Decision making during the scouting behaviour of the slave-making ant *Protomognathus americanus*

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Table of contents

Summary

In an ever-changing environment, flexible decision making can help animals to increase their fitness. Evaluating the current conditions allows them to gain information about their environment in order to choose the most beneficial among a range of possible behavioural options. In social insect societies, the colony can benefit from the integration of information gathered by several individuals, and collective decision making often takes place. However, in some situations scouting individuals have to come up with a final decision, and their decision may be based on limited information.

Here I attempted to elucidate the decision-making mechanisms and the respective key parameters during the scouting behaviour of the slave-making ant *Protomognathus americanus*. Besides the slavemakers, colonies of these ants comprise enslaved workers of closely related *Temnothorax* host species which perform all routine tasks. The slavemaker workers are specialized in searching for host colonies, attacking them and stealing their pupae in order to replenish the slave work force of their own colony.

Before the beginning of the slavemakers' scouting behaviour, decisions have to be made about when to start scouting and which individuals leave the colony as scouts. In my experiments, demographic data showed that colonies with more slavemaker workers send out more scouts, resulting in a faster discovery of host colonies. Furthermore, it could be demonstrated that a shortening of the food supply increases the activity of slavemaker workers outside the nest. Both results suggest that the number of slavemaker workers, probably measured via the nutritional status of individual slavemaker workers, serves as a key parameter to determine the need of the colony and to regulate the onset of the scouting behaviour. Additionally, not all slavemaker workers are equally likely to serve as scouts. Fertile individuals stay inside the nest, and an analysis of the cuticular hydrocarbons of slavemaker workers showed that this division of labour is reflected in the slavemakers' chemical profile.

Having eventually discovered a host colony, a scout has to decide whether or not this host colony constitutes a suitable raiding target. This decision should depend on the potential costs (e.g., worker losses due to host defence) and the potential benefit (i.e., the number of host pupae that can be raided) of attacking the host colony. In choice experiments, *P. americanus* scouts showed a general preference for *T. longispinosus* colonies that contain more host workers, although these larger host colonies represent a greater risk for a raiding party. Colonies with higher host worker numbers are more probable to engage in aggressive encounters with intruding scouts, and increased aggression rates lead to a delay until the scouts' final decision is made. The higher risk that attacking larger host colonies entails may be compensated for by the increased benefit in terms of higher slave worker numbers that can be acquired in a single raid, since in host colonies in the field worker and pupae numbers are positively correlated. As a consequence, slavemaker colonies likely reduce the need for additional scouting events during which slavemaker workers might be particularly vulnerable. Thus the number of host workers represents an easily accessible key parameter for slavemaker scouts to evaluate the value of a host colony.

In my thesis I could demonstrate that the evaluation of a few key parameters is sufficient for regulating decision-making processes during the scouting behaviour in a slave-making ant. The demography of both parasite and host colonies influences the outcome of the decision making, and the nutritional status of slavemaker workers can function as a mean to translate the need of the colony for more slaves into scouting activity. In conclusion, slave-making ants have evolved elaborate decision making processes to successfully exploit their host societies.

Zusammenfassung

Flexibilität in der Entscheidungsfindung kann Tieren dabei helfen, in einer sich stetig verändernden Umwelt ihre Fitness zu erhöhen. Durch Evaluierung der aktuellen Situation ist es ihnen möglich, Informationen über ihre Umwelt zu sammeln, um schließlich aus einer Reihe von Verhaltensoptionen diejenige zu wählen, die den größten Nutzen verspricht. Kolonien sozialer Insekten können davon profitieren, dass mehrere Individuen Informationen sammeln, die in die Entscheidung einfließen, und es kommt häufig zu einer kollektiven Entscheidungsfindung. Manche Situationen bedingen jedoch, dass kundschaftende Individuen eine endgültige Entscheidung auf der Basis unvollständiger Information treffen.

In der vorliegenden Arbeit habe ich untersucht, welche Faktoren die Entscheidungsfindung der sklavenhaltenden Ameise *Protomognathus americanus* während der Suche nach Wirtskolonien beeinflussen. Neben den Sklavenhaltern enthalten Kolonien dieser Ameisenart zusätzlich versklavte Arbeiterinnen der nahe verwandten Gattung *Temnothorax*, welche alle regulären Arbeiten innerhalb der Kolonie erledigen. Die Sklavenhalterarbeiterinnen sind darauf spezialisiert, nach Kolonien ihrer Wirte zu suchen, diese anzugreifen und Wirtspuppen zu stehlen, so dass die Arbeitskraft der Sklavenhalterkolonie durch neue versklavte Arbeiterinnen aufrechterhalten wird.

Noch vor Beginn der Suche nach Wirtskolonien muss eine Entscheidung innerhalb der Sklavenhalterkolonie getroffen werden, wann die Suche begonnen werden soll und welche Individuen als Kundschafter das Nest verlassen. Meine Untersuchungen zur Demographie der Sklavenhalterkolonien zeigten, dass mit steigender Anzahl an Sklavenhaltern in einer Kolonie mehr Kundschafter aktiv sind. Außerdem führt eine Einschränkung der Futterversorgung zu erhöhter Aktivität der Sklavenhalter außerhalb ihres Nestes. Beide Ergebnisse lassen darauf schließen, dass die Anzahl an Sklavenhalterarbeiterinnen, möglicherweise abgeschätzt mittels des individuellen Ernährungszustandes, als Hauptfaktor zur Bestimmung des Bedarfs der Kolonie dient sowie den Beginn der Suche nach Wirtskolonien reguliert. Des Weiteren unterscheiden sich die Sklavenhalterarbeiterinnen in ihrer Wahrscheinlichkeit, als Kundschafter zu fungieren. Fertile Arbeiterinnen bleiben im Inneren des Nestes, und eine Analyse der kutikulären Kohlenwasserstoffe zeigte, dass sich diese Arbeitsteilung auch im chemischen Profil der Sklavenhalter widerspiegelt.

