"The Other Side of Sociality –
Susceptibility to Parasites in Social Insects"

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1. Introduction

1.1 Host-Parasite Co-Evolution

Genotypes develop into phenotypes that can be selected to produce a next generation in the current environment. Whenever this happens changes in the frequencies of genotypes in the population will result from selection. This very general statement of the evolutionary relationships of genotype, phenotype and selection is more complex in host-parasite relationships, because the environment for either host or parasite is at the same time a phenotype – produced by the genotype of its counterpart, the parasite or the host. Thus, the selection pressure and related to this, the success of a phenotype and its genotype is strongly dependent on other genotypes.

Parasites exploit hosts for their own reproduction and the degree they harm the host is termed virulence. The virulence of parasites is a flexible trait that is dependent on the mode of transmission, competition with other parasites or parasite strains during co-infections but also due to features of its host. The host's reaction towards the parasite as well as the availability of susceptible hosts might influence the degree of virulence.

Hosts may use defence mechanisms that reduce the exposure due to anticipatory defences. Post-infection mechanisms involve physiological defences that are based on immune responses.

Components that are involved in the virulence of parasites and resistance of hosts may show strong signs of co-evolution as the basic genetic mechanisms are not independent, but the phenotype they produce is dependent on the phenotype of the counterpart they are exposed to. A general model explaining the adaptations and counter-adaptations is the Red Queen hypothesis (Van Valen 1973; Bell 1982). Very briefly, under this hypothesis it is assumed that parasites adapt to certain host genotypes having a high fitness when exposed to them, but reducing the fitness of these host genotypes. Due to the high replication rates of parasites these will become very abundant infecting host genotypes that are very abundant. Thus, rare host genotypes the parasites have not adapted to, will have a higher fitness and increase in frequency within a population. Parasites will counteract this by adapting to the new most frequent host genotypes. This is a form of negative-frequency dependent selection that will lead to a cycling of frequencies of host and parasite genotypes (Salathé *et al.* 2008).

1.2 Social Insects and Parasites

Social insects, e.g. ants, bees and wasps, might be prone to attack by parasites and pathogens due to certain features related to sociality (Schmid-Hempel 1998). Colonies of social insects are characterized by a high density of individuals enhancing parasite transmission. Furthermore, a huge amount of food resources are stored as well as the presence of large numbers of brood items (larvae, pupae), especially attracting brood parasites. Usually, nest conditions like temperature and humidity are regulated and thus are highly homeostatic representing a constant and predictable environment with respect to these abiotic factors. Last but not least, colonies are groups of highly related family-members enhancing the transmission of parasites adapted to certain host genotypes (Schmid-Hempel 1998).

All the individuals of a colony of social insects possess individual immune responses due to the action of humoral and/or cellular immune system activity. However, immune pathways seem to be well conserved across invertebrate taxa, social insects lack an extensive amount of genes related to the immune repertoire (Hultmark 2003, Evans *et al.* 2006). Two non-exclusive explanations have been put forward to explain this lack. On the one hand, other – so far unknown (novel) genes might contribute to the immune system or alternatively, group-level defences might compensate for this lack of genes (Evans *et al.* 2006). Defences at the group-level might arise from structural and/or organizational features of a social insect colony, but also from the advanced behavioural repertoire. This defence based on the integrated social activities has been termed “social immunity” (Cremer *et al.* 2007).

The social immune system is based on three key features that resemble individual immune systems to some extend (Cremer & Sixt 2009). Colonies are discrete units within their respective environment as individuals are. Individuals show certain behaviours that are related to the avoidance or removal of pathogens similar to whole colony units do due to division of labour. Organizational features are the existence of waste management with certain areas foreseen for the collection of waste. Behavioural features are found in the socially produced fever that honeybee colonies show upon attacks by wasps or heat-sensitive pathogens (Starks *et al.* 2000).

Physiological adaptations of group-living, with respect to density-dependent effects, have been studied in detail, in two distinct taxa - bees and thrips (minute insects of the order Thysanoptera). Both taxa show a huge range of group sizes, ranging from solitary to obligatory eusocial species. Evidence for a homologous density dependent immune response is given, as for both taxa a positive correlation of antibacterial activity in the hemolymph with increasing group size was shown (Stow *et al.* 2007; Turnbull *et al.* 2011).

1.3 Introduction to Specific Topics - Hosts

Social immunity has been proposed to compensate for the lack of immune genes. All so far sequenced eusocial insect genomes (honeybee and seven ant genomes) show a lack of immune genes when compared to non-social insects (Evans *et al.* 2006). The quantity of immune genes does not give information about the quality of the present immune genes during infections. We study this effect by determining the temporal immune response in the eusocial bumblebee. Therefore, workers were either infected with *Escherichia coli*, sterile buffer only or served as un-manipulated control bees. We used a housekeeping gene of *E. coli* in order to quantify its presence in infected bees over the course of the experiment (Chapter 1).

Social immunity might be based on prophylactic adaptations that are present without the presence of a pathogen in order to reduce the infection risk. Other responses might be activated in the presence of pathogens (Cremer *et al.* 2007). The degree of activated responses might differ dependent on the pathogen individuals are exposed to. As responses of hosts are based on the specific recognition of parasites, often due to molecular properties (e.g. chemical volatiles, surface recognition molecules etc.), it might be assumed that recognition of familiar pathogens is better than of uncommon ones. We will test this hypothesis using foraging bumblebees and by manipulating artificially provided food sources with a common bumblebee pathogen (*Crithidia bombi*, a trypanosome gut parasite (Lipa & Triggiani 1988)) and an uncommon pathogen (*E. coli*). Un-manipulated food sources will serve as controls for this experiment (see Chapter 2).

