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North-west European Section IUSSI

Abstract Book

Plenary Lectures

Professor Lars Chittka (Queen Mary University of London)
Are bees conscious?

Bees have a diverse instinctual repertoire that exceeds in complexity that of most vertebrates. This repertoire allows the social organisation of such feats as the construction of precisely hexagonal honeycombs, an exact climate control system inside their home, the provision of the hive with commodities that must be harvested over a large territory (nectar, pollen, resin, and water), as well as a symbolic communication system that allows them to inform hive members about the location of these commodities. However, the richness of bees' instincts has traditionally been contrasted with the notion that bees' small brains allow little behavioural flexibility and learning behaviour. This view has been entirely overturned in recent years, when it was discovered that bees display abilities such as counting, attention, simple tool use, learning by observation and metacognition (knowing their own knowledge). Thus, some scholars now discuss the possibilities like consciousness in the bees. These observations raise the obvious question of how such capacities may be implemented at a neuronal level in the miniature brains of insects. We need to understand the neural circuits, not just the size of brain regions, which underlie these feats. Neural network analyses show that cognitive features found in insects, such as numerosity, attention and categorisation-like processes, may require only very limited neuron numbers. Using computational models of the bees' visual system, we explore whether seemingly advanced cognitive capacities might 'pop out' of the properties of relatively basic neural processes in the insect brain's visual processing area, and their connection with the mushroom bodies, higher order learning centres in the brains of insects.

Professor Rebecca Kilner (University of Cambridge)
How behaviour changes evolution: experiments with burying beetles

Behavioural ecologists analyse animal behaviour to understand how it is adaptive, and therefore why it persists. In our lab, the focus is slightly different. We want to know how adaptive traits, like animal behaviour, influence the subsequent course of evolution. We address this question by focusing on one social behaviour in particular, namely parental care. Our model species is the burying beetle, a remarkable insect that breeds upon the body of a small dead vertebrate. It shows elaborate parental care, which involves preparing the carcass to make an edible nest for its offspring and provisioning larvae after hatching. I will describe experiments that manipulate the provision of parental care and measure the way in which traits then evolve and adapt, in both parents and offspring. The general conclusion is that there are diverse ways in which behaviour can change evolution.

* indicates presentations by student participants

Oral Presentations

Hamilton's rule and the recovery of inclusive fitness at the level of the individual

Michael Bentley (University College London)

Hamilton's rule shows how natural selection can favour the evolution of a social trait through direct and indirect routes. This follows from Hamilton's definition of inclusive fitness as the sum of all the effects on reproductive success a focal individual has on itself (direct fitness effects) and the effects it has on the reproductive success of others to whom it is related (indirect fitness effects). This way of thinking about the action of natural selection forms the foundations of social evolution theory, and has proved extremely useful as an organising framework for studying the adaptations organisms display for social environments. Recently, however, the theoretical foundations of Hamilton's approach have been questioned. Firstly, it has been argued that because biological interactions are typically nonlinear and fitness effects are not additive inclusive fitness cannot generally be defined at the level of the individual. Secondly, it has been argued that the general form of Hamilton's rule, based on regression coefficients, does not give rise to an inclusive fitness quantity defined at the level of the individual. Here, I unify the foundations of Hamilton's original work with the contemporary version of Hamilton's rule to recover inclusive fitness at the level of the individual. I illustrate the generality of the approach by calculating the inclusive fitness of individuals on social networks with nonlinear interaction effects and strong selection.

Assessing heterothermic fever response in individuals of model bee species across the social spectrum

Victoria L. Blanchard*, James E. Cresswell, David R. Tarpy (University of Exeter)

Bees are regional heterotherms that depend on non-flight thermogenesis (NFT) for pre-flight warm up of individuals and brood incubation at the colony level. Many organisms demonstrate a febrile response to infection either endothermically (by increasing their body temperature's "set-point") or behaviourally (by changing the environmental thermal preference), but the impact of disease on individual thermoregulation in the Apoidea has not yet been fully evaluated. This study assesses the ability of individuals from model species—across the social spectrum—to increase the rate of NFT, generate a higher thoracic temperature, and/or sustain that high temperature in response to an immune challenge. Each species was injected with lipopolysaccharides (LPS) to simulate an infection and febrile response was measured through comparative analysis of rate of warming, maximum temperature, and final temperature to begin to assess the impact of social evolution on the individual immune system. We found that rate of NFT was not affected, *Megachile rotundata* and *Bombus impatiens* generated a significantly higher thoracic temperature in 'infected' bees, and that *Bombus impatiens* maintained this higher temperature. This implies that there is an effect of social grouping on the physiological immune response.

Determining queen number in the ant *Lasius flavus* and considerations for possible causes of social polymorphism.

Gino Brignoli, Emeline Favreau and Yannick Wurm (Queen Mary University of London)

Social organisation in the ants takes a variety of forms, the number of reproductive queens in a colony is one such distinct polymorphism which is relatively easy to distinguish between species. These social structures can also vary within species and recent studies have revealed the genomic basis determining such variation in two distantly-related species. The widely-distributed yellow meadow ant, *Lasius flavus*, was commonly thought to have single queen colonies. However, further research has indicated the likelihood of a degree of social polymorphism within the species. Based on this research and the expectation that social polymorphism is under-recorded in ants we hypothesise that *L. flavus* probably exhibits more than one social form. We examine DNA microsatellite data from workers to unambiguously determine queen number for colonies of *L. flavus* sampled in south-west London (UK) and explore some of the possible factors driving social polymorphism in the ants. Understanding the evolutionary mechanisms behind the variety of ant social forms enables us to explore their highly successful ecological roles.

