. 'Urban-foraging' is one such behavioural modification, enabling individuals to exploit high energy, human-derived foods (e.g. crops and food-waste), but this behaviour can also result in conservation conflicts and challenges for the management of wild animal populations. In the Cape Peninsula of South Africa, chacma baboons (Papio ursinus) live in spatial overlap with humans and commonly urban-forage: 'raiding' fruiting trees, residential and commercial properties, even taking food directly from people. The City of Cape Town hires a management programme that employs field-rangers to effectively 'herd' the baboons out of the urban space. Here, we investigate the causes and consequences of urban-foraging for a baboon troop living at the urban edge. We combine behavioural data from custom-built tracking collars (for n=16 adults, recording high resolution GPS and acceleration data) with non-invasively assessed physiological stress levels and nutritional state, and information on environmental risks and rewards. We present preliminary findings based on individual trajectory data collected at 1Hz resolution over several months, and explore the factors that predict the frequency and duration of individual urban-foraging. Finally, we discuss our findings in the context of current management practices for reducing humanbaboon conflict on the Peninsula, and consider our results in understanding how urban-foraging species manage the costs and benefits of living alongside humans.

# Movement tracking reveals that parrots exploit cyclic, human-derived food opportunities in urban habitats

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For animals that partly exploit human-derived food, urban environments present a complex food landscape. This includes both geographical and temporal aspects, such as the flow of people having lunch in city parks over the weekend or provisioning from residential balconies before work. Predicting the availability of such resources in time and space represents cognitive and navigational challenges. Here, we present pioneering work that aims to uncover cognitive processes underlying the navigational and foraging decision making of sulphur-crested cockatoos (Cacatua galerita), a large social parrot that has successfully invaded or persisted in humanmodified habitats across Australia. Using over 30,000 record data from the long term citizen science project 'Wing-tags' we create a dynamic representation of cyclic food availabilities arising from recreational bird feeding in central Sydney, and match these with 2 years of high frequency GPS data collected on 8 sulphur crested cockatoos. Birds' activity daily patterns coincide with collective patterns emerging from human activities. In addition, birds show site fidelity and regular directional flights to specific locations in dense urban areas, suggesting knowledge and memory of regular, geographically specific foraging opportunities. Building on these maps, we discuss the role of cognitive processes such as memory and mental maps when navigating across urban landscapes to find food. Our work represents a novel representation of the city pulse from a human and a bird point of view, and advances our understanding of how cognition can facilitate some species to coexist and interact with humans in large cities.

#### The geometry of decision making

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From genetic and neural networks to ant colonies and wildebeest herds, collective behaviour has evolved across levels of biological complexity. In contrast to most artificial systems, decentralised control is often a signature of such systems. For animals in the natural world, survival often depends on the behavioural rules that individuals adopt and the decisions they make in response to the location of conspecifics, resources and threats in their environment. Most of the decisionmaking literature in both animal behaviour and neuroscience is limited to individuals exposed to a two-choice context. But this is not necessarily true of freely-moving animals in the wild. Individuals may encounter multiple options and rewards rely on the animal choosing the right option within reasonable time. My work elucidates how the brain breaks symmetry when faced with an n-choice decision scenario and how this links to consensus decision-making, previously described in fish schools and baboon troops. By linking decision-making at these two scales i.e. individual and group, I reveal unifying principles of decision-making in Euclidean space.

#### Plastic pollution impairs shell selection behaviour in hermit crabs

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Microplastics (plastics <5mm in diameter) present a major threat to marine biodiversity, reducing survival, fecundity, and growth rates in a range of species. However, the behavioural and cognitive impacts of plastic pollution are poorly understood. This study used shell selection behaviour in hermit crabs (Pagurus *bernhardus*) as a model system to investigate effects on cognition. We hypothesised that microplastic exposure would impair shell selection behaviour, measured as lower rates and higher latencies of contacting, investigating, and entering an optimal shell. To test this, 64 wild-caught female crabs were kept in tanks containing either 50g polyethylene microbeads (plastic treatment; n=35) or no plastic (control; n=29) for five days. Subjects were then moved into suboptimal shells, acclimated to an observation tank, and offered an optimal alternative shell. Their behaviour was subsequently recorded for 30 minutes. As predicted, fewer crabs in the plastic treatment contacted ( $\chi^2$ =7.401, p=0.007) and entered  $(\chi^2 = 5.343, p = 0.021)$  the optimal shell, compared to control animals. Contact latency was also greater for the plastic treatment (plastic median=1800s, IQR=1296-1800s, control median=948s, IQR=178-1800s, U=290, p=0.002), although there were no differences in either investigation time (plastic median=80.5s, IQR=63-218s, control median=129.5s, IQR=70-198.5s, U=97.5, p=0.401) or latency to enter the optimal shell (plastic median=634s, IQ=257.5-1503.5s, control median=565s, IQR=276.5-1213.5s, U=83, p=0.625). These results demonstrate that microplastic exposure can be detrimental to hermit crab shell selection. More research is necessary to establish whether similar effects are observed in natural environments and other species.

#### Sensory biology in ballooning spiders

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Some spiders and other wingless arthropods, such as caterpillars and spider mites, disperse aerially over hundreds of kilometres by ballooning. Technically a misnomer, ballooning involves the arthropod releasing strands of silk on which sufficient forces act to provide rapid lift and take off. Air movement from wind. thermals and their associated drag forces can generate the lift to make these animals air-borne, however an alternative hypothesis is that electrostatic forces could generate lift. Atmospheric electricity, or the atmospheric potential gradient (APG), is present at all times and varies with weather patterns; from around +120V/m on days with clear skies to up to  $\pm 10kV/m$  under storm clouds and mist. Under ecological conditions spiders and other arthropods will be subject to both air movements and electric fields provided by the APG. Here, the ability of spiders to detect and respond behaviourally to electric fields is tested. I show that spiders attempt to balloon in response to electric fields alone and I explore how wind and efields can interact to trigger ballooning behaviour. The discovery that terrestrial organisms can detect electric fields at atmospheric levels opens up an entirely new field in sensory biology, demanding the use of technology from the physical sciences to make measurements possible. Understanding how ballooning behaviour is triggered, and in which ecological conditions, will provide a new tool for understanding the distribution and abundance of arthropod species that use ballooning to disperse.

### Altruistic bet-hedging in an arid zone cooperative breeder

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Altruistic species are globally associated with arid and unpredictable environments, highlighting the importance of environmental conditions as a driver for the evolution of altruism. Recent theoretical work suggests that when the environment is unpredictable, altruistic behaviours can be selected to reduce variance in fitness rather than increases in mean fitness, as traditionally thought. This new hypothesis, so-called altruistic bet-hedging, provides a novel framework to test the mechanisms by which environmental conditions promote the appearance of altruism. However, the predictions of altruistic bet-hedging theory have not been explicitly tested yet. In this talk we outline our research showing that environmental and cooperative factors in white-browed sparrow weaver societies have effects on reproductive success that closely match those predicted by altruistic bet-hedging theory. We find that the presence of (female) helpers reduces variance in reproductive success but not its mean. Furthermore, we explicitly show that these differences in reproductive success are in part explained by how the presence of female helpers interacts with environmental conditions. Our results provide rare evidence suggesting that altruistic bet-hedging may explain cooperation in an arid zone bird. Furthermore, our findings reveal hidden costs of cooperation and highlight that the expected overall effect of cooperation on reproductive success will depend on the relative frequency of different environmental conditions. Variation in the relative frequency of environmental conditions due to geographical factors or climate change is expected to modify the extent to which selection for cooperation arises from effects on the mean or variance.

### Behavioural traits that define social dominance are the same that reduce social influence

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The traits that define social dominance in many societies – aggression, coercion, and influence over group decisions – may be the very traits that reduce influence in other contexts. Here we examine the behavior and influence of dominant and subordinate male cichlid fish in different contexts. We find that under standard social conditions, dominant males are the most aggressive group members and concomitantly have the greatest influence over group behavior. However, in a more complex group scenario - responding to a simple association task - dominant males have the weakest influence over group behavior. Instead subordinate males, with low aggression and little influence over typical group behavior, have the greatest influence over their groups in the context of the association task. Although subordinate males had little behavioral connection with other group members, they were highly connected both spatially and visually - likely important types of connection when responding to a visual task. Moreover, the behavioral stimuli that caused group movements had different signal-to-noise ratios for dominant and subordinate males. Response to the association task was characterized by a rapid, directional swim toward the light cue, which was kinematically different from normal swimming, but similar to the aversive chasing frequently displayed by dominant males. In contrast, subordinate males only displayed this behavior in the association task. We conclude that it was the very behaviors that made dominant males influential in one context that caused them to lack influence in another.

#### Epigenetics and environmental change: adaptation versus constraint

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If organisms are to persist in the face of climate change, they must be able to deal not only with increasing temperatures, but also greater climatic variation. One of the primary ways animals cope with environmental change is through phenotypic plasticity, the ability to respond to environmental cues through phenotypic adjustment. For many animals, plasticity during development can influence behaviour and fitness later in life, both positively (adaptation) and negatively (constraint). Using superb starlings (Lamprotornis superbus), which inhabit a range of East African environments where rainfall varies within and among years, I will explore the molecular mechanisms that underlie plasticity in the genome in the form of epigenetic change. Specifically, I will examine how patterns of DNA methylation across the starling genome vary with rainfall during development, discussing genes that show signatures of adaptive capacity versus those that instead show signatures of being constrained by early life conditions. I will then compare patterns of DNA methylation across the genome from birds collected along an ecological gradient spanning hundreds of kilometers that varies in the degree of rainfall variability and predictability. Together, these two studies will not only illustrate the different ways that environmental conditions shape patterns of DNA methylation across the genome, but they will enable me to develop an evolutionary framework for integrating ideas of adaptation and constraint in the context of climate change and behavioural epigenetics.

# Transgenerational effects of simple and complex environments on behaviour in zebrafish

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Phenotypic plasticity is a fundamental mechanism by which organisms can adapt to cope with environmental change, such plasticity represents a short-term mechanism of adaptation within the lifetime of an individual. However, recent evidence suggests that the inheritance of acquired traits via epigenetic mechanisms may also represent a mechanism for adaptation to certain environments over multiple generations. There are many outstanding questions regarding the adaptive relevance of these mechanisms, the environmental contexts under which this type of inheritance may occur, the persistence of such effects and how common they are. We examined the inheritance of acquired behavioural traits using a combination of environmental manipulations and automated animal tracking with Danio rerio. Adult male zebrafish were exposed to simple or complex physical environments and their behaviour was quantified using automated video tracking and custom analysis scripts. Males of both groups were then bred with separate unmanipulated females, and behaviour of the F1 offspring was quantified both as larvae and as adults. Social behaviour, activity and anxiety-like behaviour were all influenced by the environment in the parents, but we also found evidence for transmission of behaviour to F1 offspring. We then repeated the manipulation again using males from this F1 offspring cohort and examined the inheritance of traits in F2 offspring with varying parental and/or grand-parental environmental experience. These results suggest that paternal environmental experience can be inherited nongenetically in zebrafish, affecting behaviour in subsequent generations.

### Adaptive motor control: Slope-dependent modulation of muscle cocontraction in freely walking stick insects

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Terrestrial locomotion in a variable and unpredictable environment requires animals to adjust their limb movements appropriately. For example, the ability to cope with disturbances like changes in substrate slope is crucial for locomotion at intended speed and direction. Negotiating inclines is particularly interesting as it is associated with changes in load distribution across the body. Flexibility in motor control is thought to be achieved by either utilizing distinct motor patterns, or by closed-loop control through sensory feedback. Mammals, for example, adjust their motor output in anticipation of an incline and use functionally distinct transition strides between level and slope walking (Gottschall and Nichols, 2011). So far, slope-dependent changes in insects have been studied mainly under steady-state conditions, thus neglecting the dynamics of adaptation in response to changes in load distribution. Here, we investigated how freely walking stick insects (Carausius *morosus*) mastered a step change in walkway slope (±45°). For this, we simultaneously recorded their whole-body kinematics and hind leg muscle activity. We moreover used a simplified mechanical model to estimate the varying mechanical demand due to slope transitions. Our results suggest that these transitions involve only little kinematic adjustments, but a considerable reduction in muscle co-contraction associated with shifts in how ground reaction forces distribute. Since the observed changes occurred gradually with each subsequent leg stepping onto the incline, we conclude that stick insect motor adaptation to inclines is achieved reflexively and continuously, depending on the ongoing load sensory feedback, rather than through switching between pre-wired distinct motor programs.

### Dynamical network formation of C. elegans

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Understanding physical rules underlying collective motions requires perturbation of controllable parameters in self-propelled particles. However, controlling parameters in animals is generally not easy, which makes physical rules underlying animals' collective behaviors elusive. Here, we find that a conventional model animal, *C. elegans*, collectively forms dynamical networks of bundle-shaped aggregates with simple physical rules. We investigate the dependence of the *C. elegans* network formation on various extrinsic parameters (material of substrate, ambient humidity and density of worms). Taking advantage of well-established *C. elegans* genetics, we also control intrinsic parameters (genetically determined motility) by mutations and by forced neural activation via optogenetics. Furthermore, we develop a minimal agent-based model that reproduces the dynamical network formation and its dependence on the parameters, suggesting that the key factors are alignment of worms after collision and smooth turning. Our findings imply that the concepts of active matter physics may help us to understand biological functions of animal groups.

Ref, Sugi\* et al. Nature Commun, 2019; Sugi\* et al. PNAS, 2014; Sugi et al. Nature Neurosci, 2011

#### Bats adjust their mouth-gape to rapidly narrow their acoustic 'field of view'

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Echolocating bats are renowned for their ability to control the sensory information that they acquire. By rapidly changing their echolocation signal design and timing, bats can adjust the rate and accuracy which they acquire information about the environment. Much less is understood about bats' ability to control the spatial aspects of their emission, that is their ability to control the sector of space which they scan using a single emission (beam forming). We used a large (wideband) microphone array and a high-end tracking system to reconstruct high resolution beams and mouth movements of *Pipistrellus kuhlii* bats as they were searching for and landing on a target in a large flight room. We show that bats rapidly narrow their bio-sonar field of view when scanning a target. On-target horizontal sonarbeams were  $\sim$ 23 degrees narrower than off-target beams. By directly measuring bats' mouth-gape, we found that this beam adjustment was mediated by changes in the mouth gape: bats opened their mouth to narrow the beam and vice versa. Acoustic simulations confirmed these results and also suggested that the bats narrowed the vertical beam-width by  $\sim$  50 degrees. The bats used the same sensory strategy in the presence of loud masking noise implying that beam adjustments are not used for dealing with noise. The function of the narrowing of the beam was probably to improve signal-to-noise-ratio which increased by at least 60%. The narrowing of the beam-width could also play a role in improving spatial localization.

# Neural mechanisms of simple grouping behaviour: nonapeptide regulation of shoaling in fish

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The nonapeptides are a highly conserved family of neuropeptide hormones that have been repeatedly shown to regulate social behaviours across vertebrate taxa. In mammals the nonapeptides oxytocin and vasopressin have been shown to play key roles in complex behaviours such as pair bonding, social recognition, parental behaviour etc. However simple grouping behaviour is often difficult to study in many mammals, and recent research in other taxa has started to explore the role of nonapeptides in grouping behaviour. We have examined the role of nonapeptides in shoaling behaviour in different fish species and populations, using behavioural, pharmacological and neurobiological approaches to investigate how the teleost nonapeptides isotocin and vasotocin influence shoaling behaviour. In guppies, we have shown that administration of isotocin increases shoaling tendency, while vasotocin reduces it. We have shown that increases in shoaling tendency seen in predator-exposed guppies are associated with changes in vasotocin signalling and sensitivity. In zebrafish, we have found that increased environmental complexity leads to increased shoaling tendencies within a few weeks, and that this behavioural shift is associated with increased isotocin neuron numbers, specifically in the magnocellular portion of the pre-optic area. Unlike in mammals, behavioural phenotypes in fish seem to be associated with changes in nonapeptide signalling, rather than nonapeptide receptor distribution. This work indicates that the role of nonapeptides in social behaviour is conserved across vertebrates, but with important mechanistic differences between taxa, and that nonapeptide signalling plays a critical role in simple grouping behaviour in vertebrates, as well as complex social behaviour.

#### Escape from threat in the presence of obstacles

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Having a functional understanding of the world is fundamental for choosing and executing adaptive actions. It is not known how the mammalian brain builds and represents this understanding. Here we address this problem by studying a set of ethological actions that rely on knowledge that animals have about their spatial environment. Using new behavioural paradigms, we investigate the strategies that mice use to escape from imminent threats when there are obstacles on the way to their shelter. We find a hierarchy of strategies, in which mice first follow innate navigational rules that lead to suboptimal escape paths. Next, they learn from the spatial statistics of these inefficient escapes: in subsequent trials, they run directly to an intermediate goal that provides access to the shelter, such as an edge of the obstacle. At this stage, previously taken escape paths are also converted to memorized trajectories; when the environment changes acutely, there is a balance between exploiting these known routes and finding new, efficient paths to the shelter. These results identify strategies that mice use to select escape routes based on an understanding of their surroundings, and they provide a starting point for investigating how the brain uses internal models of the world during natural behaviours.

#### Inter-group dispersal in Vulturine guineafowl

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Dispersal is one of the primary drivers of population dynamics, connectivity, and gene flow. For social species, dispersal behaviors are not only dependent on the physical properties of their environment, but also on the social landscape. Many species use social information (e.g. conspecific densities) to decide when to depart and where to settle, possibly as an indicator of underlying habitat quality or to avoid competition. However, for group-living species, the underlying habitat is likely less important to dispersers than the distribution and social structure of groups. How do subadults disperse through the social landscape? For example, individuals who are part of more cohesive social groups, or who receive more affiliative interactions are less likely to disperse. Similarly, more cohesive social groups may be more resistant to the immigration of new individuals, thus affecting settlement. The Vulturine guineafowl (Acryllium vulturinum) is a highly-gregarious bird species which lives in highly-cohesive groups. Using a 2-year dataset comprising over 800 individuals spanning 18 groups that are permanently tracked using GPS tags, I quantify how inter-individual interactions, and the history and dynamics of interactions among groups, predict which individuals disperse and where they disperse to. These unique data provide some of the first insights into both the large-scale movements of individuals across social landscapes and the fine-scale social that dictates the decisions that individuals make.

#### Individual information access resulting from fine-scale movement decisions

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Animals must constantly make decisions that affect their fitness (e.g. where to go, what to eat, when to be vigilant). In order to make beneficial decisions, they must collect and integrate information and from their physical surroundings and social partners. In complex natural environments an animal's fine-scale behavior can strongly influence its access to such information. To study this, we used drones to film free-ranging zebra herds in Kenya and create 3D models of the surrounding environment. Using novel analytical methods, we extracted movement and behavioral data from these videos, and reconstructed individuals' visual fields. Here we present the results of our analyses, in which we explore how individuals' fine-scale movement and behavioral decisions affect their visual access to social and environmental information. By comparing observed paths to randomized and optimized paths, we explore the extent to which individuals prioritize visual information access as they move through complex habitats. We also consider the implications of individual strategies for group-level phenomena such as collective detection and information transfer.

### The influence of social relationships on leader-follower decisions in highly dynamic bird flocks

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In group-living animals, pre-existing social relationships can underlie leaderfollower decisions. Primates that live in stable groups, for instance, tend to follow their preferred affiliates during collective movements. However, such highly stable groups are relatively rare in nature; it remains therefore unclear whether such leader-follower decision rules could also take place in more fluid social systems. Here, we investigate the extent to which social relationships predict leader-follower events in collective movements of colonial birds that form fission-fusion flocks. We used a high-resolution system to track 6 flocks of 28 captive zebra finches (*Taeniopygia guttata*), using the precise record of their locations over time to calculate their social association strengths with others (i.e. their social networks) and their fine-scale movements over time (i.e. leader-follower events). Then we used generalized linear models to relate previous social associations with current leader-follower events during collective movements. Our results indicate that the probability to follow an individual is positively correlated with social association strength and negatively correlated with the distance between leader and follower prior to the movement taking place. These findings corroborate predictions of selforganizing collective movement in which individuals tend to react to their nearby conspecifics; but they also highlight that even in fluid social systems individuals can have a higher probability to follow those that they are more strongly associated with. Our study suggests that the 'follow-a-friend' rule can be detected not only in species that live in stable groups but also in more dynamic social systems.

