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Abstracts and List of Participants

Organized by University of Würzburg

Thomas Schmitt
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Queen pheromones in social bees

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In most social insect species including honey bees, bumble bees, wasps, ants and termites, queen pheromones play an important role in the regulation of worker reproduction. The proximate mechanisms by which queen pheromones affect worker reproduction are queen control or signals for queen fecundity. Based on the results of more recent studies, in which queen pheromones were found to be correlated with the reproductive activity of a queen, the general conclusion is that queen pheromones are evolutionary conserved signals mainly consisting of structurally related hydrocarbons. However, these results are mainly based on correlative studies, and queen pheromones were not tested in bioassays for their physiological or behavioral activity. Furthermore, several investigations in which behavioral experiments have been performed showed that queen pheromones in bees do not always consist of hydrocarbons. In my presentation I will survey and assess the recent literature on queen pheromones in social bees including the results of own studies on bumblebees and halictine bees. Finally, I will assess methodological approaches used in order to identify pheromonal signals of queens and discuss how they may contribute to our understanding of the evolution of queen pheromones.

Cooperation under the bark: Sociality and fungus farming in ambrosia beetles

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Ambrosia beetles obligatorily depend on fungi for nutrition, which they farm in social societies within wood. This obligate fungus farming evolved at least 10 times independently within the bark beetles (*Scolytinae*) and so they are a great model system for studying the evolution of sociality and insect-fungus mutualism. In this talk I present recent findings (i) on the ecological conditions that favor social fungiculture and how it is selectable experimentally, (ii) how beetles defend their nests against fungal pathogens and (iii) what farming practices beetles employ to maximize fungal yields. Surprisingly, farming beetles succeed by unusual methods like attraction to alcohol, child labour, crop rotation and bacterial fertilization of fungi. In my newly established group we aim for a general understanding of the ecological and genetic factors that are selecting for obligate fungus mutualisms and social behaviours in this group of bark beetles and other plant-living arthropods.

For more information about my group see: www.insect-fungus.com

Prevent a fall - save the life of the queen

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In honey bees (*Apis* spp.), only those larvae that are exclusively fed a large amount of royal jelly emerge as queen bees. For almost a century scientists tried to unravel the secret of royal jelly and searched for a particular ingredient that might serve as a queen determinator. Despite of all of these efforts, no specific compound could be singled out and eventually the balance of nutrients in royal jelly and simply the amount of food that the larvae receive turned out to be fundamental for caste determination. Yet the entire debate about the function of royal jelly has overlooked the major difference between the rearing conditions of queens and workers: the orientation of the larval position. Whereas the horizontal worker cells can harbour liquid food the vertical queen cell cannot. We here show that brood raising bees adjust royal jelly viscosity such that the queen larvae do not fall out of their vertical cells. This is conditioned by the main protein of royal jelly, major royal jelly protein 1, acting as a structural protein to hold the queen larvae on the royal jelly surface.

Social Immunisation in Ants

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Social insects fight disease as a collective. When colony members get exposed to pathogens, their nestmates perform highly sophisticated sanitary care, e.g. by grooming off infectious particles or by applying antimicrobials for disinfection. Whilst this sanitary care drastically reduces the probability of the exposed individuals to fall sick, it comes at the risk for the caregivers to contract the disease themselves. We found that pathogen transmission during sanitary care occurs frequently in ants, but is often limited to such low levels that the care-giving individuals only develop micro-infections, which typically do not cause disease. Instead, they can induce an immune-stimulation and provide protective effects upon secondary challenge with the same pathogen, meaning that social contact to exposed nestmates provides "social immunisation". In nature, ant colonies face a great diversity of pathogens. We therefore studied how broadly this social immunisation protects ant workers against pathogenic threats. We found that pathogens differ in the strength of the protective effect they elicit, and test under which conditions low-level infection with one pathogen may induce cross-protection for other pathogens. Further, we show that not only individual immunity but also the expression of sanitary behaviour of ants is affected by their previous pathogen experience.

Information use and value perception in social insects

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Social insects have many different information sources available to them when making decisions, including several types of memories, various internal states, and multiple sources of public and social information, such as communication from nestmates. An individual worker must integrate these information sources to make sensible decisions. We find that while social information is very important for both individual and collective decision making in ants, private information plays a critical, and often underappreciated role. Route memories may outcompete pheromone trails when the two conflict, and can trigger collective decisions. Combining route memories with pheromone communication allows for a composite collective decision to be made, with the strengths of both information sources. Additional information sources, such as on-trail food sharing, can completely change a workers' response to other information sources, such as memories and pheromone trails. All this information integration is aimed at choosing the most valuable course of action. Animals are often considered economically rational, in that they assign fixed values to resources of fixed absolute qualities. However, humans show relative value perception – i.e. the value assigned to a resource is affected by many things extrinsic to the resource itself. Our research shows that ants also show relative value perception. Ants which expect high quality food but receive medium quality food undervalue the medium quality food, and vice versa for an expectation of low quality. This demonstrates that ants value qualities relative to a reference point, much as humans do. We also found that value perception is affected by value-neutral changes in food quality: ants devalue food which is different, but not worse, than what they expect. Most counterintuitively, we show that ants overvalue food which they had to work hard for. The many parallels between humans, non-human vertebrates, and insects suggest that relative value perception is a strongly adaptive behaviour, and that social insects can be valuable models of behavioural economic behaviour. Only by understanding how animals perceive value can we fully understand the decisions they make.

A germline-soma-analogy for understanding the remoulding of the fecundity-longevity-trade-off in a highly social termite

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Ageing occurs in most organisms and appears to trade off with fecundity. In some organisms, such as queens of social insects, this trade-off is apparently absent, allowing individuals both long life and a high reproductive rate. An extreme example is the mound building termite *Macrotermes bellicosus*: queens and kings can live for up to 20 years and concurrently lay ~20.000 eggs per day while workers live only few weeks. Investigating the connection between fecundity, longevity and sociality we compared transcriptomes of young and old queens, kings and two sterile worker castes.

We found few/ no genes to be differentially expressed between young and old queens/ kings that differed in age by six years. By contrast, old and young major workers had several thousand genes differentially expressed while 77 showed age-related expression in minor workers. Strikingly, minor workers can develop further into soldiers, whereas major workers represent a terminal and short lived disposable caste. We compare the expression patterns between different taxa and will provide evidence supporting the superorganism concept. In this highly social termite, mechanisms underlying ageing between castes resemble those in solitary organisms separating the germline from soma, suggesting an evolutionary transition in organismal individuality.

Thymus vulgaris essential oils and their potential function in disease defence

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Host-plant-parasite interactions of pollinating insects and their foraging target plants are mainly studied on the host-parasite or host-plant but rarely on plant-parasite level. However, for pollinating insects foraged products present an additional tool for fighting against parasites and pathogens. Especially honeybees take advantage of self-produced gland secretions and foraged hive products facilitating medication and sanitation of the colony. Especially secondary plant metabolites in nectar and honey are known for their antibiotic effects which are used by individual worker bees and are transmitted via trophallaxis to the whole colony. Here we show the antimicrobial potential of several Thymus vulgaris secondary metabolites (6 monoterpenes, 3 acetates) against bacteria associated with European foulbrood disease in the honeybee *Apis mellifera*. A high-through put cell growth inhibition assay was used to estimate the substrate specific IC50 for each bacterial strain. Comparing the results across all tested strains, carvacrol and thymol showed to have the highest antimicrobial activity, whereas the three acetates performed worst. The only exception is the bacterium *Paenibacillus alvei* being more sensitive to more complex monoterpenes than the other strains. Synergistic effects may increase the inhibitory effects observed for single substances, as T. vulgaris essential oils are mixtures of monoterpenes and acetates. Overall, it seems possible that increasing chemical complexity may lead to less antimicrobial activity of the tested secondary metabolites.