Prophylactic responses involve density-dependent effects. However, their occurrence has been shown in inter-species comparisons (Stow *et al.* 2007; Turnbull *et al.* 2011), but it has been rarely studied whether these responses might be plastic within a species according to the social context individuals are exposed to. One of the examples where these effects have been studied comes from migratory locusts in which an up-regulation of immune function has been detected in the swarming phase (Wilson *et al.* 2002). However, some social insects also show variation in social context. Cyclical phases of growth as can be found in annual social insect societies are one of these examples. Usually these colonies are founded in spring by single queens carrying for the first brood. After emergence of the first workers these will take care of nest maintenance and especially care for the brood. Colonies grow until new sexual individuals will be produced and newly mated queens hibernate. Throughout the season group size changes dramatically and risk of infection as well. Initial studies have been done using bumblebees and social context has been varied experimentally. Immune function was determined for antimicrobial activity and phenoloxidase activity of the hemolymph. The overall results indicate a plastic response of immune function dependent on the social context with an up-regulation of phenoloxidase activity in group kept bumblebees and an increase of antimicrobial activity in solitarily kept bumblebees (Ruiz-González *et al.* 2009). However, inconsistency in their results with respect to a between colony effect leaves some uncertainty about the data. We study the density-dependent immune response by exposing individual bumblebee workers to different social contexts (group kept versus single kept) and study this effect on the gene expression of selected immune genes (Chapter 3).

1.4 Introduction to Specific Topics - Parasites

Microparasites (e.g. viruses, bacteria, fungi etc.) usually have much larger population sizes and infect individuals rather than colonies. Nevertheless, they can have effects at the colony level and defence mechanisms might occur at both the individual- and the group-level. High density conditions and frequent social contacts between closely related colony members enhance the transmission of these parasites. Furthermore, homeostatic nest conditions favour parasite establishment and maintenance.

In bumblebees, a parasite showing condition dependent virulence, occurs - the trypanosome gut parasite *Crithidia bombi* (Lipa & Triggiani 1988). This parasite might be transmitted vertically, but also show high frequencies of horizontal transmission due to foraging workers and infections occurring at infected flowers. It is relatively benign in individual workers, but causes infected queens to fail during colony foundation in spring (Brown *et al.* 2003). Within natural populations several strains can be identified using highly polymorphic microsatellite markers (Schmid-Hempel & Reber Funk 2004). Different genotypes of strains might be detected; knowledge about the resulting phenotypes is scarce. Here we use an *in vitro* cultivation system as well as a newly developed high-throughput cell counting system to exactly determine growth rates of different strains (Chapter 4).

C. bombi infections in natural populations have been estimated based on microscopic investigations. However, studies on strain diversity as well as co-infections by distinct genotypes are scarce. An initial study was done by Schmid-Hempel & Reber Funk (2004) showing that there is a huge diversity of strains and multiple infections are frequent. As bumblebees have annual colonies, that differ in their growth throughout the season drastically, it could be assumed that this also impacts the parasite population. As colonies grow the higher the probability becomes for intra-colonial transmission due to an increase of social contacts. With increasing size of colonies the number of foragers that might become exposed to new pathogens also increases. Together, this might result in increases of parasitic prevalence with proceeding season. However, with an accumulation of strains the probability of multiple infections also increases. Thus, interactions between strains are expected to occur (Ulrich *et al.* 2011; Ulrich & Schmid-Hempel 2012). We study the prevalence of infection as well as multiple infections in natural populations of two common bumblebee species (*B. terrestris* and *B. lapidarius*) by repeated sampling throughout the season. Polymorphic microsatellites are used to reconstruct changes in the *C. bombi* population genetic structure throughout the season (Chapter 5).

C. bombi is assumed to be a multi-host parasite with high levels of horizontal transmission on flowers (Durrer & Schmid-Hempel 1994). As flower usage is not equal between host species (Goulson & Darvill 2004), there is some potential for local adaptation towards host species. Within host species strong genotype-genotype interactions have been shown to occur (Riddell *et al.* 2009), but rigorous testing of the association of certain host genotypes and parasite genotypes in natural populations has not been done. Moreover, genotype by genotype interactions might not only occur within host species, but also between host species resulting in a signature of population differentiation of the parasite with respect to its host species.

Population differentiation might not only occur with respect to host species, but also with respect to space and time. Recently, Salathé & Schmid-Hempel (2011) have shown that population differentiation of *C. bombi* with respect to different habitats does occur, especially when population sizes of the parasite are low. Differentiation of populations within time might be due to either selection acting on the parasite population, but also effects due to genetic drift caused by population bottlenecks might contribute to temporal divergence of parasite populations. Severe bottlenecks occur in the *Bombus-Crithidia* system due to the hibernation of queens, which constitutes the primary agent of transfer to the following year. Local adaptation might be hindered by strong genetic drift as well as by frequent horizontal transmission between host species. High resolution microsatellite genotyping has been applied to samples of *C. bombi* extracted from several host species collected in subsequent years in order to test for local adaptation and interfering factors of between host horizontal transmission and temporal population differentiation (Chapter 6).

1.5 Introduction to Specific Topics - Social Parasitism

A special case of parasitism is social parasitism, which is the exploitation of resources derived from the social interactions of others. This form of parasitism is mainly based on the use of the work force of colonies by the social parasite in order to rear and take care of its own brood. The social parasites might be grouped according to their life-history and related to that, their virulence (Brandt *et al.* 2005). Queen-tolerant parasites coexisting with the host queen might represent the only true parasites, as they slowly exploit their host without killing it. Queen-intolerant might rather be classified as parasitoids as they immediately kill the resident host queen and live on the remaining ’somatic‘ body (the workers). Slave making or dulotic ants that depend on periodic slave raids might be classified as micropredators (Brandt *et al.* 2005).

