Myrmecological News | 11 | 119-132 | Vienna, August 2008

The causes and consequences of genetic caste determination in ants (Hymenoptera: Formicidae)

Kirk E. Anderson, Timothy A. Linksvayer & Chris R. Smith

Abstract

Recently there has been an explosion of research into the genetics of caste determination, especially following the discovery of systems where queen-worker caste determination has a strong genetic influence. In this review we collate and interpret research on genetic caste determination in ants and discuss this research within the historical framework of caste determination in the social insects. While early researchers disagreed over the relative importance of rearing environment and genes on caste determination, the notion that caste is determined by environment had been largely supported by both theory and empirical results – until relatively recently. The growing utility of molecular markers, together with breeding studies and other quantitative genetic approaches, has now demonstrated a genetic component to caste across numerous social insect taxa. The strength of the genetic component varies and may often remain highly conditional on the environment. In extreme cases, caste is determined almost exclusively by genotype. We review environmental and genetic factors that affect caste determination, summarize recent evidence for weak and strong genetic caste determination, and discuss the evolution of these systems. Genotypes that produce queen-biased caste ratios are often described as cheaters, and here we emphasize that the evolutionary dynamics of genetic caste determination involves the coevolution (often antagonistic) of biasing and restorer genes expressed in interacting nestmates. The evolutionary importance of such conflicts over caste fate remains unclear, but in some cases may lead to widespread dependent lineage systems, sperm parasitism, and workerless social parasites.

Key words: Polyphenism, phenotypic plasticity, genotype-by-environment interaction, social cheaters, dependent lineage, co-evolution, antagonistic selection, review.

Myrmecol. News 11: 119-132 (online 25 June 2008)
ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 14 April 2008; revision received 15 May 2008; accepted 16 May 2008

*Dr. Kirk E. Anderson** *(contact author), Department of Entomology, University of Arizona, Tucson, AZ 85721, USA. E-mail: keanders@email.arizona.edu*

*Dr. Timothy A. Linksvayer***, School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA.*

*Dr. Chris R. Smith***, School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA; Program in Ecology and Evolutionary Biology, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA.*

* *Authors contributed equally.*

Introduction

> I believe that natural selection, by acting on the fertile parents, transmitted to their fertile offspring a tendency to produce sterile members ... one set of workers of one size and structure, and simultaneously another set of workers of a different size and structure.
>
> Darwin (1859)

In social insects, the presence of sterile castes and the mechanisms that underlie caste determination have long fascinated biologists. A division of labor between reproductive queens and more-or-less sterile workers is a core trait of eusocial colonies that seems to be responsible for the extreme ecological and evolutionary success of the social insects (Hölldobler & Wilson 1990). The largest and most complex societies are characterized by further division of labor between workers, and these worker castes are often morphologically distinct. Honey bees have long been a model system for studying reproductive caste determination, and early studies established the long-standing paradigm that caste is determined exclusively by environmental factors, and that royal jelly is the "queen-producing" substance (Michener 1974). Early experiments on caste determination in ants also demonstrated the importance of the nutritional environment (e.g., Wesson 1940, Gregg 1942, Passera 1974). Such an environmentally-based process fits well with simple theoretical predictions: Genes biasing caste determination towards queen or worker development are expected to be fixed or lost, respectively, so that little genetic variation for caste is maintained within populations (Crozier & Pamilo 1996). However, other early researchers inferred genetic influences on caste based on detailed observations of aberrant phenotypes in queens and their presumed offspring. For example, individuals from a colony of *Acromyrmex* leaf-cutter ants presented a mosaic of queen and worker traits, prompting W.M. Wheeler (1937) to propose that caste determination in ants was under genetic control. Perhaps more importantly, Wheeler concluded that an understanding of caste determination in ants would only be realized somewhere beyond the "environment-versus-heredity impasse". This conclusion is equivalent to acknowledging that caste in social insects is a complex phenotype, influenced by multiple interacting genetic and environmental factors. Indeed, recent and mounting evidence from a variety of approaches supports this conclusion.

Thus, while environmental factors have long been the focus of research on morphological caste determination (WILSON 1971, OSTER & WILSON 1978, WHEELER 1986, HÖLLDOBLER & WILSON 1990, WHEELER 1991), this review approaches caste in social insects from a genetic perspective. Like any complex phenotype, caste has a heritable component. At the most fundamental level, the vast number of genes (see EVANS & WHEELER 1999) involved in the developmental process of caste determination is subject to mutation-selection balance. Additionally, caste-biasing alleles may experience opposing selection pressure within and between colonies, potentially resulting in their maintenance at intermediate frequencies. Here we review genetic and environmental factors that influence caste determination, and how these factors may interact to shape caste developmental trajectories. Our empirical foundation relies primarily on the association of genetic markers with caste phenotypes, and to this end we review studies demonstrating genetic caste determination (GCD) in social insects. We divide this influence into two basic categories according to recent data; 1) when the heritability of caste is intermediate, "weak GCD", environmental variation exerts a strong influence, and individual genetic variants differ in their probability of developing into alternative castes and 2) "strong GCD" when caste is determined exclusively or nearly so by genotype (see Tab. 1 for examples of each). Finally, we discuss the consequences of genetic influences on both reproductive and worker caste polymorphism, and how these genetic influences may evolve and be maintained.

Factors affecting caste determination

Environmental factors: While early models of environmental caste determination (ECD) focused on the quantity and quality of food given to larvae, other environmental factors have also been shown to influence caste determination (WHEELER 1986, 1991). For example, in many ant species, new queens and males are only produced at certain times of the year, and environmental cues such as changes in temperature associated with overwintering are required for queen production (ELMES 1987). In some cases, these seasonal effects seem to be mediated by the quantity of hormones the queen deposits in her eggs (SUZZONI & al. 1980, DE MENTEN & al. 2005, SCHWANDER & al. 2008a). Perhaps a more general maternal influence on caste determination is queen pheromone that signals queen presence and suppresses queen development (KELLER & NONACS 1993). Such queen signals may be received directly by larvae and influence their development, or may influence worker behavior, which in turn shapes the social environment and indirectly affects larval development.

Workers control many of the environmental factors that influence caste determination. In the majority of ants and vespid wasps, larvae are directly fed by workers (progressive provisioning) and the workers presumably have control over what larvae are given (MICHENER 1974), although larvae may often be capable of influencing worker provisioning behavior (NONACS 1986, CREEMERS & al. 2003, KAPTEIN 2005). Such adult control of larval caste developmental trajectories can be considered a type of parental manipulation (ALEXANDER 1974, MICHENER & BROTHERS 1974, LINKSVAYER & WADE 2005). In some taxa, larvae have relatively more control over their own caste determination. For example, in attine ants, larvae are placed on a pile of food, though they are likely constrained in the quality of food they can acquire and perhaps limited in what they can reach. In other taxa, e.g., *Melipona* stingless bees, larvae are provided an initial bundle of food and develop in a sealed cell (mass provisioning; MICHENER 1974) decreasing the potential for worker control of larval caste fate (RATNIEKS 2001).

Genetic factors: In fact, all of the "environmental" factors mentioned above can have genetic components. Genes expressed in care-giving workers and the queen can influence the nutritional, microclimate, and pheromonal environment experienced by larvae, and thus indirectly shape caste determination (indirect genetic effects; LINKSVAYER & WADE 2005, LINKSVAYER 2006, 2007). Thus, genes expressed in care-giving workers have a strong potential to be caste-biasing genes. Indeed, LINKSVAYER (2006) found heritable variation for queen and worker effects on reproductive caste in the acorn ant *Temnothorax curvispinosus*, indicating that queen and worker influences on larval caste determination have a genetic basis and can evolve. Brood may also influence the provisioning they receive through mechanical "begging" (KAPTEIN 2005) or chemical signaling (NONACS 1986, LE CONTE & HEFETZ 2008). In this way, genes expressed in both brood and care-giving workers interact to influence the developmental environment and resulting caste determination. Such heritable queen, worker, and brood effects on caste are a prerequisite for the evolution of caste via queen-worker-brood conflict over caste fate (LINKSVAYER 2006, 2007, 2008).

The process of caste determination is often described as polyphenism or phenotypic plasticity because the same genotype, when exposed to different environments can result in multiple discrete phenotypes (WHEELER 1986). With strict nutritional ECD, an individual that receives enough food will surpass a threshold for queen determination and develop into a queen, whereas an individual receiving less food may be below the threshold and develop into a worker (WHEELER 1986). Genetic factors may raise or lower the queen threshold, and can influence the likelihood that an individual surpasses the threshold, but can also influence how developing individuals respond to environmental signals. Some genetic variants may effectively "ignore" environmental cues and initiate queen caste determination regardless of rearing environment. When different genotypes are differentially sensitive to and respond differently to environmental cues, there is genotype-by-environment interaction (G × E, FALCONER & MACKAY 1996). Such G × E indicates genetic variation for phenotypic plasticity, and is important for the evolutionary modification and "fine tuning" of larval responses to the developmental environment (LINKSVAYER 2007). As detailed above, G × E interactions are not straightforward in social insects because the "E" term includes the highly influential social environment, which is generated in part by the collective "G"

Tab. 1: Taxonomic distribution of genetic caste determination (GCD) in ants.