Species-specific patterns of slavemaker and host phenotype evolution

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The transition to parasitism is a drastic shift in lifestyle, involving rapid changes in gene structure, function, and expression. After the establishment of an antagonistic relationship, parasites and hosts co-evolve through reciprocal adaptations resulting in an evolutionary arms-race. Repeated evolution of social parasitism and slavery among *Temnothorax* ants allows us to examine gene expression patterns as well

as selection signatures characterizing slavemaker raiding and reciprocal host defensive behavior. Previous studies of *Temnothorax* provide evidence for co-evolving adaptations between parasites and hosts. This includes diverging raiding strategies between slavemakers, as well as shifts in host defense portfolios under parasite pressure. Through comparative gene expression analyses, we find that slavemaker raiding behavior is characterized by a down-regulation of numerous genes relative to their non-raiding state, and only a small number of genes shared expression between slavemaking species. In contrast, hosts possess a higher ratio of commonly-to-privately over-expressed genes. Moreover, we were able to identify numerous genes with signature of selection. Again, there was little overlap among species pointing to species-specific adaptations rather than convergent trajectories during the evolution of the slavemaker and host lifestyles.

Saving the injured: wound treatment and selective help in the ant *Megaponera analis*

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Infections are a major hazard for social insects, being especially prone to them due to low genetic diversity and large aggregations of individuals within the nest. Open wounds in the form of cut off extremities pose a major health and infection risk for individuals. We therefore analysed the behavioural response both on the social and individual level of the termite-hunting ant *Megaponera analis* towards open wounds. *Megaponera analis* raids termites in groups of up to 600 ants at termite foraging sites.
During these raids some ants get injured by soldier termites (in the form of cut off extremities). After the fight these injured ants get picked up by their nestmates and carried back to the nest. Within the nest we now observed treatment of the injury by nestmates in the form of intense allogrooming directly at the wound. This treatment focused mostly on the first 30–60 minutes after injury and 12 hours later treated ants were observed to participate again in raids. If treatment was inhibited mortality increased from 10% to 75%. Sterile experiments support the hypothesis that treatment by nestmates prevents infection of the wound. Wound sealing (without treatment) also seems to occur extraordinarily fast, with the wound being sealed/clotted in less than 6 minutes. In addition heavily injured ants (loss of 5 extremities) are not carried back to the nest or treated, interestingly this seems to be regulated not by the helper but by the uncooperativeness of the injured individual. In conclusion we show a multifaceted help system focused on injured individuals, which is not only limited to rescuing the injured by carrying them back from the hunting ground (thus preventing predation of the injured) but moreover includes a sophisticated treatment inside the nest.

Genomic architecture of reproductive division of labor

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I will present a comparative and a functional genomic study that shed light on the genomic architecture of reproductive division of labor. The first, is using inquilines (workerless social parasites) and their hosts to determine what genomic components are worker specific and can potentially be lost in inquilines and the second, uses variation in founding strategies to determine the mechanisms that lead to social polymorphism in terms of reproductive division of labor between queens.

Direct fitness for workers in a *Temnothorax* ant

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Sociality evolved multiple times throughout the history of life, but the degree of cooperation and altruism varies among genera and species. In cooperatively breeding birds and mammals, the experience, safety and resources gained by helpers might result in an increased direct fitness when they later start to produce offspring themselves. In contrast, helpers in eusocial Hymenoptera (e.g., bees and ants), are usually not capable of mating and replacing a fully fertile queen. They therefore do not gain direct fitness in the presence of reproducing individuals.
However, as Hamilton's theory of inclusive fitness shows helpers can nevertheless benefit indirectly from their apparent altruism: helping a relative to rear offspring results in indirect fitness. In addition, helpers in societies of "primitively eusocial" insects may also have the option to obtain direct fitness by inheriting a nest or replacing the reproductive. How important direct fitness is in advanced eusocial insects has rarely been quantified.
Workers of the monogynous ant *Temnothorax crassispinus* are capable of producing males from unfertilized eggs. Previous studies under laboratory condition revealed after the loss or death of the queen workers form a hierarchy, in which high-ranking workers gain direct fitness by producing sons. Our study revealed that natural, queenright colonies contain a percentage of workers with elongated ovaries and developing eggs. We currently quantify the percentage of worker-produced males in queenright and queenless colonies in the field. Additionally, we compare whether queen- and worker-produced males differ in fitness-relevant aspects.
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Leg length, running speed and surface rugosity. An experimental test of the size-grain hypothesis

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Habitat complexity is known to shape the structure and diversity of ant assemblages and can affect competition, and foraging behavior. Many studies found a link between body size, leg length and habitat complexity which is in accordance with the size-grain hypothesis. It suggests that smaller, shorter legged species have an advantage with increasing complexity in comparison to larger and longer legged species, since the former can move through while the latter species must walk across their habitat. The hypothesis is supported by multiple studies and thus "ants in open, less complex habitats are larger and have longer legs" is a common insight. Besides, it is expected that leg length is a good predictor for running speed. While changes in species richness, composition and resource discovery in differently structured habitats are well explored, hardly any study focusses on the running speed of ants in different habitats.
We performed running experiments with differently sized ant species along an artificial gradient of surface rugosity. We measured running speed, number of steps, body size and leg length to answer the question, if morphological traits can be used to predict the running speed of ants in complex habitats. The species with the relatively longest legs were the slowest but could sustain their speed with increasing surface rugosity. Those with relatively shortest legs were the fastest on the flattest surface but their speed decreased rapidly with increasing rugosity. Similar sized species responded very different to high surface rugosity which might be related to species specific habitat preferences. Thus, ants reacted in a species specific manner towards increasing surface rugosity and leg length was not necessarily a good predictor for running speed. If habitat complexity acts as a filter for community composition this may rather be due to resource exploitation ability and competitive ability of each species.

Effect of temperature on the fitness of an ant and its endosymbiotic bacteria

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Endosymbiotic bacteria are present in all insects and their effect on hosts can range from beneficial to harmful. On the one hand, endosymbionts can provide their hosts with essential nutrients or allow digestion of otherwise toxic food sources. On the other hand, endosymbionts can manipulate host reproduction to their own benefit, which often results in substantial fitness costs to the host. Although numerous studies have identified endosymbionts in ants, it remains unclear whether these bacteria affect ant fitness. We use the model ant *Cardiocondyla obscurior* and its two endosymbionts *Wolbachia* and Candidatus *Westeberhardia* cardiocondylae to investigate the relationship between endosymbiont and host fitness. We show that high rearing temperatures significantly decrease endosymbiont levels while substantially increasing colony productivity. In contrast, endosymbiont levels are maximized but colony reproduction significantly impaired at low temperatures. These results show that endosymbionts and their ant host have contrasting temperature optima. Assuming that *Wolbachia* is a reproductive parasite, both symbiont and host should thrive in warm climates. In contrast, if infection with Candidatus

Westeberhardia is beneficial to the host, symbiont and host should fare better at more moderate climates. This complex tripartite interaction is thus predicted to determine the species' distribution range and potential to invade novel environments.