The spatial and temporal distribution of bumblebee pathogens in their hosts and the wider environment.

Joanne. D. Carnell*, Rosaline. A. Hulse, Sam Page, Dave Goulson & William. O. Hughes (University of Sussex)

Bumblebees (*Bombus* spp.) are experiencing population declines globally. The availability of floral resources and the presence of pathogens are critical factors in their health and survival. Wild bumblebees are naturally exploited by three known, longstanding microbial pathogens (*Crithidia bombi*, *Nosema bombi* and *Apicystis bombi*) and by *Nosema ceranae*, which has more recently jumped from honey bees. Bumblebee pathogens are transmitted horizontally via shared flowers and floral resources are also likely to influence bumblebee resistance or tolerance of infection. Measuring the spatial and temporal changes of all four pathogens concurrently across multiple habitats is needed to understand how food resource availability affects transmission dynamics, and how infection rates in the bumblebee hosts relates to pathogen presence on flower vectors. Here we screened common bumblebee species and the flowers they forage on for the known microbial pathogens. We investigated their distribution across three habitat types in the UK, exploring changes through the season and comparing peak prevalence periods across three years. We also attempt to distinguish between infected hosts and uninfected vectors through targeted organ screening to elucidate the infectivity of each pathogen and its prevalence in the wider environment.

Sight in a clique, scent in society: plasticity in the use of nestmate recognition cues along colony development in the social wasp *Polistes dominula*

Alessandro Cini[1,2], Federico Cappa[2], Irene Pepiciello[2], Leonardo Platania[2], Rita Cervo[2] (1. Centre for Biodiversity and Environment Research, University College London; 2. Università di Firenze - Dipartimento di Biologia)

Nestmate recognition, i.e. the ability to discriminate nestmates from foreign individuals, has been traditionally considered to be predominantly based on chemical cues. Recent empirical evidence however suggests a plasticity in the use of different communication channels according to cues availability in different contexts. In particular visual cues have been shown to influence social recognition in social wasps, but their role in nestmate recognition is still under-investigated. We tested the hypothesis of plasticity in the use of visual and chemical recognition cues in the social wasp *Polistes dominula*, in which the availability and reliability of recognition cues varies across the season. Before the emergence of workers, *P. dominula* colonies are rather small and the variability in the facial pattern might allow resident wasps to use visual cues for nestmate recognition. After workers emergence, the increase in colony members number reduces the reliability of visual cues, thus leaving chemical cues as the most reliable nestmate recognition cues. We thus predict a differential use of chemical and visual cues along colony life. We experimentally separated visual and chemical cues of nestmates and non-nestmates and presented them alone or in combination (with coherent or mismatched cues) to resident wasps to test which communication channel was used in the two colony stages and, in case, how visual and chemical cues interacted. Our results show a differential use of visual and chemical cues according to colony phase, which supports the hypothesis of a plastic, reliability related use of recognition cues in this species.

Bumblebee Social Network Analysis and the Effects of Pesticides on Colony Organisation

Sam Duckerin* (University of Bristol), Prof. Jane Memmott (University of Bristol), Dr. Richard James (University of Bath), Dr. Seirian Sumner (University College London)

The social organisation of bumblebee colonies underpins the ability of the queen and her workers to be able to forage efficiently, care for developing brood, and maintain nest homeostasis in the face of variable environmental conditions, and all without any centralized control. This flexible social behaviour is an emergent, self-organising property of the group, generated from interactions between individual bees and their social and physical environment. The social organisation of the colony is therefore partially structured on the network of interactions between individuals. A new challenge facing bees in today's agricultural landscape is exposure of foragers to sub-lethal doses of non-target insecticides. Neonicotinoids are the most widely used class of insecticides in the world and many studies have shown their negative effects on both individual behaviour and colony productivity. We don't yet understand the dynamics of the process by which

individual-level effects lead to impairments at the level of the colony. Here we use automated video-tracking techniques to produce high-throughput behavioural data for all individuals inside the bumblebee colonies, plus the colony's foraging effort. The high temporal and spatial resolution of the individual tracking data is used to automate the collection of behavioural interactions across the colony. Social network analysis of the interactions allows us to explore the relationship between individually affected bees and the social organisation of the whole colony. Colonies exposed to pesticides show a reduction in network size and in total number of edges (fewer bees and fewer interactions), but the overall structure of the network remains largely unchanged. This suggests that bumblebee colony social organisation may be resilient to the pesticide-induced behavioural changes of individuals. We explore this in more detail by tracking changes in dynamic temporal networks, the division of labour and in dominance hierarchies during pesticide exposure.