Degree of GCD	**Type**	**Subfamily**	**Taxon**	**References**
Strong	Queen-Worker	Myrmicinae	*Pogonomyrmex* DL *barbatus & rugosus*	Helms Cahan & al. (2002), Julian & al. (2002), Volny & Gordon (2002)
			Solenopsis geminata × *xyloni*	Helms Cahan & Vinson (2003)
			Vollenhovia emeryi	Ohkawara & al. (2006)
			Wasmannia auropunctata	Fournier & al. (2005)
		Formicinae	*Cataglyphis cursor*	Pearcy & al. (2004)
	Queen-Queen	Myrmicinae	*Solenopsis invicta*	Gotzek & Ross (2007)
		Formicinae	*Acanthomyops latipes* × *claviger*	Umphrey & Danzmann (1998)
Weak	Queen-Worker	Myrmicinae	*Acromyrmex echinatior*	Hughes & Boomsma (2008)
			Pogonomyrmex badius	Smith & al. (in press)
			Temnothorax curvispinosus	Linksvayer (2006)
	Queen-Queen	Myrmicinae	*Monomorium* sp. 10	Fersch & al. (2000)
			Harpagoxenus sublaevis	Winter & Buschinger (1986)
			Myrmecina graminicola	Buschinger & Schreiber (2002)
		Formicinae	*Lasius niger*	Fjerdingstad (2005)
			Formica truncorum	Bargum & al. (2004)
		Ectatominae	*Ectatomma tuberculatum*	Hora & al. (2005)
	Worker-Worker	Myrmicinae	*Acromyrmex echinatior* and *A. versicolor*	Hughes & al. (2003), Julian & Fewell (2004)
			Pogonomyrmex badius	Rheindt & al. (2005); Smith & al. (in press)
			Temnothorax rudis	Stuart & Page (1991)
		Ecitoninae	*Eciton burchellii*	Jaffe & al. (2007)
		Formicinae	*Camponotus consobrinus*	Fraser & al. (2000)
			Formica selysi	Schwander & al. (2005)

term of the individuals that form the society (Linksvayer 2006, 2007).

In line with the general observations of Kerr (1950) for *Melipona* stingless bees, more detailed studies revealed that caste ratios and size proportions of other social insects were relatively unaffected by environmental fluctuations (Wheeler & Nijhout 1984, Johnston & Wilson 1985, Passera & al. 1996, Fraser & al. 2000, Billick 2002). This stability suggests a genetic component to caste determination, yet studies manipulating aspects of the social or larval environment often revealed that caste determination remains primarily plastic. For example, hormonal manipulations of *Melipona* stingless bees drastically change queen-worker caste ratios relative to genetic expectations (Hartfelder 2006). Also, in a harvester ant where genetic determination of both queen and worker castes has been documented (RHEINDT & al. 2005, SMITH & al. in press) a change in the incoming food supply to colonies alters colony investment into queens and workers (SMITH 2007). Thus, despite genetic predispositions, environmental factors may override genetic variation in the thresholds or developmental switches that bias caste determination (HUGHES & BOOMSMA 2007).

Overview of "weak" GCD

Although colonies of most ant species are headed by a single, once-mated queen, colonies of other species consist of multiple maternal and / or paternal subfamilies. Nearly a quarter of a century ago CALDERONE & PAGE (1988) demonstrated that colonies of honey bees could be selected for different worker properties, and shortly after ROBINSON & PAGE (1988) showed that behavioral specialists within honey bee colonies tended to belong to distinct paternal subfamilies (patrilines). Since these landmark studies demonstrated a heritable basis for behavior, much has been learned about the role of genetics in behavioral and morphological caste specialization. However, we still have little understanding of how inheritance of caste specialization works in the social Hymenoptera and how selection at both the individual and colony levels act to maintain specific caste phenotypes. We return to these issues later.

As genetic markers (RFLP, allozymes, RAPD, AFLP, microsatellites, etc.) have become easier to develop and use they have been more commonly employed in assaying for GCD. Researchers tend to look at whether known sources of genetic variation differ in caste production and whether there is a statistical association between genotype and caste. This approach has demonstrated that some form of GCD exists in at least 21 ant species spanning 4 subfamilies and that genetic bias can occur between queens and workers, or within the queen or worker castes (Tab. 1). As an ever increasing number of studies use genetic markers to detect a heritable basis for caste determination, researchers must be conscious of any variation attributable to life history traits or social structure. For example, workers may selectively nurture or destroy certain genotypes depending on season. Also, signatures of GCD may be confounded by maternal or paternal effects when examining matrilineal or patrilineal caste biases.

Evidence for weak GCD: Genetic biases in caste determination (from weak to strong) have been described in many species spanning four independent evolutionary origins of eusociality (WINTER & BUSCHINGER 1986, ROBINSON & PAGE 1988, HARTFELDER & al. 2006, HAYASHI & al. 2007). Forms of caste bias include behavioral and / or morphological specialization among worker castes, morphological variation among queens, and whether individuals become queens or workers. The majority of studies describe differences within either worker or queen castes, while only a few describe a heritable basis for becoming a queen rather than worker ("royal cheating").

Genetic biases in the determination of physical worker castes may be more common because workers are often functionally sterile and there is no (or less) conflict associated with the potential for reproduction (HÖLLDOBLER & WILSON 1990). Although it is difficult to tally the actual frequencies of each type of genetic caste determination (among workers vs. between workers and queens) from the literature due to taxonomic biases (in what taxa research is performed) and publication biases (negative results are published less often) there have been more reports of genetic differences within castes compared to between queens and workers (Tab. 1).

Caste biasing alleles: The majority of studies have utilized patrilines as an easily defined source of genetic variation, so it is appropriate to explore how traits are inherited from fathers and how these are then passed to subsequent generations. Because alleles are only carried by males in alternating generations, a paternally inherited allele will only be in females in the next generation and then both males and females two generations thence. Thus, if a paternal allele biases a focal female's propensity to become a queen rather than a worker then we would expect, all else being equal, that female offspring of our focal female will also show a queen bias. Despite the superficial benefits of having an allele that favors royalty over drudgery, the resulting dynamics are not straightforward because colonies need to produce both queens and workers at specific times during a colony's life cycle (HÖLLDOBLER & WILSON 1990). Thus, alleles that strongly bias an individual toward queen development may impose a genetic load on colonies when those individuals are produced out of sync with the colony's "natural cycle" (ANDERSON & al. 2006a, CLARK & al. 2006, SCHWANDER & al. 2006). G × E interactions and maternal effects may counterbalance weak caste biasing alleles and help maintain normal caste production cycles (SCHWANDER & al. 2008a).

Selection for diversity: While a host of conditions have been hypothesized to select for polyandry in the social Hymenoptera (CROZIER & FJERDINGSTAD 2001), the data presented here suggest that diversity at caste biasing alleles may select for a higher effective mating frequency or polygyny. Under ECD, both polyandry and polygyny increase genetic diversity within colonies, which in turn increases conflict over caste determination and the theoretical likelihood that individuals, if in control of their own fate, may selfishly choose reproduction over work (REUTER & KELLER 2001). Under GCD these conflicts are actually realized and traits affecting caste bias evolve (LINKSVAYER 2006). But when genes influence caste fate, colony fitness may be adversely affected by the overproduction of expensive caste phenotypes which provide little return for their investment (HELMS CAHAN & al. 2004, ANDERSON & al. 2006a, SCHWANDER & al. 2006). Under these conditions, colony-level selection may act to maintain efficient caste ratios by removing caste-biasing alleles or by generating pressure for polygyny and polyandry according to the relative strength of the existing genetic caste bias. Where GCD is very weak (Tab. 1), colony fitness may be relatively unaffected by weak gyne-biasing alleles, and the genetic load generated by "royal cheats" may simply be compensated by other genotypes in the colony which retain plasticity. If gyne-biased alleles increase in frequency in spite of reduced colony fitness, this will generate selective pressure for allelic combinations that allow the unconstrained expression of the worker phenotype. In a manner similar to that suggested by OLDROYD & FEWELL (2007), polyandry or polygyny will increase colony fitness because it increases the chances that a colony ends up with a diverse set of caste-biasing allelic combinations.

Potential effects of genetic caste bias: Most research has focused on the role of polyandry and polygyny in con-

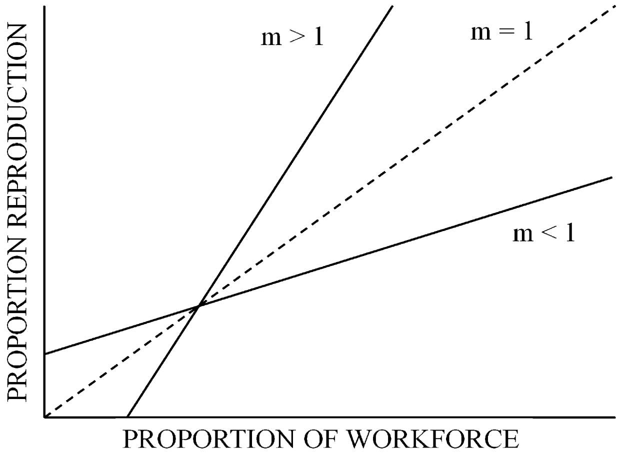

Fig. 1: Potential relationships for how lineages within colonies are distributed among the worker and queen castes. A slope, *m*, of 1 (dashed line) indicates "fair play", where the amount of reproduction gained by a lineage is directly proportional to the amount invested in the workforce. Slopes less than 1 suggest the presence of rare cheaters such that an increase in workforce investment yields a less than proportional representation among queens; patrilines rare among the workforce are "royal cheats". A slope greater than 1 hints at nepotism where the most common lineage among workers gains a disproportionate share of reproduction, potentially by preferential treatment (queen caste induction) of their relatives.

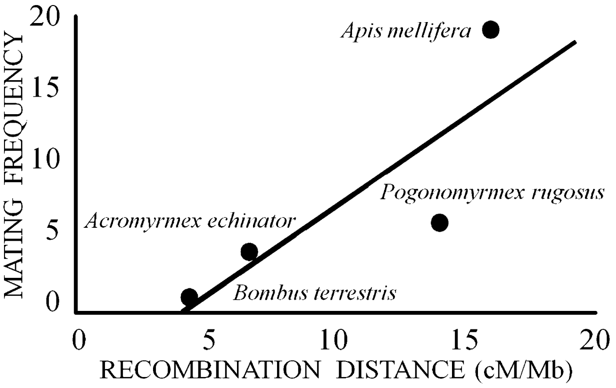

Fig. 2: Relationship between recombination rates and mating frequency in social insects. Despite a very small sample size, r = 0.83 and P = 0.17. Data on mate frequency were taken from RHEINDT & al. (2003) and SUMNER & al. (2004); recombination rates are from WILFERT & al. (2007).

tributing to colony genetic variation, but little attention has been paid to the role of males. Assuming that a genetic caste bias exists, what is the most advantageous response by males? Should they spread their seed across queens or put all of their sperm in "one basket"? If the former is the better strategy, it will drive increased genetic diversity because queens may need to mate multiply to acquire sufficient sperm (COLE 1983, TSCHINKEL 1987, FJERDINGSTAD & BOOMSMA 1998, KRAUS & al. 2004), though in many species males possess more than sufficient sperm to fully inseminate a female (WOYKE 1962). This may, indeed, be the case when royal cheaters increase in frequency in a population because these males may decrease their likelihood of being detected by remaining rare in colonies (HUGHES & BOOMSMA 2008). Moreover, males that "play fair" may also want to decrease their probability of being parasitized; if increased investment in workers does not yield a proportional increase in reproduction then donating "too much" sperm in one place may be a poor strategy if cheating is strong (Fig. 1).