Leader-follower size mismatch impairs teaching in tandem running ants

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Diversity within groups is often assumed to increase group productivity. In social insects, for example, genetic and morphological diversity among workers are thought to increase colony functioning and division of labour. During communication, however, differences between workers, e.g. in body size, could also have negative effects, either due to differences in sensory perception or due to physical constraints. Tandem running is used by ants of some species to guide nestmates to locations of interest, such as food sources or nest-sites and is considered a rare example of teaching in animals. We hypothesised that tandem running is less efficient if leaders and followers differ in size. This is expected if body size affects walking speed, leading to a mismatch in walking speeds, which is likely to increase the chance of tandem runs breaking up. To test this hypothesis, we studied tandem running in the ant *Temnothorax nylanderi* during colony emigrations. We found that larger ants walked faster and performed more successful tandem runs. The success rate of tandem runs rapidly decreased when a leader paired-up with a smaller follower, possibly because of a mismatch in walking speed. However, tandem runs remained highly successful if the follower was the larger of the two ants. Overall, followers of tandem runs were slightly, but significantly larger than leaders. Our study suggests that a leader-follower size mismatch may impair tandem running, but only if the follower is smaller than the leader. Colonies may reduce the risks of unsuccessful tandem runs by employing followers that are significantly larger than the leaders.

DNA and RNA analyses in slave-making ants and their hosts

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The development of a parasitic lifestyle is characterized by several modifications in genome structure and gene function as well as in gene expression.
Slave-making ants in the small tribe *Formicoxenini* as an evolutionary young clade are ideal model organisms to detect the underlying molecular fundament of the drastic behavioral shift from their closely related host species. Slave-makers share other traits that set them apart from their nonparasitic relatives. Therefore, our project intends to detect candidate genes involved in the **co-evolutionary interaction between slave-makers and their hosts.** The *Formicoxenini* are an exceptional hotspot in the evolution of slave making, with at least five independent origins. However, under parasite pressure, host defense patterns shift similarly, suggesting **parallel evolution not only in the different origins of slave-making ant species but also of defensive traits in their hosts.**

Comparative Genomic Analysis will elucidate the complex interplay between genes and their regulation, involving single-nucleotide mutations, contraction or expansion of gene families, transposable elements, and differential DNA methylation.
Given that variations in gene expression do not necessarily come along with changes in DNA sequences, RNA analysis will be an important complementary tool to clarify underlying mechanisms in behavioral changes. Reciprocal adaptations of the resulting co-evolutionary arms races should be reflected in shifts in gene expression. A bigger number of species in the transcriptomic comparison will underpin the genomic results and give additional statistical power.
Sequence analyses of the RNA might also shed light on the evolutionary origin of slave making.

Underground transport of excavated soil in leaf-cutting ants: Influence of CO_2, airflow direction and humidity on workers' preferences for pellet deposition

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The gas exchange in the giant underground nests of the leaf-cutting ant *Atta vollenweideri* is facilitated by a wind-induced ventilation mechanism, with fresh air entering and CO_2-rich air leaving the nest through several openings on the nest mound. On top of outflow openings workers construct small ventilation turrets using soil excavated in the underground and transported to the surface. We hypothesized that workers carrying soil pellets use the climatic conditions inside the nest tunnels to orient and to locate outflow openings. In the laboratory, we tested the preference of pellet-carrying workers for climatic variables in two binary choice experiments. In the first experiment, a group of ants was first exposed during soil transport along a tunnel to either 0.04%, 1% or 5% CO_2, simulating atmospheric levels, good or poor nest ventilation, respectively. Single pellet-carrying workers were then diverted and confronted with a choice between two tunnels providing different CO_2 levels on each side. When the CO_2 in the underground was elevated, workers significantly preferred to transport pellets along tunnels also containing higher levels of CO_2. When exposed to atmospheric or to low CO_2 levels, workers showed no preference during the test. In the second experiment, single pellet-carrying workers were diverted and given a choice between two tunnels, one providing inflow, and the other providing outflow of air with a velocity of either 0, 5 or 10 cm/s, and either 40% or 80% relative humidity. When humid air was provided, workers preferred to transport pellets along outflow tunnels for 5 and 10 cm/s airflow velocity. When dry air was used, workers also preferred the outflow tunnel for 5 cm/s, but changed their preference for the inflow tunnel for 10 cm/s. Results are discussed in the context of nest ventilation and collective climate control.

Population genetic structure of two parabiotic ant-species across French Guiana

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The two neotropical ant species *Camponotus femoratus* and *Crematogaster levior* are obligate mutualists. Both ant species co-occur in so-called ant gardens. Previous studies found that both species possess highly diverse and consistent cuticular hydrocarbon (CHC) profiles, with two distinct chemotypes per species. With a largescale sampling approach across French Guiana, we wanted to investigate whether the different chemotypes of the two mutualistic species are a product of high phenotypic plasticity, or whether these correspond to cryptic species. To this end, we sequenced the mitochondrial gene cytochrome oxidase I of one individual per colony per species. We were able to show a direct link between chemo- and genotype, indicating the existence of cryptic species. Furthermore, we found that the choice of the nest partner is random and not based on genotype (i.e. species). The two *Camponotus* genotypes show an east-west distribution, whereas the two Cr. Levior genotypes are found across the entire range. We will investigate more fine scale population genetic patterns, as well as the effect of various environmental parameters such as temperature, precipitation and canopy cover on the distribution of the four genotypes.

Teasing apart environmental vs inherited components of a termite gut microbiome

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Termites rely on a complex microbial symbiosis to digest plant material such as dead wood and grass. The core gut microbiota is thought to be transmitted vertically via dispersing alate reproductives from the parent colony to new colonies established with a mate from a different parent colony, as well as horizontally between nestmates. Previous work has defined the core microbiome in various ways: using a single colony to represent a species, including multiple colonies over a large distance, or comparing different species across locations. Here we synthesise these approaches, exploring differences between castes, colonies, species, and locations over time, to differentiate the core microbiome of a species, common but not essential gut community members, and environmentally acquired microbes. We find that the number of colonies and castes included in the analysis affects the size and composition of the resulting core. A limited set of vital microbial partners simplifies the potential co-evolutionary interactions and reduces the potential for transmission failure during the colony establishment bottleneck. Microbes common to a location may be resident or transitory, perhaps assisting with the digestion of local foodstuffs by degrading inhibitory plant secondary compounds. Work over longer time scales will be necessary pinpoint the core community and detect seasonal influences.

Oxidative stress in a clonal ant species: the roles of reproductive status and workload.

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In most organisms, the limitation of resources prevents investment in both reproduction and self-maintenance at the same time. As a consequence, fecundity is often traded off against longevity. Oxidative stress, a state of imbalance between damaging free radicals and antioxidant cell defenses, has been proposed as a proximate factor modulating this trade-off. In social insects, however, this relationship seems to be inverted, resulting in a long-lived, highly fertile queen caste and a short-lived, sterile worker caste. Previous research on oxidative stress provided equivocal results and the mechanisms underlying the trade-off in social insects are still poorly understood.
In the clonal ant *Platythyrea punctata*, workers can produce female offspring by thelytokous parthenogenesis from unfertilized eggs. Nevertheless, its colonies are characterized by a well-ordered reproductive division of labor. One, rarely several individuals monopolize reproduction through dominance interactions within the colony. These reproductives, though genetically and morphologically identical, live significantly longer than their submissive, non-reproducing conspecifics, which handle all other tasks. Therefore *P. punctata* provides an ideal model to study the proximate causes of ageing, while avoiding confounding factors. To investigate the effects of induced oxidative stress on the survival of reproductive and non reproductive workers we administered Paraquat, a common herbicide known to increase the formation of free radicals. We showed that reproductive status, as well as age and workload influence the susceptibility to oxidative stress. Our results indicate that oxidative stress could indeed play a role in mediating the reversal of the trade-off between longevity and fecundity in social insects.