Nach der Entdeckung einer Wirtskolonie muss ein Kundschafter entscheiden, ob diese Wirtskolonie ein lohnenswertes Angriffsziel für einen Raubzug darstellt. Die Entscheidung für oder gegen einen Angriff sollte von den potentiellen Kosten, wie dem möglichen Verlust

eigener Arbeiterinnen aufgrund der Verteidigung der Wirte, und dem potentiellen Nutzen in Form der Anzahl an Wirtspuppen, die geraubt werden können, abhängen. In Wahlexperimenten zeigten Kundschafter von *P. americanus* eine allgemeine Präferenz für Kolonien von *T. longispinosus*, die mehr Wirtsarbeiterinnen enthalten, obwohl diese größeren Wirtskolonien ein höheres Risiko für eine Gruppe angreifender Sklavenhalter darstellen. Wirtskolonien mit einer größeren Anzahl an Arbeiterinnen lassen sich eher auf aggressive Interaktionen mit eindringenden Kundschaftern ein, und erhöhte Aggressionsraten führen zu einer Verzögerung der endgültigen Angriffsentscheidung. Das erhöhte Risiko, das ein Angriff auf eine größere Wirtskolonie mit sich bringt, wird möglicherweise durch den größeren Nutzen in Form einer höheren Anzahl an Sklaven, die durch einen einzelnen Angriff gewonnen werden können, kompensiert, da in Wirtskolonien im Freiland eine positive Korrelation zwischen der Anzahl an Arbeiterinnen und Puppen besteht. Als Folge davon reduziert sich für die Sklavenhalterkolonien wahrscheinlich die Anzahl an zusätzlich benötigten Wirtskolonien und dadurch der Bedarf an weiteren Kundschaftern, die während der Suche nach Wirtskolonien vermutlich besonders gefährdet sind. Somit verkörpert die Anzahl an Wirtsarbeiterinnen für kundschaftende Sklavenhalter eine einfach zu bestimmende, aussagekräftige Größe zur Evaluierung des Wertes einer Wirtskolonie.

In meiner Arbeit konnte ich zeigen, dass die Bestimmung einiger weniger Hauptfaktoren ausreichend ist, um Entscheidungsfindungsprozesse einer sklavenhaltenden Ameisenart während der Suche nach Wirtskolonien zu steuern. Die Demographie sowohl der Parasiten- als auch der Wirtskolonien beeinflusst die Entscheidungsfindung, und der Ernährungszustand der Sklavenhalterarbeiterinnen kann als Mittel dienen, den Bedarf der Kolonie in entsprechende Aktivität bei der Suche nach Wirtskolonien zu übertragen. Sklavenhaltende Ameisen haben demnach ausgefeilte Entscheidungsfindungsprozesse entwickelt, um erfolgreich die Gesellschaften ihrer Wirte auszunutzen.

List of publications

Article 1:

Pohl, S. & Foitzik, S. 2011: Slave-making ants prefer larger, better defended host colonies. Animal Behaviour **81**, 61-68.

Article 2:

Pohl, S., Witte, V. & Foitzik, S. 2011: Division of labor and slave raid initiation in slave-making ants. Behavioral Ecology and Sociobiology **65**, 2029-2036.

Article 3:

Pohl, S. & Foitzik, S. Parasite scouting behaviour and host defence are regulated by colony size in a social parasite system. Submitted to Ethology.

Article 4:

von Beeren, C., Pohl, S. & Witte, V. On the use of adaptive resemblance terms in chemical ecology. Psyche, in press.

Declaration of contributions as co-author

The first three articles are predominantly based on my own work. However, my work was supported by contributions of several co-authors:

Article 1:
Susanne Foitzik participated in the conceptual design, the interpretation of the results and the writing of the manuscript.

Article 2:
Volker Witte supported me in the chemical analyses and the interpretation of the results. Susanne Foitzik participated in the conceptual design and the writing of the manuscript.

Article 3:
Susanne Foitzik contributed to the conceptual design and the writing of the manuscript.

Article 4 resulted from a joint effort of Christoph von Beeren, Volker Witte and myself. We discussed the topic in detail and outlined the manuscript together. Christoph von Beeren led the writing of the manuscript, and Volker Witte and I revised all drafts until completion.

Introduction

> *"We shall, perhaps, best understand how instincts in a state of nature have become modified by selection, by considering* […] *the slave-making instinct of certain ants:* [it has] *generally, and most justly, been ranked by naturalists as* [one of] *the most wonderful of all known instincts."*
>
> – Charles Darwin (1859)

All animals live and interact with their environment. Amongst others, they have to forage, escape from predators and gain access to mating partners. Since the environment is variable, individuals consistently face situations which differ in their specific circumstances, and in which they have different options available to them. But these various options differ in how they affect an individual's survival or reproductive success. Thus decision making, i.e. choosing one of several options in a given situation under specific circumstances, can strongly influence the fitness of an individual (Charnov 1976; McNamara & Houston 1986; Kirkpatrick & Ryan 1991). While adaptations such as enhanced olfaction or stronger legs change the frame conditions, e.g. allow a potential prey animal to better detect a predator or improve the predator's ability to chase its prey, enhanced decision making allows gaining advantages in the present situation. Accordingly, strong selective pressures will lead to adaptations that help the animals to make the "right" decision, i.e. to choose the option that increases their fitness. This can be achieved by a precise evaluation of the current circumstances, and by integrating as much information as possible into the decision-making process before a decision is made (Dall et al. 2005). However, comprehensive evaluations may be costly in terms of time and energy spent, and relying on a few key parameters might suffice (Detrain & Deneubourg 2002). Among the factors that individuals should take into account when making a decision are their current needs as well as the potential benefit and the potential risk that are associated with a specific decision. Depending on the particular situation in which an animal has to make a decision, these factors may include their own physiological condition, the availability of food in the foraging area, or the presence of predators.

In contrast to decisions made by single individuals, decision making in social animals is influenced by the needs and the interests of several individuals, which can lead to conflicts over the final decision (Kerth 2010). However, the group members can also benefit from the fact that information can be collected and processed by more than one individual, thereby reducing potential errors compared to the outcome of individual decisions (Conradt & Roper 2003; Sumpter & Pratt 2009). This benefit of collective decision making can also be found in humans, where it was described by Francis Galton as early as 1907. Galton (1907) noticed that a group of individuals, which do not necessarily need to have expertise in the field, would be able to make a good judgment about the weight of an ox, simply by taking the median value of all individual estimations. The underlying mechanisms have since been successfully applied to describe different fields like stock markets, online search engines and political opinion polls (Surowiecki 2004).

Representing one of the most prominent groups of social animals, eusocial insects such as ants, termites, bees and wasps are among the most successful organisms on Earth in terms of abundance and biomass (Wilson 1990). They form highly organized colonies with elaborate communication and division of labour (Wilson 1971; Hölldobler & Wilson 1990; Seeley 1995). Decision making in social insects is usually based on collective mechanisms such as positive feedback and quorum sensing (Conradt & Roper 2005; Couzin 2009). A well-studied example is the house-hunting behaviour in ants and honeybees (Franks et al. 2002; Visscher 2007), where several scouting individuals evaluate a potential new nest site and then decide individually whether to recruit nestmates or not. Recruited nestmates that arrive at the potential new nest site make their own decisions regarding the suitability of the potential nest site, and then also decide whether to recruit further individuals (Camazine et al. 1999; Mallon et al. 2001). If and when a certain threshold of individuals is reached, the whole colony moves without further evaluation processes (Pratt et al. 2002; Seeley & Visscher 2004). Notably, these thresholds can be variable, depending on the number and quality of potential nest sites that are available and the current urgency to find a new home (Franks et al. 2003).