The unequal representation of genetic lineages in queen and worker castes may assume two basic relationships, 1) lineages rare among workers are overrepresented among queens, and 2) the most common patrilines among workers are overrepresented among queens (Fig. 1). The former situation is that of the "rare royal cheat" described previously (MORITZ & al. 2005, HUGHES & BOOMSMA 2008), but the latter represents nepotism (for possible examples see PAGE & al. 1989, HANNONEN & SUNDSTROM 2003). The underlying genetic mechanisms that could give rise to either of these scenarios will differ as "royal cheater" larvae bias their own caste fate (allocation of resources to growth / reproduction and solicitation of nutrition) while nepotism likely involves interactions between nurses and the larvae such that provisioning a larva is conditional on the larva's genotype. In the coming years we predict many more studies will evaluate the slope of this relationship (Fig. 1); these data will be very helpful in assessing the degree of conflict within colonies and how this may play a role in the evolution of strong genetic caste determination.

Recent studies that simultaneously evaluated the role of genetics in worker-worker and queen-worker caste determination suggest that genetic variation may affect caste determination at different critical points during development and in species-specific ways. In *Acromyrmex echinatior,* the patrilines that produced a greater than expected number of queens also showed a large bias in which worker caste (minor or major) they produced (HUGHES & BOOMSMA 2008); thus, there appears to be genetic variation at multiple developmental switches. That is, some patrilines had lower thresholds to become majors and gynes while others essentially bypassed the major caste and developed as only minors or gynes. On the other hand, in the harvester ant *Pogonomyrmex badius,* the size of large workers and queens are more similar within patrilines than either are to small workers (SMITH & al. in press), and so it appears that there is genetic variation for becoming large. It seems that weak GCD can evolve in different ways both within and between species.

Many genes and pathways implicated in caste determination have epistatic effects (RÜPPELL & al. 2004, HUNT & al. 2007, LINKSVAYER 2007). Recombination rates in the Hymenoptera are among the highest reported for animals (WILFERT & al. 2007), potentially decreasing the linkage of many genes that are involved in caste determination. Although single gene function can be critical for the maintenance of social structure (i.e., *CSD, Gp-9*; BEYE & al. 2003, GOTZEK & ROSS 2007, GOODISMAN & al. 2008), caste determination is complex, and genetic caste biasing may entail fortuitous combinations of alleles which are broken up quickly in subsequent generations. Genetic caste biases may be evolutionarily ephemeral, persisting for short periods and then being broken up such that they have an inconsistent influence on social evolution.

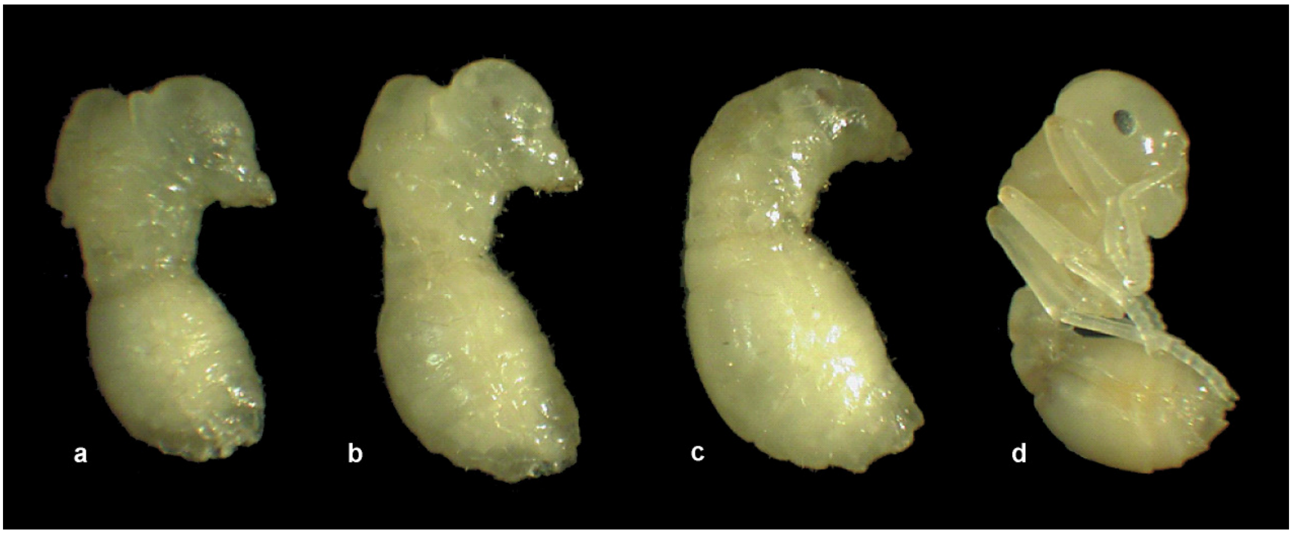

Fig. 3: The developmental cost of strong GCD in immature colonies of DL *Pogonomyrmex*. Four brood nourished simultaneously by the same incipient lab colony. The pupa at the far right (d) is inter-lineage and resulted in a normal worker phenotype. The other three broods (a - c) are intra-lineage genotypes and arrested development at different stages of metamorphosis. Photo by K.E. Anderson.

In fact, increasing recombination rates may coevolve with genetic influences on caste and polyandry. A tantalizing piece of evidence for this comes from a very small number of species where both recombination rates and mating frequencies are known (Fig. 2). These four species vary greatly in both polyandry and recombination rate, and a positive linear relationship between the two exists (though non-statisitically significant due to a very low sample size); polyandry evolved independently in each of these lineages (KRONAUER & al. 2007), all of which are reported to have some degree of queen-worker genetic caste determination (MORITZ & al. 2005, TILLEY & OLDROYD 1997, HELMS CAHAN & al. 2002, HUGHES & BOOMSMA 2008). This finding suggests that genetic caste determination is a recurrent phenomenon, though potentially short-lived, and that alleles that bias caste may usually be prevented from accumulating in discrete lineages.

Overview of strong GCD

Although recent studies have highlighted additional taxa representative of strong genetic caste determination (Tab. 1), the following section will focus on the best studied exemplar; dependent lineage (DL) populations of *Pogonomyrmex* seed harvester ants (see NONACS 2006). All of the more recent examples of strong GCD involve some form of thelytokous parthenogenesis by the queen (PEARCY & al. 2004, FOURNIER & al. 2005, OHKAWARA & al. 2006, HEINZE 2008), a reproductive mode with obvious similarities to DL *Pogonomyrmex* systems. Parthenogenesis by queens maintains linkage of alleles that bias development toward queens, while a genetically variable workforce can be generated by normal sexual reproduction. A genetically variable workforce is potentially a great advantage to the colony for adapting to variable environments or maintaining division of labor (GADAGKAR 2004, OLDROYD & FEWELL 2007). Although it has been known that thelytokous parthenogenesis is phylogenetically widespread (CROZIER & PAMILO 1996), its role in caste determination and social evolution is just beginning to be understood (SUMNER & KELLER 2008) and studies on the molecular basis of parthenogenesis are well underway (LATTORFF & al. 2007).

Dependent-lineage (DL) *Pogonomyrmex*: In some populations of morphologically defined *Pogonomyrmex barbatus* and others of *P. rugosus*, all workers were found to be heterozygous at certain genetic markers whereas the gynes in these colonies were homozygous for the same markers (HELMS CAHAN & al. 2002, JULIAN & al. 2002, VOLNY & GORDON 2002). This pattern was discovered while searching for the signatures of hybridization and initially thought to be associated with present sympatry between *P. barbatus* and *P. rugosus* (JULIAN & al. 2002), or present hybridization between subspecies of *P. rugosus* (HELMS CAHAN & al. 2002). More detailed genetic markers identified the role of hybridization in the phenomenon (HELMS CAHAN & KELLER 2003, ANDERSON & al. 2006b, SCHWANDER & al. 2007a). Morphology was misleading, and hybridization was not occurring between sub-species or species. Oddly enough, each of the morpho-species comprised a perpetually hybridizing system composed of two cryptic and reproductively isolated lineages (VOLNY & GORDON 2002, HELMS CAHAN & KELLER 2003, PARKER 2004, HELMS CAHAN & al. 2006, SCHWANDER & al. 2008b). With very few exceptions, inter-lineage (F_1) gamete combinations produced workers and intra-lineage combinations produced gynes. Each system had apparently stabilized as workers and gynes representing F1 generations did not contribute to the gene pool via the production of inter-lineage haploid or diploid genotypes (SCHWANDER & al 2007b, SUNI & al. 2007). Thus, polyandry was obligate for both the origin and perpetuation of the system because queens had to mate with a male of each lineage to produce both workers and gynes (HELMS CAHAN & al. 2002, JULIAN & al. 2002, VOLNY & GORDON 2002).

Nuclear markers coupled with a mitochondrial DNA phylogeny indicate that the *Pogonomyrmex barbatus* - *P. rugosus* complex is composed of at least six independently evolving lineages (HELMS CAHAN & KELLER 2003, ANDERSON 2006b, but see SCHWANDER 2007a); one *P.*

rugosus and one *P. barbatus* apparently with environmental caste determination (ECD), and two pairs of lineages which interbreed to form GCD colonies. In recognition of the population pressures generated by this reproductive mode it is referred to as a "dependent lineage" (DL) system (ANDERSON 2006a, b). The dependent lineage pairs are H1 / H2 and J1 / J2 based on discovery locations near Portal, Arizona, USA (HELMS CAHAN & KELLER 2003). The H1 / H2 lineage pair has the morphology of *P. rugosus* and the J1 / J2 lineage pair has the morphology of *P. barbatus*.