## The evolution of menopause in resident killer whales (and other interesting animals)

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Why females of some species cease ovulation before the end of their natural lifespan is a longstanding puzzle in life-history evolution. In humans, as well as some natural populations of toothed whales, reproductive aging occurs much faster than somatic aging and females exhibit prolonged post-reproductive lifespans (PRLSs). Determining the mechanisms and functions that underpin PRLSs has proved a significant challenge. Here I summarise our work, bring together both classic and modern hypotheses proposed to explain PRLSs and life-history evolution and discuss their application with particular reference to our studies of killer whales. In doing so I highlight the need to consider multiple interacting explanations for the evolution of PRLSs and discuss the key role of social structure.

#### Movement patterns and leadership in a multilevel social group

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Patterns in animal movement arise from interactions between moving individuals, and hence are modulated by social relations within the group. Thus, the spatial distribution and movement patterns of individuals often reflect the structure of the society the animals are living in. The occurring particular movement patterns may also influence the dynamics of leading within the group. To investigate the relationship between movement patterns and leadership, we observed the collective motion of free-ranging Przewalski horses in Hortobágy National Park, Hungary. These horses are especially suitable to such a study because in this reserve they live in a complex multilevel society: harems unite in a large herd. In this study we used novel methods, since we need the continuous and simultaneous position data at high frequency for wild animals in natural environment. Our observational method is based on aerial videos of two drones, one provides high resolution motion data for all animals in the herd, while the other ensures individual recognition. In this way, we collected trajectory data regarding the daily movements of around 250 individuals at the same time, while knowing the identity of all of them. Using the data generated from the aerial footage, we are studying the motion patterns and leadership dynamics inside the harems and inside the whole herd. Since all the horses are recognised and their life- and harem history was recorded regularly for the past 20 years, motion data can be related to many individual and group characteristics.

# Conflicts of interest and collective decision-making in white-faced capuchins (*Cebus capucinus*)

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How do groups of individuals decide where to go and what to do? To obtain the benefits of sociality, animal groups must remain cohesive, reaching consensus and coordinating important daily activities like foraging. However, foraging strategies of individual group members often vary, creating conflicts of interest about foraging choices. When conflicts of interest about when and where to feed exist in a group, some individuals must compromise their preferred behavior, presumably at a cost to themselves. This study extends the marginal value theorem to individuals living in stable social groups to generate predictions about the mechanisms underpinning how groups reach consensus. Using a six-month study of two white-faced capuchin monkey groups (*Cebus capucinus*) on Barro Colorado Island, Panama, we examine individual differences in optimal patch departure time and how these translate into collective decisions. We test the hypothesis that dominance, size, and age impact how long individuals prefer to remain in a foraging tree, creating conflicts of interest over when to leave. Using the focal tree method on group feedings in Attalea butyracea palms, we calculate exact individual feeding rates for all group members in each palm. These feeding rates generate individual foraging gain curves that predict optimal departure times. We further analyze individual attempts to initiate group movement to understand who exerts influence on group decisions. Results indicate individuals differ in their preferred departure times and group decisions are shared between adults. Together, this captures important elements of group decision-making in social primates: when to go and who decides.

### Drones and Deep Learning Reveal Visually-mediated Collective Decision Making in the Wild

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We use video recording drones and custom built computer vision algorithms to not only automatically record the location of all individuals in ungulate herds in the wild but also detect nine body key-points, things like front of the head, shoulders, and tail, for all individuals in the group. We then embed this information in finescale georeferenced 3D landscape maps with centimeter level precision. We study herds of plains zebra, Grevy's zebra, impala, and african buffalo in central Kenya. Using a relay of drones we record herds for up to an hour during which time we observe the animals in an undisturbed state and then purposely walk toward them on foot to create a disturbance they detect and respond to. Afterwards we use an additional drone to create 3D maps of the exact area the animals moved through (sometimes over more than a square kilometer) with pixel resolution of a few centimeters. Since we know each individuals location, head position and direction, and their exact position within the environment, we study the role visual communication plays in group decision making in complex environments under heavy predation risk and observe individuals' strategies for optimizing the acquisition of both social and environmental information while also effectively foraging and remaining safe from predation.

#### Energy saving in fish school

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Movement through fluids imposes steep energetic costs on organisms that swim, glide, and fly. It has long been proposed that group-living species minimise these costs through collective coordination, but while this appears to be true for flocking birds, there is little evidence that schooling fish coordinate their movement to save energy when swimming. In addition to scarce direct evidence, we also lack a biologically-plausible theory to describe how fish should behave when obtaining hydrodynamic benefits from others. Most models of collective energy savings are overly simplistic or make restrictive, unrealistic assumptions about spatial positions, which tend to be highly dynamic in real groups. Consequently, despite an abundance of predictions that energy saving is possible, we have yet to reconcile existing theory with natural behaviour. To address these problems, we employ an integrative experimental and theoretical approach. First, we use a physical model of fish-like robots to derive a new, foundational theory of hydrodynamic interactions that generalises to any group structure. Our model reveals that regardless of the specific spatial arrangement, fish can obtain energetic benefits from a leading neighbour by adjusting their swimming pattern using a simple, linear relationship. We further conduct experiments with pairs of freely-swimming goldfish (Carassius *auratus*) and find that this species engages in the same dynamical vortex phase matching predicted by our theory to save energy. Our results offer important insights into the ecology of schooling fish, and our theoretical model could be readily applied to the development of efficient underwater autonomous vehicles.

#### Deep attention networks reveal the rules of collective motion in zebrafish

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A variety of simple models has been proposed to understand the collective motion of animals. Simple models can be insightful but lack important elements necessary to predict the motion of each individual in the collective. Adding more detail increases predictability but can make models too complex to be insightful. Here we report how the modular structure of deep attention networks can obtain a model of collective behavior that is simultaneously predictive and insightful. Our model describes zebrafish pairwise interactions, *Danio rerio*, as approximately repulsive, attractive or as alignment, but only when moving slowly. At high velocities, interactions correspond only to alignment or alignment mixed with repulsion at close distances. The model captures aggregation of information from different neighbours as a weighted average. Weights are higher for neighbours that are close, in a collision path or moving faster in frontal and lateral locations. These weights effectively select a dynamical number of neighbours, from a single one to up to 12, often changing in less than a second. By fitting the model to groups of fish of different ages, we explored the ontogeny of collective behaviour. Prediction accuracies are higher for older fish. Interaction maps show stronger attraction and orientation in older fish, with smoother attention maps. We also explored the effect of group size and habituation to the environment on the rules of collective behaviour.

# idtracker.ai: tracking all individuals in small or large collectives of unmarked animals

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Understanding of animal collectives is limited by the ability to track each individual. Determining animal trajectories from video recordings faces the problem of maintaining correct animal identifications after individuals touch, cross or are occluded by environmental features. We present idtracker.ai, an algorithm and software that extracts all trajectories from video, with high identification accuracy for collectives of up to 100 individuals. First, a species-agnostic preprocessing extracts images from the video. Then, a first convolutional network detects when animals touch or cross, and a second convolutional network identifies the animals along the video. Training examples for both networks are safely extracted using a set of heuristics without humans in the loop. A training and identification protocol adapts to the conditions of the video and tracking difficulty. Post-processing steps are applied to ensure the continuity of the trajectories. Thanks to the transfer learning capacities of the convolutional networks, idtracker.ai can be used in different ways to match animal identities across videos. The modularity of this open-source and free software tracking system allows researchers to use it and adapt it to their needs. In particular, we show how we use idtracker.ai and a predictive model based on deep attention networks to study information transfer across individuals in groups of juvenile zebrafish.

#### Individual identification using deep learning in wild birds

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Individual identification is essential to most animal studies in ecology, evolution and conservation. To date, this has been achieved mostly through methods relying on marking individuals (e.g. colour rings) and using human observers for data acquisition. While presenting several advantages, these methods can be time consuming and labour-intensive, thereby hampering high rates of data collection. Recent technological and analytical advances, such as RFID and deep learning can help to overcome these limitations by automatizing data collection and analysis. Here, we present a method based on photos that allows the individual identification and behavioural study of a small passerine bird, the sociable weaver, *Philetairus* socius. First, we describe an automated method (based on RFID) for efficient collection of large samples of individually labelled images of birds in the wild, which are required for training convolutional neural networks (CNNs). Second, we go through the process of training a CNN to build an accurate classifier of the focal individuals. Finally, we test the generalization capability of our models by predicting the identity of the birds from images that were collected with different cameras and in different contexts from the ones originally used for training the CNNs. We show that it is possible to identify birds with >90% accuracy, even when the conditions of the training datasets differ from the images to which the classifier can potentially be applied. These results provide a practical solution for collecting large training datasets and illustrate the potential use of CNN for individual identification in wild populations.

#### 3D-tracking collective escape in wild groups of Damselfish

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In animal collectives, it might only take one or a few individuals to detect a threat in order to trigger a collective escape at the level of the group. For animals living in hierarchically-structured groups, it remains unclear whether, and how, dominance relationships shape the way information spreads. I will present how we investigated the impact of social hierarchy on collective sensing in socially-structured groups of damselfish *Dascyllus marginatus*. In the field, we experimentally triggered collective escape responses using a loom stimulus projected on an iPad. This allowed us to create situations where a limited number of individuals had direct access to the information. Using multiple cameras, we tracked in 3D the movements of all group members during these experimentally-induced collective escapes. In order to disentangle between private and social access to information, we then computed the visual connections between all the individuals and the loom stimulus. I will discuss whether the number and the social status of the initiator(s) affect the speed at which information spreads within the group, and the intensity of the escape response in the other individuals.

### All you need is statistical physics? Group- vs. Individual-Optimization against Predator Attacks

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Animal collectives can be framed as an ensemble of agents following identical rules modeled as social forces. This framing is also common in statistical physics, which suggests that general principles from statistical physics also hold for the description of animal collectives.

One of the most prominent ones is that a system at a transition from an ordered to an unordered state has the strongest response to an external global field. Based on this concept of maximal response at the transition it was conjectured that natural systems should evolve to this transition ('criticality'), i.e. represent examples of selforganized critical systems.

Here we investigate the validity of this concept using an individual-based model for a collective of agents being attacked by a single predator with different attack schemes. We find that under group-level optimization the order-transition is favored. However, not improved reaction but spatial structure is the main driver. On the other hand, under individual-level optimization, i.e. natural evolution like optimization, the collective is not showing self-organized criticality but rather evolves into the ordered phase away from the transition. The main cause of this trend in evolution is the spatial self-sorting of agents according to their parameters.

Our work shows how difficult it is to translate concepts from statistical physics to heterogeneous and spatially explicit biological systems. However, we also emphasize how important and fruitful the feedback between the two disciplines can be.

## La Olá' waves of the sulphur molly: adaptive anti-predator behavior of an extremophile fish

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The ability to detect and react towards a potential predator is crucial for animals as failure to respond is usually fatal. However, anti-predator responses often come at a cost and reactions while no or only inactive predators are present will reduce the prey's overall fitness. In Mexico, sulphide-rich and severely hypoxic springs are colonized by the endemic sulphur molly (*Poecilia sulphuraria*). To cope with these physicochemical stresses, sulphur mollies perform aquatic surface respiration, resulting in the build-up of large aggregations directly at the water surface, where they are particularly vulnerable to avian predation. Following a bird attack, fish schools produce a series of synchronized collective waves by repeatedly diving down in a cascade-like manner. As diving into the hypoxic water column is costly, fish may have evolved mechanisms to distinguish between potential threats and harmless environmental disturbances such as flyovers of non-predatory birds. We found that only specialized piscivores like kingfishers and egrets produce largescale, repeated collective responses of the sulphur mollies. In a laboratory experiment, we presented fish with artificial disturbance cues and found that bimodal stimulations consisting of a combined visual and acoustic cue induced significantly stronger escape behaviors than either cue alone. Most piscivorous birds produce both visual and acoustic cues during their hunting, while most nondangerous disturbances are only associated with a single cue. Thus, we assume that sulphur mollies use predator-specific cue sets to distinguish dangerous from nondangerous disturbances and react only to the latter.

## Anti-predator costs and benefits of leadership: experimental evidence using virtual prey attacked by real predators

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The major cost of leadership in moving animal groups has long been assumed to be predation, with individuals leading from the front of groups being targeted more often by predators. Nevertheless, empirical evidence for this is limited and experimental tests are entirely lacking. To avoid confounding effects associated with observational studies, we presented a simulation of virtual prey to real fish predators to directly assess the predation cost of leadership. Prey leading others are at greater risk than those in the middle of groups, confirming that any benefits of leading may be offset by predation costs. Importantly, however, followers confer a net safety benefit to leaders, as prey leading others were less likely to be attacked compared to solitary prey. We also find that the predators preferentially attacked when solitary individuals were more frequent, but this effect was relatively weak compared to the preference for attacking solitary prey during an attack. Our results suggest that goal-orientated individuals, i.e. potential leaders, are under selective pressure to maintain group cohesion, favouring effective leadership rather than group fragmentation.

### When and how: temporal patterns, defensive behaviours and adaptive benefits associated to male parental care in the glassfrog *Centrolene savagei*

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Recording information about adaptive benefits and variation of parental investment in glassfrogs, is important for a better understanding of the evolutionary behavioral ecology in anurans. In this study, we recorded variations in parental investment by males of the glassfrog *Centrolene savagei* at two temporal scales; and we performed field experiments to simulate risks of predation by small invertebrates, to test the level of aggression of males caring eggs. Between February 2016 and November 2018, we monitored 87 males and 154 egg clutches in a population of *C. savagei* in the Central Andes of Colombia. Parental investment was higher at night than at noon, and it decrease as embryos develop and become more independent. Males caring eggs exhibit higher levels of aggression than solitary males, by biting and kicking with their legs the brush tip when simulating predation attacks; moreover, these males also spent more time tolerating the stimulus before flee. Our results show that male parental care behavior in *C. savagei* is adaptive. However, parental investment is a plastic behavior and varies across embryonic development, during the day and likely across seasons or populations with different environmental conditions.

### Swarm intelligence and the avoidance of parasites in schooling fish

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Disease transmission and parasitism is thought to be one of the major costs of group living. Nonetheless, when many individuals interact, a variety of behavioral patterns emerge enhancing information processing and the ability to discriminate subtle differences in the environment. With this study, we explore how groups of fish cope with the presence of an ectoparasite and if group living facilitates disease avoidance. At the individual level, fish are manually infected and monitored for the metabolic costs and behavioral effects of the infection using physiology tests in a swim tunnel. At the group level, we use individual tracking methods and reconstruct collective dynamics and individual movement characteristics that emerge in groups containing both uninfected and infected individuals. Specifically, we ask whether groups of uninfected fish can detect and move away from infected individuals, for example using wisdom-of-the-crowd mechanisms, or via distributed mechanisms. Overall, we aim at quantifying physiological and behavioral characteristics to better understand the relationship between individual and group-level information processing in the context of antiparasite defense.

## Context dependent sociality across foraging strategies and behaviours in a colonial seabird

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Animals experience consequences and benefits from group living, thus social behaviours should be favoured only when the benefits of sociality overcome the costs. Indeed, many animal groups exhibit fission-fusion dynamics, in which groups form and separate over time, with individuals varying in their use of social behaviours. If the costs and benefits of sociality differ between behavioural contexts and external condition, individuals may alter their social behaviours in a context dependent manner. However, current studies of animal sociality have generally focussed on single behaviours in isolation. Recent advances in multilayer social network methods provide a robust way to consider the multifaceted nature of sociality. To understand the factors driving individual variation in sociality we simultaneously GPS tracked 85% of all breeding individuals from a small colony of Australasian gannets (*Morus serrator*). Individuals from this colony exhibit location specific (bay-restricted and open-strait) foraging strategies, allowing us to address the hypothesis that sociality will vary with environmental contexts. We also examine sociality across three related behavioural contexts; coordination at the colony, commuting and foraging. During foraging, individuals socially associate more than expected by chance only during open-strait foraging, highlighting the use of environmentally driven social strategies. We found low overlap in sociality between colony, commuting and foraging behaviours, highlighting some carry-over between these behaviours, but that social foraging primarily occurs separately from other social associations. Through our multidimensional analysis of social movement and foraging we provide a first quantification of individual-level variation in sociality of a colonial species across multiple contexts.

### General rules to predict the outcome of chemotaxis across species

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Many living beings navigate using chemical cues. This behavior, known as chemotaxis, is a key feature of life across several levels: It guides bacteria towards nutrients and suitable niches, it helps immune cells find the pathogenic ones, and steers animals away from predators and towards food, friends and mates.

The physiological and biophysical mechanisms that underlie chemotaxis have been extensively studied. It is however difficult to link the well-studied instantaneous behaviors of chemotacting individuals to the global features that determine the fate of the system, such as the distribution of foragers across food patches. Through a combination of theory and experiments, we aim to link these two levels of description.

Our theoretical work studies how sources of chemoattractants of different densities can be distinguished at a distance. We have obtained two interesting predictions on how this ability is limited by the physical properties of diffusion. First, we find that a difference of orders of magnitude in concentration between two sources may lead to only a small difference in the number of individuals choosing each one. Second, we find a counterintuitive trade-off: Being better at finding resources (i.e. having higher sensitivity to the chemoattractant) may lead to a lower ability to distinguish highquality sources from low-quality ones.

We test our predictions experimentally using the nematode *Caenorhabditis elegans*, but we aim to develop a general theory to link individual properties to global outcomes, which we expect will be useful across species and contexts.

#### Revealing the behavioral algorithms of insect swarms

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Discovering the algorithms that biological systems use to make decisions is a central goal of ethology and neuroscience. Fundamental to our understanding of these systems is the ability to measure and model how individual components cause the emergence of higher-level, collective phenomena. Collective behaviors in animal groups are the product of individual decisions informed by sensory interaction networks, and revealing the network dynamics underlying group decision-making is a key challenge. To achieve a truly comprehensive understanding of behavior and the mechanisms that produce it, detailed and objective descriptions are needed. Recent breakthroughs in computer vision and machine learning have drastically improved the quality and resolution of these measurements, placing these goals within reach.

To reveal the sensory networks underlying locust swarming, we measured the vision and locomotion of marching juvenile locusts (*Schistocerca gregaria*) using a combination of individual tracking, direct estimation of the visual field, and unsupervised pattern-recognition algorithms for classifying behaviors. We then applied Bayesian machine learning methods to automatically derive sensory features that are predictive of individual decision-making and use these features to generate dynamic, multidimensional networks for better understanding how information propagates across groups and causes the emergence of collective behaviors. Results from this work will provide critical understanding of how swarms coordinate their behavior and will inform next-generation models of collective decision-making. This work builds on a growing movement to shift the fields of ethology and neuroscience toward an integrative, data-driven search for parsimonious general principles by leveraging techniques from computer science, physics, and mathematics.

## Social associations and communal nesting decisions in wild house mice: who benefits?

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The benefits of sociality are often not equally distributed, even for seemingly cooperative behaviours, which can influence social decisions and consequently shape animal social systems. An example of such a behaviour is communal nursing in mammals, where multiple reproducing females cooperate to care for their combined offspring. An individual's choice of when and with whom to nurse communally will therefore have important impacts on their fitness. However, the exact mechanisms influencing these decisions and how those choices might subsequently effect reproductive success are still relatively unknown and it therefore remains unclear whether this behaviour is exploitative or cooperative. We examine communal nursing decisions and their effect on individual fitness using a long term dataset of wild house mice (Mus musculus domesticus), in which communal nursing is facultative, using detailed data on nest box usage, genetic information and reproductive success. We exploit social network analysis to relate individuals' communal nesting decisions to their previous social behaviour, relatedness and individual traits such as age, allowing us to investigate questions such as how decisions about when to nest communally or not are influenced by group structure, partner availability and the individual traits of partners. We then link these decisions to a female's reproductive success. By examining how social and individual traits combine to influence communal nursing decisions, we gain new insight into how the benefits of communal nursing are distributed and to what extent communal nursing behaviour is exploitative or cooperative.