While these nest site selection processes are based on the cumulative decisions of several individuals, in some situations single scouts have to make a final decision. Scouting honeybees are well-known for their waggle dance that informs their nestmates about the quality, direction and distance of a food source they discovered (von Frisch 1948). However, a scout that returned to the hive can decide whether to recruit nestmates to the food source or not (Dyer 2002). Once the nestmates are informed, it is though still the colony's decision (or the decision of a number of colony members) whether or not to follow a recruiting scout, which depends on the colony's need and the alternative foraging patches proposed by other scouts (Seeley 1995). The scout's influence is still more distinct in the case of foraging for mobile prey. For example, it has been demonstrated that in the group-raiding ant *Leptogenys diminuta*, single scouts decide whether to attack a prey organism directly on their own or to recruit nestmates for a collaborative attack, depending on the respective mobility of the prey organism they encountered (Witte et al. 2010). Hence the study of decision making in social insect individuals can provide insight into the mechanisms that regulate processes at the interface between individual and group decisions.

I studied decision making in a socially parasitic ant species. Social parasites exploit the resources of another social insect species, and they are particularly common among ants (Hölldobler & Wilson 1990). The degree of parasitism ranges from temporary parasitism during colony foundation to total dependence on the host during all life stages (Wilson 1971; Buschinger 2009). Among the obligate social parasites that rely completely on their hosts, slave-making ants exploit the workforce of other ant species by enslaving host workers. The slaves perform all ordinary colony tasks like foraging and brood care, and the slavemaker workers are specialized in regularly replenishing the workforce of the parasite colony via slave raids (Hölldobler & Wilson 1990; D'Ettorre & Heinze 2001). Since the behavioural repertoire of slavemaker workers is almost exclusively confined to the acquisition of new slave workers, the slavemakers' decisions should not be affected by trade-offs that are caused by competing current interests, i.e. they do not have to split their forces to satisfy simultaneously occurring needs such as the need for new slaves and the need to forage for food. Slave-making ants are hence well suited for the study of decision making in social insect individuals.

The obligate slave-making ant *Protomognathus americanus* lives in deciduous forests in the Northeast of the United States. The colonies of this small myrmicine ant can be found inside hollow acorns, sticks and hickory nuts on the forest floor. It parasitizes three closely related *Temnothorax* species: *Temnothorax longispinosus*, *T. curvispinosus* and *T. ambiguus* (Beibl et al. 2005). Colony sizes are small; a parasite colony comprises on average four to five slavemaker workers and about 30 slaves (Herbers & Foitzik 2002). Throughout most of the year, the slavemaker workers remain inside their colony, while the slaves care for the brood, forage and even feed the slavemaker workers via trophallaxis (Sturtevant 1927). However, in late summer some slavemaker workers leave the colony as scouts, searching for nearby host colonies. When a scout finds a host colony, she can either attack it directly, or she can return to her own colony in order to recruit a raiding party of nestmates via tandem running. The raiding party then attacks the host colony, killing or expelling the adult host workers and stealing the host pupae, which are brought back to the slavemaker colony (Wesson 1939; Alloway 1979; Alloway & Del Rio Pesado 1983). These raided host pupae will eventually emerge and imprint on the colony odour (Goodloe & Topoff 1987; Hare & Alloway 1987; Le Moli & Mori 1987), thus replenishing the slavemaker colony's slave workforce.

In my thesis, I focused on the scouting behaviour of *P. americanus*, i.e. I studied the events from the onset of the search for host colonies to the decision to attack a host colony. Below I will describe chronologically the course of events in more detail, and I will present in each case the specific questions I investigated.

Even before the actual scouting behaviour takes place, decisions have to be made inside the slavemaker colony about which individuals will leave for scouting and when to start searching for host colonies. Previous studies showed that *P. americanus* workers form dominance hierarchies inside their colonies, with the dominant workers becoming fertile and seldom participating in raiding events (Franks & Scovell 1983; Blatrix & Herbers 2004). These fertile workers can account for more than 70% of the male offspring (Foitzik & Herbers 2001a). Division of labour can hence be found even among the few slavemaker workers inside the slavemaker colony. Article 2 extends the work on the division of labour between *P. americanus* workers by focusing on participation during scouting events and linking the individual behaviour to individual fertility. Furthermore, the cuticular hydrocarbon (CHC) profiles of slavemaker individuals were analyzed. Originally evolved as a protective layer to prevent desiccation, CHCs adopted an important role in social insect communication, for example in nestmate recognition (van Zweden & d'Ettorre 2010) or in the display of dominance and fertility status (Liebig 2010). In accordance with studies on several ant species that showed differences in the CHC profiles between workers with different tasks (e.g., Greene & Gordon 2003; Lengyel et al. 2007) and between fertile and infertile individuals (e.g., Peeters et al. 1999; Smith et al. 2009), I expected to find chemical differences between slavemaker individuals, which might also provide information about their task and fertility status for their nestmates.

Regarding the onset of the scouting behaviour, slavemaker workers should only start searching for host colonies when there is an actual need to replenish the slave workforce, since during the dangerous slave raids an average of 19% of the participating slavemaker workers are killed by *Temnothorax* host workers that defend their colony (Foitzik et al. 2001). While the need for new slave workers is generally considered to trigger the search for host colonies, it remains unknown how this need is detected. Since slavemaker workers do not feed themselves, but are fed by their slaves, they could use their own nutritional status as an approximation to assess the colony's need for new slaves. In article 2, this hypothesis is addressed by experimentally starving slavemaker colonies and observing the resulting reaction of the slavemaker workers. Furthermore, slavemaker colony demography (number of slavemaker workers, number of slaves, slave to slavemaker ratio) likely determines the required slave workforce. The influence of colony demography on the initiation of the slavemakers' searching behaviour is investigated in more detail in article 3.

Once the slavemakers begin scouting, the course of the events can be quite variable (Alloway 1979). While the final outcome of slave raids in *P. americanus* has been studied in detail before (Alloway 1979; Foitzik et al. 2001; Foitzik & Herbers 2001b; Brandt & Foitzik 2004), a detailed examination of the scouting behaviour is lacking. Article 3 addresses this gap by recording the temporal course of the scouting behaviour. I observed the behaviour of slavemaker workers from the beginning of the search for host colonies and the discovery of a host colony to the eventual start of an attack, taking into account demography data of the slavemaker colonies to further explain the course of actions.

A key moment during scouting is the discovery of a host colony. Comparably to social insect workers that forage for food, scouts "forage" for host pupae, and therefore they should evaluate the quality of the host colony, to decide whether or not the discovered host colony is worth being raided. For that purpose, they enter the host colony. However, when host workers discover a slavemaker scout, they usually attack her, try to expel her from the nest site and sometimes even kill her, while the slavemaker scout also regularly attacks hosts without recruiting nestmates (Alloway & Del Rio Pesado 1983). In article 3 I quantify the aggressive behaviour of both scouts and host workers and investigate the interrelation between the duration of the aggression, the number of scouts and hosts involved, and the consequences for the further course of the interaction.