Ecological effects of genetic diversity in host-parasite interactions

Sophie Evison (University of Sheffield)

Many parasite infections consist of multiple parasite strains or species, leading to the opportunity for antagonistic or even cooperative interactions within a host during infection. Genetic diversity in the host adds further complexity in understanding genetically diverse parasitic infections. The ecological outcomes of such genetically diverse host-parasite interactions, and the resulting effects on host health are generally poorly understood due to a lack of empirical data. Using the honey bee *Apis mellifera*, and multiple strains of its fungal brood parasite *Ascosphaera apis*, as a model system, we have investigated how manipulating genetic diversity in both host and parasite influences the outcomes of infection in terms of parasite virulence and transmission. By combining experimental biology with genomic tools to dissect this genotype by genotype interaction, we show how trade-offs in a parasite's life history strategy might influence the evolutionary trajectory of such genetically diverse host-parasite relationships. We specifically highlight how complexities in the biology of this particular relationship such as the mating system of the parasite, its method of infection, as well as the host's multi-layered resistance mechanisms can influence infection dynamics and host-parasite co-evolution. Unraveling such complex dynamics is a significant yet often overlooked part of understanding disease epidemiology, but something that has important consequences for managing disease in insect pollinators.

Effects of neonicotinoid pesticide exposure on gene expression in *Bombus terrestris* bumblebees.

Isabel Fletcher*, Thomas J Colgan, Yannick Wurm, Andres N Arce, Ana Ramos Rodrigues and Richard Gill (Queen Mary University of London)

Insect pollinators, including social bees are key to ecosystem stability as well as agricultural yields. There have been recent concerns for declines in social bees worldwide and one of the factors implicated in these declines is the use of pesticides on agricultural crops. Such pesticides are intended against pest species in order to increase crop yields, but pesticides can negatively affect non-target wild social bees. In particular, exposure to neonicotinoid pesticides negatively impacts learning and memory abilities, foraging behaviour and colony survival of social bees. We know relatively little however about the molecular mechanisms by which pesticide exposure affects bee cognition. To address this gap in our understanding, we exposed *Bombus terrestris* bumblebee workers to sublethal concentrations of a commonly used neonicotinoid pesticide, clothianidin. mRNA was extracted from head tissues and sequenced. We found widespread differences gene expression in B. terrestris workers exposed to clothianidin in comparison to a control group. These findings provide novel insight into the molecular response of bumblebees to a common pesticide, identifying candidate pathways for further experimentation. This contributes to the evidence base of the non-target effects of neonicotinoids on wild pollinators, provides a novel manner of quantifying the effects of pesticide exposure and informs the debate on the costs of insecticide use.

Pesticide affects bee brain development resulting in adults becoming poorer learners

Dylan B. Smith, Ana M. dos Ramos Rodrigues, Philipp Bischoff, Farah Ahmed, Andres N. Arce and **Richard J. Gill** (Imperial College London)

Social bee colony success relies on effective foraging across complex landscapes requiring workers (in the case of our study) to possess a high level of learning and cognitive ability. Foragers must learn to associate floral nectar and pollen with an olfactory stimulus to bring back the necessary food to rear colony brood. This associative learning in social bees is considered to be underpinned by the mushroom bodies (MBs) in the brain, in which tissue growth and development occurs during pupal-stage metamorphosis and first few days after eclosion. Any induced stress during these phases could therefore impede MB development potentially leading to behavioural retardation of older bees such as poorer learning performance. One such stressor could be neonicotinoid pesticide exposure as residues: i) are frequently brought back in the pollen and nectar fed to the brood; ii) detected in colonies across the globe; ii) target nicotinic acetylcholine receptors (nAChRs) in Kenyon Cells found to be in high densities in social bee MBs. I will present a study that exposed individuals to a neonicotinoid during brood and early adult development of bumblebees. We investigated its effect on olfactory learning performance using proboscis extension reflex (PER) conditioning, and importantly coupled these findings with respective measures of MB development. Using the latest advances in μCT scanning and 3D image analysis we non-destructively measured the structural components of the MBs in situ at 4μm resolution, and reconstructed the separate MB components for over 90 brains allowing a comparative analysis between our experimental treatments.

Population genetics and colony structure of island and mainland *Bombus terrestris* in the UK and France.

Sophie Hedges* (University of Exeter)

Through their role as pollinators of major food crops, the economic value attributed to ecosystem services provided by bumblebees (genus *Bombus*) is considerable. The global declines observed with in the species therefore generates deserved concern. Several bumblebee species have undergone population bottlenecks and the associated loss of genetic diversity threatens the viability of populations long-term. One impact of low genetic diversity is heightened susceptibility to infection by parasites or pathogens. The varroa mite (*Varroa destructor*) is emerging world-wide and has detrimental effects on both wild and managed bee populations. In this investigation we aim to look on the effects of population genetics of *Bombus terrestris* with regards to the dispersal of Varroa. We will use a comparative network of field sites consisting of populations known to be either infected with or free from Varroa, both on islands and mainland sites within the UK and France. By using fragment analysis of 9 loci across these populations, we aim to assess the genetic diversity between island and mainland populations and how the degree of genetic relatedness of different pollinator species impact the prevalence and transmission of emerging infectious diseases.