Social parasites in most cases are queens invading colonies utilizing host workers to rear their own offspring developing into queens and males (Brandt *et al.* 2005, Schmid-Hempel 1998). Usually, the worker caste is absent or reduced in their function. In bumblebees a complete subgenus (*Psithyrus*) has specialized into this social parasitic life style. These queens invade host colonies after these have successfully established and the first batch of workers has emerged. Usually, the host queen is killed and the *Psithyrus* queen takes over reproduction forcing the host workers to rear their brood (Goulson 2010). However, within a given population not all colonies will be parasitized. Thus, the effective population size of *Psithyrus* might be smaller than that of their hosts. This has serious implications for the genetic diversity of the parasite population as it will be more strongly exposed to genetic drift. Unfortunately, reliable estimates for population sizes and the genetic diversity of *Psithyrus* and their respective hosts within a given population are not available. Prevalence has been estimated by artificially placing host colonies in the field, but this might overestimate the frequency of infected hosts due to the exposition of colonies and hence enhanced host finding by the parasite (Carvell *et al.* 2008; Müller & Schmid-Hempel 1992). Location and excavation of host nests is nearly impossible due to the cryptic nests underground (Sladen 1912). Here, we utilized foraging host workers and drones, and drones of the parasite population and apply highly resolving microsatellite markers and subsequent sibship reconstruction methods in order to determine the population structure of both, host and parasite. Thus, we are able to determine population sizes as well as estimates for the genetic diversity (Chapter 7).

Social parasites nearly always are queens that produce few or no workers. However, due to some pre-adaptations in a few species also workers might act as social parasites. This is the case, when workers have a high reproductive potential, sometimes coupled with a special reproductive system - thelytoky (parthenogenetic production of female offspring).

Thelytokous parthenogenesis occurs in a few species of ants (*Platythyrea punctata, Pristomyrmex pungens*) and in *Apis mellifera capensis*, a subspecies of the Western honeybee endemic to the Fynbos region in South Africa (Ruttner 1988). Workers of this subspecies show some unique traits distinguishing them from workers of other subspecies. Besides the thelytokous parthenogenesis, workers of *A. m. capensis* produce queen-like secretions in their mandibular glands (rich in 9-oxo-decenoic acid (9-ODA)), usually have higher number of ovarioles and may lay eggs even in the presence of the queen (Moritz *et al.* 1999). These eggs will develop into females as they are not cannibalized by other workers, which occur in other subspecies and is known as mutual 'worker policing' (removal of worker laid eggs) (Ratnieks 1988; Ratnieks & Visscher 1989). These preconditions lead to selfish reproductive behaviour and finally to social parasitism (Hamilton 1964; Greeff 1996). This became most evident, when *A. m. capensis* colonies had been transported into the area of the adjacent subspecies *A. m. scutellata* for pollination purposes in the early 1990's (Allsopp 1992). *A. m. capensis* workers entered colonies of *A. m. scutellata* and established themselves as social parasites. Within a few generations this syndrome has spread throughout the whole distribution range of *A. m. scutellata* causing thousands of colonies to die (Greeff 1997). The parasitic workers enter host colonies of the adjacent subspecies *A. m. scutellata*, kill the resident queen (Moritz *et al.* 2003), release queen substance (9-ODA) (Crewe & Velthuis 1980), suppress queen rearing and ovary development in the host workers and lay female eggs within a few days (Moritz *et al.* 2004).

Kin selection theory predicts strong selection for selfish reproduction if workers produce female offspring parthenogenetically (Hamilton 1964), because the benefits of altruistically rearing offspring due the high relatedness disappear. The relatedness between a laying worker and her offspring is much higher (r = 1) than that among supersisters (r = 0.75). Additionally, selection for selfish reproduction is driven by the higher reproductive value of queen or pseudoqueen offspring, compared to worker produced males (Greeff 1996). Here, the genetic basis of thelytokous parthenogenesis, 9-ODA production and the speed of ovary development will be determined utilizing a double-backcross (see Chapter 8).

However, the ultimate selective forces that have driven thelytoky nearly to fixation in the *A. m. capensis* population remain unclear. Several hypotheses have been stated in the past, as the high queen loss due to harsh environmental conditions (Moritz 1986). Colonies with thelytokously reproducing workers might re-queen themselves and hence, are not doomed to death when the queen gets lost. Here, this hypothesis is tested in ten hopelessly queenless colonies (Chapter 9).

Chapter 1

Dynamics of Immune System Gene Expression upon Bacterial Challenge and Wounding in a Social Insect (*Bombus terrestris*).

Erler S, Popp M & **Lattorff HMG** (2011) *PLoS ONE* **6**: e18126. (doi: 10.1371/journal.pone.0018126)