Slavemaker workers, and parasites of ants in general, have evolved various strategies to prevent being attacked and expelled or killed by host workers (Kistner 1979; Hölldobler & Wilson 1990). Since in ants CHCs carry the necessary information to allow the discrimination of colony members (van Zweden & d'Ettorre 2010), parasites frequently evolved chemical strategies to circumvent their hosts' nestmate recognition mechanism. Parasites modify their CHCs so as to be misidentified as a nestmate, or at least not to be detected as an intruder (Dettner & Liepert 1994; Lenoir et al. 2001). Unfortunately, the terms used to describe chemical strategies of parasites (e.g. chemical mimicry, chemical camouflage, chemical insignificance) are often used inconsistently by different authors, and hence the same strategy may be referred to with various terms, or the same term is applied for different strategies. Article 4 is an attempt to propose a consistent terminology for chemical resemblance strategies that is in accordance with the terms used in general biology.

When a scout discovered a host colony, she has to decide whether it qualifies as a suitable raiding target, i.e. whether or not the host colony should be attacked. It has been demonstrated before that *P. americanus* colonies have the ability to discriminate between different host colonies (Brandt & Foitzik 2004). Slavemaker colonies showed host preferences depending on the host species as well as on their own and the host colonies' population. While in these experiments the host colonies were of similar size, I wanted to study the influence of host colony demography on the slavemakers' decision. Since foraging for host pupae clearly comprises a risk component for slavemaker workers due to the presence of defending host workers, it should be selectively advantageous for scouts to evaluate not only the potential benefit in terms of host pupae they may gain, but also the potential risk represented by the workers of the host colony. In article 1, slavemaker colonies were confronted simultaneously with two host colonies of the same population, but of different demography, in order to investigate whether they favour host colonies of certain demographic compositions, and whether they show preferences for host colonies based on the benefit : risk ratio they evaluated. Furthermore, I wanted to clarify which factors, the number of host workers, the number of host pupae or the ratio between the two, are considered by scouts to decide whether a discovered host colony is worth attacking.

The particular biology of *P. americanus* allowed me to address several questions regarding the decision-making mechanisms in a social insect species. At various points both before and during the scouting behaviour, slavemaker workers have to make decisions about their upcoming actions. They have to evaluate the current situation, taking into account the conditions they encounter, in order to increase the resulting benefit. Because of the small colony sizes, every slavemaker individual is equivalent to a considerable part of the colony, and thus individual decisions account directly for a substantial part of the final outcome at the colony level. Additionally, in my thesis I observed and quantified the course of the scouting behaviour of *P. americanus* in detail. Quantifying the time spans between key events, recording interactions between parasite and host workers, and linking these observations to the demography of the involved ant colonies enabled me to gain insight into the behavioural patterns, and the factors that influence them, during a crucial part of the life cycle of *P. americanus*.

Article 1

Slave-making ants prefer larger, better defended host colonies

Sebastian Pohl and Susanne Foitzik (2011)

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Slave-making ants prefer larger, better defended host colonies

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Collective decision making is important for social insects living in highly organized societies. However, often only a few individuals acquire information relevant for the entire colony. In the slave-making ant *Protomognathus americanus*, single scouts search for colonies of their *Temnothorax* hosts, which are subsequently attacked by a group of raiding workers. Scouts and raiders risk being killed by host workers defending their colony. Considering both the raiding risk and the potential benefit, that is, host pupae that could be taken to serve as slaves after eclosion, scouts must decide whether or not a discovered host colony is worth attacking. We investigated the occurrence of slave raids, host colony assessment and the final decision making by *P. americanus* colonies during choice trials in the laboratory. We confronted slavemaker colonies with two host colonies of different demographic composition to analyse which host colony attributes are considered during the scouts' decision process. Slavemaker colonies showed increased raiding activities when the slave to slavemaker ratio inside the slavemaker colony was low. Slavemakers did not favour host colonies with more pupae, but preferentially attacked colonies with more workers. These represent riskier raiding targets, but as larger colonies usually contain more brood in the field, the increased benefit may necessitate fewer raids, decreasing the total risk during a raiding season. However, confronted with two host colonies that showed more distinct benefit to risk ratios, their decision shifted. Thus raiding behaviour and decision making in *P. americanus* are affected by a combination of external and internal stimuli.

During their lives, animals have many different choices. They can select among alternative mating partners, prey items or nesting locations. Because their decisions can strongly affect their fitness and survival, animals should optimize their decision-making processes. This includes taking into account all relevant information and weighing its importance. In group-living species, information from different group members can be integrated and in some cases the group as a whole can come to a decision (Conradt & Roper 2005). In social insects, these collective decisions become very important, although single social insect workers also take individual decisions, for example during solitary foraging. Ants are known to be able to choose between objects of varying attributes, such as potential nest sites or prey items that are subject to choice decisions (Pratt & Pierce 2001; Cerdá et al. 2009; Robinson et al. 2009). Recent studies on decision-making processes in social insects have focused mainly on contexts such as nest site choice and foraging (Seeley & Buhrman 1999; Franks et al. 2002, 2003; Detrain & Deneubourg 2008). Risks associated with the different alternatives should affect the consequences of specific decisions. Although potential risks also influence nest site or foraging decisions, only a few studies have included risk evaluations (Nonacs & Dill 1990; Franks et al. 2005; Ings & Chittka 2009).

Slave-making ants are social parasites that exploit the brood care behaviour of related host species (Hölldobler & Wilson 1990; Brandt et al. 2005a), similar to avian brood parasites (Payne 1977; Winfree 1999; Krüger 2007). They attack host colonies to replenish their slave workforce, and the host workers in turn defend their colony and regularly kill attacking intruders. Host colony choice should therefore include the evaluation of risks and benefits, deciding whether or not to raid a discovered host nest. We studied decision making in these social parasites. The decision to raid a host colony is presumably based on intrinsic factors such as the colony's need for new slaves and the number of slavemaker workers that can participate in a raid. The final decision to attack a specific host colony should be influenced by extrinsic factors such as the distance, demography and species of the host colony. Indeed, slave-making ants preferentially attack colonies of a less well-defended host species, when given a choice (Brandt & Foitzik 2004).

The North American slave-making ant species *Protomognathus americanus* is an obligate social parasite that completely relies on enslaved workers of their *Temnothorax* ant hosts. Slave workers perform all routine colony tasks such as brood care and foraging, and they even feed slavemaker workers that are unable to feed

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themselves. Slavemaker workers are specialized morphologically and behaviourally for raiding host colonies to replenish the number of enslaved host workers in the slavemaker colony. The acquisition of new slaves is a crucial part of the slavemakers' life cycle, securing the survival and reproduction of the colony (Alloway 1979). In summer, some of the slavemaker workers leave their colony as scouts, searching individually for host colonies. Scouts often enter discovered host colonies, presumably to acquire information on the suitability of these colonies, and thereby come in contact with host workers or brood. If a decision in favour of a raid is made, they will opt for one of two alternatives: either they attack the host colony directly or they return to their own colony, where they recruit nestmates (both conspecifics and slaves), and they lead a raiding party to the host colony that is to be attacked. Host pupae are stolen and carried to the slavemaker colony (Wesson 1939). Emerging host workers are imprinted on the slavemaker colony odour during the first few days after eclosion (Goodloe & Topoff 1987; Le Moli & Mori 1987), and they subsequently work for the slavemaker colony.