Differentiation of immune response with castes in termites by de novo transcriptome sequencing

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Eusociality is one major evolutionary transitions, during which the division of labor is considered as the hallmark feature. This character of evolution, also interpreted as task specialization, is associated with multiple morphological, physiological and behavioral adaptations required for brood care, foraging, and defense. With these adaptations which ultimately cause the formation of castes in insect sociality (mostly in termites, ants, some bees and wasps), while whether immune system is related to eusociality in termites is rare understood. We hypothesis that immune system in termite sociality had also differentiation along with the formation of castes. We address this issue by exploring the immune responses of different castes with de novo transcriptome sequencing. After injection with cocktail of heat-killed pathogens (*Pseudomonas entomophila, Bacillus thuringiensis, Saccharomyces cerevisiae*), the mRNAs from false workers, soldiers and reproductive of *Neotermes canstaneus* were sequenced. We found much more genes are regulated (1420 genes downregulated and 398 genes upregulated) in reproductives compared to soldiers (90 genes downregulated and 108 genes upregulated) and false workers (135 genes downregulated and 71 genes upregulated). In these upregulated genes, reproductives had 54 same genes as soldiers, while only 7 same genes as workers which almost is same number between soldiers and workers. In the downregulated genes, reproductives shared 50 and 41 same genes as soldiers

and workers, respectively. Besides, soldiers and workers had 29 same downregulated genes. From these findings, it is indicated that the immune system differentiates with division of labor during eusociality in termites.

Phylogenetic relationships and genetic variation of Australian *Amitermes*

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The Australian *Amitermes* Group (AAG; Blattodea: Termitidae) currently consists of 5 genera and 100 described species. These termites are considered to be ecosystem engineers altering their environment substantially *via* nutrient cycling and soil enrichment. In addition, they provide food and habitat for many other species and have evolved traits that are highly unusual in the termite world, including unique foraging behaviours and nest parasitism. However, almost nothing is known about the relationships between the species or how their ecological niches may have shaped and been shaped by their unique characteristics. As a first step, phylogenetic relationships and genetic variation within a selection of Western Australian *Amitermes* were investigated using whole mitochondrial genomes (mitogenomes), and mitochondrial (mtDNA) and nuclear ribosomal DNA (rDNA).
Mitogenomes of ten *Amitermes* and five *Drepanotermes* species were used to calculate Bayesian inference and maximum likelihood trees. The results suggest that *Amitermes* and *Drepanotermes* constitute a single clade rather than sister genera, whereby *Drepanotermes* are the most derived *Amitermes*.
Cytochrome oxidase II (COII) mtDNA and internal transcribed spacers 1 and 2 (ITS1 and ITS2) rDNA were used to investigate intra- and interspecific variation of *Amitermes* and *Drepanotermes*. Genetic variation between and among species was generally low, resulting in unresolved, polytomous branches in single-marker trees. Tree topology differed between the two types of markers, so although resolution improved greatly in a multi-gene tree, a few taxa were positioned erratically. Additional markers and species will be needed to test whether this is simply due to a limited number of informative sites or perhaps hybridisation/introgression between species. Further work will map ecological and reproductive traits onto our expanding AAG phylogeny.

Diet specialization in neotropical army ants

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Army ants are top arthropod predators in tropical ecosystems. During their daily mass raids thousands of army ant workers roam the forest in search for living prey, considerably affecting prey populations. Despite their important ecological role, little is known about the diet of most army ant species. We conducted a large-scale diet assessment of army ant species in a Neotropical community known to have a particularly high army ant density, i.e. that of La Selva Biological Station (Costa Rica). Over a period of nine weeks, we collected prey items of nine surface-raiding army ant species belonging to three genera: *Eciton*, *Nomamyrmex* and *Neivamyrmex*. We noted exact location, time, and the stratum (ground or on tree) of the raid location. We identified adult prey morphologically and immature prey via DNA barcoding.

Altogether, we collected more than 3200 prey items from 233 raids. The prey nearly exclusively consisted of other ants (99%), and most prey items were brood (87%). A first predator-prey network analysis revealed a high degree of diet specialization among army ant species. We also noted a temporal and spatial (ground vs. canopy raiders) differentiation among the studied species. Our results suggest that an important ecological factor facilitating the coexistence of diverse army ant communities is a differentiation in their food niche.

Bees foraging without waggle dance information achieve greater foraging success through a change in foraging strategy

Robbie I'Anson Price *and Christoph Grüter*

The honey bee waggle dance helps bees find high quality food sites, however, its benefit to colony foraging success is less clear. Both empirical and theoretical studies have suggested that the vector information contained in the dance often does not improve foraging success, particularly in environments with evenly spread, relatively poor quality or short lived food sources. We carried out an 18-day experiment in a human-modified temperate environment using colonies that either have normal dance information or disrupted dance information. Surprisingly, we found that colonies with disrupted dances had greater foraging success and showed greater foraging effort than the ones with normal dances. Our results suggest that the bees with access to disrupted dance information reduce the use of social information and increase private information-use and/or exploration when searching for food. We used an agent based model to replicate the conditions of our experiment and found that there are indeed environmental conditions in which it is better not to use social information. Foraging conditions were overall poor during the summer, both in terms of the quality and quantity of food collected by individual bees and we provide evidence to the possibility that human impact may have created landscapes to which the honey bee foraging method is not well adapted.

Phylogenomics and taxonomy: Species delimitation in the fungus-farming ant genus *Sericomyrmex*

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Ants in the Neotropical genus *Sericomyrmex* cultivate fungi for food, and both ants and fungi are obligate, coevolved symbionts. The taxonomy of *Sericomyrmex* is problematic because the morphology of the worker caste is generally homogeneous across all of the species within the genus, species limits are vague, and the relationships between them are unknown. Ultraconserved Elements (UCE's) are phylogenomic markers that have proven useful in resolving both deep and shallow phylogenetic relationships. We used UCEs as to reconstruct evolutionary history and to infer species boundaries in *Sericomyrmex*. We recovered an average of ~990 UCE loci for 88 *Sericomyrmex* samples from across the geographical range of the genus as well as for 5 outgroup taxa. Using maximum-likelihood and species-tree approaches, we recovered nearly identical topologies across data sets with 50% to 95% matrix completeness. We integrated the results of the UCE analyses with the results of morphological studies, which consist of morphological characters and measurements of workers, queens, males, and larvae. Both molecular and

morphological data show that *Sericomyrmex* consists of a lesser number of species than previously described. We identify 9 species-level lineages in *Sericomyrmex*, including 2 new species. This is less than the previously described 19 species, even accounting for 2 species for which we had no UCE samples, which brings the total number of *Sericomyrmex* species to 11. Divergence-dating analyses recovered 4.3 million years as the crown-group age estimates for *Sericomyrmex,* indicating a recent, rapid radiation.

Number and distribution of Yellow Crazy Ant supercolonies across different land use systems in Jambi, Sumatra, Indonesia

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Anoplolepis gracilipes is an invasive species in the tropics and on several oceanic islands. *A. gracilipes* can affect entire ecosystems by forming large polydomous and polygynous supercolonies with extremely high worker densities. In a plot-based study design we compared the occurrence of *A. gracilipes* in the different land use systems forest, jungle rubber, and rubber and oil palm monocultures in Jambi Province, Sumatra (Indonesia). Based on the number of bait plates at which it was encountered within 50 x 50 m plots, *A. gracilipes* was similarly abundant in jungle rubber, rubber, and oil palm but did not occur in forest at all. Furthermore, we conducted a population genetic analysis using mtDNA (900 bp sequence based on concatenated fragments of COI and Cytb) to determine the number and spatial distribution of supercolonies of *A. gracilipes* in Jambi Province. We found six distinct mtDNA lineages of which four were closely related and two were genetically distinct from these four. The six lineages form at least six different supercolonies. In two cases, workers from the same lineages were found in plots as far as 60 km apart, which is suggestive of supercolony budding coupled with human-mediated jump-dispersal. Within plots the distribution of workers from different lineages was spatially distinct, regardless whether mtDNA sequences of the lineages were one mutational step apart or six mutational steps apart. This further supports the assumption that workers from different lineages belong to different supercolonies and that a difference of one single base pair is sufficient to discriminate between supercolonies.