The innate immune system which helps individuals to combat pathogens comprises a set of genes representing four immune system pathways (Toll, Imd, JNK and JAK/STAT). There is a lack of immune genes in social insects (e.g. honeybees) when compared to Diptera. Potentially, this might be compensated by an advanced system of social immunity (synergistic action of several individuals). The bumble bee, *Bombus terrestris*, is a primitively eusocial species with an annual life cycle and colonies headed by a single queen. We used this key pollinator to study the temporal dynamics of immune system gene expression in response to wounding and bacterial challenge. Antimicrobial peptides (AMP) (abaecin, defensin 1, hymenoptaecin) were strongly up-regulated by wounding and bacterial challenge, the latter showing a higher impact on the gene expression level. Sterile wounding down-regulated TEP A, an effector gene of the JAK/STAT pathway, and bacterial infection influenced genes of the Imd (relish) and JNK pathway (basket). Relish was up-regulated within the first hour after bacterial challenge, but decreased strongly afterwards. AMP expression following wounding and bacterial challenge correlates with the expression pattern of relish whereas correlated expression with dorsal was absent. Although expression of AMPs was high, continuous bacterial growth was observed throughout the experiment. Here we demonstrate for the first time the temporal dynamics of immune system gene expression in a social insect. Wounding and bacterial challenge affected the innate immune system significantly. Induction of AMP expression due to wounding might comprise a pre-adaptation to accompanying bacterial infections. Compared with solitary species this social insect exhibits reduced immune system efficiency, as bacterial growth could not be inhibited. A negative feedback loop regulating the Imd-pathway is suggested. AMPs, the end product of the Imd-pathway, inhibited the up-regulation of the transcription factor relish, which is necessary for effector gene expression.

Keywords immune pathways, antimicrobial peptides, gene expression

Supplementary material

(http://www.plosone.org/article/fetchSingleRepresentation.action?uri=info:doi/10.1371/journal.pone.0018126.s001; http://www.plosone.org/article/fetchSingleRepresentation.action?uri=info:doi/10.1371/journal.pone.0018126.s002; http://www.plosone.org/article/fetchSingleRepresentation.action?uri=info:doi/10.1371/journal.pone.0018126.s003)

Figure S1. Effector protein TEP A, gene expression within 24 hours post-treatment.

Figure S2. Relish and prophenoloxidase gene expression within 24 hours compared to bacterial growth.

Table S1. Primer summary.

Chapter 2

Recognition and Avoidance of Contaminated Flowers by Foraging Bumblebees (*Bombus terrestris*).

Fouks B & **Lattorff HMG** (2011) *PLoS ONE* **6**: e26328. (doi: 10.1371/journal.pone.0026328)

Bumblebee colonies are founded by a single-mated queen. Due to this life history trait, bumblebees are more susceptible to parasites and diseases than polyandrous and/or polygynous social insects. A greater resistance towards parasites is shown when the genetic variability within a colony is increased. The parasite resistance may be divided into different levels regarding the step of the parasite infection (e.g. parasite uptake, parasite intake, parasite's establishment in the nest, parasite transmission).

We investigate the prophylactic behaviour of bumblebees. Bumblebees were observed during their foraging flights on two artificial flowers; one of these was contaminated by *Crithidia bombi*, a naturally occurring gut parasite of bumblebees (in a control experiment the non-specific pathogen *Escherichia coli* was used).

For *C. bombi*, bumblebees were preferentially observed feeding on the non-contaminated flower. Whereas for *E. coli*, the number of visits between flowers was the same, bumblebees spent more time feeding on the non-contaminated flower.

These results demonstrate the ability of bumblebees to recognise the contamination of food sources. In addition, bumblebees have a stronger preference for the non-contaminated flower when *C. bombi* is present in the other flower than with *E. coli* which might be explained as an adaptive behaviour of bumblebees towards this specific gut parasite. It seems that the more specific the parasite is, the more it reduces the reward of the flower.

Key words prophylactic behaviour, co-evolution, pollinators, social insect, parasite

Supplementary material

(http://www.plosone.org/article/fetchSingleRepresentation.action?uri=info:doi/10.1371/journal.pone.0026328.s001)

Figure S1. Frequency distribution of number of flights.

Chapter 3

Social context dependent immune gene expression in bumblebees (*Bombus terrestris*).

Richter J, Helbing S, Erler S & **Lattorff HMG** (2012) *Behavioural Ecology & Sociobiology* (in press, doi: 10.1007/s00265-012-1327-2).

Social insects are prone to attack by parasites as they provide numerous resources of food and brood, homeostatic nest conditions and a high density of individuals, enhancing the transmission of parasites. The defence of social insects might occur at different levels, the individual and the group. Individual defence occurs in part via the innate immune system resulting in the expression of antimicrobial substances. Group level defences, summarized as 'social immunity', represent a suite of behavioural and organizational features.

Here, all effects contributing to social immunity except for the social context were removed from bumblebee (*Bombus terrestris*) workers, kept either in groups or solitarily. The gene expression of 6 effector molecules of the immune system was monitored in both groups and in controls from the same source colonies. The social treatment has a highly significant effect on immune gene expression; with groups exhibiting higher levels of two antimicrobial peptides (AMPs) and two lysozymes. Phenoloxidase is affected at the regulatory level, with a strong up-regulation of its suppressor Spn27A in groups suggesting a trade-off with antimicrobial activity. AMPs are strongly up-regulated in groups, whereas lysozymes are strongly down-regulated in solitary treatments suggesting another trade-off. Clearly, 'social immunity' impacts elements of individual immunity.

Keywords innate immune system, social immunity, quantitative real-time PCR, antimicrobial peptide, lysozyme, phenoloxidase

Supplementary material

(http://www.springerlink.com/content/5t2t36061133j933/265_2012_Article_1327_ESM.html)

Material and Methods

Table S1. Primer sequences.

Richter *et al.* 2012 *Behav Ecol Sociobiol* (in press). 43

Chapter 4

A Quantitative *In Vitro* Cultivation Technique to Determine Cell Number and Growth Rates in Strains of *Crithidia bombi* (Trypanosomatidae), a Parasite of Bumblebees

Popp M & **Lattorff HMG** (2011) *Journal of Eukaryotic Microbiology* **58**: 7-10. (Erratum **58**: 273).