#### Footage of the communication function by cheetah at scent-marking sites

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Scent-marking is an essential form of communication, particularly for solitary species, as the information persists and does not rely on individuals encountering one another. Scent-marking conveys information on individual presence/area use, sex, rank and reproductive status. However, not enough is known about such communication in cheetah, Acinonyx jubatus, a predominantly solitary felid, and the possible role of scent-marking sites. Using camera-traps, we assessed the behaviour of cheetahs at scent-marking sites, asking how individuals of different demographic and dominance classes use the sites for intraspecific communication. We show that the inferred function of communication at scent-marking sites differs not only by sex but also by rank. Accordingly, females visit the sites infrequently, 8% of all visits, to signal estrus events, while males visit the sites frequently, 91% of all visits. Moreover, among males, dominant individuals scent-marked during 77% of their visits and reacted to a female by vocalizing during 52% of visits, but submissive males neither scent-marked nor vocalized while at the sites. We demonstrate how indirect monitoring can deliver significant behavioural information, and our study showcases the importance of scent-marking sites to cheetah populations, with potential consequences for cheetah reproduction that needs to be further explored.

# Group foraging bats individually discriminate group members based on search-phase echolocation calls

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Animals have evolved diverse strategies to utilize social information for increasing foraging success and efficiency. Echolocating bats can eavesdrop on changes in echolocation calls of nearby bats to gain information about prey availability. A few of these species coordinate flight to search for patchy prey together with their small social group. Yet to access the social information produced by their group members, group foraging bats must be capable of identifying these individuals to maintain contact with them in flight. Here we investigated whether search-phase echolocation calls, produced by bats to scan large areas for prey, can additionally convey individual identity. We caught and recorded search-phase calls of free-flying Molossus molossus with known identity. Then we recaptured 25 of these bats from five different social groups and tested them in habituation-dishabituation playback experiments to determine if they can discriminate between individual group members based on their search-phase calls. In playback trials subject bats habituated to calls one group member, then dishabituated to calls of a second group member, and finally rehabituated to new calls of the first group member. Thus they perceived the individual signatures of their group members and not simply the differences between playbacks. Acoustic analysis also supported the presence of individual signatures in search-phase calls. Our results provide the first step in testing the hypothesis that search-phase echolocation calls convey identity to enable *M. molossus* to maintain contact with group members in foraging flight.

#### Help thine enemy- the evolution of short ranging signals

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Honest signalling of aggressive intent relies on the proximity risk model in biology. This model assumes that the probability of successful attack is a function of the distance between the contestants and that this distance can be correctly estimated. This later assumption may not hold in nature where contestants have to estimate this distance under noisy conditions. Here I investigate whether short-range ranging signals can be evolutionarily stable under such conditions with the help of a game theoretical model. These signals can help the opponent to estimate the correct distance, thus they can promote honest signalling of intentions. Here I show that ranging signals that help the estimation of distance between opponents can be evolutionarily stable. However, such help only benefits those individuals who are able and willing to attack. As a result, ranging signals in themselves are an honest cue of proximity and in turn they are honest cues of aggressive intent. I give an example: 'soft-song' in birds, and I discuss why these signals are expected to be embedded in the threat display of the species.

#### The Cocktail Party Problem: How do field crickets solve it?

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The Cocktail Party Problem arises when multiple signallers signal simultaneously resulting in acoustic masking interference. It is likely to be a major obstacle to effective signalling in loud and dense animal choruses. Crickets are acoustically active insects which call from spatial aggregates and broadcast loud stereotypic and species-specific calls to attract females over long distance. Under these conditions, it is expected that these calls from multiple males may interfere in both spectral and temporal domains resulting in masking. It is reasonable to expect that males must employ strategies to avoid masking and signal effectively. In this study, we examined the conspecific acoustic masking in males of the field cricket Acanthogryllus asiaticus by determining their spacing and signal transmission. Playback experiments were conducted to examine acoustic response of focal male towards its real conspecific neighbour in field and towards the simulated masking neighbour under laboratory conditions. We found that males call from spatial aggregates and that their call transmit upto 3 m, thereby demarcating the broadcast area for a given male. Given natural spacing and signal transmission, males on an average have the nearest neighbour at 3 m distance and one acoustic masker on an average. Further, we found that males avoid masking by alternating their calls and modulating their call SPL with their neighbour. Our study provides insights into how males deal with conspecific masking which in turn leads us one step further in understanding how multiple males may signal effectively in the seeming cacophony of a loud chorus.

# Good singers find more eggs in their nest: Song consistency predicts fecundity in blue tits (*Cyanistes caeruleus*)

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Songbirds listen, learn and practice their vocal skills to deliver their conspecific song. The neuro-motor patterns involved demand a fine coordination of respiratory and syrinx muscles, including two independent sound sources. It has been proposed that the accuracy with which a bird delivers its song may indicate the general neuromotor functioning and therefore be subjected to sexual selection. In addition, females would theoretically be able to assess song consistency quickly in contrast to other song traits such as repertoire size. We studied the song characteristics of individually marked blue tits in a monitored breeding population at Lancaster, UK. We hypothesised that if an individual's vocal control is finely tuned, the sound output of notes of the same type should be consistent. To test that, we designed a custom-made acoustic analysis protocol in R to measure note consistency based on spectrogram correlation. We analysed 14000 individual notes from 1500 songs of 70 individuals (48 males and 22 females). Our results show that male blue tits that performed songs with more consistent notes were paired with females that laid larger clutches of eggs. Furthermore, male song consistency increased throughout the season peaking at the egg-laying period as predicted if consistency was under sexual selection. Finally, vocal consistency in female song is significantly lower than in male song, suggesting female choice might be the evolutionary driver of this trait. In conclusion, we argue that song consistency is a crucial aspect of communication and is likely to play a central role in the evolution of birdsong.

## Sensorimotor perception and integration of multiple-simultaneous visual stimuli in locusts

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In marching insects such as desert locusts, the extraction of relevant visual information amidst the noisy background is of critical importance for coordinating movement and avoiding collision with conspecifics. This study addresses two major facets of insect visual behavior: multiple target tracking and discrimination, during variable visual stimuli encounter. Experiments with walking desert locusts, Schistocerca gregaria, were performed in controlled conditions to understand the associated sensorimotor processes and decision-making. We investigated if a) locusts exhibit preferential response to selective stimulus when presented with multiple relevant stimuli simultaneously, and b) locusts respond differently to multiple copies of the same stimulus presented differently along different axes, orientations and speeds. Numerous visual stimuli including video clips of swarming locusts, random dot kinematograms and geometrical shapes with varying parameters were presented to tethered locusts walking on an air-cushioned trackball. High speed video recordings recorded the locusts' response by tracking the head pose, body angle and movement trajectory. In addition, neurophysiological responses from the neck connectives of locusts were monitored. Our results suggest that the desert locust does respond deferentially to selective stimulus when presented with multiple contradicting stimuli simultaneously. The pause duration between the walking bouts, known to be critical for swarm formation, varies with the complexity of stimuli and appears to be critical feature of decision-making in a visually rich environment.

#### Meat ants cut more trail shortcuts when facing long detours

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Engineered paths increase efficiency and safety but also incur construction and maintenance costs, leading to a trade-off between investment and gain. Such a trade-off is faced by Australian meat ants, which create and maintain vegetation-free trails between nests and food sources, and thus their trails are expected to be constructed selectively. To test this, we placed an artificial obstacle consisting of 300 paper grass blades between a sucrose feeder and the colony, flanked by walls of either 10 or 80cm length. To exploit the feeder, ants could detour around the walls or take a direct route by traversing through the obstacle. We found that, when confronted with a long alternative detour, 75% of colonies removed more grass blades and ants were also 60% more likely to traverse the obstacle instead of detouring. An analysis of cut patterns revealed that ants did not cut randomly, but instead concentrated on creating a trail to the food source. Meat ants were thus able to collectively deploy their trail clearing efforts in a directed manner when detour costs were high, and rapidly established cleared trails to the food source by focussing on completing a vertically aligned trail which is then followed by the ants.

#### Baboons unequally modulate their behavior to maintain group cohesion

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Animals must modulate their speed and coordinate their behavior to stay in contact with other members of their group. Due to differences in body size and locomotor capacity, some individuals may need to walk faster (or slower) than their preferred pace to allow groups to stay together. To test whether individuals modulate their speed to facilitate group cohesion, we simultaneously tracked members of a troop of olive baboons (Papio anubis) in Laikipia, Kenya with GPS collars and integrated accelerometers. We identified the footfalls of walking baboons and defined each group member's 'characteristic walking profile' based on the distribution of stride frequencies observed when walking alone. We then measured their stride frequency when walking as part of a group, finding that smaller baboons increased their stride frequency and showed larger deviation from their characteristic walking profile compared to larger baboons, which decreased their stride frequency during group movement. Smaller baboons had higher dynamic body acceleration, a measure that correlates with energy expenditure, than larger baboons. These results stress the importance of considering the role of movement capacity in shaping a species' movement ecology and illustrate an approach for accomplishing the effects of differences in movement capacity under socially and ecologically relevant field conditions. Together, our findings suggest that group movement imposes consensus costs which are borne disproportionately by smaller group members and highlight how individuals' decisions are constrained by the need to maintain cohesion.

#### Social allocation maintains bond stability in a wild rock hyrax population

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The structure and dynamics of animal social networks affect ecological and evolutionary processes. Social networks impact pathogen and information transmission, as well as reproductive success and survival. However, little is known about how animals maintain stable social relationships with their conspecifics. Until recently social relationships could be described using only coarse measures, mostly based on human observation of social interactions. Here, we used proximity sensors to document 32,726 interactions in a wild rock hyrax population at 1Hz resolution. We found that most hyrax pairs maintained stable relationships of varying strengths over a couple of months. We analyzed a two-months period, and found that hyraxes employed social allocation on a daily basis to maintain bond stability. That is, in a given day, hyraxes interacted more with conspecifics for whom the cumulative interaction time was lagging the one predicted by their daily mean. This compensation mechanism suggests that hyraxes keep record of past interactions and actively correct their 'social path' to maintain their social relationships. Our study opens new directions regarding the adaptive value of social stability and the mechanisms that maintain it.

### Hidden floral signals used by bumblebee pollinators

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Pollinating insects use a variety of floral signals to identify more rewarding flowers in their environment. This learning of floral displays is critical for maximizing foraging success. Some floral signals are salient to humans, while others are hidden to humans without use of modern technology. Here recent work from the University of Bristol Bee Lab investigating two such signal modalities is presented. Insect pollinators have previously been shown to respond to differences in flower temperature between flower species. Similarly, elevated humidity generated by evening primroses has been shown to be used by hawkmoths to locate rewarding evening primrose flowers. However, floral humidity's occurrence and use by pollinators outside of this single hawkmoth-primrose pollination system is unclear. Recent advances in thermal imaging technology have allowed surveys that reveal floral temperature differs across the flower surface, creating a temperature pattern. Similarly, use of affordable humidity probes and new robotic tools reveals many flower species produce floral humidity. Using captive bumblebees and conditioning techniques we demonstrate bumblebees can learn to distinguish artificial flowers that differ in each of these traits in a way comparable to real flowers. The presence of these 'hidden' floral signals, and the capacity of at least bumblebees to respond to them in a foraging context, expands our understanding of the range of multimodal floral signals pollinators respond to and the foraging decisions pollinators may make when visiting floral displays.

# Juvenile cleaner wrasses can learn socially about the consequences of cheating

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Social learning is often highlighted as an important driver of the evolution of human cooperation as it can facilitate the spread of cooperative behaviours and lead to large scale-cooperation and to the cultural evolution of behavioral traits. In contrast, evidence for the use of social learning by cooperating non-human animals is currently limited, and they are thought to mostly rely on individual learning or instinct alone. Here we show that juvenile bluestreak cleaner wrasses (Labroides *dimidiatus*) can learn socially about the consequences of cheating in cooperative interactions and adjust their strategic behavior accordingly. Observation of a conspecific adult interacting with model clients that flee when the cleaner 'cheats' by eating a preferred food item (which corresponds to cheating by eating mucus rather than ectoparasites in nature), caused the juvenile cleaners to eat more against their preference - a behavior that equates to increased cooperation in natural settings. Observation of an adult interacting with model clients that differ in their responses to such cheating, influenced the observers' subsequent partner choice, leading them to choose a partner that is less responsive to being cheated. These results suggest that juvenile cleaner fish can extract and use information from observing the outcomes of cleaning interactions, indicating an active role for social learning in the development of cooperative strategies in a non-human animal. Our results further show that client's responses to cheating have reputational effects: they modulate the subsequent behaviour of observing cleaners and can thus influence cooperation dynamics at a larger scale.

#### Necessity creates opportunities for chimpanzee tool use

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While social transmission mechanisms of animal cultures are well studied, little is known about the origins of behavioural innovations, even in established tool-users such as chimpanzees. Previous work has suggested that wild chimpanzees are especially prone to engaging with tools during extended periods of low food availability and after long travel, supporting the hypothesis that cultural innovation is facilitated by necessity revealing opportunities. Here, we tested this hypothesis with a field experiment that directly compared subjects' immediate variation in measures of current energy balance with their interest in a novel foraging problem, liquid honey enclosed in an apparatus accessible by tool use. We found that the previous distance travelled directly predicted subjects' manipulations of both the apparatus and the tool, while previous feeding time was negatively correlated to manipulation time. We conclude that 'necessity' augments chimpanzees' likelihood of engaging with ecological 'opportunities', suggesting that both factors are scaffolding foraging innovation in this and potentially other species.

### Male and female song: intra-sexual versus inter-sexual song learning by New Zealand Bellbirds

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Despite female song being an ancestral trait for songbirds, research has predominantly focused on species where only males sing. Here, we compare song of male and female New Zealand bellbirds, Anthornis melanura, across a metapopulation with varying levels of connectedness via male and female dispersal. We measured song sharing between the sexes for six populations and found that although populations had little repertoire overlap, sharing of syllables by males and females within populations was between 10 22%. We asked: 1) do shared syllables reflect inter-sexual song learning? 2) is inter-sexual learning a result of syllable prevalence within male and female populations? 3) are shared syllables similar for different populations? and 4) do shared and unshared syllables have distinct acoustic characteristics? We found that chicks of both sexes learnt male and female syllables, but that attrition of opposite sex syllables, presumably through social reinforcement, resulted in significant sexual dimorphism of adult repertoires. We found no correlation between the prevalence of syllables and the likelihood that a syllable was shared, nor between the prevalence of male and female shared syllables. Shared and unshared syllables had similar acoustic properties and shared syllables differed between populations. We conclude that the sexual dimorphism found in bellbird song is likely the result of social interactions within social networks prior to breeding. This research leads the way for future work on modelling how male and female song cultures develop and how they spread via social interactions.

# Koe: web-based software to visualise, segment and classify acoustic units in animal vocalisations

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Vocal communication is fundamental to the behaviour of many animal species. Vocal information can be encoded in the types of acoustic units employed (repertoire) and their temporal arrangement (sequence structure). To study repertoire and sequence structure requires classification of acoustic units, but this is currently hindered by a lack of tools, especially for large and diverse datasets. Here I introduce Koe, an application for classifying and analysing animal vocalisations. Koe offers bulklabelling of units via interactive ordination plots and unit tables, as well as visualisation and playback, segmentation, measurement, data filtering/exporting and new tools for analysing repertoire and sequence structure - in an integrated environment. I demonstrate Koe with a real-world case study of New Zealand bellbird *Anthornis melanura* songs from an archipelago metapopulation. Having classified 21,500 units in Koe, I compare population repertoires and sequence structure between sites and sexes. Koe is web-based (koe.io.ac.nz) and easy to use, making it ideal for collaboration, education and citizen science. By enabling largescale, high-resolution classification and analysis of animal vocalisations, Koe expands the frontiers of bioacoustic research.

### The Role of Team Heterogeneity in the Dynamics of Human Conversational Turn-taking

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Social groups can benefit from collective intelligence, where group members achieve an outcome superior to that which they could achieve on their own. In human social groups, such as project teams, conversation is a primary behavior that mediates the sharing, promotion and aggregation of differing knowledge and perspectives. However, heterogeneity in team members' traits can lead to systematic differences in interaction patterns, and thus, the extent to which each individual influences the group outcome. Here we examine the role that variance in communication behaviors play in team conversation dynamics by developing a data-driven simulation model of conversational turn-taking behavior. Data on the start and end times of individual speaking turns were coded from continuous audio recordings of meetings for seven self-organized engineering teams (3 - 4 students each, 24 total) during two summer engineering design internships in 2016 and 2017. Results indicate Americans (n = 13), who were more likely to be perceived as team leaders, had significantly shorter inter-turn intervals and were significantly less likely to interrupt others compared to non-Americans (n = 7 Malawians, 4 Brazilians), while turn duration and likelihood of being interrupted did not differ. Additional analyses will explore the roles of language proficiency, personality, and topical experience. Results are informing the development of a simulation model of conversational turn-taking behavior that we will use to explore how varying levels of heterogeneity in communicative behaviors influences emergent properties of the communication network. This study will promote understanding, and prediction, of the collective properties of human conversation.

# Transgenerational transmission of predator-induced phenotypic plasticity during sexual reproduction in a cyprinid fish

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Transgenerational phenotypic plasticity is a mechanism by which organisms attempt to predict future environmental conditions so as to adaptively match their offspring's phenotypes to their environment. Predator-induced defenses, ranging from behavior to morphology, are a well-studied example of phenotypic plasticity where first attempts have been made to understand their transgenerational transmission. However, most of these studies focus on asexually reproducing organisms with short generation times, thus little is known about the transmission of such defenses during sexual reproduction, which adds another important layer of phenotypic variation to transgenerational plasticity. Here, we report the first results of a comprehensive study on transgenerational antipredator phenotypic plasticity in a sexually reproducing common prey cyprinid fish with allopaternal care, the fathead minnow *Pimephales promelas*. Predation risk was simulated by continuously exposing fish in split-clutch rearing designs to either conspecific alarm cues that are released across aquatic taxa upon injury by a predator, or a control water treatment. Afterwards, we set up breeding combinations allowing us to control for parental vs. offspring effects via environmental match/mismatch designs, paternal vs. maternal precopulatory effects, postcopulatory effects of parental care by parents from different environments and grandparental vs. parental effects. Over a 2-year period, we then assessed morphology, shoaling behavior and boldness in up to 4200 fish across 18 treatments during three generations. Our results may allow inferences about how environmental information is transmitted across generations and interacts with an individual's own perception of the environment as well as about the evolutionary consequences of transgenerational phenotypic plasticity.

# Species-specific strategies increase unpredictability of escape flight in eared moths

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Many prey animals form mixed-species groups, which provide various benefits ranging from increased food intake to increased chance of predator detection. The escape-tactic diversity hypothesis predicts another benefit. It postulates that the overall unpredictability of evasive movement is increased if multiple species with different evasive tactics mix, resulting in enhanced predator protection for the whole group. However, escape-tactic diversity could also be a functional consequence of morphological differences that correlate with evasive capabilities. Echolocating bats and eared moths are a textbook example of predator-prey interactions. Moths exhibit evasive flight with diverse tactics; however, the variability of their evasive flight within and between species has never been systematically quantified. In addition, moth species show variation in size, which correlates with their flight capability. We recorded flight strength during tethered flight of eight sympatric moth species in response to the same level of simulated bat predation. Our method allowed us to record kinematic parameters that are correlated with evasive flight in a controlled way to investigate species-specific differences in escape tactics. We show species-specific and size-independent differences in both overall flight strength and change of flight strength over time, confirming the escape-tactic diversity hypothesis for eared moths. Additionally, we show strong inter-individual differences in evasive flight within some species. This diversity in escape tactic between eared moths increases the overall unpredictability experienced by bat predators, likely providing better protection against predatory bats for the single individual.