Are bumblebees primitively eusocial? The complexity of social complexity

Jacob G. Holland & Guy Bloch (Dept. of Ecology, Evolution & Behaviour, A. Silberman Institute of Life Sciences, Hebrew University of Jerusalem)

Understanding the evolution of social complexity, how originally distinct entities can become integrated parts of larger entities, is key topic in evolutionary biology, which is being increasingly opened up by the ‘big data’ of the post-genomic age. Now more than ever, research in this area must be guided by carefully framed questions with appropriate labelling of social complexity. We suggest that commonly used classifications of social complexity across species falsely imply that social evolution always progresses along a single trajectory, and so have the potential to confuse or hinder research in social evolution. To demonstrate this, we employ published data from several species of bumblebees, and compare them with stingless bees and Attine ants to show that a single organism can have conflicting degrees of social complexity in different traits. Bumblebees possess several social traits consistent with ‘primitive eusociality’, including moderately sized colonies and egg-laying workers, but size-variation across workers, as well size differences between queens and workers, are greater than in most ‘advanced eusocial’ Attine ant and all stingless bee genera tested. These findings reveal both higher and lower levels of complexity compared to other species, depending on the trait measured, demonstrating inconsistencies with species-level definitions of social complexity that do not reflect different trajectories in social evolution. Instead, we propose that focusing on the social complexity

of individual social traits, rather than species, more usefully allows researchers to focus on the mechanisms of social evolution under different selection pressures.

Horizontal transmission of vertically inherited fungal symbionts of *Acromyrmex* leaf-cutter ants

Jack Howe, Morten Schiøtt & Jacobus J. Boomsma (Centre for Social Evolution, University of Copenhagen)

Species belonging to the leaf-cutting ant genus *Acromyrmex* live in an obligate symbiosis with a fungus, which they grow as a clonal cultivar within their nest and upon which they are nutritionally dependent. As in many other symbioses, the fungal symbiont is vertically transmitted through the maternal line: as a virgin queen embarks on her nuptial flight, she carries a fungal inoculum from her natal colony in her infra-buccal pocket, which she then uses to initiate her own colony's fungus garden after mating. This has led many to postulate long-lasting, faithful associations between cultivar and ant lineages, particularly as the ants and fungus possess behavioural and chemical adaptations to prevent the contamination of established fungus gardens by strains from other *Acromyrmex* colonies [1-4]. Although these mechanisms secure monocultures in established gardens, they have also been predicted to allow horizontal transfer of fungi in founding colonies [2]. Such swaps were indeed shown to readily occur in laboratory experiments using garden fragments from mature colonies as replacement cultivars [2], but they have not been documented with natural incipient fungus-gardens in situ. In a large-scale field study, conducted over three years in Gamboa, Panama, we identified clusters of recently settled non-claustral *Acromyrmex* queens, that were still actively foraging before the eclosion of their first workers. We created experimental mosaics of nests, from which either the incipient garden or the tending queen was removed, as well as control nests nearby, that were left intact. We then tracked the movements of colour-marked queens by direct observation, and of fungi by barcoding with 10 microsatellite markers. This showed horizontal transmission of incipient fungus gardens to be surprisingly common, with queens actively searching for nearby nests that they then either stole from or usurped. Our results suggest that there may be active host-symbiont conflicts, not unlike partner choice in other symbioses where symbionts are transmitted horizontally by default.

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4. Ivens, A.B.F., et al., Caste-specific symbiont policing by workers of Acromyrmex fungus-growing ants. Behavioral Ecology, 2009. 20(2): p. 378-384.

Eco-evolutionary modelling of bumblebee communities under environmental stress

Jacob Johansson, Jörgen Ripa and Richard Gill (Lund University, Sweden and Imperial College London)

We develop theory for how the seasonal availability of floral resources shapes the evolution of pollinator communities and how such communities respond to global warming and agricultural intensification. We focus on bumblebees (*Bombus* spp.) and the social phase of their yearly life cycle. Specifically we study adaptation of timing of the colony growth and reproductive phases and one diet preference trait, tongue length. We use mathematical modelling to link resource use, growth and reproduction at the colony level to population dynamics and co-evolution of multiple competing species. We identify evolutionarily stable strategy mixtures, representing species which co-exist in a given environment as the result of long-term evolution, and analyze their responses to environmental changes such as earlier plant growth seasons or the introduction of mass-flowering crops causing intense but short seasonal resource peaks. These evolved communities are relatively stable to resource variation with extinctions expected only for severe resource declines. This is partly due to density-dependent competition. For example, early peaks increases the abundance of worker bees but also competition later in the season, with little net effect on population growth. Environmental changes may however open up the evolved communities for invading species which may outcompete native ones. In particular, we predict that with advancing plant growth seasons, species which establish nests early in the season will benefit strongly from low interspecific competition during the initial colony growth phase. Our analyses thus demonstrates how interspecific competition may influence both the evolution of bumblebee communities and their responses to environmental changes.

Spatial stratification of tropical ant assemblages: do ground ants restrict the foraging distribution of arboreal ants?