The protozoan parasite *Crithidia bombi* and its host, the bumblebee *Bombus terrestris* are used as a model system for the study of the evolutionary ecology of host-parasite interactions. In order to study these interactions we established a method for in vitro cultivation of single parasite strains. Additionally, a high-throughput method for determining cell numbers in cultures by means of optical density (OD) measurements is developed. The protocol for in vitro cultivation allowed for growing different strains on agar plates as well as in culture medium. A calibration curve for the relationship between cell number and OD has been developed. Subsequently, growth rates for different genotypes of *C. bombi* have been recorded. Significant differences in the growth rates and generation times between these genotypes were demonstrated. As this might be related to the virulence of the parasite, this relationship might be confirmed by in vivo growth rate determination. In comparison to conventional cell-counting the application of OD measurements allows for high-throughput experiments by reducing the time per sample 30 times. The in vitro cultivation method allows for controlled infection experiments in order to study host-parasite interactions.

Keywords: host, parasite, *Crithidia bombi, Bombus terrestris,* infection, transmission, cultivation, optical density

Supplementary material

(http://onlinelibrary.wiley.com/doi/10.1111/j.1550-7408.2010.00514.x/suppinfo)

Figure S1.	Light-microscopic picture of *Crithidia bombi* (20-fold magnification).
Figure S2.	Correlation between OD_{600} and cell number/ml.
Table S1.	List of genotypes.
Table S2.	Strain M-A12 (dilution 10^{-3}) and strain M-A06 (dilution 10^{-2}) with their absorbance at 600 nm (OD) and their corresponding cells per ml.

Chapter 5

Seasonal variability of prevalence and occurrence of multiple infections shapes the population structure of *Crithidia bombi*, an intestinal parasite of bumblebees (*Bombus spp.).*

Popp M, Erler S & **Lattorff HMG** (2012) *Environmental Microbiology* (submitted).

Ergonomic growth phases of annual social insect societies strongly influence horizontally transmitted parasites. Seasonal fluctuations in prevalence and the occurrence of multiple infections of the gut parasite *Crithidia bombi* were analysed in repeatedly sampled populations of two common bumblebee (*Bombus* spp.) species. Prevalence of *C. bombi* was greatest in the middle of the foraging season and coincided with the maximal occurrence of multiple infections. The genetic structure of the parasite population also showed strong seasonal fluctuations with a drastic decline in effective population size and an increase in linkage disequilibrium when infection rates were highest. These effects are mainly attributable to significant changes in parasite allele frequencies, leading to selection of specific alleles and increasing the frequency of homozygote genotypes in the middle of the season. Towards the end of the season, selection appears to relax and we observe a recovery in linkage equilibrium as well as an increase in effective population size.

Keywords host-parasite interaction, multiple infections, intensity of infection, effective population size, heterozygosity

Supplementary material

Popp *et al.* 2012 *Evironm Microbiol* (submitted). 63

Chapter 6

Sex, horizontal transmission and multiple hosts prevent local adaptation of *Crithidia bombi*, a parasite of bumblebees (*Bombus* spp.).

Erler S, Popp M, Wolf S & **Lattorff HMG** (2012) *Ecology & Evolution (in press,* doi: 10.1002/ece3.250*).*

Local adaptation within host-parasite systems can evolve by several nonexclusive drivers (e.g. host species - genetic adaptation; ecological conditions - ecological adaptation and time -temporal adaptation). Social insects, especially bumblebees, with an annual colony life-history not only provide an ideal system to test parasite transmission within and between different host colonies, but also parasite adaptation to specific host species and environments. Here we study local adaptation in a multiple-host parasite characterized by high levels of horizontal transmission. *Crithidia bombi* occurs as a gut parasite in several bumblebee species. Parasites were sampled from five different host species in two subsequent years. Population genetic tools were used to test for the several types of adaptation.

Although we found no evidence for local adaptation of the parasite towards host species, there was a slight temporal differentiation of the parasite populations which might have resulted from severe bottlenecks during queen hibernation. Parasite populations were in Hardy-Weinberg equilibrium and showed no signs of linkage disequilibrium suggesting that sexual reproduction is an alternative strategy in this otherwise clonal parasite. Moreover, high levels of multiple infections were found, which might facilitate sexual genetic exchange. The detection of identical clones in different host species suggested that horizontal transmission occurs between host species and underpins the lack of host specific adaptation.

Keywords host-parasite interaction**,** co-evolution, population genetic structure, bumblebee, *Bombus*, *Crithidia bombi*

Supplementary material

(http://onlinelibrary.wiley.com/doi/10.1002/ece3.250/suppinfo)

Table S1.	Overview on diversity of bumblebee samples.
Table S2.	Population genetic analysis of microsatellite loci.
Table S3.	Estimated pairwise F_{ST}.

Erler *et al.* 2012 *Ecology & Evolution* (in press). 81

Chapter 7

The degree of parasitism of the bumblebee (*Bombus terrestris*) by cuckoo bumblebees (*Bombus (Psithyrus) vestalis*).