# Should I change or should I go? How colour change and behavioural choices combine for camouflage

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Camouflage is driven by matching the visual environment, yet natural habitats are rarely uniform and comprise many backgrounds. Therefore, species often exhibit adaptive traits to maintain crypsis, including colour change and behavioural choice of substrates. However, previous work largely considered these solutions in isolation, whereas many species may use a combination of behaviour and appearance to facilitate concealment. Here we show that green and red chameleon prawns (*Hippolyte varians*) closely resemble their associated seaweed substrates to the vision of predatory fish, and that they can change colour to effectively match new backgrounds. Prawns also select colour-matching substrates when offered a choice. However, colour change occurs over weeks, consistent with seasonal changes in algal cover, whereas behavioural choice of matching substrates occurs in the short-term, facilitating matches within heterogeneous environments. We demonstrate how colour change and behaviour combine to facilitate camouflage against different substrates in environments varying spatially and temporally.

### Iridescence as Camouflage

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Iridescence is a striking form of animal coloration which is taxonomically widespread, but the adaptive function of iridescence is still poorly understood. Here, we will present new and unpublished data to show that biological iridescence, produced by multilayer cuticular reflectors in real jewel beetle (Sternocera *aequisignata*) wing cases, provides effective protection against predation by birds. Importantly, we also demonstrate that the most likely mechanism to explain this increase in survival is effective camouflage, and not some other protective coloration function, such as aposematism. In two separate field experiments using wild birds and humans as surrogate 'predators', we measured both the 'survival' and direct detectability of iridescent and non-iridescent beetle models, demonstrating that the iridescent treatment fared best in both experiments. We also demonstrated an overall effect of the specular reflection (glossiness) of the leaf background: an increased level of background specularity led to a decrease in both predation rates and direct detectability of targets. The latter suggests that iridescent prey can increase their chance of survival against visually hunting predators even further by choosing glossier backgrounds. Our study is the first to provide empirical evidence for the hypothesis that biological iridescence can work as a form of camouflage in a natural setting, thus providing an adaptive explanation for the taxonomically widespread occurrence of iridescence in prey.

### Movement behaviour demonstrates precocial abilities of African savannah elephant (*Loxodonta africana*) calves

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Cooperating with conspecifics has many benefits including predator protection and information sharing that can outweigh associated costs. Within groups, divergence in optimal behaviour can cause group fissions (separation) if the costs outweigh the benefits. African savannah elephants (Loxodonta africana) are nonsynchronous breeders that live in a matriarchal fission-fusion social structure meaning that herds can merge or split depending on the relative costs of group living. Despite this, little is known about how unsynchronised breeding, including a 22-month gestation period, parturition and the presence of a neonatal calf, affects movements and hence group fusion in African savannah elephants. Here, we examined the relationship between reproductive state and movement characterized using GPS tracking data collected during 20 births from multiparous elephants ( $\geq$  second calving). We analysed the data using three-state hidden Markov models to determine whether parturition results in a distinctive change in movement behaviour, characterized as hourly and daily speed, 95% minimum convex polygon (MCP) and sinuosity index. Overall, parturition had little impact on movement in multiparous females. Using linear mixed-effects models, we determined that speed increased and sinuosity index decreased during the  $\sim$ 18 days after parturition, but, overall, movements before and after birth were not significantly different. Our results demonstrate the precocial abilities of elephant calves, which could be advantageous given both the matriarchal fission-fusion social structure of elephants and the mothers nutritional and water requirements. We speculate that, alongside cognitive development, elephants may have evolved an unusually long gestation period to facilitate an advanced stage of foetal physical development.

# Social hubs of an unsocial cat: cause and solution for the human-cheetah conflict

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Cheetahs naturally occur at low densities, which makes it unlikely for two individuals to meet by chance. With GPS data of >200 collared cheetahs (*Acinonyx jubatus*) we investigated their socio-spatial organisation. We detected a striking intraspecific communication network consisting of a regular pattern of communication hubs within the landscape. Each of these hubs was owned by territorial cheetah(s) which maintained numerous marking sites within the hubs. These marking sites were regularly visited by non-territorial males, which oscillated between two or three hubs, and irregularly by females. This spatial pattern was stable over consecutive cheetah generations. The is a unique system within mammalian species and offers exciting further research questions in understanding territoriality, mate choice, intraspecific communication and providing a key to mitigate human-cheetah conflicts. Namibia hosts one of the worldwide largest freeranging cheetah populations. Most cheetahs roam on farmland where they come in conflict with livestock farmers. We showed that regular visitations of the communication hubs by various cheetah individuals created local 'hotspots' of cheetah density in these hubs and thereby increased the local predation risk for livestock animals. Shifting the cattle breeding herds away from these hotspots during the calving season drastically reduced losses. This is because cheetahs retained their spatial distribution pattern and preved on naturally occurring prev species. Our approach of exploiting research insights of the socio-biology of conflict species to promote coexistence between humans and predators opens a promising area to develop solutions also in other conflict species with non-homogenous space use.

## Long-term movements and home range changes: rapid territory shifts in meerkats

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Territoriality is a common space use pattern among animals whereby territories provide its inhabitants with important resources and can thus be associated with increased fitness. While the role of territory quality and changes of territory ownership have frequently been investigated, the changes of boundaries are less studied. We investigated space use changes in kalahari meerkats (Suricatta *suricatta*) and applied a novel analytical approach, based on calculating dissimilarity matrices based on the earth movers distance and periodic utilization distributions. We analyzed meerkat movements of 24 different groups distributed over a 16-year period. Groups had stable territories for several years before they abandoned their home range completely to move quickly to new areas where they again remained for several years. These shifts were often preceded by more frequent group interactions but did not seem to be a product of direct displacements by other groups. NDVI as a measure of food productivity and social factors such as dominance changes did not correlate to changes in territory boundary. Against our expectation space use changes were not accumulations of small changes, but instead, groups did long distance moves into unknown ranges. As groups can thus not profit from previous local knowledge, these moves likely have important fitness consequences on the group and population level.

### Foraging site selection from GPS telemetry in a marine foraging bat

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Habitat selection models can provide insight into how animals respond to their environment at multiple scales. Here we investigate GPS tracks of the Mexican fisheating bat as it forages in the open ocean. The dynamic marine environment provides a challenge for animals attempting to reliably find prey as often the same location between nights will yield very different results. Our previous research found that bat foraging areas are on average several kilometers apart over consecutive nights, suggesting that bats cannot reliably predict prey location. Playback experiments and on-board audio recordings revealed that these bats rely on social information to find ephemeral prey patches, yet consistency in the direction of their foraging flights suggesting habitat selection at some level.

Here we ask if environmental variables measured by remote sensing are associated with foraging at two spatial scales, (nightly path, foraging patch) to identify predictors of habitat selection by fish-eating bats. We determined foraging locations through evaluation of behavioral segmentation methods with on-board audio recordings of buzzes. Using the best performing method, hidden Markov model, we parse tracks into foraging and commuting behavioral states and then use randomization tests to determine associations with environmental variables. Our results show that environmental variation fails to predict foraging patches, but at a larger scales bats choose to forage in areas with higher chlorophyll and steeper ocean slope, likely increasing the general presence of prey.

Habitat selection in a marine bat provides opportunities for comparison with other marine organisms foraging in the same unpredictable environment.

## Do nonapeptides regulate parental care depending on experience in zebra finches?

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Recent research suggests that the nonapeptide neurohormones regulate parental behaviors in a diverse array of vertebrates. However, it remains unclear how these neurohormones regulate parental care among birds, especially those which exhibit biparental care, common across birds, or whether hormonal effects are contingent on a bird's previous experience as a parent. I measured the effects of nonapeptides on parental behaviors by injecting, over three treatment days, a short-acting oxytocin receptor antagonist (OTA) or a saline control into breeding pairs of zebra finches (*Taeniopygia guttata*) that either did or did not have previous parental experience. I then compared how the duration and/or frequency of parental behaviors changed over the five days of observation (including one day before and two days after injections were administered). To compare treatment effects on parental outcomes, I also measured chick growth and mortality rates for each pair. OTA and experience significantly affected the amount of time birds spent nest guarding, with inexperienced birds receiving the OTA increasing nest guarding relative to inexperienced controls or experienced OTA birds. Chicks reared by parents that received the OTA had significantly lower growth rates than chicks reared by control parents and, among experienced birds, higher mortality relative to control birds. Together, these results provide some support for the hypothesis that nonapeptides play a role in regulating parental outcomes and some parental behaviors in both experienced and inexperienced zebra finches.

# Parental provisioning behaviour and inheritance of social networks in a colonially-breeding bird

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Parental care period is costly for parents and offspring face various risks such as predation. Many bird species mitigate these costs by breeding colonially, with colonies consisting of many breeding individuals that generally tend totheir own nests. However, relatively little is known about how colonial species behave and care for their young after offspring have fledged the nest but remain dependent on their parents. This period often involves the formation of chick creches, and parents are thought to almost exclusively feed their own chicks mainly to maximise their investment. However, this creching period could also represent an opportunity for adults to feed potential extra-pair young or to provide social support to the offspring of their close associates. Thus, parents can foster their social environment and juveniles can gain the opportunity to form social bonds with unrelated and/or genetic parents. We explore these possible mechanisms using an automated monitoring system to identify and track the adults and offspring in replicated colonies of zebra finches. We find that adults feed both unrelated and related offspring. Long-term tracking, from the period of pair formation and through the reproductive season, allows us to link the care provisioning network to the adults' social networks. In doing so, we help revealing the process by which juveniles develop their own social network as they integrate into an existing social environment and identifying whether they inherit their parents' social networks.

# Postnatal care compensates for prenatal inequalities in wild banded mongooses

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In vertebrates prenatal conditions during gestation and postnatal care during development both have important, lifelong consequences for offspring health and survival. Where mothers raise their own young, variation in maternal condition is expected to amplify prenatal inequalities among offspring, because mothers in good condition can invest more in both prenatal and postnatal periods. However, in many animal societies postnatal care is provided by other group members, not just mothers. Where carers are uncertain about their relatedness to offspring, theory predicts they should direct care in a manner that levels offspring inequality in case the poorer quality offspring are closer kin. We tested this hypothesis by manipulating maternal condition in wild banded mongooses (*Mungos mungos*) where relatedness between adult carers and communal litters of pups is uncertain. We conducted a 3-year field experiment feeding half the females from the each breeding attempt, producing 50 pups from fed females and 50 pups from non-fed control females. Fed females produced heavier offspring and provided more postnatal care. As predicted, they targeted this extra care at the smaller, lighter offspring of control females, rather than their own offspring, so that by nutritional independence the initial differences in body mass between the offspring of fed and control mothers had been eliminated. Our study shows that postnatal care can compensate for prenatal inequalities in maternal condition. The evolution of such mechanisms may buffer societies which communally care for offspring from inequalities in maternal condition and could weaken transgenerational effects on offspring fitness.

### Ontogeny of foraging via assisted learning by mothers in Egyptian fruit bat pups

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The transfer of information between parents and offspring is particularly important in mammals with relatively long periods of offspring dependency, such as fruit-bats. Offspring might learn several important skills during this period, especially how to and what to forage. Previous findings in non-bat species have revealed that juveniles learn a significant amount of what they know about foraging through social learning. Numerous bat species have been observed carrying non-volant young in flight, while both foraging and roost switching. This behavior is likely costly for mothers, and it is the benefits for the offspring that are still not fully clear. In this study, the developmental process from non-volant to independently foraging pups was monitored using high resolution GPS and telemetry tracking. Successful tracking of over 35 mom-pup pairs provides the first evidence of assisted learning of foraging by Egyptian-fruit-bat mothers. This process includes five distinct stages: (1) Pups are attached to their mothers 24/7 (2) Gradual-detachment: Mothers carry pups for shorter bouts, drop-off pups on a tree, forage alone, then pick-up pups on their way back to the cave (3) Pups are left alone in the cave (4) Pups fly independently to known sites, where their mothers previously dropped them off (5) Pups expand foraging to new sites unique to them. Our data shows that mother bats actively mediate learning of independent foraging by repeatedly placing pups on trees, which they then visit on their first foraging bouts.

### Collective decision making in fish schools

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Decision making, perception, and cognition are concepts that have been thoroughly studied in neuroscience. However, these processes are not restricted to the brain of a single animal. Through collective information processing, groups of animals exhibit responses to their surroundings that require information that exceeds the perceptive capacity of any individual. In order to study collective information processing, we have adapted strategies for studying perceptual decision-making from neuroscience to animal collectives. By presenting visual stimuli to schools of fish ranging in size from 8 to 1024, and tracking their movement with computer vision, we were able to quantify and investigate collective decisions of varied difficulty. We observed and quantified emergent properties of collective responses, and found that the accuracy and dynamics of collective processing scale with group size. We identified characteristics of collective responses that are analogous to processes observed in the brain, including evidence accumulation and working memory. Through comparison with other distributed information processors (such as neuronal networks), we aim to explore the use of animal collectives as a system to study self-organizing network processors.

### Context-dependent decision-making in house sparrows

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Adaptive foraging decisions depend on choosing food-related cues associated with high value of reward, as well as on recognizing or classifying such cues correctly. However, the relative weight that should be given to expected value versus the likelihood of correct recognition may differ across contexts. In a set of experiments, we examined how reward visibility and accessibility affect the relative weight house sparrows give to two parameters - the expected net value associated with a cue and the similarity of this cue (or its contextual setting) to those experienced in the past. The results suggest that sparrows considered both contextual similarity and netvalue in their foraging decisions but gave them different weights based on reward visibility and accessibility: When rewards were visible and easily accessible the sparrows showed no preference for neither of the cues. When rewards were visible but reaching them required considerable handling time, the sparrows preferred color cues previously associated with shorter handling time (i.e. higher perceived net value) over cues presented in a context similar to that experienced during training. Finally, when the rewards were hidden, sparrows preferred the cue presented in a context similar to that experienced during training. Thus, sparrows seem to dynamically adjust the weight given to previously learned cues according to current context, relying on cues that increase the chances of finding food when it is hidden and on cues that were associated with handling it more efficiently when it is exposed.

### Heritable variation in cognitive traits in a semi-natural system, the pheasant

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In order to understand the evolution of cognitive abilities, which underpin behaviours critical to an individual's fitness, we need to understand both how selection acts upon them and their patterns of heritability. Recent work has started to explore the fitness consequences for free-living individuals with particular cognitive abilities. However, our current understanding of the heritability of these abilities is predominantly restricted to domesticated species (poultry, rodents, model lab species) that have been subjected to artificial selection and these studies generally only look at the heritability of single cognitive abilities. We investigated the heritability, as well as their covariation of four cognitive abilities: inhibitory control, visual and spatial discrimination, and spatial learning ability in four generations of > 450 pheasants. Pheasants were reared in captivity but bred from adults that have lived and survived natural hazards for at least a year in the wild. Hence, they have been subject to selection on survival. Pheasant chicks are precocial and can be reared without parents, enabling us to standardise environmental effects during early life and remove effects of parental care. We constructed a pedigree for our birds and used animal models to account for genetic and environmental contributions to heritability. We found that performances on the different cognitive tasks varied in their genetic contributions, from moderate to no heritable component. We discuss possible mechanisms that may constrain or enhance the evolution of cognitive traits and discuss these findings in terms of modular models of the structure of animal cognition.

# Relationship between population densities, forebrain measurements and social competence in cleaner fish

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Several "intelligence" hypotheses attempt to unravel the links between ecology, cognitive abilities and brain neuroanatomical traits, but tests based on comparative research remain contentious. To reduce the effects of potentially confounding variables, it has been proposed to study the effects of naturally occurring variation in the ecology of a species on brain features. Here, we show that in a wild fish species, the mutualistic cleaner wrasse *Labroides dimidiatus*, abundance of individuals as a proxy for social complexity in natural habitats correlates positively with the relative cell counts in the cleaner forebrain. Furthermore, forebrain relative size increased with the increase in the social complexity but only in the brains of individuals with high cognitive performance. Thus, within a species, a measure of cleaner abundance, as a proxy for both intra- and interspecific social complexity, correlated with forebrain complexity as a function of cognitive performance. The results thus provide evidence for the hypothesis that social challenges and their solution promote an increase in brain complexity.

### Social behavior and disease transmission

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Although group-living may increase the overall fitness of individuals, it also facilitates the transmission of infectious diseases. Understanding the impact of population size, density, social interactions and environmental complexity on transmission is critical for being able to predict epidemic spread under novel conditions. We use the carpenter ant *Camponotus pennsylvanicus* to study the spread and transmission of a GFP-(green fluorescent protein)-labeled generalist pathogen (*Metarhizium robertsii*) as model system. Using modern microscopy and tracking of individual ant movement based on deep-learning algorithms allows us to study disease dynamics in complex scenarios. We will present empirical data on ant movement, proximity networks, pathogen distribution and transmission collected from 48 ant nests.

# Being flexible in a rigid trait: modulation of Lévy walks in termite workers under distinct social encounter context

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Movement is a crucial element of behaviour: animals displace themselves in space in search of suitable conditions for survival and reproduction. It is hence expected that movement patterns in animals will be determined by the way they efficiently balance (i) their intrinsic individual displacing abilities with (ii) the spatial distribution of food, enemies, mates, etc. However intuitive, this notion needs better evidence, as it lies in the core of the still unsolved mechanisms generating search strategies in animals. That these searches are typically described as a Lévy walk process is consensual, though.

Here we explore such a balance in the context of social interactions among termites. We checked whether changes in the density of nestmates and the density of castes would trigger search-modulation in termite workers of *Cornitermes cumulans* when searching for social interactions. Our results seem to point to a two-fold process. Termite workers confined in petri dishes do displace them- selves in a Lévy-like walking, no matter the density or the type of targets therein present (targets being other workers or soldiers, which do differ in interactivity). Such movements, however, seem fine-tuned by group composition: as the density of workers increases so does the  $\mu$  exponent of the power law describing the frequency of their step lengths.

In contrast, the mean speed of focal termites decreased exponentially with the increments of both the density of nestmates and the density of termite workers. Whereas indicative of interindividual movement obstruction, these results also point out that such an obstruction is affected by the type of interaction (worker-worker or worker-soldier). It is hence plausible to suspect that their general Lévy displacement pattern would indeed be affected by social interactions more than simply by the obstruction effect of inert targets.

It seems, therefore, that (i) while termites do have an innate propensity to perform Lévy walks, (ii) external constraints, at least in the form of opportunities for social interactions, would add an important modifier to these displacements.

# Parasite-induced bioluminescence deters predation of infected hosts by nocturnal rodent predators

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Anti-predator defences are ubiquitous in nature with aposematism a common and well-studied example. Aposematism normally combines a repellent defence, such as a toxin with a warning signal, usually visual, olfactory or acoustic. There is increasing evidence that bioluminescence can act as an aposematic signal to deter predation of prey that have chemical defences. We examine a novel example of such signalling; the bioluminescence of infected insect cadavers that is induced during infection by the parasitic nematode *Heterorhabditis bacteriophora* and its symbiotic bacterium *Photorhabdus luminescens*. This nematode-bacterium complex infects and kills soil-dwelling hosts within which it reproduces for around two weeks before new infective nematodes emerge. During this incubation period the insect cadaver. and the reproducing nematode-bacterium complex, is susceptible to predation, which is fatal for the developing parasites. We hypothesise that bioluminescence in this system acts as a warning signal to deter predation of infected hosts by nocturnally active, foraging predators. Using non-invasive CCTV monitoring, we tested both olfactory and bioluminescent deterrents by assessing the behavioural responses of house mice (*Mus musculus*) towards infected or uninfected insect prey. IVIS Spectrum In Vivo Imaging system was specifically used to evaluate bioluminescence signals under different light conditions. Mice did not respond to the olfactory cue but did spend less time near bioluminescent prey, indicating an avoidance of prey based on a luminescent signal. Bacterial symbionts in this system may have evolved exaggerated luminescent signals in order to protect a parasitic colony from predation.