Leaf-cutting ant foragers recall olfactory memories to avoid plants they previously experienced as hard to cut

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Leaf-cutting ants are known to reject previously accepted plants if they prove to be unsuitable for their symbiotic fungus, a phenomenon that involves avoidance olfactory learning. We addressed the question of to what extent olfactory memory also underlies the avoidance of plants previously experienced as hard to cut. Would ants associate an odor with a high cutting effort and would the odor be sufficient to recall such a negative association, leading to a subsequent plant avoidance? In the laboratory, subcolonies of

the leaf-cutting ant *Acromyrmex lundii* were offered "pseudo-leaves" of two inert materials of different thickness scented with different odors over three days, to allow workers to gain experience with them. Before the foraging experience, the spontaneous preference of workers for the two odors was individually tested using a Y-maze-olfactometer. After the foraging experience, individual odor preferences were quantified again, as well as the group-level foraging preferences for uniform thin leaves scented with the odors previously combined with the thick and thin materials. After having gathered foraging experience on the two materials of different thickness, individual workers developed a preference for the odor they initially experienced on the thin material, and subcolonies foraged more on leaves with the odor paired to it. A similar learned preference for the odor paired with the lower cutting effort was also observed when subcolonies were offered scented leaves of different toughness instead of pseudo-leaves. In an additional experiment offering only scented, transportable discs of tough and thin leaves over three days, i.e., when no cutting effort was needed at all, ants showed no change in their spontaneous odor preference and foraged similarly on both odors, providing indirect evidence for the association of odors with the increased effort required to cut a hard leaf.

Antimicrobial activity of honey against European foulbrood associated bacteria

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In the honeybee *Apis mellifera*, honey is an essential component in brood rearing. It contains several compounds (e.g. sugars, secondary plant metabolites and peptides) with significant antimicrobial properties to fight of a variety of pathogens. Across several brood diseases, European foulbrood (EFB) is one important bacterial disease in honeybees. EFB affects young larvae and can have a severe impact on honeybee colonies. Besides the causative agent *Melissococcus plutonius,* several secondary invading gram-positive bacteria have been identified and were shown to contribute to typical EFB symptoms. Regional and seasonal variation of EFB outbreaks as well as variation in host susceptibility have been observed making it an interesting model to study host-parasite interactions. Here, we investigated potential specific inhibitory effects of honeys from different floral origins against bacteria associated with EFB. We performed a high-throughput microtiter plate assay to determine the antimicrobial activity of several monofloral honeys against EFB associated bacterial species. Comparing growth inhibition effects of tested honeys, significant differences across different bacterial species and a marked specificity of certain honeys could be detected. Furthermore, we tested graded combinations of honey pairs for interaction effects. Our results elucidate the specific antibacterial effects of honey from different floral origin on certain bacterial species while there is no effect on others. These observations most likely are attributed to the diverse compounds varying between honeys and highlight a potential adaptive feature of plant-pollinator-pathogen interactions.

The role of octopamine and dopamine signalling for social learning in honeybees

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Honeybees can learn socially about profitable feeding sites by following waggle dances performed inside the nest by successful foragers. Followers can choose between using this social information to be recruited or use their private memory of a food source they have visited previously. The decision to use social vs. private information may depend on molecular mechanisms of the reward system. In particular, octopamine (OA) and dopamine (DA) signalling in the mushroom bodies might play important roles as these signalling pathways are involved in reward processing. First, we addressed the influence of orally administered OA and DA on dance following behaviour and recruitment probability. We trained bees to artificial feeders and tested whether OA and DA mediated the decision to follow dances to be recruited to an unknown feeder or to be reactivated to their familiar feeder. Due to their different effects on reward perception, we hypothesized that OA would enhance the use of private information and suppress the use of social information, whereas we expected the opposite for DA. Second, we analysed the expression of OA- and DA-receptor genes in the mushroom bodies. In support with our hypothesis, we found that treatment with OA reduced dance following and bees with increased OA-receptor expression preferred private information. DA-treatment increased dance following, but also increased the probability to use private information. The DA-receptor genes showed opposing patterns, with *DopR1* showing a trend to be up-regulated in social learners and *DopR2* being down-regulated in social learners. Overall, our results suggest that OA- and DA-signalling influences social learning in different but potentially cross-linked ways.

Nestmate recognition in Asian honeybees

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In social insects, colony integrity is challenged by intruders from foreign colonies: non- nestmates can try to rob resources or lay foreign eggs, and thereby might transfer pathogens. To maintain colony integrity, a recognition and defending system is required. Cuticular hydrocarbons (CHCs), long chain hydrocarbons attached to insects' cuticles, are known to serve as discrimination cues and trigger defense behaviour in social insects. Within the genus *Apis,* most studies in nestmate recognition and CHCs focus on *A. mellifera*. In our study, we focus on two open-nesting species from south Asia: the dwarf honey bee, *A. florea* and the giant honey bee, *A. dorsata*. In comparison to *A. mellifera and A. cerana*, which nest in cavities, they have a larger colony surface which has to be defended. Furthermore, the spatial distribution of nests differs between *A. florea* and *A. dorsata*. While *A. florea* nests are spread out in the landscape, *A. dorsata* forms nest aggregations in trees containing up to 200 colonies. Due to the low spatial distance between colonies within an aggregation, we assume that the integrity of these colonies is specially challenged. Therefore, we hypothesize that *A. dorsata* shows a more fine-tuned nestmate discrimination than *A. florea*. Support for our hypothesize was found linking behavioural assays and analysis of CHC-profiles of *A. florea* and *A. dorsata.* In addition, comparisons of the CHC- profiles of both species with

those of *A. mellifera* and *A. cerana* reveals general trends in how differences in nesting behaviour are associated with variation in cuticular nestmate discrimination cues.

Life expectancy affects the expression of pro-social and anti-social behaviour in ants

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The effect of experimental shortening of life expectancy on ant pro-social and anti-social behaviour was investigated in tests in which a single worker (normal or moribund) was confronted with another worker (nestmate or alien) attacked by a predator (captured by an antlion larva). During confrontations of workers, several different behavioural categories were observed, classified as either rescue behaviour (towards nestmate ants) or aggressive behaviour (towards alien ants). Analysis showed that soon-to-die ants display reduced propensity for pro-sociality (rescue behaviour towards nestmates) but higher propensity for anti-sociality (aggressive behaviour towards alien ants) than normal ants. Such effect can be considered adaptive and in line with other studies showing similar behavioural changes in moribund individuals of social insects.

Long live the queen, the king and the commoners? Transcript expression differences between old and young in *Cryptotermes secundus.*

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In most animal species a trade-off between self maintenance and reproduction exists but in eusocial insects this trade-off is absent: reproductives of these species live long and have plenty of offspring throughout their lives. To better understand the lack of the longevity-fecundity trade-off and aging in *Cryptotermes secundus* (Kalotermitidae), whole body transcriptomes of old and young individuals were compared. The significantly differentially expressed transcripts between old and young were then contrasted between the castes. The results showed unique patterns in each caste, but more similarities between the reproductives. Our results suggest aging in the reproductives but not in the workers. Taking into account that workers can become reproductives, these results are in accordance with life history theory where low extrinsic mortality can lead to postpone reproduction and to invest in maintenance. Comparing our results to another termite species with a high social complexity and with Hymenoptera we provide evidence that the level of (eu)sociality impacts the aging process.