Stephanie Law* & Kate Parr (University of Liverpool)

In tropical rainforests ants dominate arthropod fauna in their ecological impact, diversity and abundance. Primary tropical rainforest is vertically stratified into the forest floor, understory and canopy. A growing body of research has shown that the distribution of ant species in tropical rainforest corresponds with this vertical stratification. Ants are abundant in all strata yet species distributions between ground and canopy ants show little overlap, with many species occupying only one strata. Community structure of ants within a stratum has been explained by habitat complexity, associated microhabitat specialisations and by competitive interactions. However reasons behind the existence of vertical stratification and differences between strata are less comprehensive. This research aims to look at how removing competitive interactions influences vertical stratification. We quantified the contribution that ground foraging ants have on the vertical stratification of ant species above the ground. We investigated this using a novel, large-scale manipulative field experiment in an old growth tropical rainforest in Malaysian Borneo where ground ants had been suppressed in treatment plots. By eliminating a whole assemblage of ants and the associated competitive interactions the degree to which it influences the composition of other ant assemblages can be determined. In order to survey vertically, baited traps were placed at 5 m vertical intervals from the ground to the canopy on 3 emergent trees in each experimental plot (4 ant suppression and 4 control plots). Species richness, ant abundance and assemblage composition were compared between suppression and control plots. Suppression of ground ants significantly impacted ant abundance and species richness in the canopy.

The search for genomic imprinting in the social insect, *Bombus terrestris*.

Hollie Marshall*, Zoe Lonsdale and Eamonn Mallon (University of Leicester)

Genomic imprinting is the expression of only one allele in a diploid organism; expression being dependent upon the sex of the parent the allele was inherited from. Haig's kinship theory predicts imprinting exists because of conflict between the matrigenes (maternal alleles) and patrigenes (paternal alleles) of an individual over maternal resource allocation. This theory is also applicable to haplodiploid social insect species, predicting genomic imprinting should, for example, occur with relation to worker reproductive behaviour in social bees. However the existence of genomic imprinting in social insects is currently unknown. Genomic imprinting in mammals and plants is mediated by DNA methylation, many social insects including the bumblebee, posses a working methylation system, meaning the tools for imprinting are in place. While some previous research suggests genomic imprinting may exist, it is only based on gene expression data, methylation as a regulatory mechanism has not yet been associated. To begin to explore this, reproductive and non-reproductive workers from three distinct bumblebee (*Bombus terrestris*) colonies were collected. DNA and RNA were extracted from head samples and sent for whole genome bisulfite sequencing and transcriptome sequencing. Current data analysis has revealed 203 differentially methylated genes between reproductive and non-reproductive workers. These genes were enriched for functions including alternative-splicing, gene silencing and epigenetic regulation of gene expression. These data are now being paired with the RNA-Seq data from the same bee's to further clarify the role of methylation in reproductive behaviour of worker bumblebees.

Bees taste the pollen they collect

Muth, F., Francis, J.S., Leonard, A.S (University of Nevada, Reno)

Pollen is a critical source of protein for bees, but little is known about how these pollinators assess it. Pollen is a contradictory reward from the plant perspective, since it plays a dual role as both gametophyte and a nutritional reward for pollinators. We asked whether foraging bees taste the pollen they collect. Using putatively sweet and bitter pollen blends, we found that chemical composition influenced two aspects of bee behaviour relevant to plant fitness. These findings offer a new perspective on the nutritional ecology of plant–pollinator interactions, as they show that pollen’s taste may mediate its collection and transfer. We are now carrying out follow-up experiments investigating the role neonicotinoids may play on pollen taste perception.

Individual learning performance and exploratory activity are linked to colony foraging success in a mass-recruiting ant

Grégoire Pasquier* and Christoph Grüter (Royal Holloway, University of London)

Learning plays an important role in the life of many animals. In social insects, colony foraging success depends on the combined actions of many individuals and learning contributes to individual foraging success. In many ants, for example, route learning helps foragers to navigate between the nest and a food source. I will present our study exploring the link between foraging success of a colony and the route-learning performance of its individuals. We used a T-maze to assess the route-learning performance of single ants from 12 *Lasius niger* colonies. We also measured workers' pheromone deposition and exploratory activity. We then tested colony foraging performance in a complex maze, set up either as a poor environment (one food source at the end of one tip) or a rich environment (a food source at the end of each tip). We found that individual learning performance was linked to colony foraging success in the rich, but not the poor environment. The propensity of individual ants to lay pheromone correlated negatively with their learning performance and only predicted colony foraging success in colonies with poor learning abilities in a rich environment. The strongest predictor of colony foraging success was exploratory activity, which differed consistently between colonies. Our results suggest that the importance of individual learning for colony foraging success depends on the environment and that explorative activity is an important factor for colony foraging success.

Co-founding ant queens prevent disease by performing prophylactic undertaking behaviour

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Social insects form densely crowded societies in environments teeming with pathogens, but have evolved collective defences that mitigate the impact of disease. However, colony-founding queens that leave the safety of their parental nest lack this protection and consequently suffer high rates of mortality. The impact of pathogens may be exacerbated in species where queens found colonies together, as healthy individuals may contract pathogens from sick co-founders. Here, we investigated two ways in which ant queens may reduce their risk of contracting diseases from infectious co-founders. Firstly, we tested whether ant queens avoid infectious queens when deciding whom to co-found with. Secondly, we studied the behaviour of queens when a co-founder dies, to see if they can prevent diseases spreading from the corpse. Our results reveal that ant queens do not avoid founding nests with pathogen-exposed conspecifics. But, if a co-founder dies, queens perform a variety of “undertaking behaviours” towards co-founder corpses, which have previously only been observed in workers. Importantly, we found evidence to suggest that these undertaking behaviours improved queen survival and hence should also improve their chances of colony founding success.