# Parasite infection affects individual and thereby collective movements of three-spined sticklebacks

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Parasitism is ubiquitous in the animal kingdom. While many fundamental aspects of host-parasite relationships have already been unravelled, few studies have systematically investigated the effects of parasites on organismal movement. Focusing on the stickleback - S. solidus model system, here we combine detailed behavioural experiments with agent-based model simulations to get a mechanistic understanding of how parasitism can drive individual and collective movement dynamics. By individual-based tracking of fish with different levels of infection, we found that parasitized individuals swam slower, accelerated slower, and turned slower than healthy fish, and were more predictable in their movements. These effects were stronger the higher the parasite load of the fish, and were consistent across different solitary and social contexts that affected the average movement patterns of the fish. In turn, pairs composed of two parasitized individuals were not only slower, but also less cohesive, less aligned, and less coordinated than healthy pairs, with mixed pairs showing intermediate levels of behaviour. Furthermore, in such pairs, healthy fish were much more likely to lead their parasitized partner, and increasingly so the higher its parasite load. These social patterns emerged naturally in model simulations of self-organised groups composed of individuals with differences in speed and turning ability. Together, these results show how S. solidus parasite infection impacts both the motivation and capacity of individuals to move and how this in turn affects collective patterns without the need for active parasite manipulation, providing new mechanistic insights into the effects of parasitism on host movement dynamics.

### Soldiers, workers and their moves: group structure and collective motion in termite societies

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Coordination is fundamental for large-scale animal groups on the move. When foraging, termite societies coordinate movement by establishing a series of interconnected pathways, thus facilitating navigation through complex environments. Several studies have elucidated the chemical ecology behind the formation of such trails, but little is known about behavioural mechanisms modulating the patterns. In this research, we developed an empirical framework to investigate the underlying mechanisms of coordinated collective motion in termite societies. Specifically, to test how group structure affects collective patterns, we evaluate both the emergence and maintenance of self-organised trails in different caste-ratio configurations. Using high-resolution videos and image-based tracking technologies, we detect trajectories and extract posture data for individuals over time. By performing quantitative analysis of movement, we gather information about the spatiotemporal dynamics, allowing comparisons of performance between groups in different scenarios. Our results provide evidence that the singularity of each termite caste goes beyond their innate morphological differences. The behavioural patterns observed for soldiers and workers indicates that the rules governing the collective motion of each group are unique. This means that workers and soldiers should not be interpreted as equal contributors in shaping collective patterns. Still, although castes operate in different ways, we reveal phase transitions in the behavioural response and an optimal caste-ratio configuration in which consistent coordination is more likely to emerge. We argue that mechanisms of coordinated motion in termites have been shaped under specific selective pressures, not necessarily those acting in Hymenoptera, as often assumed or suggested in the past.

### How ant-to-ant feeding interactions lead to colony-level regulation of foodintake rate

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Ant colonies send only a small fraction of their workers to do the foraging. Upon finding a source of liquid food, these foragers perform repeated bouts of filling their crop (their 'social stomach') at the food source, and unloading it in local mouth-tomouth interactions to recipient ants in the nest. In this decentralized system, how can it be assured that the food brought in by the foragers matches the needs of the bulk of the colony? By imaging the real-time flow of fluorescent food in a colony of individually barcoded ants, we quantitatively describe an emergent colony-level regulation: the total rate of food flow into the colony is proportional to the colony's total level of hunger. This relationship is mediated by the amounts of food passed in local interactions, which are governed non-trivially by the food loads of the recipients. Additionally, on average, the frequency of trips of a single forager are also proportional to the colony's level of hunger. By analyzing the foragers' exits from the nest as outcomes of a Markovian decision process, we gain insight to the local factors that may translate colony hunger into individual foraging frequencies. Our findings suggest that the observed colony-level regulation may emerge without the need for individual foragers to actively assess the state of their colony.

### Multimodal navigation in ants: How do different strategies interact?

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Ants have long been a model organism for the study of navigation, due to their robust and impressive natural foraging performance. Effective navigation is a multimodal process taking into account information from different sources tuned to the sensory ecology of a navigator. For ants, the combination of innate navigational strategies and the learning of environmental information is a key to their success, with the main innate strategy being Path Integration (PI). We recorded ants being guided by PI and found that (i) ants' walking speed decreases significantly along homing paths and stays low during subsequent search paths and (ii) ants are influenced more strongly by novel or learnt visual cues the further along their homing path they are. These results suggest that PI modulates speed along the homing path in a way that might help ants search for, utilise or learn environmental information at important locations. Ants walk more slowly and sinuously when encountering novel or altered visual cues and occasionally stop and scan the world, this might indicate the re-learning of visual information. We also investigated how two learned sensory modalities interact by looking at visual and olfactory guidance in navigating ants. We see that multiple cues lead to more accurate and efficient ants, but with more complex paths. Moreover, if olfactory and visual cues are learnt together, both of the cues are necessary for successful navigation. However, this binding seems to depend on the 'usefulness' of the available cues.

### Using automated tracking to show how honey bees move within their nest

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The ecological dominance of the social insects is due in part to how colonies allocate tasks between individuals. In honey bees, age polyethism regulates task allocation, with tasks being performed in well-defined areas of the nest. It is unknown, however, how movement patterns within the nest get workers to the appropriate location at the appropriate age. To address these questions, we require methods that cover spatial and temporal scales at both the level of the individual bee, and the whole colony. This requires continuous tracking of multiple individuals, which fortunately has become possible with recent advances in automated tracking software. In collaboration with the Landgraf Lab and their BeesBook tracking system, we tracked honey bees throughout their lives, and their changing nest environment. Using analysis techniques from movement ecology, but scaled down to the nest environment, we show how workers change their use of different nest areas as they age, and how these techniques can be used to back-calculate task allocation among workers. Unlike multicellular organisms, whose units are mostly fixed to a location, a honey bee colony is comprised of movable units that interact with each other and with their nest environment. The focus of this research is to understand how movement patterns generate a superorganism whose subunits interact as a collective.

# Whistleblower: Variability of call combinations in a cooperatively breeding primate

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The great variation in vocal complexity across the animal kingdom is proposed to be associated with aspects of sociality, such as group size and breeding system. Analyses of such relations rely on properly assessing vocal complexity, which not only incorporates the vocal repertoire. We hence investigated complexity of call combinations in a cooperatively breeding primate species: Common marmosets (Callithrix jacchus), which form comparatively intermediate to small groups and are highly vocally active. Previous studies described 13 to 20 adult call types occurring singly, in series and combinations. We recorded vocalisations of five wild groups across different contexts in their natural environment and thus captured most variation in adult call types and combinations. We focussed on combinations with long-distance, whistle-like phee calls emitted by the dominant pair. This call type was given singly, in series and in 68 different combinations with nine different call types and two to seven calls per combination. Context analyses so far did not reveal significant differences between selected call combinations (preliminary results), yet our study revealed highly variable and intermediate call types that did not fit into previously described categories. The variability in call types and combinations is thus much higher than previously thought and demands new methods to characterise the vocal repertoire, assess vocal complexity and clarify the meaning of call types, combinations and modifications. Such variability in vocalisations provides the scope for complex information transfer and adds to the evidence that vocal complexity of cooperatively breeding primates rivals that of non-human great apes.

### Do Starlings use 'contact calls' to coordinate group foraging behaviour?

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Many group-living animals travel together and are thought to use calls to coordinate group movement. 'Contact calls' are a category of calls that are thought to be important in this group coordination. However, while very common across many taxa, how 'contact calls' function has not been especially well studied. While some experiments have addressed how individuals or groups use contact calls, how individuals use and respond to calls to influence the group itself remains unknown. Starlings are a social species thought to use 'contact calls' extensively to coordinate group movement and therefore provide a useful species to investigate group movement coordination. To determine how these birds use 'contact calls' to coordinate group movement, we, first, examined group movement events to determine how calls are used to coordinate group movement to and from food resources. Next, we explored the social context of these calls. We used both 3D visual and acoustic localization technology to determine both who instigates and responds to movement events, and who vocalizes during these events. By tracing who calls, when, and from where, we can determine both how these calls serve to coordinate group movement and who drives this behaviour.

# Experience of the signaller explains the use of social versus personal information in the context of sentinel behaviour in meerkats

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To maximise foraging opportunities while simultaneously avoiding predation, group-living animals can obtain personal information on food availability and predation risk and/or rely on social information provided by group members. Although mainly associated with low costs of information acquisition, social information has the potential to be irrelevant or inaccurate. In this study we use playbacks of individually distinct sentinel calming calls produced during sentinel behaviour, a form of coordinated vigilance behaviour, to show that meerkats (Suricata suricatta) discriminate between social information provided by different sentinels and adjust their personal vigilance behaviour according to the individual that is played back. We found that foraging group members acquired the lowest amounts of personal information when hearing social information provided by experienced individuals that act as sentinels most often in their group. Our study shows that social information can be flexibly used in the context of sentinel behaviour in order to optimize the trade-off between foraging and vigilance behaviours dependent on discrimination among signallers. We also provide novel evidence that the experience of sentinels rather than their age or dominance status is the main factor affecting the extent to which individuals use social information.

# Female song repertoires in the New Zealand bellbird: sexual and temporal variation

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How song repertoires vary between species and change over time is well studied in male songbirds. However, female song is much more common and widespread than once assumed, making it timely for more research on how female song repertoires compare to male counterparts, especially in species where females have complex song. We investigated the syllable repertoire of the New Zealand bellbird (Anthornis melanura), a species where both sexes have complex but sexually dimorphic song. Songs were recorded at the individual and population level to assess syllable repertoire size and temporal variation. Overall, 96 syllable types were detected in the population over four recording years, of which 58% were unique to males, 32.3% unique to females and 9% were shared between the sexes. Individual syllable repertoire sizes ranged from 15 to 32 (n = 7) syllables for males and 6 to 15 (n = 6) syllables for females. The population syllable repertoire of both sexes changed across years at a similar rate based on Jaccard's similarity coefficient (female 52.6-67.9%; male 58.6-73.7%). For males and females, certain syllable types also appeared to vary in their prevalence in the population across the years. The individual variation found suggests both sexes may be influenced by potential phenotypic or condition-based factors that can influence song repertoires. The sexes' syllable repertoires changing over time at a similar rate also suggests selection pressures may be acting on both sexes for an analogous function of their song.

## Multimodal communication in wild primates: comparing sociality and multimodal communication in two lemur species

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Animals exhibit an astonishing diversity of communicative systems, with substantial variation in both the nature and the number of signals they produce. Variation in communicative complexity has been conceptually and empirically attributed to social complexity. The 'social complexity hypothesis for communicative complexity' (SCHCC) suggests that animals living in more complex social environments exhibit more signals and/or more complex signals than animals living in simpler social environments. Much research in the context of the SCHCC has focused on a single modality, whereas several good reasons exist for acknowledging the multimodal nature of both signals and communicative systems in this framework. First, multimodal signals are by definition complex because they involve more than one signalling and perceptive system. Second, the flexible use of different modalities in multimodal signals permits another level of complexity embedded in multimodal signalling. At the system level, focusing on one modality may lead to over- or underestimation of the relationship between social and communicative complexity. Using such a comprehensive approach, we compared the communicative systems of two closely-related species of Eulemur with similar morphology and habitats, but different social systems. We studied 33 wild E. rufifrons (5 groups) and 10 wild E. mongoz (3 groups) in Madagascar. Based on 449 hours of focal behavioural observations and 284 hours of recordings, we compared their social and communicative complexity. We established a cross-modal signal repertoire to contribute to a more comprehensive assessment of communicative complexity, and to allow for more meaningful tests of the SCHCC.

### Morphogenesis of networks in polydomous ants

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Many biological systems are dependent on transportation networks for the efficient distribution of resources and information. Network builders face the challenge of balancing conflicting network properties such as robustness, efficiency and costs. Polydomous ant colonies are split between multiple spatially separated nests. They build and maintain physical trails that connect their nests to each other and to food resources. The resulting transportation network is used to distribute workers, brood, and food. The morphogenesis of these complex networks and in particular the individual mechanisms underlying them have not yet been quantified. There is empirical evidence that networks are organised at the local level between neighbouring nests and not at the colony level. We test this hypothesis in the species *Formica lugubris* with a model developed at the scale of the colony. The model consists of simple rules of interactions between nests based mainly on distance metrics. The model is validated against empirical data collected for 7 years on 9 colony networks in England. We find a good agreement between simulated and empirical data on many emergent quantities such as the number of trails per nests and centrality measures. We infer the mechanisms possibly involved at the scale of the individuals, with a focus on the diffusive behaviour of motion of scouts. This work provides for the first time a model of morphogenesis of networks in polydomous ants quantitatively validated against empirical data and will be the basis of the development of a unifying theory of dynamic transport networks across biological systems.

# Dynamic ant networks: how does social structure respond to changes in the resource environment?

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Animal social structure is shaped by environmental conditions, such as food availability; this means that changing conditions can alter social structures and result in cascading ecological effects. Understanding both how the resource environment causes certain social structures to arise, and also how resilient such structures are in the face of environmental change, is essential to understand the relationship between animal societies and their ecological context. Wood ants are an ideal study system for this, because they depend on discrete identifiable food resources (trees), and form large networks enabling resource sharing between socially connected nests of the same colony. We have collected data on the social network dynamics of 13 large multi-nest colonies of the wood ant *Formica lugubris* over 7 years, and manipulated resources to test social resilience. Our dynamic network analysis results show that nest survival is affected by social position; specifically, the flow of resources through a nest, a result of its position within the wider network, determines a nest's likelihood of surviving. Combined with sizebased 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 colony networks to split into smaller components, but without reducing growth or survival. Taken together, these results show a dynamic social structure that responds flexibly to both gradual and abrupt changes in the resource environment.

### The distributed regulation of multiple nutrients in ant colonies

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Nutritional regulation by ants is an intriguing process in which food collected by a small fraction of workers, and then distributed among the rest, satisfies the distinct nutritional requirements of the entire colony. It was previously shown that ants can regulate their protein and carbohydrate intake at both the collective and individual levels. This control is especially impressive considering that information about the global supply and demand is not available to any single individual. Here we present, for the first time, preliminary results on multi-nutrient dynamics in ant colonies using a two-color fluorescent imaging setup. Colonies of individually barcoded ants were presented with two food sources, each containing a different protein:carbohydrates ratio (P:C) and a distinct fluorescent color. We tracked the nutritional state of the colony throughout time until the P:C intake target was reached. On the individual level, we directly examined the behavior of the forager ants and their decision-making at the food source in relation to the colony's nutritional state. This information can shed light on how colony-level regulation emerges from individual behavior.

# Multi-level structure in feral horse society: Evidence from the aerial observation from drones

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Some mammalian species of different taxonomic groups, including humans, have developed social structures with nested levels of organization. This multilevel society is one of the most complex social systems in animals, but their function and evolutional process are still poorly understood especially for non-primate species because it requires good observation of large numbers of identified individuals. Equine groups are one of the taxa that have nested social structure, and there are some studies on several species such as plains zebras and Przewalski's horses, but not on domestic horses (*Equus caballus*). Studying the inter-group relationships of feral horses and comparing those of the other equine species may help understanding their origin and their ecological and social meanings. In this study, we aimed to reveal whether domestic horses form multilevel societies. We took aerial photos of feral horse herds in Serra D'Arga Portugal in 30 minutes interval using drones, identified all the individuals and collected their position data. In the field, we observed 21 harems, 2 bachelor groups and several solitary bachelors. Their home range were largely overlapped and the area of convex hull of these groups were significantly smaller than each home range, which suggests harems and bachelors aggregates to form a herd. Moreover, this herd had a structure that large harems were likely to be in the center, while bachelors were in the peripheral zone, and small harems were located somewhere between that. The presence of this stable spatial pattern strongly indicates the multilevel structures of feral horse society.

### Within-group variation and synchronization in nocturnal activity of freeranging olive baboons

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Despite decades of detailed behavioral data collection on diurnal primates, we still know exceedingly little about what these animals do during the night. Assessing the behavior of primates during their most vulnerable hours is critical to our understanding of their behavioral ecology. We fit over 80% of the adults and subadults in a group of free-ranging olive baboons with collars bearing GPS and triaxial accelerometer units, and collected high-resolution bursts of accelerometry data once every minute overnight. We applied a machine learning classifier to determine when each baboon was in motion, indicating that it was active, or was sedentary, indicating that it was resting or sleeping. We quantified the amount of nocturnal activity in the baboons and evaluated the individual consistency and within-group variation in the amount of rest they experienced overnight. We then used permutation tests to assess synchronization between groupmates in their nocturnal activity patterns and investigated the underlying reasons for synchrony. Our results indicate that baboons are active quite frequently during the night, suggesting nocturnal vigilance as a potential antipredator strategy. We also found substantial variation between groupmates in their nocturnal restlessness. Given the importance of sleep to health and cognition, this result suggests that variation in sleep quality could contribute to within-group variation in fitness. We also discovered that baboons often synchronize their bouts of nighttime activity with their groupmates. The time that baboons allocate to maintaining their social relationships might therefore not be limited to daylight hours.

# The ManyPrimates Project: Establishing an infrastructure for collaboration in primate cognition research

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Tracing back the evolutionary history of cognitive abilities requires large and diverse samples. Particularly in primatology, such samples are usually beyond the reach of individual researchers or institutions. Therefore, studies are often limited to small numbers of individuals and species, which prevents researchers from answering questions regarding the structure of individual and species differences in cognitive abilities. The ManyPrimates project was created to address these questions by providing a large-scale collaborative framework for comparative studies in primate cognition. Here we present data from a pre-registered pilot study on short-term memory. In this delayed-response task, individuals could access food rewards by remembering under which of three opaque cups the reward was hidden after a 0, 15, or 30-second delay. We tested 176 individuals from 12 primate species housed at 11 sites. Overall, individuals performed better with shorter delays, in line with previous research. A phylogenetic analysis revealed a strong phylogenetic signal for short-term memory abilities even though, with only 12 species, the validity of this analysis is limited. Our initial results demonstrate the feasibility of a large, collaborative open-science project in primate cognition research. In the future, the ManyPrimates project will provide the opportunity to address longstanding questions in primate cognition and behavior with large and diverse datasets.

# Do capuchin monkeys show strategic information seeking to fill gaps in their knowledge?

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Previous research found that capuchin monkeys (Sapajus apella) seek information about the location of food (Marsh MacDonald, 2012). In chimpanzees (Pan troglodytes) searching extends to functional tools which can be used to obtain food (Bohn et al., 2017). However seeking functional information is yet to be shown in monkeys. We presented 12 capuchin monkeys with a novel information seeking task where information could be sought from two locations; looking below a barrier provided information about a cups contents, looking above a barrier provided information about a cups functionality (open or sealed). Cups were presented in three configurations; all baited (all cups were baited but only one was open), all open (all cups were open but only one was baited), and mixed (two cups were baited and two were open, but only one was open and baited). Initially monkeys were trained to select open-baited cups when all information was visible. Then a barrier occluded the cups so individuals had to search before choosing in order to make an informed decision. Searching was more likely once information was occluded (LRT:  $\chi^2$ =17.95, df=2, p<0.001). However search location was not significantly affected by cup configuration (above search LRT:  $\chi^2$ =0.832, df=3, p=0.841; below search LRT:  $\chi^2$ =2.565, df=3, p=0.464). This supports previous findings that capuchins will search for information to fill gaps in their knowledge. However we found no evidence that searching was sensitive to which piece of information was required. We conclude that capuchin monkeys show selective but not strategic information searching.