Prevent a fall - save the life of the queen

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In honey bees (*Apis* spp.), only those larvae that are exclusively fed a large amount of royal jelly emerge as queen bees. For almost a century scientists tried to unravel the secret of royal jelly and searched for a particular ingredient that might serve as a queen determinator. Despite of all of these efforts, no specific compound could be singled out and eventually the balance of nutrients in royal jelly and simply the amount of food that the larvae receive turned out to be fundamental for caste determination. Yet the entire debate about the function of royal jelly has overlooked the major difference between the rearing conditions of queens and workers: the orientation of the larval position. Whereas the horizontal worker cells can harbour liquid food the vertical queen cell cannot. We here show that brood raising bees adjust royal jelly viscosity such that the queen larvae do not fall out of their vertical cells. This is conditioned by the main protein of royal jelly, major royal jelly protein 1, acting as a structural protein to hold the queen larvae on the royal jelly surface

Effects of the insecticide Chlorpyrifos on the ant *Cardiocondyla obscurior*

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Widespread application of pesticides in agricultural landscapes have been linked to a decline in insect abundance and diversity worldwide. Especially the decline of the economically relevant social insects serving as pollinators and pest control sparked an increased interest in understanding the effects of pesticides. The organophosphate pesticide Chlorpyrifos is one of the most widely used toxins worldwide since 1965, and acts by inhibiting acetylcholinesterase in the nervous system. We use the worldwide distributed invasive ant *Cardiocondyla obscurior* to study the effects of sub-lethal doses on direct and indirect fitness of experimental colonies. We find differences in egg-laying rates of queens as well as differences in exploratory behavior and efficiency of brood care of workers between colonies from Brazil and colonies from Tenerife and Japan. A genomic comparison of the Brazil and the Japan population shows that the gene Cobs_00487 which codes for the nicotinergic acetylcholinreceptor nAChRα6 is potentially duplicated in the Japan popuation, which is confirmed with RT-qPCR at the DNA level in the Japan and the closely related Tenerife population. Together these data show the negative effects of sub-lethal doses of Chlorpyrifos on the fitness of social insect colonies. Furthermore, the genomic differences suggest that different history of exposure to pesticide application could have led to the evolution of pesticide resistance, which would make the application of toxins against invasive ants superfluous.

RNA viruses as a driver of bumble bee populations decline

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Managed and wild bee populations have been significantly declining worldwide over the past three decades. While there are a number of reasons why this might be occurring, the increase in prevalence and virulence of viral pathogens is one of the most likely causes of this decline. In bumble bees, some species have remained common while others are declining and we hypothesize that these differences are linked to their ability to evolve resistance towards viruses. In order to test this hypothesis, we collected rare and common bumblebee species from different populations in the Hebrides in Scotland. We will analyze virus prevalence within and across species to determine if there is indeed a difference in viral load between rare and common bumblebees. Moreover, we will look for variation in selection pressure in immunologically linked regions of the genome of common vs rare bumblebees. If common species are resistant to viruses, we should be able to see marked and consistent differences in both these measures across bumble bee species and populations. Overall this work aims to identify potential sites of coevolution between bumble bees and their viruses and ultimately to determine if viruses are a key factor driving bumble bee population decline

Age- and daytime affect octopamine and dopamine receptor expression in the mushroom bodies of honeybee foragers

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Honeybees use the waggle dance to acquire information about the location of profitable food sources. Experienced foragers (older) were reported to follow fewer dances and rely more on memory to locate a food sources compared to younger foragers. Octopamine (OA) and dopamine (DA) signalling in the brain might play important roles in mediating the decision to follow dances (use social information) or return to known food locations (use private information), as they are involved in reward perception. In accordance with this, a recent study has found that systemic treatment with OA and DA affects the use of social and private information in honeybee foragers (see talk by Melissa Linn). Thus, age related changes in dance following might be linked to age related changes in OA and DA signalling. Here, we explore whether the expression of OA and DA receptor genes (*DopR1, DopR2, OctR1 & Octβ2R*) depends on forager age and the time of day. To this end, we introduced newly emerged, marked bees into observation hives and captured them when they were either ~3 weeks (young foragers) or ~5 weeks (old foragers) old. Bees were caught either early in the morning (~9 a.m.), around noon (~12 a.m.), in the afternoon (~4 p.m.) or at night (~10 p.m.). We used qPCR to quantify gene expression in the mushroom bodies, a brain area known to be important for information processing and integration. We found that expression levels of all four receptors were significantly higher in older foragers than in younger foragers. Furthermore, *DopR1* showed significant down-regulation in the morning, whereas *OctR1* showed significant up-regulation in the morning. The expression of the other genes did not change during the day. These results are consistent

with the hypothesis that age and/or experience related changes in waggle dance following are linked to age and/or experience related changes in OA and DA signalling.

Chronic ethanol tolerance in the honey bee

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Honey bees willingly consume ethanol as it is available in their natural environment, for example fermented floral nectar or fruits. To date, several behavioral effects of ethanol intoxication have been described in honey bees, including changes in motor function, disorientation and immobility.
We investigated if chronic ethanol tolerance occurs in honey bees. Our experiment consisted of four groups of bees, lasted for five days and was repeated four times on four different colonies. On each day, we performed a single treatment in which bees were exposed to water or ethanol. Bees received water on each day in group one, water for four days, and then ethanol in group two, ethanol on each day in group three, and ethanol for four days, and then water in group four. Results of motor performance, measured on each day, showed that individuals which were repeatedly exposed to ethanol (group three) developed better ability to cope with intoxication than individuals which previously did not have an ethanol experience (group two). Further, bees with past ethanol experience (group four) showed no motor impairment when compared to normal individuals (group one).
Chronic ethanol tolerance is one of the hallmarks of alcohol abuse. Here, we present the first evidence that it occurs in honey bees and thus expand our knowledge about these animals as models in alcohol research.

Bees rely on their sense of taste to assess pollen nutritional composition

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Pollen represents a main source of nutrients for many flower-visiting animals including honeybees and bumblebees. Studies have shown that an unbalanced protein supply is detrimental to bee colonies. Hence, the ability to differentiate between different pollen types, to detect the pollen nutrient content and to assess its overall quality would be highly beneficial as it allows for composing an optimal diet. In previous studies, we could already show that bees are able to discriminate between different pollen types and pollen qualities. However, the mechanisms behind this capability are still not understood.
For a better understanding of these mechanisms, we (1) used chemotactile conditioning of the proboscis extension reflex (PER), (2) developed a new technique to measure electroantennogram (EAG) activity with chemotactile stimulation and (3) performed feeding assays to test how bumblebees (*Bombus terrestris*) and honeybees (*Apis mellifera*) are able to differentiate between pollen of different nutrient concentrations.
Both *Bombus terrestris* and *Apis mellifera* workers use their sense of taste to discriminate pollen of different nutrient content. Bees seem more sensitive to fatty acids and less to amino acids, as revealed by PER experiments as well as in feeding assays. However, EAG activity indicated that receptors of the antennae are principally able to receive amino acids.