Erler S & **Lattorff HMG** (2010) *Insectes Sociaux* **57**: 371–377. (doi: 10.1007/s00040-010-0093-2)

Host–parasite systems are characterised by coevolutionary arms races between host and parasite. Parasites are often the driving force, as they replicate much faster than their hosts and have shorter generation times and larger population sizes, resulting in higher mutation rates per time interval. This scenario does not fit all host–parasite systems. Socially parasitic cuckoo bumblebees (*Bombus (Psithyrus) vestalis*) parasitise colonies of *Bombus terrestris* share most life history characteristics with their hosts. As they parasitise only a subset of all available colonies, their population size should be lower than that of their hosts. This might have strong negative effects on the genetic diversity of *B. vestalis* and their adaptability. Here, we study for the first time the population structure of a *Bombus/Bombus* (*Psithyrus*) system. Highly polymorphic DNA markers were used to reconstruct sibships from individuals collected in the wild. The analysis of the host and parasite populations revealed a rate of parasitism of about 42% (range 33–50%). The population size of *B. vestalis* was lower compared to their hosts, which was also reflected in low within-group genetic distance. An analysis of the reconstructed queen genotypes revealed more supersisters amongst the *B. vestalis* queens when compared to the *B. terrestris* host. The data suggest that *B. vestalis* females and males do not disperse over long distances. This shows a potential for local adaptation to their hosts.

Keywords social parasitism, *Psithyrus*, bumblebee, sibship reconstruction

Supplementary material

(http://www.springerlink.com/content/j0813787818g3406/40_2010_Article_93_ESM.html)

Figure S1. Distribution of genetic distance values for 1000 replicates of 6 randomly chosen queens versus 6 other randomly chosen queens for A) *Bombus terrestris* and B) *Bombus vestalis*.

and its parasite *Harpagoxenus sublaevis* have adapted to each other on a very local scale (Fischer & Foitzik 2004; Foitzik *et al.* 2009).

Dramatic declines in pollinators have been observed, e.g. *Bombus*, and also for their cuckoo bumblebee parasites (Goulson *et al.* 2006, 2008; Kosior *et al.* 2007). Many bee species have decreased in their number or have become extinct during the last 60 years. The reasons for this phenomenon are a range of both, anthropogenic and environmental factors (Goulson *et al.* 2005, 2008; Kosior *et al.* 2007; Moritz *et al.* 2007). We have developed the tools and methodology to monitor these populations simultaneously. Goulson *et al.* (2008) asked for the development of long-term monitoring of bumblebee populations to increase the knowledge of the current status of bumblebee species and their populations, as well as their changes over time. Using the combined power of highly polymorphic DNA markers with recent developments in sibship reconstruction, we are able to determine the exact origin of individuals and hence to estimate the degree of parasitism and population sizes in space and time.

Acknowledgement

We would like to thank the students of the 2008 summer course in Ecology for the help with sampling and DNA analysis. Financial support was grant by the BMBF program FUGATO-Plus (HMGL).

Chapter 8

Control of reproductive dominance by the *thelytoky* gene in honeybees.

Lattorff HMG, Moritz RFA, Crewe RM & Solignac M (2007) *Biology Letters* **3**: 292–295. (doi: 10.1098/rsbl.2007.0083).

Differentiation into castes and reproductive division of labour are characteristics of eusocial insects. Caste determination occurs at an early stage of larval development in social bees and is achieved via differential nutrition irrespective of the genotype. Workers are usually subordinate to the queen and altruistically refrain from reproduction. Workers of the Cape honeybee (*Apis mellifera capensis*) do not necessarily refrain from reproduction. They have the unique ability to produce female offspring parthenogenetically (thelytoky) and can develop into 'pseudoqueens'. Although these are morphologically workers, they develop a queen-like phenotype with respect to physiology and behaviour. Thelytoky is determined by a single gene (*th*) and we show that this gene also influences other traits related to the queen phenotype, including egg production and queen pheromone synthesis. Using 566 microsatellite markers, we mapped this gene to chromosome 13 and identified a candidate locus *thelytoky*, similar to *grainy head* (a transcription factor), which has been shown to be highly expressed in queens of eusocial insects. We therefore suggest that this gene is not only important for determining the pseudoqueen phenotype in *A. m. capensis* workers, but is also of general importance in regulating the gene cascades controlling reproduction and sterility in female social bees.

Keywords thelytoky, pleiotropy, *Apis mellifera*

Supplementary material

(http://rsbl.royalsocietypublishing.org/content/3/3/292/suppl/DC1)

Table S1. Characteristics of newly developed microsatellite loci of *Apis mellifera* L.

Lattorff *et al.* 2007 *Biol Lett* **3**: 292-295. 111

Chapter 9

Social parasitism of queens and workers in the Cape honeybee (*Apis mellifera capensis*).

Moritz RFA, **Lattorff HMG**, Crous KL & Hepburn HR (2011) *Behavioural Ecology & Sociobiology* **65**: 735–740. (doi: 10.1007/s00265-010-1077-y).

Workers of a queenless honeybee colony can requeen the colony by raising a new queen from a young worker brood laid by the old queen. If this process fails, the colony becomes hopelessly queenless and workers activate their ovaries to lay eggs themselves. Laying Cape honeybee workers (*Apis mellifera capensis*) produce female offspring as an additional pathway for requeening. We tested the frequency of successful requeening in ten hopelessly queenless colonies. DNA genotyping revealed that only 8% of all queens reared in hopelessly queenless colonies were the offspring of native laying worker offspring. The vast majority of queens resulted from parasitic takeovers by foreign queens (27%) and invading parasitic workers (19%). This shows that hopelessly queenless colonies typically die due to parasitic takeovers and that the parasitic laying workers are an important life history strategy more frequently used than in providing a native queen to rescue the colony. Parasitism by foreign queens, which might enter colonies alone or accompanied by only a small worker force is much more frequent than previously considered and constitutes an additional life history strategy in Cape honeybees.

Keywords Cape honeybee, parasitic workers, parasitic queens, queen rearing

Supplementary material

(http://www.springerlink.com/content/n86237wl04848784/265_2010_Article_1077_ESM.html)

Table S1. Queen genotypes.