Compared with nest site choices and foraging decisions, slavemaking ants face two additional challenges during their search for new slaves. The first major difference concerns the risk component of host colony choices. In raiding decisions the target itself, the host colony, additionally represents a major source of risk for the slavemakers, owing to defending host workers, which kill about one-fifth of all attacking slavemaker workers (Foitzik et al. 2001). As attacking slavemaker workers risk their lives during fights with defending host workers, wrong raiding decisions could result in significant fitness costs for the slave-making ant colony. A second main difference to previous studies on decision-making processes in social insects is that these far-reaching decisions about potential raiding targets can be made by single scout ants. Previous studies usually focused on highly collective decision-making processes with low individual power to make a decision (Visscher 2007; Edwards & Pratt 2009), whereas decision making in slave-making ants includes a strong component of individual judgement. As in nest site choices in ants (Mallon et al. 2001), a slavemaker colony's decision about raiding a host colony depends on the scout's estimation of whether a host colony is worth raiding. However, in contrast to nest site selection, a single slavemaker scout can take the decision to attack a host colony on its own and does not necessarily depend on a collective decision. In *P. americanus*, the evaluation by single individuals plays a major role during decision making, as the colonies of this slave-making ant are small, comprising on average only four to five slavemaker workers (Herbers & Foitzik 2002).

Decision-making processes in slave-making ants are under strong selection. We hypothesized that they could follow one of two distinct strategies. They might reduce the particular risk during each attack by preferring smaller host colonies with fewer host workers because these colonies are less well defended, but as smaller host colonies usually contain fewer pupae that can be stolen, they would then have to discover and raid more host colonies to obtain the same number of new slaves. However, scouts are more at risk than the members of a raiding party, because a single slavemaker worker can be more easily subdued by defending host workers if discovered. Raiding more and smaller host colonies instead of a few, large colonies with many host workers might increase the total risk during a raiding season. Conversely, attacking a large host colony is riskier for a raiding party and it could lead to heavy losses among slavemaker nestmates, but it should reduce the total number of raids and thus the number of scouts needed. By preferring larger host colonies, *P. americanus* colonies might be able to decrease the total risk during a raiding season. With regard to this aspect, the search for host colonies resembles behavioural patterns during foraging, and choosing a host colony is similar to the well-studied optimal foraging problems (Bartumeus & Catalan 2009). The higher the expected search costs, the more the attention is shifted towards more difficult to overcome targets.

Scouts need to assess host colony size to improve raiding outcomes by selectively choosing optimal host colonies. They should estimate the potential risk and the potential benefit in terms of killed nestmates on the one hand and of available host pupae on the other, before they start a raid. One possibility to achieve this goal is to acquire and evaluate information on the demography of a potential raiding target. Here, we investigated host colony choice by *P. americanus* slavemakers using raiding experiments, offering two differing host colonies as potential raiding targets. We thus questioned whether they preferentially attack host colonies of a particular demographic composition, which might allow them to increase the success of their raids. Reducing raiding risks also includes starting a raid only if necessary. In this study, we investigated intrinsic factors that could influence the decision of slavemakers to initiate raids. These included parameters that reliably indicate the need of the colony for new slaves.

METHODS

Study Species

The small myrmicine slave-making ant *P. americanus* is an obligate social parasite (Wesson 1939). It parasitizes three closely related *Temnothorax* species: *Temnothorax longispinosus*, *T. curvispinosus* and *T. ambiguus*. The social parasite colonies are small; besides the queen, a colony on average comprises four to five slavemaker workers and about 30 slaves (Herbers & Foitzik 2002). Both parasite and host colonies can be found in hollow acorns, twigs and hickory nuts on the ground of mixed deciduous forests in the northeastern United States and the adjacent Canadian regions. At our New York study site, *T. longispinosus* is the main host, with *T. ambiguus* occurring only rarely and *T. curvispinosus* being absent (Herbers & Foitzik 2002).

Collection and Maintenance of Ant Colonies

During June 2008, we collected 159 colonies of the social parasite *P. americanus* and 415 colonies of its host species *T. longispinosus* on various sites at the Edmund Niles Huyck Preserve, Rensselaerville, New York, U.S.A. (42°31′32.7″N, 74°09′22.5″W). We placed discovered colonies, still in their opened nest sites, together with some leaf litter in resealable plastic bags and stored them at 5 °C until their transport to Germany. Meanwhile, we fed the ants with pieces of cookies and tuna every 5 days. To ensure adequate humidity, we inserted moistened pieces of cotton in the bags during feeding. In the laboratory, we transferred the colonies into artificial nest sites in three-chambered plastic boxes (9.5 × 9.5 cm and 2.7 cm high) with a moistened plaster floor to provide sufficient humidity (Buschinger 1974). We kept the ants in a climate chamber on a 14:10 h light:dark cycle at 20:15 °C. We fed them ad libitum with honey and pieces of house crickets twice a week. During the raiding season, which takes place from mid-July until the end of September, we kept the colonies of *P. americanus* at 27 °C under a natural light regime to stimulate raiding activities (Buschinger et al. 1980).

Raiding Risk and Benefit

For the New York community that we investigated in this study, it is known that a third of all attacking *P. americanus* colonies suffer the loss of at least one worker during a raid (Brandt & Foitzik 2004). Moreover, on average 19% of all slavemaker workers that

Table 1
Raiding outcomes depending on the number of discovered host colonies for all three trial series

Chosen host colony	Trial series 1			Trial series 2			Trial series 3		
	No host colonies discovered	1 host colony discovered	2 host colonies discovered	No host colonies discovered	1 host colony discovered	2 host colonies discovered	No host colonies discovered	1 host colony discovered	2 host colonies discovered
Better benefit:risk ratio	N/A	5	4	N/A	5	1	N/A	9	1
Worse benefit:risk ratio	N/A	9	3	N/A	16	1	N/A	4	1
No raid	7	6	4	10	4	3	13	10	1

In trial series 1, host colonies had different numbers of pupae but not workers, in trial series 2 they had different numbers of workers but not pupae, and in trial series 3 one host colony had many workers and few pupae and the other host colony had few workers and many pupae.

participate in a raid are killed by the defending *Temnothorax* host workers (Foitzik et al. 2001). A reanalysis of these data sets showed that the fraction of killed raiding workers increased with the size of the attacked host colony (Spearman rank order correlation: $r_S = 0.18$, $N = 156$, $P < 0.025$). However, slavemaker colonies also obtained more host brood from larger host colonies (Spearman rank order correlation: $r_S = 0.24$, $N = 156$, $P < 0.003$), so that the greater risk might be compensated by a larger benefit in terms of raided host worker pupae.