Origins of the DL system: The first breakthrough concerning the origin of the dependent lineages focused on the site of original discovery (Portal, AZ) and revealed the footprints of ancient hybridization (HELMS CAHAN & KELLER 2003). This analysis pooled allelic data from gynes of all four dependent lineages (near Portal, AZ) and both putative ECD species (*P. barbatus* from Texas and *P. rugosus* from central Arizona), and argued that alleles found in each putative ECD parent formed a unique mix of alleles in all four putative hybrid lineages H1 / H2, J1 / J2. These results suggested that ancient hybridization had played either a dominant or subordinate role in the origin, transmission, or detection of GCD. However, more extensive geographic and molecular sampling confirmed that lineage J2 was not of hybrid origin, but had a parental-like *P. barbatus* genome (HELMS CAHAN & KELLER 2003, ANDERSON & al. 2006b, SCHWANDER & al. 2007a). This was enigmatic because the genetic signatures of the other three lineages (J1, H1, H2) revealed large contributions from both of the putative parental ECD species (HELMS CAHAN & KELLER 2003, ANDERSON & al. 2006b, SCHWANDER & al. 2007a). This suggested a non-hybrid origin for lineage J2 (ANDERSON & al. 2006b), or that the taxonomic units chosen to represent the putative ECD *P. barbatus* ancestor were incorrect (HELMS CAHAN & al. 2006), or that the evolution of the J1 / J2 lineage pair was largely unassociated with the evolution of H1 / H2 (SCHWANDER & al. 2007b).

Hybridization and strong GCD: The causal link between hybridization and strong GCD remains unclear (HELMS CAHAN & KELLER 2003, LINKSVAYER & al. 2006, ANDERSON & al. 2006b, SCHWANDER & al. 2007a, b, ANDERSON & al. in press). At two geographic sites SCHWANDER (2007a) detected interspecific hybridization within the *P. barbatus-rugosus* group but found no evidence of GCD. Similarly, a different *Pogonomyrmex* hybrid zone containing two distantly related and highly polyandrous species shows that some populations are composed entirely of hybrids. But while most workers in these colonies are F_1 hybrids, the molecular data only hints at weak GCD (ANDERSON & al. in press). However, hybridization is strongly associated with reproductive GCD in the fire ant *Solenopsis*. In hybrid zones, pure *S. xyloni* offspring have seemingly lost the genetic potential to develop as workers such that the perpetuation of a non-hybrid germ line relies on males of *S. geminata* to generate the F_1 hybrid worker caste (HELMS CAHAN & VINSON 2003).

The fact that hybrid dynamics differ for haplodiploid and eusocial species may facilitate the evolution of strong GCD under hybridization. Under conditions of polyandry or polygyny, sterility and reductions in fecundity can be easily averted from reproductive offspring and shunted into workers (HELMS CAHAN & al. 2002, JULIAN & al. 2002, HELMS CAHAN & VINSON 2003). If F_1 inter-lineage genotypes are intrinsically unable to develop as queens, hybridization may also relax male-male competition over representation in the queen caste (JULIAN & al. 2002). Additionally, the fitness loss associated with inter-lineage mating may be offset by the competitive advantages of F_1 workers through increased niche breadth and a subsequent decrease in intra-specific competition (UMPHREY 2006, ANDERSON & al. in press). Finally, a colony may benefit from heterosis in hybrid workers resulting in selection for hybridization (UMPHREY & DANZMANN 1998, UMPHREY 2006, JULIAN & HELMS CAHAN 2006, ANDERSON & al. in press).

Persistence and maintenance of DL systems: In mature colonies of *P. rugosus* and the lineage pair H1 / H2, gyne production is initiated by a seasonal effect (SCHWANDER & al. 2008a). During early colony growth however, dependent lineage populations seem to differ in their abilities to regulate gyne production. In general the available data indicate that either the young founding queen or incipient colony does not, or cannot supply gyne-destined eggs and brood with the elements needed to complete gyne programming (Fig. 3). Data from incipient lab colonies shows that gyne-destined genotypes either die or develop poorly during the colony founding stage and are often culled due to arrested development or worker recognition, most disappearing as either eggs or second-instar larvae (HELMS CAHAN & al. 2004, CLARK & al. 2006, VOLNY & al. 2006). However, over 50 % of immature colonies (6 - 12 months old) from one J1 / J2 lab population produced many worker-gyne intercastes (sensu HEINZE 1998) associated with gyne-destined programming (Fig. 4). Over a 6 month period, one of these lab colonies averaged only 14 workers, but produced 15 small intercastes which were about half the size of field produced gynes. Most intercastes were submissive to the queen, but in two different colonies, intercastes repeated attacked and eventually killed the resident queen (Fig. 5). In another well-fed colony, a cohort consisting of four intercastes cannibalized their developing sisters in what could only be described as a feeding frenzy (ANDERSON 2006c).

It is clear that one primary constraint on GCD colony success is early and sustained worker production that relies on the acquisition of worker-destined sperm stores. As levels of polyandry increase, common lineage queens have less colony founding success because they randomly mate with increasingly more males wielding gyne-destined sperm. However, rare lineage queens randomly encounter more worker-destined sperm while simultaneously increasing their chances of encountering a male with gyne-destined sperm. As detailed above, gyne-biased sperm stores represent a nutritional load for the incipient colony because resources are diverted to energetically expensive gyne-destined brood (CLARK & al. 2006). It was suggested that the advertisement of lineage (ASHE & OLDROYD 2002) or sperm recognition (HOSKEN & PITNICK 2003) should evolve to compensate for the genetic load that would result from a low mating frequency. Alternatively, evolving towards a higher mating frequency would promote lineage coexistence (YAMAUCHI & YAMAMURA 2006). While two of the lineages (J1 / J2) have significantly different hydrocarbon profiles (VONLY & al. 2006), the genotypes of eggs produced by newly mated queens indicate that queens mate randomly, there is no sperm recognition, and that initial (egg) caste ratios produced within colonies

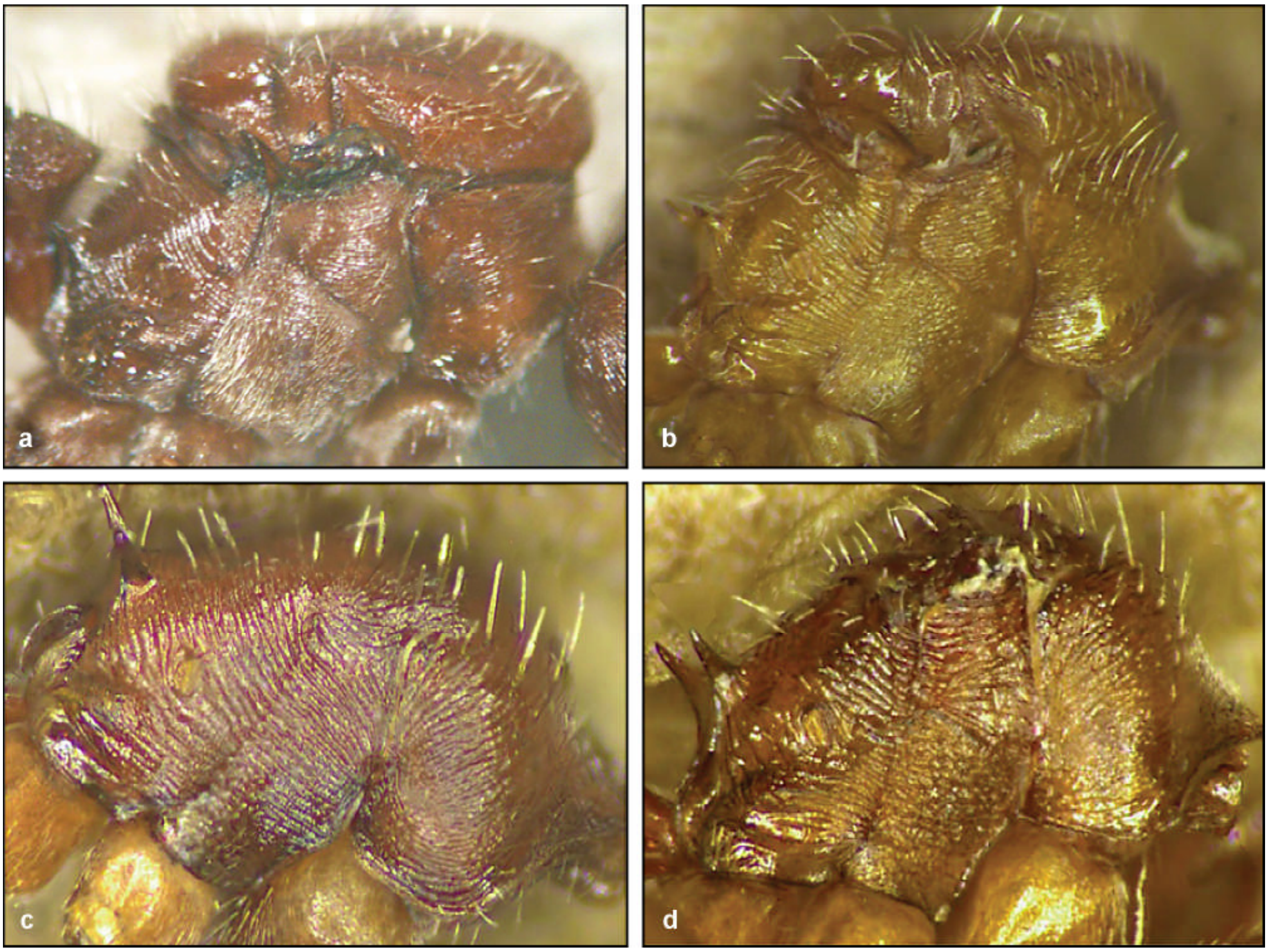

Fig. 4: Worker-gyne intercastes resulting from strong GCD in immature colonies of DL *Pogonomyrmex*. Alitrunk morphology resulting from intra-lineage genome expression. Photos are not to scale; alitrunks are shown at the same size to emphasize sclerite distinctions. (c) is an inter-lineage genome which produced a normal worker alitrunk, and (a) is a field caught intra-lineage queen. (b) and (d) are intra-lineage genomes nurtured by incipient lab colonies; both had abnormal wings that were removed prior to photography. Photos by K.E. Anderson.