Table S2. Workers genotyped with a subset of five loci to identify the maternity

Moritz *et al.* 2011 *Behav Ecol Sociobiol* **65**: 735-740. 119

3. Summary / Conclusion

3.1 Hosts – Flexibility in Immune Responses

The relatedness asymmetries in social Hymenoptera that create a high intra-colonial relatedness not only favour cooperation, but also enhance proneness to parasites (Schmid-Hempel 1998). Once parasites have adapted to certain host genotypes, colonies with low genetic diversity and high densities of individuals provide an optimal space for a parasite to establish itself. Moreover, the large food store, the presence of large amount of brood, and the nest homeostasis further facilitate the establishment of parasites in the colony (Schmid-Hempel 1995).

Nevertheless, social insects are not helpless as they have mechanisms and strategies to counteract parasite attacks (Cremer & Sixt 2009). At the individual level, the innate immune system provides a line of defence to combat the intrusion of microparasites (Hultmark 2003, Siva-Jothy *et al.* 2005). Surprisingly, recent genome sequencing efforts on social insects revealed that they actually have lower numbers of genes which contribute to innate immunity (Evans *et al.* 2006; Wilson-Rich *et al.* 2009), when compared to other non-social insects (e.g. *Drosophila, Tribolium, Bombyx*). Compensation for the effect of a lack of immune genes might come from colony level defences - known as 'social immunity' (Cremer *et al.* 2007). These might constitute prophylactic and activated defence mechanisms resulting from a cooperative action of several individuals.

Although, the innate immune system seems to lack flexibility, various potential pre-adaptations might allow for flexible responses. One indication for such a pre-adaptation is the transcriptional response of antimicrobial peptides (AMPs) elicited by non-septic wounding (Erler *et al.* 2011). Moreover, a flexible adjustment of the immune response can also depend on the social context (Ruiz-González *et al.* 2009; Richter *et al.* 2012). Individuals within groups show an up-regulation of antimicrobial peptides and lysozymes, eventually due to the higher risk of infections spreading within groups (Richter *et al.* 2012). Nevertheless, the immune system of bumblebees is not able to completely clear infections, as bacterial growth still occurs 24h post infection (Erler *et al.* 2011). This is in contrast to studies on *Tenebrio molitor*, which showed that the beetles could clear bacterial infections within 30 min

(Haine *et al.* 2008). Again, the reduced efficiency of the immune response at the individual level might be compensated by group-level defences.

Selection might also act to reduce the parasite uptake from the environment (Cremer *et al.* 2007). As *C. bombi* is horizontally transmitted by foraging workers due to shared flower use (Durrer & Schmid-Hempel 1994) avoidance of previously used flowers might reduce the uptake of parasites at flowers. This avoidance behaviour might result from pheromones passively deposited at flowers by foraging workers (Goulson 2010), but also from the parasite itself. Avoidance of flowers contaminated by *C. bombi* occurs on a long-distance resulting in less frequent choice of the flowers (Fouks & Lattorff 2011). In contrast to that, contaminations caused by a pathogen bumblebees have not adapted to – *E. coli* – did not change the initial choice of flowers, but reduced the time of nectar uptake, potentially caused by a negative gustatory response to metabolic products of the bacteria (Fouks & Lattorff 2011).

3.2 Parasites - Population Level Dynamics

Flexible adjustments of the immune response might be adaptive, whenever the host is exposed to variable threats by a variety of pathogens. At the population level, the epidemiological processes are an interaction of several factors in both the host and the parasite population. Many factors, including the frequencies of genotypes, the availability of susceptible hosts, and their immune status result in highly dynamic epidemiology (Anderson & May 1982; Ewald 1983; Ebert & Herre 1996). Social insects with an annual life cycle, e.g. social bumblebees, might represent a very strong selective force for parasite populations due to the enormous growth rates of the worker population after establishment of colonies. This results in a rapid increase in the abundance of potential host individuals which might enhance horizontal transmission of parasites. However, whenever colonies break down before winter and only individual queens hibernate, this not only results in a strong bottleneck for the host, but even more so for the parasites (Erler *et al.* 2012). The prevalence of *Crithidia bombi*, an intestinal gut parasite (Lipa & Triggiani 1988), shows seasonal trends following the population development of its host *Bombus* sp. As the host populations grow, more and more individuals become infected not only due to intra-colonial but also due to inter-colonial transmission resulting from shared flower use

(Durrer & Schmid-Hempel 1994). The population wide prevalence of parasites increases, eventually resulting in multiple infections by different genotypes of the parasite. These multiple infections might have very different outcomes. Parasite strains might either compete or cooperate in exploitation of the host. Depending on the relatedness of the parasite strains inclusive fitness concepts might come into play resulting in more complex evolutionary scenarios (Schjorring & Koella 2003). *C. bombi* strains seem to compete with each other early in the season, most strongly visible by selection on a gene closely linked to an otherwise neutral marker Cri4. Popp *et al.* (2012) found suggestive evidence for selection at this locus. Competition among strains leads to drastic reductions in the effective population size of the parasite. Initially strong linkage disequilibrium became relaxed later in the season, probably as a result from genetic exchange between different parasite strains. Genetic exchange certainly occurs under controlled laboratory conditions (Schmid-Hempel *et al.* 2011), but it also seems to play a major role in natural populations (Schmid-Hempel & Reber Funk 2004; Salathé & Schmid-Hempel 2011; Erler *et al.* 2012; Popp *et al.* 2012).