Raiding Experiments

We counted all individuals (i.e. queens, workers, larvae and pupae of both the parasite and the host) in the colonies of the social parasite and in the host colonies that we used in the raiding experiments on the day of the trial. We placed the parasite colony in its artificial nest site at the base of an Y-shaped experimental arena (2.7 cm wide and 2.5 cm high, 15 cm arm length, all angles 120°) that allowed slavemaker scouts to discover both host nests in a reasonable time. We confronted the slavemaker colony with two host colonies placed at the ends of the two arms of the Y to analyse which host colony the social parasites raided or, if they discovered a single host colony, to see whether they considered it a suitable raiding target. These host colonies were selected so that they differed in one or two demographic parameters, depending on the trial series: either in the number of worker pupae, or in the number of adult workers, or in both. Colonies that were selected to differ in a demographic characteristic, such as the number of workers, did so by at least the factor 2. We considered host colonies to be similar in a parameter when the difference between them in this parameter was less than 10%.

For the experiments, we selected those slavemaker colonies that showed scouting activity in the mornings. Slavemakers walking around outside their nest site are a good predictor that these parasite colonies will discover host colonies and initiate raids. On some days only a few slavemaker colonies showed scouting activity, so we decided to reuse active slavemaker colonies. Most slavemaker colonies (58%) were used in a single trial ($N = 18$), four colonies were involved in two trials, five colonies in three, three colonies in four and a single colony in six trials. When we reused slavemaker colonies, we tested them the next day at the earliest, and breaks between two trials could last up to 28 days. For reused colonies the order of trials followed the sequence reported below.

Experiments were successfully completed by 31 *P. americanus* colonies. Fourteen colonies performed a raid in the first trial series, 13 in the second and 13 in the third. Colonies completed a maximum of three trials within a specific trial series, with the exception of a single colony. We used 105 *T. longispinosus* colonies in total and reused host colonies only when they had no direct contact with slavemaker workers.

We observed the raiding trials, checked for the discovery of one or both host colonies by a *P. americanus* scout and examined the subsequent occurrence of a raid. In all trials, only one host colony was raided. We defined a host colony as being chosen by the slavemaker either when the scout started to attack and expel the host workers or when it recruited other slavemaker workers to one of the two host colonies, or when a complete raid took place. We recorded a trial as having ended without a raid taking place when the total experimental time was more than 3 h and we did not record any slavemaker activity outside the slavemaker colony for at least 90 min. We set up 117 raiding trials over a period of 46 days; in 59 of these, slave raids were successfully completed. In 48 of the 59 completed trials, the *P. americanus* colonies attacked a host colony without having discovered the second host (Table 1). Either *P. americanus* colonies do not regularly compare host colonies directly or the slavemaker colonies in our trials were especially eager to raid, as they had had no host contact for about a month prior to the experiments. However, even when only one host colony is discovered, scouts and subsequently slavemaker colonies have to decide whether or not to raid it. Hence, it is of interest also to analyse the results of trials in which only one host nest was discovered.

Slavemaker colonies varied with respect to slavemaker worker numbers, slave numbers and slave:slavemaker ratios (Table 2). We performed three trial series with different experimental set-ups:

Table 2
Demography of slavemaker colonies used in the experiments

	Trial series 1 (N=21)	Trial series 2 (N=23)	Trial series 3 (N=15)	Trial series 1–3, all raids (N=59)	Trial series 1–3, no raid (N=58)
Slavemaker workers	6	6	3	6	4
	5–9, 3–13	5–15, 3–58	2–4, 1–35	3–9, 1–58	2–7, 1–35
Slaves	20	13	11	14	15
	13–25, 3–54	8–19, 3–40	8–15, 7–40	9–21, 3–54	8.3–22, 2–57
Slave:slavemaker ratio	3.5	1.5	4.0	2.7	3.8
	2.0–5.2, 0.8–7.7	0.9–2.7, 0.3–6.7	3.0–9.0, 0.3–23.0	1.2–4.7, 0.3–23.0	2.2–5.5, 0.3–27.5

Medians are given with quartiles and ranges. In trial series 1, host colonies had different numbers of pupae but not workers, in trial series 2 they had different numbers of workers but not pupae, and in trial series 3 one host colony had many workers and few pupae and the other host colony had few workers and many pupae. The column labelled ‘Trial series 1–3, all raids’ combines the data of the first three columns.

Table 3
Demography of host colonies used in the experiments

		Trial series 1 (*N*=21)	Trial series 2 (*N*=23)	Trial series 3 (*N*=15)
Host workers	Colonies with better benefit:risk ratio	19 12–27, 7–48	10 7–14, 2–21	11 9–17, 7–24
	Colonies with worse benefit:risk ratio	21 12–28, 7–49	25 19–30, 16–43	28 26–36, 20–45
Host pupae	Colonies with better benefit:risk ratio	19 15–28, 6–52	6 5–22, 1–35	25 20–30, 14–46
	Colonies with worse benefit:risk ratio	4 2–8, 0–17	8 5–19, 2–40	3 1–6, 0–11
Pupae:worker ratio	Colonies with better benefit:risk ratio	1.1 0.8–1.4, 0.1–2.8	0.8 0.5–2.4, 0.1–7.5	2.3 1.5–3.4, 0.8–4.3
	Colonies with worse benefit:risk ratio	0.2 0.1–0.4, 0.0–1.6	0.4 0.2–0.8, 0.1–1.5	0.2 0.0–0.2, 0.0–0.4

Medians are given with quartiles and ranges. In trial series 1, host colonies had different numbers of pupae but not workers, in trial series 2 they had different numbers of workers but not pupae, and in trial series 3 the worker:pupae ratios differed. Colonies with better benefit:risk ratio are the colonies with more pupae in trial series 1, the colonies with fewer workers in trial series 2 and the colonies with more pupae and fewer workers in trial series 3.

Trial series 1: different numbers of pupae

In the first trial series, we confronted slavemaker colonies with two host colonies that differed only in the number of worker pupae (Wilcoxon test: $W = 231$, $N = 21$, $P < 0.0001$), but had similar numbers of adult workers (Wilcoxon test: $W = 92.5$, $N = 21$, $P = 0.76$; Table 3).

Trial series 2: different numbers of workers

In the second trial series, we offered two host colonies differing in the number of adult workers (Wilcoxon test: $W = 276$, $N = 23$, $P < 0.0001$), but which had similar numbers of worker pupae (Wilcoxon test: $W = 86.5$, $N = 23$, $P = 0.33$; Table 3).