Mechanisms of social organization in honeybees (*Apis mellifera*)

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Division of labor is a hallmark of social insects. In honeybees, social organization involves sequential transition of sterile female workers from one task to the next. While young bees remain in the center of the nest and provide food for the larvae ("nurse bees"), older bees produce wax and build new combs ("builders"), or remove dead bees from the colony ("undertakers"). The oldest bees of a colony leave the hive and become foragers. Among the foragers, some bees collect pollen, others collect nectar and again others forage for water or propolis. The social organization of a honeybee colony is highly plastic and can rapidly adjust to changes in the environment or within the hive. How the complex and yet plastic division of labor is regulated is still a mystery.
A widely accepted hypothesis suggests that workers performing different tasks should differ in their sensory response thresholds for task-related stimuli. Individuals whose response threshold is exceeded, begin to perform the associated task. Division of labor works, because individuals of a colony differ in their sensory response thresholds.
Our data provide direct support for this hypothesis, showing that bees performing different tasks in the hive indeed differ in their sensory response thresholds. Looking for molecular mechanisms underlying division of labor in honeybees, we identified a number of candidate genes for sensory responsiveness and division of labor. These include genes encoding biogenic amine receptors. We show that bees performing different tasks differ in the expression of these genes. Activating the respective proteins pharmacologically modulates sensory responsiveness of bees. Immunohistochemistry with our specific antibodies against the respective proteins reveals their expression in brain areas involved in the processing and integration of sensory information. Taken together, our data suggest that division of labor is based on different sensory response thresholds which, in turn, are modulated by specific biogenic amines and their receptors.

Visual memory formation in bees: neuroanatomy and genetics

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Honeybees and bumblebees provide valuable model organisms for memory formation in miniature brains, as they are capable of an astonishing variety of cognitive performances despite their small brain sizes. However, in contrast to odor learning, processes that facilitate storage of visual information are poorly understood in bees. By combining behavioral learning experiments with the analysis of neuroanatomical changes and differential gene expression, we aim at shading light on the mechanisms of visual memory formation. Here we examined the capacity of eusocial bees to learn and retrieve color information in different behavioral assays, including conditioning of the proboscis extension response (PER). Additionally we investigated the functional role of central brain parts, the mushroom bodies, in color learning and monitored differential expression of immediate early genes associated with visual stimulation.

Distribution of parabiotic ant species from South America with highly diverse cuticular hydrocarbon profiles

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Mutualistic interactions often lead to diversification in complex phenotypic traits among the mutualistic partners. Diversification in a sexually selected trait may ultimately lead to separation between populations and as a result to speciation. One complex phenotypic trait is the insect cuticular hydrocarbon (CHC) profile. CHCs primarily are crucial as a barrier to water-loss but secondarily evolved important functions in insect communication, e.g. nestmate recognition in social insects. In tropical South America, the parabiotic *Crematogaster levior* and *Camponotus femoratus* ants, which commonly share a so called ant garden as a nest, show highly diverse cuticular hydrocarbon profiles. Both of the species occur as two qualitatively different chemotypes, although there are no known morphological differences. One chemotype of either species shows a higher abundance of unsaturated hydrocarbons and the other one more saturated methyl-branched substances. However, also within the distinct chemotypes, there is a rather unusual quantitative diversity of different hydrocarbons. To quantify and explain this diversification we used a large-scale sampling approach in French Guiana along an east-west gradient. With this we aimed to (1) examine the CHC differences within and between the chemotypes, (2) find out if there is any geographical pattern in the distribution of chemotypes, (3) if there are any climatic influences on the CHC profiles and the distribution of chemotypes and (4) if there are preferred associations between the two mutualistic partners. In both genera we found the chemotypes to be clearly distinct from each other. For the distribution, we found one of the *Camponotus* chemotypes to be nearly missing in the eastern part of French Guiana, which is known to have a higher precipitation. However, there was no geographical pattern in the distribution of the *Crematogaster* chemotypes. Furthermore, it seems that there is no preferred association among the different mutualistic partners.

Do caste-specific or female state-specific distances of cuticle odor bouquets reflect the social level in halictid bees?

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Chemical communication is crucial for the maintenance of the colony organization found in social insects, and chemical signals are known to mediate several aspects of social life including the regulation of reproduction. It is thought that a higher social level may also require more complex chemical communication and consequently odor signals. However, so far, most studies focused on highly eusocial species. Indeed, only little is known about the evolution of chemical communication on the transition from solitary living to eusociality. Halictid bees are especially suitable to study the evolution of sociality as they exhibit a high variability of sociality ranging from solitary to primitively eusocial species including social polymorphism. Wittwer et al. (2017) recently indicated that social halictid species invest more in

communication than solitary ones. Moreover, they showed that solitary and social populations of a single species could be separated by their chemical profiles indicating a shift in the production of chemical signals on the transition from solitary living to eusociality. The aim of our study was to investigate whether the distinction of cuticle chemical signals in females of different castes and states reflects the social level of halictid bees. Our hypothesis was that a higher social level should require more distinct chemical profiles between castes or female states. We analyzed cuticular chemical profiles of foundresses, breeding females or workers of ancestrally solitary, socially polymorphic and primitively eusocial halictid species and calculated Euclidian distances. Besides analyzing the whole chemical bouquet, we also focused on certain substance classes thought to be involved in regulating the reproduction in social halictid bees and checked whether a higher social level is also associated with a higher investment in potential queen signals. The results of this study deepen the knowledge on the link between chemical communication systems and the evolution of eusociality in insects.

Exocrine secretions: internalized medicine?

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Antimicrobial and toxic secretions delivered to the environment of an organism play a major role in mediating the outcome of several host-parasite interactions. These compounds improve an organism's survival and manipulate the microbial community surrounding it. Although external immune defence in the form of such secretions can be found in many different taxa, the extension of parasite defence to the environment is especially well documented for antimicrobials from exocrine glands in social insects. The evolution of external immune defence has likely been favoured in social insects due to their lifestyle, as the nest needs to be kept clean, valuable resources such as stored food need to be preserved and group members need to be protected from becoming sick. Here we explore whether in social insects the increased risk of parasite transmission due to the commonly observed exchange of food has been countered using external immune defence in the form of antimicrobial secretions. In a series of experiments, we find that the ant *Camponotus floridanus* ingests antimicrobials from exocrine glands as a form of internalized medicine thereby minimizing the risk of disease transmission due to food exchange within the colony. With this, our work highlights antimicrobial secretions as an extended arm of the immune system that needs to be integrated with other immune defence traits.

Transgenerational Effect of Rifampicin on Sperm Length in *Cardiocondyla obscurior* males

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The ant species *Cardiocondyla obscurior* hosts two endosymbionts, *Wolbachia* and *Candidatus Westeberhardia*. To study the role of these bacteria, we use antibiotic rifampicin treatment to eliminate the bacteria. Among various direct phenotypic effects on queens, such as decreased productivity, here we report that F1 males from treated queens have shorter sperm length compared to males from untreated

queens. This suggests a toxic transgenerational effect of rifampicin on spermatogenesis. In addition to the effects of rifampicin on prokaryotes, it has also been shown to directly affect mitochondrial RNA synthesis. Mitochondria play a critical role in spermatogenesis and thus sperm motility. This suggests a transgenerational toxic effect of the applied antibiotic on male fitness. There is increasing evidence that environmental factors can induce epigenetic changes that are transmitted to offspring. Together our data call for further investigation of transgenerational effects of rifampicin on male reproductive success and life history trait.

Role of nutrition in the division of labor in a clonal ant species

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Reproductive division of labor is one of the main characteristics of social insects. One or few individuals reproduce while workers perform all other non-reproductive tasks in the colony. Nutrition has been reported as a major factor for the emergence of reproductive division of labor. However, it remains largely unknown how it can affect fecundity, longevity and task allocation. Clonal ants, such as *Platythyrea punctata*, are a suitable model to study direct effects of nutrition while avoiding any other confounding factors. Despite their clonality, colonies are characterized by a well-ordered reproductive division of labor based on rank orders established through fighting. As a consequence, each colony contains only one, rarely several, reproductive workers, while the majority of individuals has inactive ovaries.
In this study, we investigated how different food regimes influence fecundity, lifespan and task allocation in *P. punctata* workers. Our results showed that ants confined to a high-protein diet lived longer and laid more eggs than ants raised on a low-protein diet. When we induced a nutritional bias between same-aged workers, ants fed with a high-protein diet showed a tendency to become dominant and to have better developed ovaries than workers raised on a low-protein diet. Lastly, we investigated nutritional requirements of reproductive and non-reproductive individuals. In the presence of different protein to carbohydrate ratios, reproductive workers favored high protein diet. This study shows the importance of nutrition in task allocation and highlights the mechanisms that might lead to the evolution of division of labor in social insects.