are primarily a function of relative lineage frequencies (HELMS CAHAN & al. 2004, CLARK & al. 2006, VOLNY & al. 2006). Thus negative frequency dependent selection on colony founding success is a major factor promoting lineage coexistence (HELMS CAHAN & al. 2004, ANDERSON & al. 2006a, SCHWANDER & al. 2006). By the same mechanism, relative lineage frequencies and mating frequency will influence sex ratios following colony maturity (3 - 5 years), and the strength of balancing selection may determine a frequency threshold beyond which the potential for rare lineage recovery decreases sharply as rare lineage colonies that attain reproductive maturity show a marked decrease in gyne production due to a lack of gyne-destined sperm. A mathematical consideration of these obvious life-history constraints indicates that DL systems may only persist under a narrow set of conditions, with convergence of lineage frequencies towards 0.5 (YAMAUCHI & YAMAMURA 2006).

Independent lineage trajectories: Analogous to the selection acting on sexually antagonistic alleles, the constraint imposed on each reproductively isolated gene pool for the continued production of the worker caste may substantially restrict the adaptive evolution of each lineage (VOLNY & GORDON 2002). The genetic elements necessary to produce a caste functional colony require the continued interaction of two reproductively isolated gene pools. Selection must act antagonistically to simultaneously maintain a viable inter-genome (worker caste) and two viable and fertile intra-genomes (reproductive caste of each lineage). Each intra-lineage genome reaps the first hand benefits of recombination, and may evolve towards a co-adapted genome. However the effects of drift, selection, and mutation accrue independently in each lineage which may result in negative epistasis in inter-lineage genomes (Fig. 6). Strong selection should preserve sets of genes that contribute to colony level caste determination, such that many of these interacting genes may become fixed in each lineage. This fixation may also produce a genetic load via background selection (ANDERSON & al. 2006b), when inferior genes linked to the caste network have a negative effect on overall development.

Genetic models for GCD origin: There have been four main genetic models proposed to explain the evolution of strong GCD found in the *Pogonomyrmex* dependent lineage system. Briefly, the first suggests that a single locus determines caste, such that homozygotes at this locus develop

Fig. 5: The behavioral cost of strong GCD in immature colonies. The resident queen (23 mg) being attacked by an intercaste gyne (9 mg) which was produced by a 7 month old lab colony containing only 6 workers. The gyne sustained some wing damage, but eventually killed the queen. Photos by K.E. Anderson.

into gynes and heterozygotes develop into workers (Volny & Gordon 2002). The next states that the dependent-lineage system arose due to recent hybridization between ECD *P. barbatus* and ECD *P. rugosus*, and GCD is the result of incompatibilities between two interacting nuclear loci brought together by inter-specific hybridization (Helms Cahan & Keller 2003). Under this model, double heterozygote females retain bi-potency, but almost always develop into workers because double homozygote females are genetically predestined to develop into gynes and monopolize colony resources, or otherwise prevent most heterozygotes from developing into gynes. This model provides a genetic mechanism for the origin of the system, but unlike previously thought, bipotency has been lost in both intra-lineage and inter-lineage crosses (Helms Cahan & al. 2004).

A third model suggests that GCD may originate through mutation of a gene with a major influence on caste determination, e.g., a repressor allele in the caste regulatory network (Anderson & al. 2006b). This model stresses the premise that developmental networks are highly conserved, but network interruptions are evolutionary labile (Abouheif & Wray 2002, Goodisman & al. 2008). In the heterozygous state the mutant repressor allele generates a slight propensity to become a queen. In the homozygous state this mutant allele precludes worker development and results in a queen phenotype. Thus the allele behaves as a "selfish" genetic element because it biases its possessor toward queen development, and thereby increases its representation in the reproductive caste relative to other alleles. As the frequency of such a repressor increases, it would result in strong selective pressure to retain an efficient caste repressor (or repression network) in the same population, potentially generating genome evolution analogous to a general modification / rescue system (Werren 1997). One stable resolution may be genome partitioning and the evolution of dependent lineages seen in *Pogonomyrmex* (Anderson & al. 2006b).

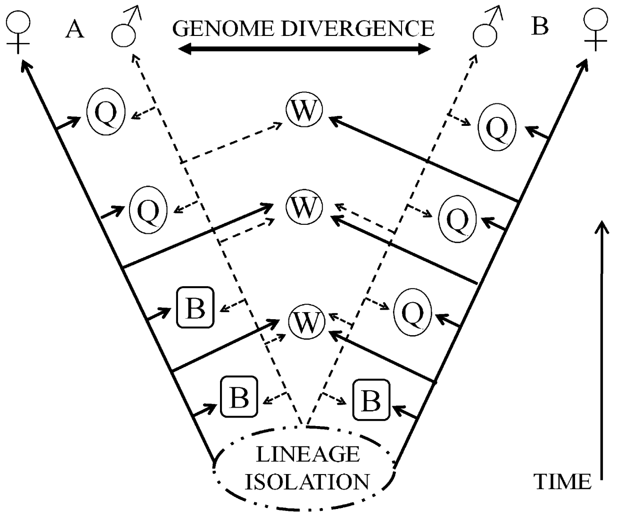

Fig. 6: Hypothesized dependent lineage co-evolution. The "V" represents the accrual of genetic divergence over time due to differences in drift, mutation and selection experienced independently by each lineage (A and B). Each arm of the "V" contains patrilines (dotted) and matrilines (solid). Diploid genome expression is "B" when plasticity remains for both workers and queens, "Q" when only queens result and "W" when only workers result. Time from lineage isolation is represented by the length of vertical arrow. Following isolation, lineage "B" becomes reliant on "A" for the production of a worker caste. Near the top, a diploid genome combination becomes unable to produce a worker caste potentially resulting in inquiline parasitism or localized extinction of the DL system.

The fourth model assumes that the ancestors of the two dependent lineages diverged for interacting cytoplasmic (i.e., mitochondrial) and nuclear genes (Linksvayer & al. 2006). Offspring with matching nuclear and mitochondrial genes, resulting from intra-lineage matings are biased to develop into gynes, while individuals with mismatched nuclear / mitochondrial genes, resulting from inter-lineage matings develop only into workers. This model explains the maintenance of distinct mitochondrial lineages, and is also biologically compelling because queens likely require higher metabolic rates than workers (see EDER & al. 1983), so it makes sense that queens have coadapted combinations of mitochondrial and nuclear genes while workers have disrupted cyto-nuclear combinations (LINKSVAYER & al. 2006).

A recent study shows that maternal effects influence caste in both ECD and GCD *Pogonomyrmex* populations (SCHWANDER & al. 2008a). STRASSMANN & QUELLER (2008) proposed that conflict between queens and developing larvae over caste fate explains the origin of strong GCD. Although not explicitly stated in their formulation, this model also involves epistasis, between maternal and larval genes. As queens transmit both their cytoplasm and maternal effects to their offspring, the maternal effect model is very similar to the cyto-nuclear model and in some situations can also lead to the maintenance of distinct mitochondrial lineages. STRASSMANN & QUELLER (2008) also describe a scenario of queen-larva conflict over caste fate for the evolution of weak to strong GCD, and below we explain how this model complements previously proposed, and very similar scenarios (ANDERSON & al. 2006b, LINKSVAYER & al. 2006).

Weak to strong GCD, royal cheaters, and social parasites

Weakly caste-biasing nuclear genes ("royal cheater genes", HUGHES & BOOMSMA 2008) may spread in a population but incur a cost at the colony level because colonies produce gynes at the expense of workers, required for colony maintenance and growth (ANDERSON & al. 2006b, LINKSVAYER & al. 2006). These alleles may simply be held at low frequency or may spread, depending on the balance of selection between selfish cheater genotypes and non-biasing genotypes within colonies (Fig. 1), and selection between colonies for maximal colony survival and productivity. If caste-biasing cheater alleles spread, restorer mitochondrial or nuclear alleles may be favored and spread, removing the caste bias (ANDERSON & al. 2006b, LINKSVAYER & al. 2006). Over the long term, populations may cycle between caste-biasing nuclear genes that effectively are selfish cheater genes (favored by within-colony selection between different offspring genotypes), and mitochondrial or nuclear genes that remove the caste bias and are favored by colony-level selection that maximizes colony productivity (ANDERSON & al. 2006b, LINKSVAYER & al. 2006). Such cycling can be described as antagonistic coevolution or conflict. In theory such caste-biasing and restorer loci could include any sort of interacting loci, such as nuclear-nuclear or cyto-nuclear loci expressed within larvae, a locus expressed in queens and a locus expressed in larvae, or queen-worker loci (LINKSVAYER & WADE 2005, ANDERSON & al. 2006b, LINKSVAYER & al. 2006, LINKSVAYER 2007, 2008). STRASSMANN & QUELLER (2008) described how caste-biasing and restorer alleles may be expressed in developing larvae and queens, respectively (i.e., queen-brood conflict).