Urban land-use is linked to higher fitness in a key pollinator

Ash Samuelson* (Royal Holloway, University of London)

Urbanisation represents a major expanding driver of global land-use change, and has been shown to impact negatively upon species abundance and diversity for many taxa. Some groups successfully exploit the anthropogenic habitat, and there is evidence to place wild bees among this number. However, the question of whether land-use directly affects fitness – the ultimate driver of ecological success and evolutionary change – remains a largely neglected missing link in the correlations between urbanisation and species abundance. Here we show that urban land-use is linked to colony reproductive success in a key pollinator by monitoring bumblebee (*Bombus terrestris*) colonies across an urbanization gradient from inner city to rural farmland. Our land-use cluster analysis identified three site categories, and this categorization was a strong predictor of colony performance. Crucially, colonies in the two clusters characterized by urban development produced more sexual offspring than those in the cluster dominated by agricultural land, most likely because they reached higher peak size, had more food stores, encountered fewer parasite invasions and survived for longer. Our results show a link between urbanisation and bumblebee colony fitness, supporting the theory that urban areas provide a refuge for pollinator populations in an otherwise barren agricultural landscape.

Stable isotopes nutritionally link leafcutter ants and their co-evolved fungal symbionts

Jonathan Z. Shik, Winnie Rytter, Anders Michelsen (Department of Biology, University of Copenhagen, Denmark)

Leafcutter ants are the ultimate insect superorganisms, with millions of specialized farming ants and their coevolved fungal cultivars. And, while leafcutter ants are dominant herbivores across neotropical ecosystems, little is known about how these resources are converted to fungus-based food for ants once they are returned to massive underground nests. To better understand these ecological dynamics, we used a stable isotope enrichment experiment to track the flow of 13C- and 15N-labeled nutrients as they were harvested by foragers of the Panamanian leafcutter ant Atta colombica, were used to produce fungus food, were assimilated by ants of different castes, and were disposed of in the trash. Our results highlight rapid conversion of nutrients into edible fungal tissue (swollen hyphal tips ingested by the ants called gongylidia) in the center of fungus gardens. We also find nutrient-specific processing dynamics, with ant workers assimilating 13C-labeled glucose during its ingestion, but requiring several days to metabolically process ingested 15N-labeled ammonium nitrate. By reconstructing nutrient ingestion timelines, we also help resolve a 40 year-old hypothesis, finding that foragers (but not gardeners) nutritionally bypass their fungal crops to directly assimilate fractions of harvested resources. Tracing these nutritional pathways with stable isotopes helps visualize how physiological cohesion within symbiotic networks gives rise to the ecologically dominant herbivory of leafcutter ants in habitats ranging from Texas to Argentina.

Identifying and understanding innovations in social evolution

Daisy Taylor (University of Bristol)

The evolution of sociality in insects is linked with increased differentiation and mutual dependence of queen and worker castes. In insects exhibiting complex social behaviours, individuals lose totipotency, with queens and workers fixed in their roles as reproductive or helpers. This caste commitment is one of the hallmarks of the transition to sociality.

In species with simple societal organisation, totipotency is retained throughout the lifecycle. Any individual has the ability to switch role, and dominance and reproductive status is regulated through social interactions. In some eusocial species, workers lose completely the ability to reproduce over the course of their lifetime. Metapolybia cingulata is one such species; newly emerged females all have the ability to become queens, but older females lose this ability (loss of plasticity). Species such as this offer a valuable opportunity to understand the causes and drivers of losses in reproductive plasticity, since this is likely to be an evolutionary precursor to the developmental commitment of the worker caste displayed in the more complex species, where queen and worker pathways are determined during larval development.

Poster Presentations

Social organisation of the Tree Bumblebee (*Bombus hypnorum*)

Ryan Brock* & Andrew F. G. Bourke (University of East Anglia)

Worldwide declines of bumblebee populations are a major concern because of their importance as pollinators. In this respect, the Tree Bumblebee (*Bombus hypnorum*) represents an enlightening case study, having rapidly spread across the UK since first being recorded in southern England in 2001, and becoming one of the most abundant UK bumblebee species in the process. Thus, in contrast to the majority of other bumblebees, whose populations are either stable, declining or at future risk, *B. hypnorum* appears to represent a species increasing in both range and abundance. Although a few studies have investigated the ecology of *B. hypnorum* in the UK, little is known regarding its colony demography, social organisation, and genetic structure, or whether any of these have contributed to its ecological success. *B. hypnorum* queens exhibit facultative polyandry, which creates within-population, between-colony kin structure variation, so allowing tests of predictions from inclusive fitness theory regarding relationships between kinship, colony productivity, and worker reproductive behaviour. Hence the aims of this recently-started project are threefold: i) to characterise the demography of *B. hypnorum* colonies in the UK population; ii) to investigate their social organisation in light of inclusive fitness theory; and iii) to investigate their genetic structure (including levels of diploid male production). Overall, the results should both help elucidate the ecological success of *B. hypnorum* in the UK and further test the role of kin selection in social evolution in the eusocial Hymenoptera.