3.3 Social Parasitism – When Hosts Turn into Parasites

Obligate social parasites are most often species that have retained queen-derived individuals and lost the worker caste (Bourke & Franks 1995; Brandt *et al.* 2005). Usually, these species are expected to show smaller population sizes compared to their hosts. Moreover, it is expected that social species evolve much faster, because more meiotic divisions occur until sexuals are produced increasing the likelihood of accumulating novel mutations (Bromham & Leys 2005). We confirmed this expectation using an approach combining molecular markers and sibship reconstruction methods in order to comparatively study the census population sizes of host and social parasite under natural conditions. The socially parasitic bumblebee (*B. vestalis*) has a census population size of one third compared to its host species (*B. terrestris*). The genetic diversity of *B. vestalis* queens was much lower than in the host species with respect to allelic richness, observed heterozygosity and the genetic distance between queens when compared to the host species (Erler & Lattorff 2010). Using six pairs of host-social parasites species within the genus *Bombus*, we could show that the socially parasitic bumblebees show lower levels of adaptive evolution than the social host species for some fast evolving anti-viral genes (Helbing 2011), indicating that reduced effective population sizes and the lack of a worker caste have a significant impact on the evolution at the molecular level. Small effective population sizes, resulting in a higher impact of genetic drift and in the long-term in lower levels of genetic diversity, are one of the major problems in socially parasitic species. Especially queen-intolerant inquilines species are affected which makes them prone to population declines and extinction, a trend that has been observed in recent times (Kosior *et al.* 2007).

The evolution of a socially parasitic life history in individuals derived from workers is an exception. Nevertheless, these rare systems are valuable as they might allow studying the factors that allow for the evolution of such a complex behavioural syndrome. One of these rare cases is the Cape honeybee, *Apis mellifera capensis*, where workers show a predisposition to social parasitism due to their ability to produce diploid female offspring by means of thelytokous parthenogenesis (Onions 1912). It appears to be a form of clonal reproduction (Baudry *et al.* 2004) as diploidy is restored by automixis with central fusion (Verma & Ruttner 1983). Usually, the lack of recombination results in a decrease of the effective population size (Gordo & Charlesworth 2001; Charlesworth 2002) which in turn accelerates genetic drift that leads to reduced levels of genetic variation (Begun & Aquadro 1992). Thus, the ability to reproduce by thelytokous parthenogenesis might not be sufficient in order to establish successfully as a social parasite. They have to overcome existing mechanisms of nest-mate recognition and acceptance as reproductive individual within the host colony and these traits might not evolve that easily under the constraint of reduced effective population sizes and clonal reproduction.

Using a forward genetics approach I could unravel the simple genetic basis for social parasitism. A single gene pleiotropically influences a set of traits that predispose worker bees to becoming social parasites. The gene was mapped to chromosome 13 and identified as a transcription factor (*gemini*) influencing the type of parthenogenesis, the queen-like pheromone production and the onset of egg-laying (Lattorff *et al.* 2007). Especially the pheromonal mimicry of the queen by socially parasitic workers (Moritz *et al.* 2003) is essential getting acceptance in the host colony. Subsequent studies showed that this gene acts via alternative splicing producing four distinct transcripts, highly correlated to the reproductive state of queens and workers (Jarosch *et al.* 2011).

In Cape honeybees not only workers show a predisposition to act as social parasites, but also queens might enter, alone or supplemented with a small number of workers (Moritz *et al.* 2011), foreign colonies to reproduce in there. Usually, the resident queen will be killed during these takeovers (Moritz *et al.* 2003) leading to the (genotypic) death of the colony. However, successful reproduction of resident workers might counteract such takeovers. The speed of ovary activation in Cape honeybees is very high and occurs even in presence of the queen (Moritz *et al.* 1999) so that resident workers might start with egg-laying activity immediately after their queen gets lost. As these workers reproduce clonally they might preserve their natal genotype to a large extend. The predisposition of workers due to the thelytoky gene might help them suppress or at least postpone takeovers of foreign workers and queens and ultimately prevents the ‘genotypic‘ death of the colony (Moritz *et al.* 2011). Hence, this is one of a few systems, where the very same genotype determines both, virulence of the parasite and resistance of the host.

3.4 General Conclusion

Social insects have evolved a highly cooperative behaviour mainly enforced by the high relatedness within colonies. The concept of inclusive fitness and kin selection (Hamilton 1964) has been used to explain the genetical evolution of social behaviour. However, close genetic relatedness coupled with high density of individuals leads to proneness of such colonies to intrusion by pathogens and parasites (Schmid-Hempel 1998). In order to counteract these attacks, a suite of behavioural and organisational features have been evolved in social insects. A number of activated and prophylactic responses based on cooperative activities of colony members, summarized under the term ’social immunity‘ (Cremer *et al.* 2007), supplementing the innate immune response of individual workers. However, traits related to parasitism and even for resistance do not necessarily be complex, as the very simple genetic basis of social parasitism in Cape honeybees shows that a single gene with pleiotropic effects (Lattorff *et al.* 2007) might be sufficient to turn workers into parasites and on the other hand, the very same gene might also be responsible for resistance to parasitism (Moritz *et al.* 2011). This simple genetic regulation might be surprising, but studies on other social insect species showed similar trends. In the lower termite *Cryptotermes secundus* a single gene was identified to be responsible for the reproductive division of labour between queen and workers (Korb *et al.* 2009) by signalling the absence or presence of a queen to the workers. In the fire ant *Solenopsis invicta*, a single gene is responsible for the complete change of the social organisation of a colony with colonies being either mono- or polygynous depending on the genotype of workers at the GP9 gene (Keller & Ross 1998; Ross & Keller 1998).

Complex phenotypes like the social organisation affecting also the cooperation among workers might be under control of quite simple genetic mechanisms as well as the other side of social insect colonies – their ability to act as parasites themselves and the resistance to parasites may also be under quite simple genetic mechanisms.

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