In populations with colonies headed by single, singly-mated queens, caste-biasing alleles transmitted from the queen or her mate will be present in at least half of their offspring. Any bias these alleles cause may strongly impact colony productivity so that strongly-biasing alleles may be held at very low frequency. As described above, polyandry may reduce this constraint because if a single male passes on the caste-biasing allele, only a fraction of the offspring produced by the colony will possess the allele. Thus, in polyandrous populations, caste-biasing alleles may reach a higher equilibrium frequency. Furthermore, in polyandrous populations, lineages of parasitic cheater genotypes that strongly bias caste may evolve (LINKSVAYER & al. 2006). The dependent lineage system may represent one stable result of two lineages with strong caste biasing genotypes that parasitize each other (ANDERSON & al. 2006b). In some cases, strong caste biasing parasites may lead to the evolution of workerless social parasites that rely on the workforce of distinct host lineages (Fig. 6). In these cases, conflict occurs between interacting parasite and host lineages, or lineages that are simultaneously both host and parasite in the case of the dependent lineage system (ANDERSON & al. 2006b, LINKSVAYER & al. 2006). When interbreeding lineages are fixed for alternate biasing and restorer alleles, hybridization may break up matching biasing / restorer complexes and reveal cryptic evidence of conflict (ANDERSON & al. 2006b, LINKSVAYER & al. 2006).

Conclusions and perspectives

GCD systems reveal the genetic complexity hidden in the reproductive modes of social organisms, from reproductively isolated dependent lineages (as in *Pogonomyrmex,* see previous section), to male and female gene pools being nearly separate (as in *Wasmannia*, FOURNIER & al. 2004), to the inability of queens to produce new queens (as recently described in a termite, HAYASHI & al. 2007), and other unexpected situations (SUMNER & KELLER 2008). As pointed out in recent reviews (KELLER 2007), caste phenotypes resulting from GCD are probably far more common than currently appreciated because our current knowledge reflects taxonomic research bias, and efficient techniques permitting molecular detection are relatively recent. GCD may be common because genetically heterogeneous colonies are susceptible to cheaters and caste differentiation involves a multitude of genes interacting at many levels, all of which are exposed to mutation, recombination, and drift followed by subsequent selection bias. Additionally, the evolution of GCD may be facilitated by conflict over reproduction and the selective benefits of within-colony genetic diversity.

Although many studies have identified genes and pathways expressed differently in queens and workers in species with ECD (GOODISMAN & al. 2008), little is known of the functional genomics that underlie either weak or strong GCD. Elucidating the proximate mechanisms responsible for GCD is an obvious next step for caste determination research. Intuitive starting points are the metabolic pathways that translate nutrition into growth, for example the insulin signaling pathway, which is associated with the synthesis and release of juvenile hormone (WHEELER & al. 2006), and plays a diverse role in caste determination (AMENT & al. 2008). However, we predict that there are many mechanisms biasing caste determination across social insect species; furthermore, as suggested by HUGHES & BOOMSMA (2008), genetic variation for different mechanisms may occur even within a species. While even less well understood, variation for genes expressed in nestmate queens, workers, and brood may also strongly influence caste trajectories of developing larvae (LINKSVAYER 2006, 2007). Advances in molecular biology have already made medium to large scale sequencing fast and cheap (e.g., TOTH & al. 2007) which makes the transition to more detailed studies of developmental gene expression feasible for non-model species. In the foreseeable future, the application of bioinformatics to caste determining pathways may bring us a step closer to understanding the molecular basis of social evolution.

Acknowledgements

This project was supported by NIH-IRACDA-PERT postdoctoral award to KEA, a NSF postdoctoral fellowship to TAL, and a Graduate College Fellowship from the University of Illinois to CRS. The suggestions of Diana Wheeler and two anonymous reviewers improved the manuscript.

Zusammenfassung

In jüngster Zeit nahm die Erforschung der Genetik von Kastendetermination drastisch zu, insbesondere nach der Entdeckung von Systemen mit starkem genetischem Einfluss auf die Königinnen-Arbeiterinnen-Determination. In diesem Übersichtsartikel stellen wir Forschungsergebnisse zur genetischen Kastendetermination bei Ameisen zusammen und interpretieren sie, auch im Zusammenhang mit der historischen Entwicklung dieser Forschungsrichtung bei sozialen Insekten. Frühe Wissenschafter waren sich darin uneinig, wie die relative Bedeutung der Umwelt während der Aufzucht auf der einen und der Gene auf der anderen Seite für die Kastendetermination sei. In Folge und bis vor kurzem hatte sich aber eine breite Unterstützung für die Auffassung gefunden, dass die Umwelt ausschlaggebend sei, basierend auf theoretischen Überlegungen und empirischen Ergebnissen. Die zunehmende Verfügbarkeit von molekularen Markern, zusammen mit Zuchtergebnissen und anderen, quantitativ-genetischen Hinweisen, hat jetzt ermöglicht, eine genetische Komponente in der Kastendetermination bei zahlreichen Taxa sozialer Insekten nachzuweisen. Die Stärke der genetischen Komponente variiert und ist offensichtlich häufig stark von der Umwelt abhängig. In extremen Fällen wird die Kaste fast ausschließlich vom Genotyp bestimmt. Wir fassen Umwelt- und genetische Einflüsse auf die Kastendetermination zusammen, einschließlich jüngster Nachweise von schwacher und starker genetischer Kastendetermination und diskutieren die Evolution dieser Systeme. Genotypen, die königinnenlastige zahlenmäßige Verhältnisse der Kasten zueinander bedingen, werden häufig als Schwindler bezeichnet. Wir betonen hier, dass die evolutive Dynamik von genetischer Kastendetermination die Koevolution (oft als Antagonismus) von Genen, die Königinnenlastigkeit bedingen, und solchen, die die Zahlenverhältnisse wieder ausgleichen, in miteinander interagierenden Nestgenossen involviert. Die evolutive Bedeutung solcher Konflikte das Schicksal von Kasten betreffend, bleibt ungeklärt, aber es könnte zu weit verbreiteten Systemen untereinander abhängiger Linien, zu Spermienparasitismus und zu arbeiterinnenlosen Sozialparasiten führen.

References

ABOUHEIF, E. & WRAY, G.A. 2002: Evolution of the gene network underlying wing polyphenism in ants. – Science 297: 249-252.

ALEXANDER, R.D. 1974: The evolution of social behavior. – Annual Review of Ecology and Systematics 5: 325-383.

AMENT, S.A., CORONA, M., POLLOCK, H.S. & ROBINSON, G.E. 2008: Insulin signaling pathways are involved in the regulation of worker division of labor in honey bee colonies. – Proceedings of the National Academy of Sciences of the United States of America 105: 4226-4231.

ANDERSON, K.E., GADAU, J., MOTT, B.M., JOHNSON, R.A., ALTAMIRANO, A., STREHL, C. & FEWELL, J.H. 2006b: Distribution and evolution of genetic caste determination in *Pogonomyrmex* seed-harvester ants. – Ecology 87: 2171-2184.

ANDERSON, K.E., GADAU, J., MOTT, B.M., JOHNSON, R.A., ALTAMIRANO, A., STREHL, C. & FEWELL, J.H. 2006c: Reproductive division of labor. – Bulletin of the Ecological Society of America 87: 194-195.

ANDERSON, K.E., HÖLLDOBLER, B., FEWELL, J.H., MOTT, B.M. & GADAU, J. 2006a: Population-wide lineage frequencies predict genetic load in the seed-harvester ant *Pogonomyrmex*. – Proceedings of the National Academy of Sciences of the United States of America 103: 13433-13438.

ANDERSON, K.E., NOVAK, S.J. & SMITH, J.F. in press: Populations composed entirely of hybrid colonies: Bidirectional hybridization and polyandry in harvester ants. – Biological Journal of the Linnean Society.

ASHE, A. & OLDROYD, B. 2002: Genetic determination of caste in harvester ants. – Trends in Ecology and Evolution 17: 448-449.

BARGUM, K., BOOMSMA, J.J. & SUNDSTRÖM, L. 2004: A genetic component to size in queens of the ant, *Formica truncorum*. – Behavioral Ecology and Sociobiology 57: 9-16.

BEYE, M., HASSELMANN, M., FONDRK, M.K., PAGE, R.E. & OMHOLT, S.W. 2003: The gene csd is the primary signal for sexual development in the honeybee and encodes an SR-type protein. – Cell 114: 419-429.

BILLICK, I. 2002: The relationship between the distribution of worker sizes and new worker production in the ant *Formica neorufibarbis*. – Oecologia 132: 244-249.

BUSCHINGER, A. & SCHREIBER, M. 2002: Queen polymorphism and queen-morph related facultative polygyny in the ant, *Myrmecina graminicola* (Hymenoptera, Formicidae). – Insectes Sociaux 49: 344-353.

CALDERONE, N.W. & PAGE, R.E. 1988: Genotypic variability in age polyethism and task specialization in the honey bee, *Apis mellifera* (Hymenoptera, Apidae). – Behavioral Ecology and Sociobiology 22: 17-25.

CLARK, R.M., ANDERSON, K.E., GADAU, J. & FEWELL, J.H. 2006: Behavioral regulation of genetic caste determination in a *Pogonomyrmex* population with dependent lineages. – Ecology 87: 2201-2206.

COLE, B.J. 1983: Multiple mating and the evolution of social behavior in the Hymenoptera. – Behavioral Ecology and Sociobiology 12: 191-201.

CREEMERS, B., BILLEN, J. & GOBIN, B. 2003: Larval begging behaviour in the ant *Myrmica rubra*. – Ethology Ecology and Evolution 15: 261-272.

CROZIER, R.H. & FJERDINGSTAD, E.J. 2001: Polyandry in social Hymenoptera: disunity in diversity? – Annales Zoologici Fennici 38: 267-285.

CROZIER, R.H. & PAMILO, P. 1996: Evolution of social insect colonies: Sex allocation and kin selection. – Oxford University Press, Oxford, 306 pp.

DARWIN, C. 1859: On the origin of species by means of natural selection. – Murray, London, 490 pp.

DEMENTEN, L., FOURNIER, D., BRENT, C., PASSERA, L., VARGO, E.L. & ARON, S. 2005: Dual mechanism of queen influence over sex ratio in the ant *Pheidole pallidula*. – Behavioral Ecology and Sociobiology 58: 527-533.

EDER, J., KREMER, J.P. & REMBOLD, H. 1983: Correlation of cytochrome c titer and respiration in *Apis mellifera*: adaptive responses to caste determination defines workers, intercastes and queens. – Comparative Biochemistry and Physiology B 76: 703-716.