Infection of ant pupae by parasitoid mites

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A great variety of parasites and parasitoids exploit ant societies. Among them are the Mesostigmata mites, a particularly common and diverse group of ant-associated arthropods. While parasitism is ubiquitous in Mesostigmata, parasitoidism has only been described in the genus *Macrodinychus*. Yet, information about the basic biology of most *Macrodinychus* species is lacking. Out of 24 formally described species, information about basic life-history traits is only available for five species. Here I review the current knowledge about *Macrodinychus* mites with special focus on two hitherto undescribed species which were discovered inside pupal cocoons of the Southeast Asian army ant *Leptogenys distinguenda*. Juvenile development of *Macrodinychus* mites took place as ecto-parasitoids on a single ant pupa. By piercing the developing ant with their chelicera, the mites apparently sucked ant hemolymph, ultimately killing host individuals. Pupal infection rates ranged from 1% to almost 90% depending on the *Macrodinychus*-ant system studied. Especially invasive ants suffered from high pupal infection rates, which might derive from

missing countermeasures against parasitoidism in newly established host-parasitoid associations. The cryptic lifestyle of *Macrodinychus* mites has certainly hampered their scientific discovery and it is safe to say that many more species await scientific discovery. With this contribution, I would like to encourage the social insect community to specifically screen ant brood for these fascinating and rather unexplored parasitoids.

Fitness of worker-produced males in the ant *Temnothorax crassispinus*

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In ant colonies there is a division of labor between reproductive queens and non-reproductive workers, which take care of the colony's needs. According to Hamilton's theory of inclusive fitness, worker altruism is stable in evolution because they indirectly gain fitness by increasing the queen's reproductive output. In addition, workers of many species are capable of producing sons by laying unfertilized eggs. Little is known about the fitness of these worker-produced males.
In this study we aim to compare the fitness of queen- and worker-produced males in the ant *Temnothorax crassispinus*. We concentrated on the survival rate of males, sperm viability, and mating behavior.

Gonadal development in *Cardiocondyla obscurior*

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The development of ovaries in eusocial ants is a crucial point in setting the reproductive division of labor between the queen and worker caste. In the polygynous ant *Cardiocondyla obscurior* workers lack ovaries and queens are the only reproducing members of the colony. This makes *Cardiocondyla* a suitable model to investigate how reproductive division of labor in a higher ant species via differential gonadal development occurs. Vasa is a member of the class of DEAD box proteins and a maternal effect gene. It is consecutively expressed throughout the development of germ cells. Vasa is also found in cells that are involved in oogenesis and is therefore considered germline specific. This makes it a useful marker to follow gonadal development in *C. obscurior*. Confocal imaging in combination with an antibody against Vasa was used to detect VASA expressing cells in *C. obscurior* queen larvae and pupae.

Collective temperature homeostasis in bumblebees: social environment modulates individual fanning behavior

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Workers within social insect colonies show division of labor, where individuals perform only a subset of all tasks necessary for colony life. The mechanisms underlying the behavioral differentiation among workers of a colony are only partly understood. Morphological and genotypic variations, and age play important roles. In addition, feedback loops between an individual's actions, its shared stimulus environment and interactions with its nestmates presumably modulate individual task selection, playing an important role in integrating the behavior of many individuals into a functioning unit.

I will discuss our recent experiments, addressing the questions: (1) whether individual response behavior is modulated by effectiveness experienced while performing a task, and (2) how the social environment modulates individual stimulus-response behavior. Specifically, I ask whether bumblebee workers (*Bombus terrestris*) measure and respond to their own effectiveness when thermoregulating brood and how the presence and behavior of nestmates impacts response decisions.
Bumblebee colonies control the temperature of their brood and maintain it at stable temperatures of around 32°C, ensuring rapid brood development. This collective property is based on the response of individual workers, which can either actively increase brood temperature by incubating or decrease brood temperature by fanning. Using temperature controlled brood dummies, we can induce fanning behavior in experimental arenas under controlled conditions and manipulate both stimulus environment and social environment.
The findings of our studies suggest that individuals assess and immediately respond to their effectiveness in decreasing super-optimal brood temperatures when fanning and that the fanning response to temperature is modulated by their social environment.
Together with a detailed analysis of the movement and interaction patterns from individual tracking data, our study highlights the degree of individual plasticity depending on social environment, providing valuable information on the underlying mechanisms of social feedback.

Individual ant workers show self-control

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Self-control – the ability to forego immediate rewards for larger rewards later – is an important aspect of human behaviour, and is strongly associated with success in many aspects of life. Animals too, when under time or processing constraints, would benefit from foregoing immediate consumption to increase overall consumption. This is especially the case for animals that regularly exploit multiple semi-permanent food sources, such as ants or bees. While self-control has been extensively investigated in humans and vertebrates, little is known about it in invertebrates. Here, we investigate self-control in the ant *Lasius niger*.
We ask whether individual ants can exert self-control by foregoing a newly discovered poor food source nearby in order to exploit a previously visited higher quality food source further away. Most ants (69%) successfully ignored the closer, poorer reward in favour of the further, better one. However, when both the far and the close rewards were of the same quality, most ants (83%) chose the closer feeder, indicating that the ants were indeed exercising self-control, as opposed to a fixation on an already known food source. When the new feeder was of only slightly poorer quality (0.75M), most ants (86%) failed to reject the poorer food source, although further experiments suggest this was due to an inability to reliably distinguish 0.75M from 1M sucrose, rather than an adaptive trade-off. The ability to reject food sources when superior sources are available may be critical in coordinating an ant colony's simultaneous foraging from multiple food sources.

Nestmate recognition in colonies of the facultative slave-making ant *Formica sanguinea*

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Mixed colonies of ants give a unique opportunity for studying the capacity of ants to learn recognition odors of nestmates. However, most studies use artificially formed associations of heterospecific ants, which in natural conditions live in pure (homospecific) colonies. The European slave-making ant *Formica sanguinea* usually live in mixed colonies containing slaves of the *Serviformica* subgenus. I compared discriminatory abilities of the slave-making ants and their slaves looking for the differences which could be explained by the fact that parasite, and not slaves, is subject for the selection pressure on living in mixed colonies. I found that *F. fusca* slaves are poor at discriminating against alien *F. sanguinea* ants. In contrast, slave-making ants respond with aggression onto the contact with alien conspecific ants. Both species are similar in that they tolerate alien slaves, however, the underlying mechanism seems to be different and related to the species. Whereas slaves are apparently incapable of accurate discrimination against alien slaves, slave-makers are postulated to be intrinsic tolerant to each individual which is likely to be a slave. Such inherited tolerance would be associated with low or none costs of false acceptance (erroneous acceptance of alien individuals) and would reduce the risk that slaves from a new source colony will be rejected as being unrelated to and chemically different from currently used slaves. Thus, inherited or imposed by the social environment tolerance toward individuals which are likely to be slaves, facilitates replenishment of the slave workforce. Moreover, results of behavioral tests show that an individual to be recognized be a slave needs to be contaminated with the slave-makers'

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