Trial series 3: different numbers of workers and pupae

In the third trial series, we presented two host colonies that differed in both the number of workers (Wilcoxon test: $W = 120$, $N = 15$, $P = 0.0006$) and the number of worker pupae (Wilcoxon test: $W = 120$, $N = 15$, $P = 0.0007$; Table 3). One of the colonies used in a specific trial contained a high number of pupae and a low number of host workers, resulting in a high pupae:worker ratio (all ratios ≥ 0.8), whereas the other colony comprised a high number of host workers and a low number of pupae and therefore showed a low pupae:worker ratio (all ratios ≤ 0.4; Table 3).

To compare the demography of host colonies chosen for the raiding trials with naturally occurring host colony composition data, we analysed the most recent field collection data that were available for our study site. These data were obtained in 2003 during field mappings at the Edmund Niles Huyck Preserve, Rensselaerville, New York (Foitzik et al. 2009). We found that in *T. longispinosus* field colonies the number of worker pupae increased with the number of workers that lived in a colony (median of pupae:worker ratio: 0.8, quartile range 0.2–1.7, total range 0–13.5; best-fitting linear model: $y = -0.007x^2 + 1.1x + 1.77$, $R^2 = 0.24$, $P < 0.0001$). This function is nearly linear for small to medium-sized host colonies, but levels off at very large colony sizes. In our experiments, we used host colonies with a maximum of 49 workers and 52 host worker pupae, and the curve levelled off mainly beyond these colony sizes. In the field, only 10% of all host colonies contained more workers or more worker pupae. Hence, for the parameter range studied, the benefit:risk ratio can be taken as constant.

For statistical analyses, we used the computer programs Statistica 6.0 (StatSoft, Inc., Tulsa, OK, U.S.A.) and PAST version 1.84 (Hammer et al. 2001). Power analyses were performed with the freeware program G*Power 3.1.2. The linear model was fitted using R version 2.8.1 (R Core Development Team, Vienna, Austria).

RESULTS

Trial series 1: Different Numbers of Pupae

When confronted with two host colonies that differed in the number of pupae, *P. americanus* showed no preferences (chi-square test: $\chi^2_1 = 0.43$, $N = 21$, $P = 0.65$; Fig. 1a). Of the seven completed trials in which both host colonies were discovered, four ended with a raid of the host colony that provided the better benefit:risk ratio and three with a raid towards the host colony with the worse benefit:risk ratio.

Trial series 2: Different Numbers of Workers

In the second trial series, *P. americanus* colonies raided host colonies with more host workers more often than those with fewer workers (chi-square test: $\chi^2_1 = 5.26$, $N = 23$, $P = 0.037$; Fig. 1b), although both types of colonies contained the same number of worker pupae.

Trial series 3: Different Numbers of Workers and Pupae

In the third trial series, with host colonies with increased differences in the benefit:risk ratio, we could not find any preference of *P. americanus* for either type of host colony (chi-square test: $\chi^2_1 = 1.67$, $N = 15$, $P = 0.30$; Fig. 1c). A power analysis revealed that, owing to the lower sample size, the effect that could still be detected in trial series 3 (effect size $w = 0.93$) was greater than those in trial series 1 and 2 (effect size $w = 0.79$ and $w = 0.75$, respectively).

Raiding outcomes in trial series 3 were shifted towards colonies with fewer host workers, although the host colonies differed in the number of host workers like the host colonies presented in trial series 2. Host colonies used in these two trial series were unequal regarding the differences in worker pupae numbers. If we disregard these differences, trial series 3 can be seen as a repetition of trial series 2, both presenting host colonies that differed in the number of host workers. However, the results of the two trial series differed from each other (17:6 in favour of colonies with more workers in trial series 2 versus 5:10 against colonies with more workers in trial series 3; chi-square test: $\chi^2_1 = 6.13$, $P = 0.013$).

Internal Parameters

We also investigated the conditions leading to the beginning of slave raids. As both the number of slavemakers and the slave:slavemaker ratio of a given colony varied between trial series, we give here the results for all trials combined. We performed a total of 117 trials in

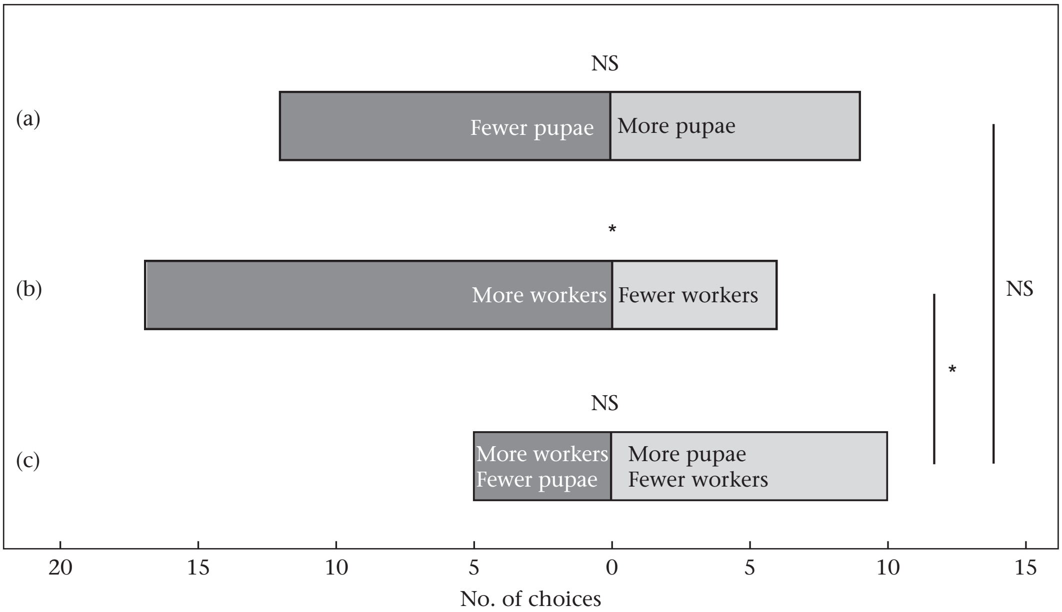

Figure 1. The number of host colony choices for the demographically differing types of host colonies presented for all three trial series: (a) different numbers of pupae ($N = 21$), (b) different numbers of workers ($N = 23$) and (c) different numbers of workers and pupae ($N = 15$). Light grey bars represent the alternative with the better benefit:risk ratio, dark grey bars the alternative with the worse benefit:risk ratio. $^*P < 0.05$, within (above bars) or between (beside bars) trial series.

which scouts searched for host colonies, with 59 of those ending with a raid. In 28 of the remaining 58 trials, *P. americanus* scouts discovered at least one host colony, but did not start a raid, and in 30 trials host colonies were not detected by slavemakers (Table 1). Our experiments revealed that the ratio of slaves per slavemaker in a slavemaker colony was smaller in trials in which slave raids occurred than in trials not ending with a raid (Mann–Whitney *U* test: $U = 1319, N_1 = 59, N_2 = 58, P = 0.033$; Fig. 2). In contrast, neither the total number of slavemaker workers nor the number of slaves in the slavemaker colony affected the occurrence of a raid (Mann–Whitney *U* tests: $P \geq 0.10$ for all trial series). Of the 59 completed trials, 36 ended with the attack of a single scout (61%), whereas in the remaining 23 trials (39%) a group of slavemakers attacked the host colony. We could not find any differences in the number of slavemaker workers, slaves, host workers or host worker pupae or in the slave:slavemaker ratio between the two attacking options (Mann–Whitney *U* tests: all $P > 0.17$).