ELMES, G.W. 1987: Temporal variation in colony populations of the ant *Myrmica sulcinodis*: II. Sexual production and sex ratios. – Journal of Animal Ecology 56: 573-583.

EVANS, J.D. & WHEELER, D.E. 1999: Differential gene expression between developing queens and workers in the honey bee, *Apis mellifera*. – Proceedings of the National Academy of Sciences of the United States of America 96: 5575-5580.

FALCONER, D.S. & MACKAY, T.F.C. 1996: Introduction to quantitative genetics. Edition 4. – Longmans Green, Harlow, Essex, UK, 464 pp.

FERSCH, R., BUSCHINGER, A. & HEINZE, J. 2000: Queen polymorphism in the Australian ant *Monomorium* sp.10. – Insectes Sociaux 47: 280-284.

FJERDINGSTAD, E.J. 2005: Control of body size of *Lasius niger* ant sexuals – worker interests, genes and environment. – Molecular Ecology 14: 3123-3132.

FJERDINGSTAD, E.J. & BOOMSMA, J.J. 1998: Multiple mating increases the sperm stores of *Atta colombica* leafcutter ant queens. – Behavioral Ecology and Sociobiology 42: 257-261.

FOURNIER, D., ESTOUP, A., ORIVEL, J., FOUCAUD, J., JOURDAN, H., LE BRETON, J. & KELLER, L. 2005: Clonal reproduction by males and females in the little fire ant *Wasmannia auropunctata*. – Nature 435: 1230-1234.

FRASER, V.S., KAUFMANN, B., OLDROYD, B.P. & CROZIER, R.H. 2000: Genetic influence on caste in the ant *Camponotus consobrinus*. – Behavioral Ecology and Sociobiology 47: 188-194.

GADAGKAR, R. 2004: Sex ... only if really necessary in a feminine monarchy. – Science 306: 1964-1965.

GOODISMAN, M.A.D., KOVACS, J.L. & HUNT, B.G. 2008: Functional genetics and genomics in ants (Hymenoptera: Formicidae): The interplay of genes and social life. – Myrmecological News 11: 107-117.

GOTZEK, D. & ROSS, K.G. 2007: Genetic regulation of colony social organization in fire ants: an integrative overview. – Quarterly Review of Biology 82: 201-226.

GREGG, R.E. 1942: The origin of castes in ants with special reference to *Pheidole morrisi* FOREL. – Ecology 23: 295-308.

HANNONEN, M. & SUNDSTRÖM, L. 2003: Worker nepotism among polygynous ants. – Nature 421: 910.

HARTFELDER, K., MAKERT, G.R., JUDICE, C.C., PEREIRA, G.A.G., SANTANA, W.C., DALLACQUA, R. & BITONDI, M.M.G. 2006: Physiological and genetic mechanisms underlying caste development, reproduction and division of labor in stingless bees. – Apidologie 37: 144-163.

HAYASHI, Y., LO, N., MIYATA, H. & KITADE, O. 2007: Sex-linked genetic influence on caste determination in a termite. – Science 318: 985-987.

HEINZE, J. 1998: Intercastes, intermorphs, and ergatoid queens: who is who in ant reproduction? – Insectes Sociaux 45: 113-124.

HEINZE, J. 2008: The demise of the standard ant (Hymenoptera: Formicidae). – Myrmecological News 11: 9-20.

HELMS CAHAN, S., JULIAN, G.E., RISSING, S.W., SCHWANDER, T., PARKER, J.D. & KELLER, L. 2004: Loss of phenotypic plasticity generates genotype-caste association in harvester ants. – Current Biology 14: 2277-2282.

HELMS CAHAN, S., JULIAN, G.E., SCHWANDER, T. & KELLER, L. 2006: Reproductive isolation between *Pogonomyrmex rugosus* and two lineages with genetic caste determination. – Ecology 87: 2160-2170.

HELMS CAHAN, S. & KELLER, L. 2003: Complex hybrid origin of genetic caste determination in harvester ants. – Nature 424: 306-309.

HELMS CAHAN, S., PARKER, J.D., RISSING, S.W., JOHNSON, R.A., POLONY, T.S., WEISER, M.D. & SMITH, D.R. 2002: Extreme genetic differences between queens and workers in hybridizing *Pogonomyrmex* harvester ants. – Proceedings of the Royal Society of London B- Biological Sciences 269: 1871-1877.

HELMS CAHAN, S. & VINSON, S.B. 2003: Reproductive division of labor between hybrid and nonhybrid offspring in a fire ant hybrid zone. – Evolution 57: 1562-1570.

HÖLLDOBLER, B. & WILSON, E.O. 1990: The ants. – The Belknap Press of Harvard University Press, Cambridge, MA, 732 pp.

HORA, R.R., DOUMS, C., POTEAUX, C., FENERON, R., VALENZUELA, J., HEINZE, J. & FRESNEAU, D. 2005: Small queens in the ant *Ectatomma tuberculatum*: a new case of social parasitism. – Behavioral Ecology and Sociobiology 59: 285-292.

HOSKEN, D.J. & PITNICK, S. 2003: Do queens select sperm? – Trends in Ecology and Evolution 18: 107.

HUGHES, W.O.H. & BOOMSMA, J.J. 2007: Genetic polymorphism in leaf-cutting ants is phenotypically plastic. – Proceedings of the Royal Society B-Biological Sciences 274: 1625-1630.

HUGHES, W.O.H. & BOOMSMA, J.J. 2008: Genetic royal cheats in leaf-cutting ant societies. – Proceedings of the National Academy of Sciences of the United States of America 105: 5150-5153.

HUGHES, W.O.H., SUMNER, S., VAN BORM, S. & BOOMSMA, J.J. 2003: Worker caste polymorphism has a genetic basis in *Acromyrmex* leaf-cutting ants. – Proceedings of the National Academy of Sciences of the United States of America 100: 9394-9397.

HUNT, G.J., AMDAM, G.V., SCHLIPALIUS, D., EMORE, C., SARDESAI, N., WILLIAMS, C.E., RUEPPELL, O., GUZMAN-NOVOA, E., ARECHAVALETA-VELASCO, M., CHANDRA, S., FONDRK, M.K., BEYE, M. & PAGE, R.E. Jr. 2007: Behavioral genomics of honeybee foraging and nest defense. – Naturwissenschaften 94: 247-267.

JAFFE, R., KRONAUER, D.J.C., KRAUS, F.B., BOOMSMA, J.J. & MORITZ, R.F.A. 2007: Worker caste determination in the army ant *Eciton burchellii*. – Biology Letters 3: 513-516.

JOHNSTON, A.B. & WILSON, E.O. 1985: Correlations of variation in the major minor ratio of the ant *Pheidole dentata* (Hymenoptera, Formicidae). – Annals of the Entomological Society of America 78: 8-11.

JULIAN, G.E. & FEWELL, J.H. 2004: Genetic variation and task specialization in the desert leaf-cutter ant, *Acromyrmex versicolor*. – Animal Behaviour 68: 1-8.

JULIAN, G.E., FEWELL, J.H., GADAU, J., JOHNSON, R.A. & LARRABEE, D. 2002: Genetic determination of the queen caste in an ant hybrid zone. – Proceedings of the National Academy of Sciences of the United States of America 99: 8157-8160.

JULIAN, G.E. & HELMS CAHAN, S. 2006: Behavioral differences between *Pogonomyrmex rugosus* and dependent lineage (H1/H2) harvester ants. – Ecology 87: 2207-2214.

KAPTEIN, N., BILLEN, J. & GOBIN, B. 2005: Larval begging for food enhances reproductive options in the ponerine ant *Gnamptogenys striatula*. – Animal Behaviour 69: 293-299.

KELLER, L. 2007: Uncovering the biodiversity of genetic and reproductive systems: Time for a more open approach. – American Naturalist 169: 1-8.

KELLER, L. & NONACS, P. 1993: The role of queen pheromones in colonies of social insects: Queen control or queen signal? – Animal Behaviour 45: 787-794.

KERR, W.E. 1950: Genetic determinants of castes in the genus *Melipona*. – Genetics 35: 143-152.

KRAUS, F.B., NEUMANN, P., VAN PRAAGH, J. & MORITZ, R.F.A. 2004: Sperm limitation and the evolution of extreme polyandry in honeybees (*Apis mellifera* L.). – Behavioral Ecology and Sociobiology 55: 494-501.

KRONAUER, D.J.C., JOHNSON, R.A. & BOOMSMA, J.J. 2007: The evolution of multiple mating in army ants. – Evolution 61: 413-422.

LATTORFF, H.M.G., MORITZ, R.F.A., CREWE, R.M. & SOLIGNAC, M. 2007: Control of reproductive dominance by the thelytoky gene in honeybees. – Biology Letters 3: 292-295.

LE CONTE, Y. & HEFETZ, A. 2008: Primer pheromones in social Hymenoptera. – Annual Review of Entomology 53: 523-542.

LINKSVAYER, T.A. 2006: Direct, maternal, and sibsocial genetic effects on individual and colony traits in an ant. – Evolution 60: 2552-2561.

LINKSVAYER, T.A. 2007: Ant species differences determined by epistasis between brood and worker genomes. – Public Library of Science One 2: E994.

LINKSVAYER, T.A. 2008: Queen-worker-brood coadaptation rather than conflict may drive colony resource allocation in the ant *Temnothorax curvispinosus*. – Behavioral Ecology and Sociobiology 62: 647-657.

LINKSVAYER, T.A. & WADE, M.J. 2005: The evolutionary origin and elaboration of sociality in the aculeate Hymenoptera: Maternal effects, sib-social effects, and heterochrony. – Quarterly Review of Biology 80: 317-336.

LINKSVAYER, T.A., WADE, M.J. & GORDON, D.M. 2006: Genetic caste determination in harvester ants: possible origin and maintenance by cyto-nuclear epistasis. – Ecology 87: 2185-2193.

MICHENER, C.D. 1974: The social behavior of the bees; a comparative study. – Belknap Press of Harvard University Press, Cambridge, MA, 404 pp.