Analysis of dynamic networks of ant nests

Dominic Burns* & Elva Robinson (University of York)

In most ant species a single colony inhabits a single nest. However, some species demonstrate a trait called polydomy, whereby a single colony inhabits multiple nests with resources being shared between those nests. *Formica lugubris* is a polydomous species of wood ant that farms aphids for sugary excretions derived from tree sap for their primary food source. By recording the locations of nests in a colony, trees the ants are feeding on, trails of exchange between nests and foraging trails researchers have previously used techniques from network analysis to investigate the way that polydomous wood ant nest networks function and the way that they are structured. However, previous work has focused mostly on the static structure of the networks, yet nest networks are dynamic. Consequently, little is understood about how nest networks change over time, the factors important in influencing change and how they adapt to change. In this project I am using a variety of network methods to investigate dynamicity in polydomous nest networks. Initially I am designing mathematical models and performing statistical analyses of nest networks to produce hypotheses about the way that polydomous nest networks function. I am then using these hypotheses to inform experimental work.

How does individual personality modulate colony level personality? A study in *Myrmica rubra*.

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In eusocial insects, a range of different personality phenotypes have been noted at both the individual and colony level. However, despite the hypothesised importance of colony level personality, the link between individual and group level personality is not yet fully understood. A major difficulty in the investigation of this link is that removing individuals to study the effects of different personality types changes not only the personality profile of the colony, but also the size and composition of the colony. In this study on *Myrmica rubra*, we take a novel approach to the problem of modulating the influence of different individual personalities without altering colony structure. Using a combination of unique RFID tags attached to ants assayed for individual personality, and a sliding colony entrance door controlled by a RFID reader we are able to alter which individuals can leave the colony to respond to different stimuli, without changing the colony size or composition. We hope that this approach will provide new insights into the link between individual and colony level personality.

Information flow through honeybee networks during collective foraging

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Effective coordination of collective behaviour relies upon rapid information transmission between group members. During collective foraging, honeybee workers can use information gained through multiple interaction types to guide their decision-making. The waggle dance provides information on the availability, quality, and spatial location of foraging resources, while olfactory information about food sources can be gleaned from trophallactic interactions or antennal contact with successful foragers. However, we still lack a clear understanding of how the information encoded within these alternative information networks combines during collective foraging and how their relative importance shifts according to behavioural context—e.g., reactivation to known food sites versus recruitment to novel ones. Here, we used a novel variant of network-based diffusion analysis (NBDA) to examine the spread of information through honeybee networks. Two groups of individually marked foragers were trained to separate feeders containing high-quality sucrose solution, one of which was subsequently made unrewarding. We then recorded in-hive interactions between these individuals in order to construct social networks based on dance following, trophallaxis, and antennal contacts. Using NBDA, we assessed the relative contribution of each network in reactivating workers to the feeder on which they were trained, as well as in recruiting workers to a novel feeder. By quantifying fine-scale adjustments in the use of information, our work provides insight into how colony-level outcomes are regulated by multi-layered and dynamic networks of interaction.

Plastic male reproductive investment in the solitary megachilid, *Osmia bicornis*

Rosie Knapp*, Jens van Eeckhoven, Amanda Bretman, Elizabeth Duncan (University of Leeds)

High relatedness, and hence ancestral monandry, is considered critical to the evolution of eusociality. In social Hymenoptera, evidence suggests that polyandry evolved only after the 'point of no return' in which female workers lost their reproductive totipotency. For males, the evolution of polyandry and resulting sperm competition between rivals leads to sexual selection on a range of pre-and post-copulatory mating behaviours. Although it has not yet been studied in Hymenoptera, males from a wide range of taxa are highly responsive to their social environment, and exhibit differential investment in these behaviours depending on the level of reproductive competition encountered. Polyandrous social insects show highly complex mating behaviours, and understanding the mating behaviour of related solitary species may shed light on how these behaviours have evolved. We examined whether the level of reproductive competition influenced male investment in reproductive behaviour in the solitary bee *Osmia bicornis* (Megachilidae) by observing matings of males kept alone or with a rival prior to mating. We found that mounting voracity (the vigour with which the male mounted the female) was higher on average for males kept with a rival. This provides the first evidence that *O. bicornis* males respond plastically to the level of reproductive competition encountered prior to mating. Coupled with previously published data indicating high investment by males in post-copulatory mate guarding and mating plugs, it seems likely that *O. bicornis* females may not be strictly monandrous. This suggests that within Hymenoptera, polyandry may not be restricted to social species, and may have multiple independent origins in both social and solitary lineages. Future studies using genetic markers in wild populations are required to confirm the occurrence and extent of polyandry in *O. bicornis*.

The effect of internal nectar reservoir concentration on commercial bumblebee foraging activity

Callum D. Martin*, Callum Toner & Mark J. F. Brown (Royal Holloway, University of London)

The commercial bumblebee trade is a multi-million pound industry with colonies being transported around the globe to enhance the pollination of a variety of crops. Despite their widespread use, there is little published research on the foraging activity of commercial colonies. Optimisation of their foraging should be a key consideration, as it could enhance crop yields and agricultural efficiency. Commercial bumblebees are shipped with a nectar reservoir directly underneath the nest. If the reservoir is open, bees can access nectar at any time from within the nest. It is possible that this internal nectar resource could affect the foraging activity of bumblebees outside the nest. To test this, commercial bumblebee colonies were placed on Royal Holloway University campus. Colonies were assigned to one of three treatments: access to undiluted nectar reservoir (control), access to diluted nectar reservoir, and no access to a nectar reservoir. Nest traffic was significantly higher in the diluted nectar treatment colonies than in the undiluted and closed reservoir colonies. The highest numbers of pollen foragers were observed in the diluted treatment colonies, followed

by the control, and then the closed reservoir colonies. The colonies in the two treatments with access to nectar also gained significantly more weight during the experiment. These results highlight a possible method of increasing the number of bees foraging outside the nest, which could help maximise the pollination efficiency of commercial bumblebees. This could have important implications for crop production and agricultural efficiency.