### Green monkey responses to drones: insights into the evolution of alarm call systems

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One of the core facets of the human language faculty is the ability to designate objects and events in the environment. A prerequisite for conventionalized communication in the auditory-vocal domain is flexibility in both vocal production and comprehension of sounds. To evaluate the flexibility in vocal production and comprehension in a nonhuman primate species, we presented a novel aerial threat, namely a drone to West African green monkeys, Chlorocebus sabaeus. Calls given in response to the drone were clearly distinct from alarm calls given to other potential predators, but highly similar to those given by East African vervet monkeys, C. *pygerythrus*, to eagles. An analysis of > 3000 calls revealed that the alarm call repertoires of both species were structurally highly similar, although the green monkeys' call types were overall less distinct. To probe how rapidly the animals attached meaning to the sound of the drone, we conducted playback experiments after 1-3 exposures to the drone. Subjects immediately responded with orienting responses, including scanning of the sky and running into cover. In conclusion, the structure of the alarm calls in this genus is highly conserved, while comprehension learning is rapid and open-ended. Our findings support the view of a deep dichotomy in the flexibility in vocal production vs. auditory learning in terrestrial mammals; this dichotomy has also been found in other species, such as domestic dogs and suggests that in this clade, flexibility in the auditory domain evolved prior to the flexibility in vocal production.

# Using thermography to understand third-party social evaluation in cooperatively breeding common marmosets

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Third-party social evaluation is crucial for group living species to navigate social networks and to keep track of potential cooperation partners. Experiments with human actors have shown that marmosets are able to evaluate social interactions between humans but experimental evidence of social evaluation of conspecifics is lacking. Additionally, behavioral 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 (noninteraction control playback) by playbacks of food, chatter or begging vocalizations. Our results suggest 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 behavioral data and argue that thermography is more sensitive measure of arousal marmosets.

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### HSP90 increases individual behavioural consistency in the desert locust

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All organisms can tailor their phenotype to changing environmental conditions whilst remaining robust to environmental perturbations. Heat shock protein 90 (HSP90) has been proposed as a key mediator of this robustness. HSP90 canalises intracellular machinery in yeast and morphological traits in animals and plants. HSP90 may have a role in synaptic function, but its role in regulating behaviour is almost entirely unexplored.

We investigated the role of HSP90 in behavioural consistency in the desert locust, *Schistocerca gregaria*, a species which shows extreme phenotypic plasticity. In response to crowding or isolation, locusts transform between a cryptic 'solitarious phase' that avoids other locusts and a brightly coloured and highly mobile 'gregarious phase' that is attracted to conspecifics.

We analysed the effect of pharmacological inhibition of HSP90 in a simple locomotor hesitation assay that measures the time a hungry locust takes to walk upwind across a beam towards a food odour. Locusts were starved and assayed twice daily for 4 days after daily injection with the selective HSP90 inhibitor 17-AAG or a vehicle control. The eight repeat observations per individual permitted Bayesian estimation of both between- and within-individual variability.

Solitarious locusts showed considerably greater between- and within-individual variability in locomotor hesitation than gregarious locusts. Inhibition of HSP90 had no effect on mean crossing time in either phase, but caused a clear increase in within-individual variance in both phases. It did not affect between-individual variance. Our data provide the first evidence that HSP90 canalises behaviour towards greater individual consistency.

### Identity domains in complex behavior: Toward a biology of personality

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Personality traits offer considerable insight into the biological basis of individual differences. However, existing approaches toward understanding personality across species rely on subjective criteria and limited sets of behavioral readouts, resulting in noisy and often inconsistent outcomes. Here, we introduce a mathematical framework for studying individual differences along dimensions with maximum consistency and discriminative power. We validate this framework in mice, using data from a system for high-throughput longitudinal monitoring of group-housed mice that yields a variety of readouts from all across an individual's behavioral repertoire. We describe a set of stable traits that capture variability in behavior and gene expression in the brain, allowing for better informed mechanistic investigations into the biology of individual differences.

### Personality-dependent movement, space use and fitness in wild house mice

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The causes and consequences of consistent individual differences in behaviour, called animal personality, have been thoroughly investigated and stimulated their incorporation into ecology and evolution. Personality is frequently measured using standardised behavioural tests such as open field or dark-light tests. Measures from these tests are often used to draw conclusions about ecological and evolutionary processes in natural conditions, although the direct relevance of standardised measurements for natural situations is not often validated. We compared measures of activity/exploration and anxiety-like behaviour from standardised behavioural tests to to spatial measurements for colonization of a novel, large-scale environment using a grid of antennae to track individual mouse movements. We measured home-range size and quality as well as offspring recruitment after mice established permanent territories in our semi-natural enclosures.

We found that mice which were more active/explorative in standardised tests visited fewer locations during the colonisation period of the experiment, suggesting that comparing results from laboratory test setups to those from more natural situations should be done with care. The relationship between personality and space use after territory formation proved to be more complicated. We did not find a direct relationship between activity/exploration or anxiety-like behaviour and territoriality in the semi-natural enclosures, nor did we find a direct relationship between personality and offspring recruitment. Taken together, these results suggest that a more thorough investigation of movement behaviour and spatial components will further broaden our understanding of the causes and consequences of animal personality.

### Cortisol coregulation between dogs and owners

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Cortisol coregulation' refers to the ability of social dyads to bidirectionally modulate each other's physiological stress levels. Traditionally, research into cortisol coregulation has focused on human social interactions, but a recent study has demonstrated this phenomenon in fish, suggesting that cortisol coregulation is not unique to humans. In fact, new research exploring inter-instead of intra-specific cortisol coregulation suggests that dogs and their owners coregulate their cortisol levels. This PhD research investigates cortisol coregulation between companion dogs (Canis familiaris) and their owners and aims to evaluate the factors that influence the strength and direction of coregulation between the dog-owner dyad. Participants repeatedly collect their own and their dog's saliva samples across workdays and non-workdays. In addition, participants also complete a number of questionnaires allowing us to assess daily/weekly routines, the personality of the owner and the dog, and the relationship and attachment levels between dogs and owners. By combining salivary cortisol measures with questionnaire data, we evaluate the influence of dog and owner behaviour and lifestyle, personality, and relationship 'quality' on cortisol coregulation between dogs and owners. This presentation will include an overview of our findings to date and discuss their implications for expanding our knowledge of physiological stress modulation, as well as assessing and improving companion animal welfare.

# The role of edge enhancement in background matching and disruptive camouflage

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Disruptive camouflage is defined as patterning that breaks up the outline of an object, potentially making it more difficult to detect and recognise a target. Recent work has suggested that enhancing the edges of disruptive markings may act to further increase their effectiveness, particularly for identification of targets. However, it is not known whether this edge enhancement effect is specific to disruption, or whether it could also benefit other forms of camouflage, such as background matching. It is also unclear how background-specific the effects are. Here, we conducted two experiments to test how detection and identification of camouflaged targets is influenced by edge enhancement, both for disruptively patterned targets and for background matching targets. In the first experiment, we used a psychophysics-inspired paradigm to measure the critical duration the target had to be presented for to be detected or recognised. In the second experiment, we created an online 'citizen science' game and measured detection times for targets on different types of visual backgrounds. Overall, we found that disruptively patterned targets were generally harder to find than background matched targets, in accordance with previous results. However, surprisingly, we did not find a clear advantage for edge enhancement in any condition, and in some cases, it in fact made the task easier. Therefore, while edge enhancement may sometimes aid disruption, this effect seems to be highly background specific, and we find no evidence that it can extend to other camouflage strategies.

# Where pheasants go to die: does cognitive ability predict where pheasants get predated?

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Most animals utilise a home range. This is assumed to reflect the importance of being knowledgeable about the location of patchily distributed and unpredictable resources such as refuges, food and mates, and also areas that are most safe from predators. Ultimately, the question of why animals exhibit home ranging behaviour is therefore a cognitive one, and yet no studies to date have explicitly addressed whether variation in cognitive ability relates to space use and mortality within an animal's home range. Using the common pheasant, *Phasianus colchicus*, we tested birds on a battery of spatially-related cognitive tasks before releasing them into the wild, where they were then continuously tracked for their entire lifespans until the point they were predated. We found that birds were disproportionately more likely to be predated on the periphery of their home range, although this did not relate to any of the cognitive measures we tested. I will discuss these results in light of the assumed selection pressures driving the formation of animal home ranges.

### Impacts of artificial lighting on the visual ecology of nocturnal hawkmoths

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Artificial lighting at night is a conspicuous and widespread form of anthropogenic pollution, with demonstrated effects on the natural world, impacting the behaviour of nocturnal animals, plant growth, and the interactions between plants and their pollinators. We studied nocturnal hawkmoths (Sphingidae), which have excellent vision and are ecologically-important pollinators, to comprehensively model the effects of different types of artificial lights on their visual ecology. We tested how multiple light types would affect perception in the context of several key visuallydriven behaviours, from intra-specific communication to predator avoidance and detection of floral signals for foraging and pollination. Using spectrometry, we measured colours from museum specimens of 14 hawkmoth species found in the UK, as well as the flowers and leaves of hawkmoth-pollinated plants and surrounding vegetation. We then modelled how well the relevant colour signals would be perceived, either by the hawkmoths themselves or by potential avian predators, under different lighting types. Our results suggest that artificial lights differentially affect colour perception by hawkmoths and their avian predators, so that some light types, particularly with narrow-band long-wavelength spectra, could be detrimental to hawkmoth behaviour without affecting the ability of potential predators to detect their prey. Our analyses will suggest which aspects of hawkmoth visual ecology may be most vulnerable to disturbance by artificial lighting, and determine which types of lights are likely to be more or less harmful to hawkmoths, providing valuable information to policy-makers considering changes to artificial lighting, such as a move from more traditional lighting types to LEDs.

# Social network structure, long-term associations and reproduction in white rhinoceros

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An understanding of a species' social environment and grouping patterns can be vital for their conservation management. Southern white rhinoceros (Ceratotherium *simum simum*) require intensive management and protection due to the threat from illegal poaching. To maintain genetic diversity, rhinoceros are frequently translocated between different populations. Current translocation strategies take into account the sex, age, and when available, the genetic background of each individual. However, they often do not consider existing social bonds and group dynamics, which may influence individual wellbeing and fitness. White rhinoceros show substantial variation in reproductive success between populations. The impact social conditions have on white rhinoceros reproduction remains unexplored. In this study, we applied social network analysis to two white rhinoceros populations in Kenya, to investigate social structure and natural grouping patterns in the wild. We investigated daily group compositions from two different time-periods, over six months apart, to determine if network structure and inter-individual associations persisted over time. Furthermore, we used individuallevel network metrics to determine if network position relates to female reproductive success. Our results show that whilst network structure changed over time, re-association between pairs of individuals remained higher than expected if individuals were associating randomly, suggesting that associations do persist over time. Moreover, our results suggest that females that preferentially associated in cliques, or that frequently connected sub-groups together, had greater reproductive success. Our study provides new insights into white rhinoceros social structure and reproduction that may be relevant to their conservation and breeding management.

# The importance of animal behaviour in conservation science: the example of cheetahs in Namibia

Bettina Wachter<sup>1</sup>, Jörg Melzheimer<sup>1</sup>, Lisa Giese<sup>1</sup>, Vera Menges<sup>1</sup>, Heribert Hofer<sup>1</sup>

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Studies on the behaviour of elusive and endangered species are challenging and therefore often have to rely on indirect methods such as GPS-collars and camera traps. Nevertheless, such methods have a huge potential, particularly when applying state-of-the-art devices that collect an enormous amount of different data in high temporal resolution and do not interfere with the secretive life of the animals. We used such devices in a long-term study of free-ranging cheetahs (Acinonyx jubatus) living on farmland in Namibia. Many farmers live in conflict with the cheetahs because they perceive them as threat to their livestock animals and thus often kill them. The GPS-collars with integrated acceleration (ACC) devices revealed various movement and behavioural patterns of cheetahs. The most conspicuous patterns were different types of clusters, i.e. locations that cheetahs (re-)visited regularly. Physical visits to the clusters in the field and additional behavioural information from camera traps revealed that clusters (i) were used for intra-and intersexual communication, (ii) displayed a feeding event of a prey animal, (iii) showed the death of a cheetah or (iv) indicated a lair of a female that recently gave birth. This information let us identify risky areas for the cattle calves on the farms and assess the intensity of the farmer-cheetah conflict. Additional GPS data of sympatric living leopards revealed very different movement and cluster patterns. We included all this information to develop new research-based conservation strategies for cheetahs and to evaluate current mitigation methods such as translocations of 'problem animals'.

## Visual tracking of tiny insects using a freely moving camera while reconstructing their environment

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Automatic locomotion analysis (i.e. tracking) of animals has gained popularity in Biology and Ecology. However, current visual tracking systems fail to track tiny animals like insects in their natural environments for three main reasons: (1) the highly imbalanced foreground / background pixel ratio given small or high recording altitude; (2) the highly varying animal / environment appearance (in particular across different species / habitats); and (3) the presence of clutter, frequent occlusions and low foreground contrast. In addition the necessity to recover the 3D structure of the environment and advanced behavioural features like bearing further aggravate the overall task. To address these challenges we developed a global optimisation scheme using factor graphs to detect even tiny animals like ants (< 5 pixel) in videos recorded with a freely moving camera. Novel machine learning techniques featuring rotation equivariance and optic flow strategies yield additional behavioural characteristics and becomes agnostic to the appearance of the animal and environment. This detection mechanism is accompanied by an adjusted Structure-from-Motion pipeline to also recover the environmental reconstructions and globally referenced camera trajectories while addressing so-called critical configurations potentially corrupting correct threedimensional reconstructions. Here we will present the latest results of our tracking and reconstruction system in which we particularly investigate the limits of visual object tracking and the impact of critical configurations on the overall performance.

### Studying Behaviour in 3D

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Most animals live in a three-dimensional environment and interact with it, yet studying collective behaviour in 3D remains a challenging task. To study naturalistic behaviour of a group or an individual it is crucial to develop methods, which enable high throughput measurement of the animal's movement in 3D space. Furthermore, 3D position is often not sufficient, and details such as body posture, orientation, or head position are important to answer many questions in behaviour. We introduce a new set-up design for studying collective behaviour of multiple animals in a relatively large indoor 3D environment (15m x 7m x 4m). The setup consists of a commercially available motion capture system capable of real-time tracking using infrared reflective markers, with additional video cameras to compute posture details of animals using computer vision and machine learning algorithms.

Real time tracking allows the possibility of conducting interactive stimuli based experiments with animals.

Lower tracking latency also allows integration of Augmented and Virtual Reality displays as part of experimental setup and interactive data visualisation. The current methods used for tracking 3D posture and action recognition are largely limited to humans due to lack of appropriate datasets for animals. Our goal is thus to create large-scale datasets with our setup that can then be used by researchers in the field of machine learning to develop new solutions for animal posture tracking. Such collaborations are crucial for the development of methods and gaining new insights from collective behaviour studies in the lab and in the wild.

### Swarm formation characteristics and fear-based modeling of Tetra fish

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Self-organizing motion portrayed by flocking birds, insect swarms, fish schools and even bacterial colonies is perhaps one of the most fascinating and yet inadequately understood phenomena in the field of collective behavior. Swarming is utilized as a primary mechanism for defense against predators, better foraging and mating capabilities and increased hydro/aerodynamic efficiency in long-distance migration events. Although the dynamics of swarming motion has received much scientific attention, more work is required to connect the mechanisms responsible for swarm initiation and formation to modeling efforts. This study investigates swarming in Black Tetra (*Gymnocorymbus Ternetzi*) fish triggered by pseudo predators in the form of approaching objects. High-speed video and tagging techniques are used to analyze the swarm and individuals. Observations include reaction times, swarm formation shapes, velocity, density, leadership within the group, etc. A model is then proposed wherein fish have a simple fear vector based on points they can see in their field of view. Friends appear as small collections of dots but if they are moving quickly a fear threshold is heightened in the observer. Large, fast moving objects exceed the observers fear threshold and they propel themselves opposite to the stimulus. Experiments and simulations reveal similar behavior, patterns, response times and wave speeds. Further, the data reveal that fish can transfer information across large groups faster than their individual reaction times and that the wave propagation is not dependent on fish density.

### Individual heterogeneity and intergroup variance in collective behavior

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Cooperative group activity requires consensus and synchronization among individuals. Thus, individual behavioral tendencies must homogenize within the group. This raises the question of whether individuality disappears altogether in collective behavior, or rather somehow manifested in the overall group behavior.

An extreme example of synchronized group behavior is that of collective motion, the concurrent spatial translation of many individuals. Swarming insects, in particular, can organize in synchronized groups of millions that cover vast areas. We studied marching locust nymphs under controlled conditions in order to uncover the interdependency between variability in the behavior of individuals and that of groups. To this end, hoppers were individually tagged with barcodes, enabling their consistent identification and tracking while walking in a ring-shaped arena. We compared the behavior of single animals, small groups, and virtual, non-interacting groups composed of randomly-shuffled trajectories of individuals from real groups. Two types of behavioral characteristics were identified: (1) those that differ between single animals and groups, while remaining conserved among groups, suggesting their importance in the formation of collective motion; and (2) those that are heterogeneous among groups, but homogenized within a group, and thus give rise to distinct group characteristics. Computer simulations showed that the observed intergroup variance could result solely from the unique combination of the individual locusts composing the group, differing only in their socio-behavioral tendencies. These findings indicate that individual variance can generate distinct group-level characteristics, even in the highly synchronized collective motion phenomenon; and thus demonstrate the importance of individual variance in collective behavior.

# Shall I come again? Site fidelity in a group of Northern Bald Ibis (*Geronticus eremita*)

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With only about 700 individuals left in the wild in the Souss Massa National Park in Morocco, the Northern Bald Ibis (*Geronticus eremita*) is a highly endangered avian species. Little is known about the general spatio-temporal patterns of these birds, which is very important for conservation to protect the remaining colonies and for the success of reintroduction projects. Especially local enhancement and hence simple socially transmitted information of the location of food plays an important role regarding foraging decisions. In the present study, thirty-two Northern Bald Ibises of the free-flying and individually marked colony of the Konrad Lorenz Research Station in Upper Austria were fitted with GPS transmitters from 2013 to 2016. The colony was established in 1997 for basic research of social behaviour and to gain knowledge for reintroduction projects. We studied their movement behaviour with a focus on site fidelity and revisitation rate of foraging grounds within their home range. Generally, individuals showed a high site fidelity and preferred specific foraging grounds over the years with seasonal patterns in the revisitations of the preferred locations. Our results indicate that Northern Bald Ibises are conservative in their use of space and resources and further contribute core-knowledge for reintroduction projects. As the colony forages together or splits up in small groups during foraging, habitat quality cues from specific individuals could be used by other colony members. This knowledge can help to identify such target areas to subsequently protect them in remaining populations or reintroduction projects.

# Signal manipulation alters the integration of social behavior, physiology, and performance.

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Signals that mediate repeated social interactions have the potential to drive dynamic feedback between signaling phenotype, physiology, and the social environment. Thus, signals might play a causal role in generating integrated phenotypes among a set of flexible traits. We previously found that the brightness of the white breast feathers in female tree swallows is correlated with social behavior, corticosterone, and stress resilience. We hypothesized that integration of this suite of traits might be maintained by the experience of repeated social interactions that are mediated by signaling. In this study, we experimentally dulled female breast feathers during the breeding season. We identified ~40,000 instances of an individual visiting a box at which they were not part of the breeding pair using an RFID network. Relative to controls, dulled females initiated fewer trips and were visited less often by neighboring males. Dulled females also differed in several physiological measurements and fed their own nestlings at a higher rate. Ultimately, dulled females fledged significantly more offspring at their own nest despite having similar clutch sizes and initiation dates as controls.

### Distributed information transfer in slime mold Physarum polycephalum

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*Physarum polycephalum*, despite lacking neurons, has demonstrated information processing capabilities that help it thrive in challenging environmental conditions. It is a single-celled, macroscopic, multi-nucleated protist that self-organizes into a complex system of intersecting tubules. *P. polycephalum* is capable of remarkable problem-solving behaviors, but the mechanisms underlying these behaviors are poorly understood. They are believed to be encoded in the cyclical contractionrelaxation pattern of its membrane, which is composed of multiple contractile regions that respond to the quality of the local environment and the contractile pattern of the neighboring regions. In a recent study, we showed that, when P. *polycephalum* tubule segments were given a choice between two food sources, the direction of information transfer varied with the difference in quality between the food sources. In particular, when the food sources differed in quality, the contractile regions near the rejected food source acted as the information sources (i.e., as the drivers of the behavior) and the regions near the chosen food source acted as the information destinations. To explain this counterintuitive result, we will present here a mechanistic model suggesting that the behavior of the slime mold may actually be driven by an increased relaxation of the membrane near the chosen food source relative to the baseline contraction-relaxation activity of the rest of the tubule. Under this new paradigm, we can reproduce our experimental results and propose new testable hypotheses to explore the link between the behavior of *P*. polycephalum and the active matter characteristic of its membrane.