MICHENER, C.D. & BROTHERS, D.J. 1974: Were workers of eusocial Hymenoptera initially altruistic or oppressed? – Proceedings of the National Academy of Sciences of the United States of America 71: 671-674.

MORITZ, R.F.A., LATTORFF, H.M.G., NEUMANN, P., KRAUS, F.B., RADLOFF, S.E. & HEPBURN, H.R. 2005: Rare royal families in honeybees, *Apis mellifera*. – Naturwissenschaften 92: 488-491.

NONACS, P. 1986: Ant reproductive strategies and sex allocation theory. – Quarterly Review of Biology 61: 1-21.

NONACS, P. 2006: Interspecific hybridization in ants: at the intersection of ecology, evolution, and behavior. – Ecology 87: 2143-2147.

OHKAWARA, K., NAKAYAMA, M., SATOH, A., TRINDL, A. & HEINZE, J. 2006: Clonal reproduction and genetic caste differences in a queen-polymorphic ant, *Vollenhovia emeryi*. – Biology Letters 2: 359-363.

OLDROYD, B.P. & FEWELL, J.H. 2007: Genetic diversity promotes homeostasis in insect colonies. – Trends in Ecology & Evolution 22: 408-413.

OSTER, G.F. & WILSON, E.O. 1978: Caste and ecology in the social insects. – Princeton University Press, Princeton, NJ, 352 pp.

PAGE, R.E. Jr., ROBINSON, G.E. & FONDRK, M.K. 1989: Genetic specialists, kin recognition and nepotism in honey-bee colonies. – Nature 338: 576-579.

PARKER, J.D. 2004: A major evolutionary transition to more than two sexes? – Trends in Ecology and Evolution 19: 83-86.

PASSERA, L., RONCIN, E., KAUFMANN, B. & KELLER, L. 1996: Increased soldier production in ant colonies exposed to intraspecific competition. – Nature 379: 630-631.

PASSERA, L. 1974: Differenciation des soldats chez la fourmi *Pheidole pallidula* NYL. (Formicidae: Myrmicinae). – Insectes Sociaux 21: 71-86.

PEARCY, M., ARON, S., DOUMS, C. & KELLER, L. 2004: Conditional use of sex and parthenogenesis for worker and queen production in ants. – Science 306: 1780-1783.

RATNIEKS, F.L.W. 2001: Heirs and spares: caste conflict and excess queen production in *Melipona* bees. – Behavioral Ecology and Sociobiology 50: 467-473.

REUTER, M. & KELLER, L. 2001: Sex ratio conflict and worker production in eusocial Hymenoptera. – American Naturalist 158: 166-177.

RHEINDT, F.E., STREHL, C.P. & GADAU, J. 2005: A genetic component in the determination of worker polymorphism in the Florida harvester ant *Pogonomyrmex badius*. – Insectes Sociaux 52: 163-168.

ROBINSON, G.E. & PAGE, R.E. Jr. 1988: Genetic determination of guarding and undertaking in honey-bee colonies. – Nature 333: 356-358.

RÜPPELL, O., PANKIW, T. & PAGE, R.E. Jr. 2004: Pleiotropy, epistasis and new QTL: The genetic architecture of honey bee foraging behavior. – Journal of Heredity 95: 481-491.

SCHWANDER, T., HELMS CAHAN, S. & KELLER, L. 2006: Genetic caste determination in *Pogonomyrmex* harvester ants imposes costs during colony founding. – Journal of Evolutionary Biology 19: 402-409.

SCHWANDER, T., HELMS CAHAN, S. & KELLER, L. 2007a: Characterization and distribution of *Pogonomyrmex* harvester ant lineages with genetic caste determination. – Molecular Ecology 16: 367-387.

SCHWANDER, T., HUMBERT, J., BRENT, C.S., HELMS CAHAN, S., CHAPUIS, L., RENAI, E. & KELLER, L. 2008a: Maternal effect on female caste determination in a social insect. – Current Biology 18: 265-269.

SCHWANDER, T., KELLER, L. & HELMS CAHAN, S. 2007b: Two alternate mechanisms contribute to the persistence of interdependent lineages in *Pogonomyrmex* harvester ants. – Molecular Ecology 16: 3533-3543.

SCHWANDER, T., ROSSET, H. & CHAPUISAT, M. 2005: Division of labor and worker size polymorphism in ant colonies: the impact of social and genetic factors. – Behavioral Ecology and Sociobiology 59: 215-221.

SCHWANDER, T., SUNI, S., HELMS CAHAN, S. & KELLER, L. 2008b: Mechanisms of reproductive isolation between an ant species of hybrid origin and one of its parents. – Evolution doi: 10.1111/j.1558-5646.2008.00387.x

SMITH, C.R. 2007: Energy use and allocation in the Florida harvester ant, *Pogonomyrmex badius*: are stored seeds a buffer? – Behavioral Ecology and Sociobiology 61: 1479-1487.

SMITH, C.R., ANDERSON, K.E., TILLBERG, C.V., GADAU, J. & SUAREZ, A.V. in press: Caste determination in a polymorphic social insect: nutritional, social and genetic factors. – American Naturalist.

STRASSMANN, J.E. & QUELLER, D.C. 2008: Social evolution: ant eggs lacking totipotency. – Current Biology 18: R299-R301.

STUART, R.J. & PAGE, R.E. Jr. 1991: Genetic component to division of labor among workers of a leptothoracine ant. – Naturwissenschaften 78: 375-377.

SUMNER, S., HUGHES, W.O.H., PEDERSEN, J.S. & BOOMSMA, J.J. 2004: Ant parasite queens revert to mating singly. – Nature 428: 35-36.

SUMNER, S. & KELLER, L. 2008: Social evolution: Reincarnation, free-riding and inexplicable modes of reproduction. – Current Biology 18: R206-R207.

SUNI, S.S., GIGNOUX, C. & GORDON, D.M. 2007: Male parentage in dependent-lineage populations of the harvester ant *Pogonomyrmex barbatus*. – Molecular Ecology 16: 5149-5155.

SUZZONI, J.P., PASSERA, L. & STRAMBI, A. 1980: Ecdysteroid titer and caste determination in the ant *Pheidole pallidula* (NYL.) (Hymenoptera, Formicidae). – Experientia (Basle) 36: 1228-1229.

TILLEY, C.A. & OLDROYD, B.P. 1997: Unequal subfamily proportions among honey bee queen and worker brood. – Animal Behaviour 54: 1483-1490.

TOTH, A.L., VARALA, K., NEWMAN, T.C., MIGUEZ, F.E., HUTCHISON, S.K., WILLOUGHBY, D.A., SIMONS, J.F., EGHOLM, M., HUNT, J.H., HUDSON, M.E. & ROBINSON, G.E. 2007: Wasp gene expression supports an evolutionary link between maternal behavior and eusociality. – Science 318: 441-444.

TSCHINKEL, W.R. 1987: Relationship between ovariole number and spermathecal sperm count in ant queens: a new allometry. – Annals of the Entomological Society of America 80: 208-211.

UMPHREY, G.J. 2006: Sperm parasitism in ants: selection for interspecific mating and hybridization. – Ecology 87: 2148-2159.

UMPHREY, G.J. & DANZMANN, R.G. 1998: Electrophoretic evidence for hybridization in the ant genus *Acanthomyops* (Hymenoptera: Formicidae). – Biochemical Systematics and Ecology 26: 431-440.

VOLNY, V.P. & GORDON, D.M. 2002: Genetic basis for queen-worker dimorphism in a social insect. – Proceedings of the National Academy of Sciences of the United States of America 99: 6108-6111.

VOLNY, V.P., GREENE, M.J. & GORDON, D.M. 2006: Brood production and lineage discrimination in the red harvester ant (*Pogonomyrmex barbatus*). – Ecology 87: 2194-2200.

WERREN, J.H. 1997: Biology of *Wolbachia*. – Annual Review of Entomology 42: 587-609.

WESSON, L.G. 1940: An experimental study on caste determination in ants. – Psyche 47: 105-111.

WHEELER, D.E. 1986: Developmental and physiological determinants of caste in social Hymenoptera: evolutionary implications. – American Naturalist 128: 13-34.

WHEELER, D.E. 1991: The developmental basis of worker caste polymorphism in ants. – American Naturalist 138: 1218-1238.

WHEELER, D.E., BUCK, N. & EVANS, J.D. 2006: Expression of insulin pathway genes during the period of caste determination in the honey bee, *Apis mellifera*. – Insect Molecular Biology 15: 597-602.

WHEELER, D.E. & NIJHOUT, H.F. 1984: Soldier inhibition in the ant *Pheidole bicarinata*: Inhibition of soldier development by adult soldiers. – Journal of Insect Physiology 30: 127-135.

WHEELER, W.M. 1937: Mosaics and other anomalies among ants. – Harvard University Press, Cambridge, MA, 95 pp.

WILFERT, L., GADAU, J. & SCHMID-HEMPEL, P. 2007: Variation in genomic recombination rates among animal taxa and the case of social insects. – Heredity 98: 189-197.

WILSON, E.O. 1971: The insect societies. – Belknap Press of Harvard University Press, Cambridge, MA, 548 pp.

WINTER, U. & BUSCHINGER, A. 1986: Genetically mediated queen polymorphism and caste determination in the slave-making ant, *Harpagoxenus sublaevis* (Hymenoptera, Formicidae). – Entomologia Generalis 11: 125-137.

WOYKE, J. 1962: Natural and artificial insemination of queen honeybees. – Bee World 43: 21-25.

YAMAUCHI, A. & YAMAMURA, N. 2006: Persistence of symmetrical social hybridogenesis in haplodiploid Hymenoptera. – Journal of Theoretical Biology 240: 24-31.

Zeitschrift/Journal: Myrmecological News = Myrmecologische Nachrichten

Jahr/Year: 2008

Band/Volume: 011

Autor(en)/Author(s): Anderson K.E., Linksvayer Timothy A., Smith C.R.

Artikel/Article: The causes and consequences of genetic caste determination in ants (Hymenoptera: Formicidae). 119-132