Metabolic rate scaling and ventilation patterns in Formica rufa

Craig Perl* (University of Sussex)

Metabolic rate and its relationship with body size is a fundamental determinant of organismal fitness. Alongside various environmental and physiological factors, the metabolic rate of insects is linked with distinct ventilation patterns, defined as either continuous, cyclic or discontinuous. Though associated with higher or lower metabolic rates, the precise role of these ventilation patterns remains uncertain. We determine the allometric scaling of metabolic rate and respiratory water loss in the red wood ant, *Formica rufa*. We also assess the effect of movement upon metabolic rate and ventilation pattern. Metabolic rate and respiratory water loss are both negatively allometric. We observed both continuous and cyclic ventilation associated with relatively higher and lower metabolic rates, respectively. In wood ants, however, movement not metabolic rate is the primary factor determining which ventilation pattern is performed. Conversely, metabolic rate and not ventilation pattern is the primary determinant of respiratory water loss. Moreover, metabolic rate scaling is invariant among wood ant nests unlike some aspects of morphological scaling, suggesting that these two forms of scaling respond to environmental factors in different ways.

The genetic basis of worker reproduction in *Bombus terrestris*

David Prince, Timothy Huggins, Anders Wirén, Irina Mohorianu, Tamas Dalmay, Andrew Bourke (University of East Anglia)

Workers within eusocial insect colonies rarely reproduce in the presence of the queen. While the ultimate reasons for the loss or retention of worker reproduction can be explained in terms of inclusive fitness theory, their molecular basis is less well understood. The bumble bee *Bombus terrestris* is an excellent system in which to investigate the genes involved in worker reproduction in eusocial insects. *B. terrestris* has an intermediate level of eusociality where workers retain a relatively high degree of reproductive ability while generally refraining from reproducing until the end of the colony cycle. We profiled genes differentially expressed in brain, fat body and ovary tissue in ovary-active versus ovary-inactive *B. terrestris* workers using RNA-seq. We found few differences in genes expressed in the brain, an intermediate number of genes differentially expressed in the fat body, and many differentially expressed genes in the ovary. Comparisons with studies conducted in the highly eusocial honeybee *Apis mellifera* identified sets of genes that appear to have conserved roles in worker reproduction. Our results help elucidate the molecular basis of eusocial evolution and enhance our understanding of the reproductive biology of bees.

Testing bee cognition using a radial arm maze

Gregoire Pasquier, **Christopher D. Pull**, Ellouise Leadbeater (Royal Holloway, University of London)

Bees rely upon memory acquisition, retention and retrieval in order to efficiently navigate the complex floral environment in which they forage. Consequently, assaying memory is of interest for social insect biologists from two perspectives: understanding the evolution of insect cognition, and assessing the impact of anthropogenic stressors on foraging behaviour. In this poster, we will present a novel protocol for standardised testing of bee memory, based on an analogue of the radial arm maze (RAM)- a classical psychological apparatus that is typically used to assay pharmacological effects on learning and memory in rodents. We will show how the RAM can be used to assay various aspects of memory, discuss the benefits and drawbacks of applying this approach to bees and present preliminary data on the performance of bees in the RAM. Ultimately, we hope that developing the RAM for use with bees will help us to understand how natural selection shapes and drives the evolution of cognition.

From reproductive control to reproductive constraint; studying honeybee worker sterility through comparison with a related solitary species.

Jens Van Eeckhoven* & Elizabeth Duncan (University of Leeds)

Reproductive division of labour is central to eusociality. In *Apis mellifera*, worker bees are reproductively constrained when a queen is present. Forgoing their reproduction, they: care for brood, forage, thermoregulate and defend the nest. To investigate the evolution of reproductive constraint, we compare the reproductive morphology of a eusocial species (*A. mellifera*, Apidae) to that of a related solitary species (*Osmia bicornis*, Megachilidae; mrca 100 mya). By comparing ovarian morphology and also by examining expression of genes shown to regulate reproductive constraint in honeybees, we aim to discern how molecular pathways were co-opted into regulating worker sterility. Notch signalling, for instance, represses egg-laying under queenright conditions in *A. mellifera*. *Anarchy* and *gemini* (*A. m. capensis*) have been implicated in haploid and diploid egg laying respectively, by workers under queenright conditions. We have established in situ hybridisation to visualise gene expression in the *O. bicornis* ovary and have begun to examine expression of these genes. In future, RNA interference will also be used to determine the function of these genes in the ovary of *O. bicornis*. Did these genes become co-opted in *A. mellifera* from a historical role in control of ovary activity and oogenesis in relation to: food or protein availability, hibernation, nest availability or as a response to mating? Understanding the role of these genes and pathways in related solitary species will help us understand how, over the course of evolutionary time, they have become co-opted into controlling honeybee reproduction.

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