## Fighting cichlids: morphometric and hormonal analysis to understand female and male aggression

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Even though aggression in males has been historically linked to androgens, recent evidences suggest that the key step regulating this behavior involves aromatization to estrogens. Even if females from different species also display aggressive behavior, aggression has been usually studied in males competing for resources and female aggression is still understudied. The challenge hypothesis suggests that behavioral interactions lead to an increase in plasma androgen levels in response to social instability. Cichlasoma dimerus is a monogamous Neotropical cichlid with biparental behavior, in which both males and females show aggressive behavior. In this context, the aims of this study were: a) to perform network correlation analysis of morphometric and hormonal variables in order to understand individual variability in aggressive behavior; b) to determine whether there is a relationship between sex steroids plasma levels and intrasexual aggression in the context of the challenge hypothesis. Sex steroids were determined before and after intrasexual dyadic agonistic encounters and morphometric variables were measured. All agonistic interactions were recorded for one hour and aggressive and submissive displays were determined in each animal. Network correlation analysis suggests that morphometric and hormonal variables can differentially explain individual aggression not only in males but also in females. Moreover, initial estradiol plasma levels can predict winner status and aggression in females, but not in males. Finally, during male encounters there was not only an increase in androgen levels but also in estradiol levels, suggesting that the challenge hypothesis could be extended to estrogens.

### Primate socio-endocrinology revisited: new tools to tackle old questions

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Links between fitness proxies and individual differences in sociality are repeatedly reported in human and non-human primates. Generally, individuals with more social contact or stronger social bonds enjoy benefits such as increased survival and reproductive output. The supporting body of endocrinological evidence, in turn, highlights the negative correlation between physiological stress-levels and secure social bonds. However, due to methodological restrictions, questions regarding the mechanisms that connect social environment (and particularly sociopositive exchanges) and hormone-behaviour interactions remain unanswered. Bio-logging techniques allow continuous and synchronous monitoring of the behaviour and position of multiple individuals within a group, revealing a fine-scale representation of each individual's social environment. Thus, we can address how sociopositive behaviours are given, reciprocated, and distributed across a network of potential partners. This, together with regular and frequent non-invasive assessment of physiological stress-levels (i.e. from urine and faeces), allows us to link short- and long-term hormone profiles to sociopositive interactions. Sixteen Cape chacma baboons (Papio ursinus) were tracked on the Cape Peninsula, South Africa using high-resolution collars built at Swansea University, collecting both accelerometer and GPS data (40 Hz and 1Hz sampling frequency, respectively) for several months. During this period, observational data were also collected, allowing for the comparison of traditional and new methods in the field of socio-endocrinology. Here, we demonstrate the first steps of obtaining grooming data from bio-loggers and present preliminary findings from behavioural and hormone analyses. This work will contribute to a better understanding of the relationship between sociopositive interactions and physiological stress-levels in primates.

### Let it go: macaws wait for better rewards in a self-control paradigm

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The ability to control impulsiveness to gain higher, but delayed pay-offs has been suggested to increase individual fitness and has been demonstrated in several species across different taxa. One of the methods used to investigate self-control is the delayed gratification task that requires subjects to avoid an immediate but less preferred reward in order to obtain a better but delayed one. First results indicate that birds perform comparable to primates in this complex impulse control task.

We performed a delay of gratification test with two different but closely related parrot species: great green macaws (*Ara ambiguus*, AA) and blue-throated macaws (*Ara glaucogularis*, AG). During the task, subjects were given a choice between an immediate lower quality reward (= LQR) and a delayed higher quality reward (= HQR) presented sequentially on a rotating tray. Control conditions were implemented to test for location preferences (i.e. both options contain LQR) and avoidance learning (i.e. HQR comes first). Our preliminary results showed that the AA, on average, tolerated a greater delay ( $\bar{x}$ =23.12s) than AG ( $\bar{x}$ =10.00s), although both species had a maximum delay of 30 seconds. However, the AG showed higher individual variation (SD=10.95) than the AA (SD=8.42).

Notably, the individuals of both species that tolerated higher delays distracted themselves (e.g. manipulating objects) while waiting, which compares with some previously tested species. Overall, the macaw species tolerated delays lower than the few previously tested parrot species, suggesting that the differences in their self-control abilities may reflect adaptations to species-specific foraging ecology.

# High CO2 conditions disrupt cleaner fish cognition but reveals potential for adaptation

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Ocean acidification due to increased CO2 absorption is one of the many consequences of climate change. Various studies suggest that marine organisms' sensory functions will be impaired under extreme scenarios (980 µatm). However, these studies involved short term CO2manipulations and do not consider the potential for adaptation through natural selection. Here we show that the cognitive performance of Indo-Pacific cleaner wrasse, Labroides dimidiatusis unlikely to suffer, at least as long as 750 µatm is not exceeded. After gradual change of pCO2 levels, we acclimated cleaners to both pre-industrial and future scenario levels over 30 days before we tested fish in an ecologically relevant task, the ability to prioritise an ephemeral food source over a permanent one. Fish cognitive performance remained stable from pre-industrial (275 µatm) to present-day pCO2levels (404 µatm). While performance was drastically reduced under both mid and high CO2 scenarios, some cleaners retained a normal cognitive performance under mid CO2, suggesting the existence of tolerant individuals among today's cleaners standing genetic variation where natural selection can act on, as long as strong selection pressure on cognitive performance exists.

### Neurally underdeveloped cuttlefish newborns exhibit social learning

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Learning can occur through self-experience or through the experience of others. The latter allows for adaptive behaviour without trial-and-error, and generally maximizes individual fitness. Given their mostly solitary lifestyle, cuttlefish have rarely been tested under observational learning scenarios. Here we tested if neurally-underdeveloped *Sepia officinalis* hatchlings (up to 5 days) incorporate social information, by observing conspecifics perform a task where inhibition of predatory behaviour is learnt. Our results show that more observers than demonstrators learned the task, while also reaching learning criterion in fewer trials. Moreover, observers always reported less attacks and higher latency time to attack during trials. Our findings reveal the vicarious capability of cuttlefish newborns to learn inhibition of predatory behaviour, potentially through emulation (i.e. affordance learning). Despite ongoing changes on neural organization during early ontogeny, this cognitively-demanding form of learning is already present in cuttlefish early stages, facilitating behavioural adaptation and potentially improving individual fitness in the environment.

# Problem solving in cockatoos and robots: emulating animal cognition with synthetic intelligence

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The growth of comparative cognition has yielded discoveries of Surprisingly Complex Behaviour (SCB) in taxa as different as apes, birds and social insects. Interpretations of SCB based on 'mental' representations, consciousness, or insight have recently re-appeared in scientific publications, but are hard to define operationally and can turn into empirical dead-ends. An alternative is to emulate SCB observations in experimentally accessible frameworks, combining prior predispositions, learning by experience, generalization, working and reference memory, and explicit models of internal representations. This integrates behavioural biology with the rapidly growing field of synthetic intelligence systems, especially autonomous robotics. We are pursuing such an approach, investigating complex problem-solving behaviour by Goffin cockatoos and emulating their SCB in virtual and physical synthetic systems. Our basic task is gaining access to a reward (food or self-plugging in a mains outlet) after opening a cascade of inter-connecting locking devices, and our theoretical tools are both model-based and model-free reinforcement learning algorithms with strong dedicated prior features.

## Heterospecific song quality constitutes social information for settlement decisions in a wild bird

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Heterospecific social information use for breeding habitat selection, i.e. information derived from the observation of other heterospecific competitors and their settlement decisions, is considered as an important behaviour structuring multiguild populations. Because gathering information about possibly dominant competitors may involve agonistic costs, the use of cues acquired from a distance but reliably predicting local success should be favoured. In particular, bird songs are conspicuous signals assumed to reliably reflect producer quality, and thereby local site quality, and could thus constitute valuable information sources for conspecific and heterospecific competitors. It is however unknown whether fine-song features other than simple contact calls may cross species boundaries. We experimentally tested this hypothesis on a wild population of collared flycatchers (Ficedula albicollis), a species known to eavesdrop on great tits (Parus major) presence and performance. Using a playback experiment, we tested whether flycatchers preferred to settle near broadcasts mimicking the presence of a high quality great tit (songs with large repertoire size, long strophes, high song rate), a low quality great tit or a chaffinch (control). Among old females, aggressive ones preferred to settle near broadcasts of high quality tit song, while less aggressive old females preferred to settle near broadcasts of low quality tit song. Male traits did not influence settlement decisions. Thus collared flycatcher females use great tit song qualityfeatures as information for settlement decisions, but differently depending on their own competitive ability and age or experience. These results extend our view of heterospecific social information to fine sexual signals compositions.

## Development and retention times of behavioural performance predict the evolution of plastic behaviour in unstable environments

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Theory shows that high environmental instability selects for fixed rather than plastic phenotypes, because of lag-time constraints (i.e., the time to adapt to environmental change). Since behaviour can change rapidly, the lag-time constraint has been dismissed as not relevant for behavioural plasticity, and it is often argued that responsive behaviour (i.e., plastic behaviour that responds to the environment) should evolve to cope with unstable environments. But performing a behaviour efficiently may require time for learning, practicing or, in social animals, for the group to adjust. Likewise, not using a behaviour can over time reduce its level of performance due to memory constraints, lack of practice, or mismatch with the group. We show, using individual-based simulations, that the evolution of responsive behaviour does not depend on the absolute length of time to develop or to retain behavioural performance, but instead depends on the relation between the two. Above a threshold of development/retention times, increasing environmental instability leads to the evolution of fixed behaviour; below that threshold, responsive behaviour is selected even in maximally unstable environments. Our results generate novel predictions as for when responsive behaviour should evolve, as opposed to more fixed behavioural strategies, such as those seen in animal personality.

## When water meets temperature: behavioral thermo-hydroregulation in a terrestrial ectotherm

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The regulation of body temperature (thermoregulation) and regulation of water balance (define here as hydroregulation) are key processes underlying ecological and evolutionary responses to climatic conditions in wild animal populations. In terrestrial or semi-terrestrial ectotherms, thermoregulation and hydroregulation closely interact and combined temperature and water constraints should directly influence individual performances. However, in ectotherms studies, behavioral and physiological hydroregulation have been overlooked. Behavioral hydroregulation is also often studied independently of thermoregulation, and too few studies highlighted the effect of water on body temperature regulation. We demonstrate how thermo-hydroregulation provides a framework to investigate functional adaptations to joint environmental variation in temperature and water availability. We detail for example why we expect some behavioral conflicts between thermoregulation and hydroregulation, as a heating organism also loses more water. In a second part, we aim at showing some empirical support of this framework with empirical behavioral studies on the common lizard (Zootoca vivipara) in controlled and semi-controlled conditions. The first results of our team highlight different patterns of activity and micro-habitat selection in response to both water and temperature constraints in the environment. This knowledge that still have to get deepened could have important ecological but also evolutionary implications.

# How viewing objects with the dorsal or ventral retina affects colour-related behaviour in guppies (*Poecilia Reticulata*)

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Colours are used for species recognition, aposematic signals, camouflage, and mate choice. In aquatic environments, coloured cues can be viewed from above or below individuals. For small fishes, such as guppies (*Poecilia reticulata*), food is usually found either at the water surface or on the stream bed. These two locations have very different visual backgrounds. Moreover, during courtship, the male generally displays in front of or slightly below the female. Those differences in behaviours may be related to differential expression of opsin genes in the dorsal and ventral retina and between females and males. We tested the spectral sensitivity of guppy males and females with stimuli viewed from below and above the body axes. Twelve different wavelengths, collectively stimulating all of the guppy cones, were tested. We found that wavelength, position and speed of the stimuli influenced male and female behaviour and seems to be mediated by the long wavelength sensitive photoreceptors. Males also had stronger behavioural responses than females whereas females performed more foraging-related pecking behaviour. Our results suggest that the spatial requirement of visual tasks and their ecological context are important and appear to be partly correlated with photoreceptor arrangement in the retina.

### Chimpanzee (Pan troglodytes) navigation in a virtual 3D foraging game

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Primate navigation has been studied in the wild and in captive environments. While captive studies allow for greater experimental control, space limitations severely limit the generalizability of results to natural contexts. We introduced six chimpanzees at Leipzig Zoo, Germany, to a novel virtual 3D testing game. Chimpanzees operated a touchscreen to guide an avatar through a cartoon style arena that contained grassy hills and bushes as well as trees and other obstacles, in order to collect virtual fruit. After training subjects to reliably navigate to the same goal location (a tree with multiple pieces of fruit under it), we presented subjects with novel challenges (e.g. navigating to the same location from different starting points and with different starting orientations; navigating to a novel goal location). Most subjects learned to steer the avatar (walking, turning, orienting on the spot) over a small number of testing sessions. All six subjects learned to navigate to the same goal from different starting points over the course of six to twelve testing days, even when they could not see the goal at first. In addition, three subjects quickly learned to travel to a second, hidden goal location when no fruit was present at the original goal location, with one subject even taking novel shortcuts on its way to the new location. We propose to use virtual 3D testing environments such as this to study potential mechanisms of primate navigation (e.g. path integration, landmark use, cognitive maps) in greater depth than was previously possible.

# Factors shaping the gut bacterial communities of wild red-fronted lemurs *(Eulemur rufifrons)*

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The gut microbiome is important for the development of the gastrointestinal immune response, food digestion, vitamin production, susceptibility to disease and regulation of the physiological stress response. Thus, it plays a pivotal role for the health of an animal. The composition of the gut microbiome of an individual can be shaped by several factors. These include intrinsic factors like age, sex, genetics, and the physiological stress response, and extrinsic factors like diet, social interactions, and gastrointestinal parasites. Particularly, social interactions appear to be key in shaping the gut microbiome composition. To determine the composition of the bacterial gut communities of wild lemurs and their potentially impacting factors, we studied 4 groups of red-fronted lemurs in Kirindy Forest in Madagascar for a period of one year. Fecal samples were collected monthly per individual to determine the gut microbial community accompanied with daily behavioral observations. Preliminary results from 16S rRNA gene analysis showed that the main bacterial phyla present are *Bacteroidetes*, *Firmicutes*, *Spirochaetes*, and *Gammaproteobacteria*. Particularly, abundances of *Bacteroidetes* differed between the groups, suggesting that group membership is key to the gut microbiome composition. Further processing and analysis of the data and samples will address the effects of seasonality, diet, and social interactions on the bacterial community of individuals. Herewith, we contribute to the emerging understanding of the interrelationship of factors influencing gut microbiota compositional dynamics and, thus, central links of the sociality-health nexus in a wild primate.

# Spatial organization of food distribution on the nests of the primitively eusocial paper wasp *Ropalidia marginata*

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In social insect colonies, food transferred through space and time via nestmates carries both nutrition and information. We followed, spatially and temporally, food brought into semi-natural colonies of a tropical paper wasp *Ropalidia marginata*, to understand the mechanism and efficiency of its distribution among adults as well as to larvae. Wasps divided the tasks of bringing food to the nest and feeding larvae, among themselves. Using the analogy of the travelling salesman problem and the Hamiltonian path problem, we found that individuals optimized their routes in order to feed the randomly distributed larvae. Within each feeding bout, different feeders randomly fed larval cells resulting sometimes in repetitive feeding of the same cells by different wasps. This lack of spatial segregation of their feeding effort helped provide redundancy that should avoid larvae going hungry. Considering all the bouts put together, the larvae closer to the centre of the colony were fed significantly more frequently than larvae at the periphery. The cause of this variation could be the nest's geometry and needs to be studied further. The consequence of differential rates of larval feeding can, however, shape the fate of these larvae; previous work has shown that well-fed larvae develop into adults that are more likely to become egg-layers while poorly-fed larvae develop into adults more likely to become non egg-layers. Understanding the spatial organization of food transfer may be a key to understanding how insect societies achieve efficient social organization and division of labour.

## Locomotor adaptations reflect differences in habitat use between four frugivorous rainforest mammals

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Foraging animals move through their habitat responding to a diverse set of environmental and social cues. The exact paths they take as they navigate between resources depends on the interaction between their motion capacity and the physical constraints imposed by habitat structure. We compared the fine-scale movement decisions of four Neotropical frugivorous mammals--capuchins (Cebus capucinus), spider monkeys (Ateles geoffroyi), kinkajou (Potos flavus) and coati (Nasua narica)--during a season when Dipteryx oleifera was the only available fruiting tree species. Using data from high resolution GPS-tracking, drone-based mapping of fruit trees, and LIDAR derived metrics of habitat structure, we built step selection functions to elucidate the environmental features driving individuals movement decisions, and test the hypothesis that species with more specialized locomotor adaptations and stricter canopy use (spider monkeys and kinkajou) show stronger habitat preferences than species with a more generalized locomotor morphology and less restricted canopy use (capuchins and coati). All species preferred taller canopy and avoided routes with high elevation gain, with the strongest effect on spider monkeys and the weakest effect on kinkajou. Semiterrestrial species avoided heavily sloped terrain, with strictly arboreal species unaffected. All species except capuchins avoided canopy gaps and preferred areas with canopy cover, with the strictly arboreal species the most strongly affected. All species minimize their distance to fruiting trees. Species-specific trends in habitat use reflected locomotory specialization, but there was also surprising interindividual variation. Our results demonstrate how different motion capacities result in discrete strategies of habitat utilization given shared environmental constraints.

# Estimation of attraction and repulsion forces working among individuals in feral horses

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Life is dictated by the forces acting upon us. In animal groups, the most representative example is the attraction and repulsion forces that influence group cohesion. The low of attraction and repulsion proposes individuals adjust distance to neighbors, following force working among individuals. Although theoretical studies have reported the effectiveness of this rule, field studies are relatively few, especially in large non-human mammals. Therefore, it is still unknown how these forces actually work among individuals and the effective range of both attraction and repulsion forces. In the present study, we quantified both forces and estimated the effective range by combining the field observation in feral horses with verification by mathematical simulation. Horses are highly social and maintain constant membership within one group. We constructed agent-based models based on a simple repulsion and attraction model and compared it to observed data recorded with UAVs. Metric, topologic, and exponential decay were the interaction types considered in our models. Our results are threefold results. First, metric interaction in our simulated models best fit the observation data. Second, repulsion force was estimated to be a maximum of four body lengths. In other words, horses perceived personal space may be within four body lengths. Third, inter-group differences were found which suggest group interaction range can be plastic or other types of forces influence group cohesion. Our study is one of first to quantify attraction and repulsion forces in feral horses.

### Quantifying exploitative competition in Neotropical frugivores

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Understanding the strength of competition between species over a food resources is an essential element in ecology. When multiple species are dependent on a single common food resource exploitative competition should be at its highest. In 2015-2016 and 2017-2018 we fitted three neotropical frugivores (white-faced capuchin, Geoffrey's spider monkey and white-nosed coati) with high-resolution GPS collars on Barro Colorado Island, Panama, during a season where the primary fruit resource comes from *Dipteryx oleifera*. Flowering *D. oleifera* were identified from drone footage for both years. To ensure the frugivores were in audible or visual range of each other dyadic distances was set to max. 50 m and with at least one individual being within max. 20 m of a fruiting *D. oleifera*. Data from 200 fruit-fall traps (grams/m2/week) was investigated as predictor for number of encounters and encounter durations. GPS data was randomized to investigate if our encounter data was different to random chance. Encounter outcomes were assessed by creating videos of the tracks for the individuals and scored according to three possible outcomes: co-occurrence, displacement and avoidance. Number of daily encounters and daily encounter durations were predicted by *D. oleifera* fruit-fall as both positive, neutral and negative relationships. Encounters were different from random and the primates had the strongest level of competition of in the form of displacements, short durations and fewer encounters. Niche differentiation theory explains how the strength in exploitative competition changes with food availability and this study provides framework to quantify it.

# Which factors influence movement and association patterns of non-breeding ravens?

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Most animal social groups show some form of temporal variation in group size and composition i.e. fission-fusion dynamics. It remains largely unknown which social and ecological processes drive these group dynamics. Common ravens (Corvus *corax*) live as non-breeders in highly dynamic fission-fusion groups during their first three to even more than ten years. They show large individual variation in movement distances (few to hundreds of kilometres) and different durations of temporary settlements close to rich food sources (from days to years). This system leads to repeated associations of many individuals at the same and different locations, where socio-positive behaviour and alliance formation in agonistic interactions can frequently be observed. We studied the effects of sex, age and genetic relatedness on movement and association patterns in non-breeding ravens. Over the last 10 years we individually marked around 300 ravens, estimated their age, collected blood samples, recorded almost daily their associations at a rich food source and additionally GPS-tagged more than 50 non-breeders. Our results revealed no indication for sex differences but with increasing age non-breeders associate with local groups less frequently. Further, non-breeding ravens increase their use of a specific food source, if their nest siblings are present as well. This is also supported by observations from captivity, where siblings often form strong social bonds to outcompete others in rank and access to resources. Together, these results underline the importance of the social environment as a driver for individual movement decisions.

# Visual landmarks and experience affect where and how wild hummingbirds search

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Currently, there are two methods for studying how spatial memory shapes animal movement: the comparative cognition approach which trains animals to use specific cues, but rarely examines the details of movement beyond a few key behaviours; and the movement ecology approach which uses animal-borne trackers to collect the details of animal movement but can only indirectly infer the role of spatial memory. While each approach has its advantages and limitations, they are rarely used in combination. In this study we combined the methods used in comparative cognition and movement ecology to examine how the learning about visual landmarks affects the searching behaviour of wild hummingbirds. We trained wild hummingbirds to find a reward relative to a pair of landmarks, and in tests the reward was removed and the birds' movements tracked in 3D. Using Hidden Markov Models, we classified hummingbird movements into different behavioural states, including 'travelling' and 'searching' and analysed how experience and presence or absence of the landmarks in the test affected: 1) where and when states occurred; 2) the probability of transitions between states; 3) the patterns of speed and turning within each state. The presence of the landmarks not only influenced where hummingbirds searched, but also how birds allocated their time, as well as when birds changed between states, and even the properties of the behavioural states themselves. This study demonstrates the benefits of combining experiments from comparative cognition with analyses from movement ecology, providing both experimental control and insights into the details of animal movement.

# Fruit investigation behaviors vary with color vision phenotype in wild capuchin monkeys

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Senses serve as the interface between animals and their environment and play a critical role in food detection and evaluation. Color and/or scent changes during ripening may attract frugivores and inform their investigation behaviors. While numerous studies have assessed the impact of color on fruit selection, comparatively little is known about fruit scent, and how olfactory and visual data are integrated during foraging. We combine 25 months of behavioral data on 75 white-faced capuchins (*Cebus imitator*) with measurements of fruit reflectance spectra (color) and plant volatile organic compounds (scents) from 18 dietary plant species at different ripeness stages. We show that the frequency of sniffing behaviors - a proxy for reliance on the sense of smell - is positively correlated with increases in the volume of fruit odorants during ripening. Additionally, monkeys with red-green colorblindness (dichromacy) sniffed fruits more often, indicating that increased reliance on olfaction may be a general behavioral strategy that mitigates decreased capacity to detect red-green chromatic contrast. These results demonstrate a complex interaction among fruit traits, sensory capacities and foraging strategies. By examining fruit traits and sensory investigation of seed dispersing mammals, we help elucidate the evolutionary relationships between plants and frugivores and explain variation in primate behavior.

### A Comprehensive Framework for the Analysis of Colour Patterns in Nature

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The behaviour, ecology and evolution of almost all animals is affected by vision, whether that of a competitor, potential mate or predator. Animal vision is hugely diverse, particularly when considering spatial acuity and the range of wavelengths their eyes are sensitive to. What might look like a powerful visual signal to one animal could be perfectly camouflaged to another. Quantifying the appearance of scenes based on the vision of the receiver is therefore essential. To date, colour and pattern have typically been analysed separately, often without appropriate control for viewing distance. A number of sophisticated spatio-chromatic analysis techniques have been devised, but these have rarely been adopted by researchers because they require expensive equipment, prohibitively laborious data collection, and computer coding skills. We have therefore developed the 'quantitative colour and pattern analysis' (QCPA) framework, which offers an unprecedented range of different spatio-chromatic analysis and data visualisation tools, all based on free, open-source user-friendly software. The framework uses calibrated digital imaging, supporting almost any camera type (even smart-phones). These images are converted to animal-vision cone-catch quanta, and then a series of novel algorithms are used to apply acuity and viewing-distance correction, reconstruction of sharp chromatic edges, and the clustering of images into discrete colours. All of the processing makes use of the 'receptor noise limited' colour model together with spatial acuity correction, which we believe makes our framework the most comprehensive, sophisticated and behaviourally validated suite of animal vision analysis tools to date.

# Towards automatic receptive field mapping in 'social state space' by 3D videography

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Measuring mouse social behavior is difficult. Mice are small, their movements are fast, and mice move in 3 dimensions (during mounting, for example). Currently, most studies of social behavior rely on labor-intensive methods, such as manual annotation of individual video frames. These methods are susceptible to experimenter bias and have a very limited throughput. We present an experimental setup and a robust calibration and tracking method that allows us to measure the behavior of multiple freely moving mice in 3 dimensions with high spatial and temporal precision (90 frames/s). In addition to this 3D data, we collect accelerometer data and record ultrasonic vocalizations (which are classified into call types using unsupervised clustering methods). These data allow us to construct a matrix representation of the 3D postures and movements (within and between mice) and patterns of ongoing ultrasound vocalizations - a kind of 'social state space'. This representation gives us a fine-grained read-out of social behaviors and how they change with manipulations of neural circuits. We are currently doing two things: (1) We are working on approaches to analyze this type of data to discover structure in social behavior in a purely data-driven manner. (2) We are combining this behavior setup with silicone probe neural recordings to map firing patterns of both single neurons and networks in the social state space.

### Windows of perception and collective sensing in animal groups

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Pooling of information often allows larger groups to make more accurate decisions than smaller groups. Many models suggest this improved accuracy depends on group members gathering information relatively independently from one another. Is there evidence that group-living animals coordinate the behaviour to sample information independently? Using a virtual prey experiment, I will first show that the visual perceptual abilities of individual fish are limited both in space and time, with self-induced motion reducing individuals' capabilities of detecting prey. This will demonstrate, therefore, that individuals have key 'windows' when their likelihood of detecting information is higher. I will then show that in groups, individuals offset these perceptual windows, thereby making information gathering more independent between one another. Consequently, I will show this independent gathering of information allows groups to detect visual information in their environment that individuals are less likely to detect if alone. This work lends new insights into the strategies animals use to collectively detect information, ultimately leading to more accurate collective decision-making.

# Pair-bond stability does not benefit reproductive performance of breeding pairs

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Pair-bond formation and stability is key for reproduction of mated individuals. Pairbonded individuals engage in reciprocal interactions that facilitate the emergence of cooperative activities that increase reproduction and therefore fitness. Thus, it is key to understand the role of pair-bond stability and the social mechanisms by which individuals can increase their reproductive performance. Here we used a captive population of zebra finches, *Taeniopygia guttata*, a species that form lifelong pairs resulting from mutual mate choice, to characterise the process of pair bond formation, its temporal stability, and how these translate to reproductive outcomes. We used a state-of-the-art high-resolution tracking method to monitor social associations across 180 individuals in 4 replicated aviaries occurring during the prebreeding season, quantifying the strength and stability of the pair-bond, and measuring parameters of following reproduction. Our results indicate that pairbond formation is a complex process. Contrary to our expectations, socially pairbonded pairs that were stable before the breeding season did not started their clutch earlier in the season, nor did they have larger clutch compared to those that were less stable during the pre-breeding season. This indicates, that other mechanisms that favour reproductive performance should be in place, and that perhaps pair-bond stability may have other non-reproductive benefits. These results contribute to better understand the dynamics of processes, such as the development of social structure, and sexual selection, especially in monogamous species.

### Mate encounter in a multimodal duetting system

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Pair-formation strategies are affected by the spatiotemporal distribution of potential mates. The paleotropical false-leaf katydid *Onomarchus uninotatus* exhibits a unique multimodal duetting system. Males use long-range acoustic signals and females respond with short- range vibratory signals, which are then used by males to localise the females. Being a canopy species, this presents a paradox. While male acoustic signals can be perceived over relatively long distances and thus by females located on a different tree, female vibratory responses cannot be perceived by males across trees. For the across-tree scale, we studied the spatial structure of calling males in their natural habitat and, together with information on female hearing thresholds and host plant (Artocarpus spp.) distribution, computed the perceptual spaces of male calls and found that females could hear calls of males from neighbouring trees with a probability of 0.6. We then investigated female responses to male acoustic signals played back from loudspeakers that were not connected to the substrate on which the females were placed. Females typically tremulated first, followed sometimes by initiation of flight, suggesting that females may perform flight phonotaxis to locate calling males on a different tree. We then used a simulation framework to study the optimal mate encounter strategies that males and females can employ at the across-tree spatial scale. We varied the across-tree spatial distribution of the sexes and quantified the encounter efficiencies for different movement patterns, using the data on spatio-acoustic patterning of callers in this system.

# Within-individual variation in divorce and extra-pair paternity in blue tits (*Cyanistes caeruleus*)

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Several studies investigated variation in the frequency of divorce and extra-pair paternity (EPP) between individuals. However, our knowledge about withinindividual consistency and about environmental factors that influence withinindividual changes in mating patterns remains limited. We used a dataset based on 18 breeding seasons from two populations of blue tits to investigate withinindividual consistency in pairing status (divorce), the occurrence of EPP, the number of extra-pair young (EPY), and the number of extra-pair partners (EP partners). We further tested whether between-year changes in levels of EPP could be predicted by changes in the local social breeding environment. Repeatabilities for mating patterns were low to moderate, but significant for the likelihood to divorce in females and for the occurrence or levels of EPP in males and in females. We found no evidence that the presence of the former social partner, the proportion of familiar individuals or phenotypic traits of the neighbours influenced levels of EPP. For females, an increase in territory size was associated with an increase in the number of EP partners and an increased likelihood to gain EPP. Our study indicates that mating behaviour is primarily a context-dependent trait. The expression of EPP might be highly flexible depending on suitable opportunities or coincidental 'meetings' of two individuals leading to variation in within- and extra-pair copulations and on post-copulatory processes. We propose that future research should now focus on potential carry-over effects of the non-breeding or early breeding season on the mating patterns.

### Empirical dynamic modelling for the study of complex mate choice systems in *Poecilliidae*

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Sexual Selection is perhaps the most complex idea in evolutionary biology. It is this seemingly unbound creative potential which makes it so interesting and seemingly difficult to study quantitatively. By leveraging machine-learning and statistical physics, we are beginning to develop robust quantitative descriptions of behavior. Here we present empirical data driven dynamic models of behavior in freely interacting male and female guppies as well as generative models of male ornamentation patterns. The metrics calculated from this representation provides quantitative insight on essential elements of courtship including control and information transfer between individuals and provide an equation-free predictive framework to explore. We highlight the relationships between the variation in ornamental signals and courtship behavior as well as robust quantitative description of female preference and male reproductive tactics. In the future, these techniques and others from complex systems science will provide a rich toolset to further explore the strange manifolds of co-evolutionary aesthetics across taxa.

# A simple efficient foraging strategy to exploit a replenishing resource under competition uncertainty

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Every spring tens of thousands of female lesser long-nosed bats (Leptonycteris yerbabuenae) arrive pregnant to a maternal cave in the Sonoran Desert of Mexico after a long migration of more than 1000 km from central Mexico. During the lactation period, they rely on the nectar, pollen, and fruit of the Saguaro cacti (*Carnegiea gigantea*) as their main food source, while the Saguaro relies on these bats as its main pollinator. In order to reveal the foraging strategy of the lesser longnosed bats, we used miniature GPS devices with an ultrasonic microphone to track bats' movement and behaviour. We used a drone to create a 3D model of the visited cacti fields, characterized the cacti distribution and the number of open flowers. Analyzing bat movements in relation to their food distribution allowed us to identify visits to a specific cactus. We found that lesser long-nosed bats conduct long commutes every night, flying up to 103 km each way from the cave to the foraging site. They concentrate their feeding in a specific area inside the cacti field, visiting specific cacti very often thus maintaining a foraging home-range throughout the night and during consecutive nights. Using a model with minimum memory, we show that bats revisit cacti according to their previous experience. Our results demonstrate a simple efficient strategy for foraging under competition uncertainty.

### Dive Like a Penguin - Foraging Flexibility of Chinstrap Penguins in the South Shetland Islands

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With the expansion of the krill fishery in Antarctic waters, and the disproportionate effects of climate change on the continent, understanding how krill-feeding animals respond to changes in the abundance and distribution of their prey is necessary for the mitigation of anthropogenic threats on Antarctic wildlife. Chinstrap penguins feed almost exclusively on krill, and cannot switch prey species when krill availability is low, thus their capacity to dynamically adapt their foraging behaviour to the distribution and availability of krill will affect their survival into the future. To understand their foraging flexibility, we studied the diving behaviour of chinstrap penguins across 4 islands in the South Shetlands between 2011 and 2016. We compiled GPS and temperature depth recorder (TDR) data from foraging trips of 171 chinstrap penguins, totaling over 388,000 dives, and used unsupervised machine learning to identify the number of dive types, and categorize these dives. We calculated the maximum depth, duration and time spent at the bottom phase of each of each dive, and used the Calinski-Harabsz criterion to identify the number of clusters in the dives based on these three variables. The algorithm identified 3 types of dives overall. Comparing the dives employed during the day and night across foraging trips in the 4 islands, provided novel insights into the diversity of foraging behaviour in the Antarctic predator.

# Resource competition can explain coexistence and switching of collective states in fish shoals

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Animal aggregations are known to exhibit distinct collective forms (or 'states'), such as swarms or polarised groups. While these states can be recreated in simulations, empirical evidence for their adaptive value, and why groups might switch between them, is lacking. We show that responding to an ephemeral food stimulus is faster when fish shoals are in a disorganised, swarm state because of the reduced overlap in the visual fields of individuals. However, once social information becomes available, subsequent arrivals to the food are faster in more organised, polarised groups. By tracking individual identities, we reveal consistent inter-individual variation in the optimal group state. This conflict can explain switching between collective states, driven by competition for resources.

### Stochastic motor control of search behaviour in the model organism C. elegans

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Previous research on *C. elegans* search behaviour has been largely undertaken in short spatiotemporal scales and mainly focused on stereotyped turning behaviour. However, the structural organization of *C.elegans* search trajectories is more complex and spans a wide range of scales, so classic experiments are not able to explore generative mechanisms in whole detail. Here we expanded such classic scales up to 90 min and 24.5 mm2 in an effort to capture high-order trajectory dynamics and patterning. Our results show that *C. elegans* unfolds looping behaviour covering a wide range of sizes and in a time-ordered manner. Based on a microscopic (Langevin) stochastic model we are able to explain the observed variability in terms of speed and curvature motor control, and analyze how the movement of *C.elegans* departs from an elementary stochastic generative process, suggesting that neuromotor control of key movement variables at the microscopic scales modulate a program of (macroscopic) trajectory motifs, such as loops of multiple sizes and variability. We use these results to discuss the theoretical impact of the observed motor control and looping patterns under the perspective of sampling behaviour and search theory.

### The art of diplomacy in vocally negotiating barn owl siblings

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When rivalries are facing to compete for resources, the dynamic behavioural adjustments to the contestant's signalling can be as crucial as the average/maximum signal strength to prevail in competition. Unfortunately, the importance of the realtime signal modulation in conflicts resolution remains understudied, especially using an experimental approach. Here we developed a novel "automatic interactive playback" that directly interacts with a live individual in order to experimentally test the efficiency of different real-time adjustment strategies to become vocally dominant in nestling barn owls (*Tyto alba*) that negotiate for food when parents are absent. We found that to induce the withdrawal of a nestling from competition it is more efficient to match its call duration (i.e. mimicking the live nestling's change) and to mismatch its call rate (i.e. behave contrary to the live nestling's change). In addition, we showed that these strategies are the costliest because they require a larger investment of the playback (more and longer calls) than the less efficient ones, thus indicating the honesty of such behaviours. Our results therefore highlight the importance of real-time signalling adjustment in communication processes over resource competition and emphasize the power of using interactive playback settings to investigate the conflict resolution in animals.

# Cuckoldry in the family: Inclusive fitness benefits can mitigate costs of paternity losses

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Reproduction in many socially monogamous species is not always confined to the pair bond. Females may also mate with extra-pair males, and while this infidelity benefits the cuckolders it also incurs costs for the males that are pair-bonded to those females. Inclusive fitness gains that arise through genetic relatedness among reproducing individuals may dampen the costs that cuckolded males suffer, however this possibility has received scant attention to date. Here, we combine theoretical modeling with a genetic field study to ask whether 1) mating with close kin, or 2) allowing oneself to be cuckolded by close kin, can be adaptive for paired males when they are faced with rampant paternity losses. Using a socially monogamous wild fish, Variabilichromis moorii, we show that paired males possess a higher than expected level of relatedness to their cuckolders causing them to be measurably related to the extra-pair offspring in their nests. We also show that elevated relatedness between paired males and their cuckolders can be adaptive for both parties when competition for fertilizations is strong. Overall, our results show a long-postulated but largely untested -- and therefore under-appreciated -- effect of inclusive fitness on mating interactions; namely that cuckoldry by relatives can offset males' direct fitness losses with inclusive fitness gains, and this effect can be substantial in systems where paternity losses are frequent.

### Impacts of inter-group interactions on intra-group behavioral changes in Javan gibbons (*Hylobates moloch*)

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Agonistic inter-group interactions can cause individual costs such as physical injuries, increased physiological stress, and disrupted intra-group social relationship. Therefore, individuals employ various behavioral strategies to minimize the cost associated with the aggressive inter-group encounters. However, studies on impacts of inter-group encounters on intra-group behaviors are generally lacking, especially in species that live in small groups. We investigated behavioral strategies of territorial and pair-living Javan gibbons in response to inter-group aggression such as I) affiliative behaviors 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 behaviors between pair-partners following the inter-group encounters. However, we found a decrease in grooming interactions after more aggressive encounter but not after lost encounters. During inter-group encounters gibbons significantly altered their activity budgets: they foraged and socialized 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 behavior in gibbon pairs, but provide evidences of changes in activities during encounter and inter-group avoidance through sleeping site selection in gibbons.

#### Foraging as an evidence accumulation process

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The patch-leaving problem is a canonical foraging task, in which a forager must decide to leave a current resource in search for another. Theoretical work has derived optimal strategies for when to leave a patch, and experiments have tested for conditions where animals do or do not follow an optimal strategy. Nevertheless, models of patch-leaving decisions do not consider the imperfect and noisy sampling process through which an animal gathers information, and how this process is constrained by neurobiological mechanisms. We formulate an evidence accumulation model of patch-leaving decisions where the animal averages over noisy measurements to estimate the state of the current patch and the overall environment. We solve the model for conditions where foraging decisions are optimal and equivalent to the marginal value theorem, and perform simulations to analyze deviations from optimal when these conditions are not met. By adjusting the drift rate and decision threshold, the model can represent different 'strategies', for example an incremental, decremental, or counting strategy. These strategies yield identical decisions in the limiting case but differ in how patch residence times adapt when the foraging environment is uncertain. To describe sub-optimal decisions, we introduce an energy-dependent marginal utility function that predicts longer than optimal patch residence times when food is plentiful. Our model provides a quantitative connection between ecological models of foraging behavior and evidence accumulation models of decision making. Moreover, it provides a theoretical framework for potential experiments which seek to identify neural circuits underlying patch-leaving decisions.