Influence on Raiding Decision

Supporting evidence for the relevance of the number of host pupae comes from further analysis of slave raid onsets. We analysed the slavemakers' decision whether or not to perform a raid for all cases in which the scouts discovered only one host colony, irrespective of trial series. Host colonies that were raided contained more pupae than those that were discovered, but not attacked (Mann–Whitney *U* test: $U = 329$, $N_1 = 48$, $N_2 = 20$, $P = 0.043$; Fig. 3), whereas we could not find any influence of worker number (Mann–Whitney *U* test: $U = 449.5$, $N_1 = 48$, $N_2 = 20$, $P = 0.69$) or pupae:worker ratio (Mann–Whitney *U* test: $U = 377$, $N_1 = 48$, $N_2 = 20$, $P = 0.17$) in the host colony on the decision to raid in the selected cases over all trial series.

DISCUSSION

Slave raids are crucial for the survival of a slavemaker colony. Thus, accurate host colony choice can strongly increase the raiding performance and ultimately the fitness of a slavemaker colony.

In most trials, slavemaker colonies initiated raids even when the scouts only discovered a single host colony. Although slavemaker colonies could thus not choose between two alternative hosts, they had to take an active decision whether or not a discovered host colony was a suitable raiding target. As we observed a substantial number of trials in which no raid occurred after the discovery of at

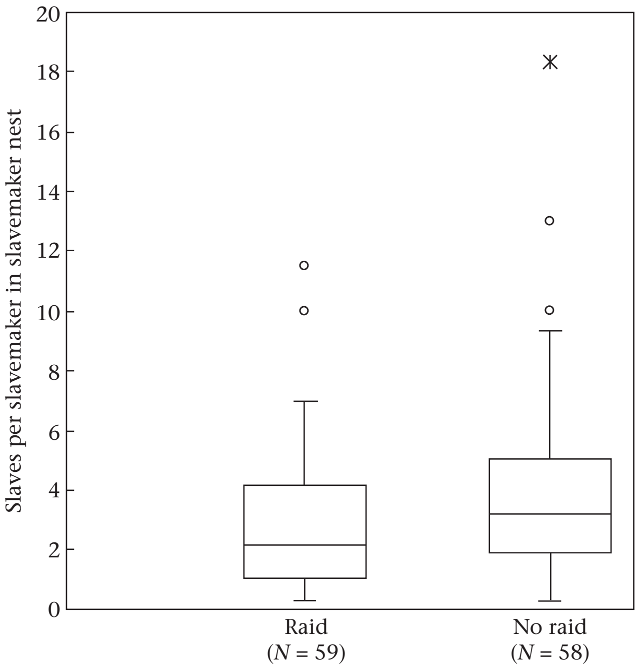

Figure 2. The ratio of slaves per slavemaker inside the slavemaker colony for trials in which slave raids did or did not take place. Boxes show medians and lower and upper quartiles; whiskers represent the lowest datum still within 1.5 interquartile ranges (IQR) of the lower quartile, and the highest datum still within 1.5 IQR of the upper quartile, respectively; the star shows an outlier outside 3 IQR, whereas the circles show outliers between 1.5 and 3 IQR. The number of trials is also shown.

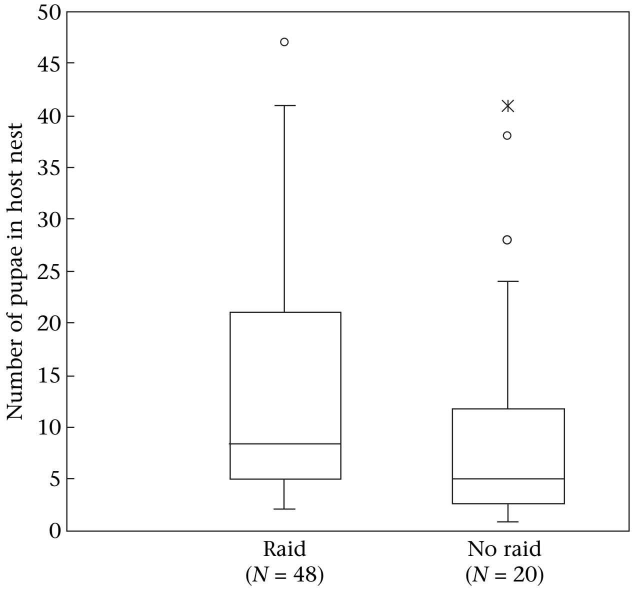

Figure 3. The number of host pupae present in a host colony for trials in which slave raids did or did not take place. Only those trials are included in which only one host colony was discovered. Boxes show medians and lower and upper quartiles; whiskers represent the lowest datum still within 1.5 interquartile ranges (IQR) of the lower quartile, and the highest datum still within 1.5 IQR of the upper quartile, respectively; the star shows an outlier outside 3 IQR, whereas the circles show outliers between 1.5 and 3 IQR. The number of trials is also shown.

least one host colony (Table 1), we conclude that the observed decisions are not merely the consequence of host colony discovery, but are influenced by the characteristics of the host colony and the raiding motivation of the slavemaker colony. During house hunting in *Temnothorax* colonies, single workers regularly discover only a single nest site (Edwards & Pratt 2009). This well-studied decision-making process is thus similarly based on decisions not involving direct comparisons between two or more options. The workers decide whether or not a nest site found is suitable and consequently either recruit or do not recruit nestmates.

The first two trial series revealed that *P. americanus* colonies preferentially attacked larger colonies of their host *T. longispinosus* despite the higher number of defending host workers, whereas they showed no preference for host colonies that contained more pupae. These results suggest that slavemaker scouts use the number of host workers as a measure of host colony size, with the number of host pupae having no primary effect on their decision.

Conversely, the third trial series indicated that the number of host pupae is not completely ignored during the decision-making process of slavemaker scouts when evaluating whether or not to raid a host colony. In the second trial series, slavemakers preferred host nests with more workers, whereas this was not the case in the third trial series, in which, in addition to worker number, pupae number was also varied. These two trial series differed in their outcome, with the slavemakers' decision being shifted towards the colony with a better benefit:risk ratio in the third trial series. Our results therefore indicate that the number of worker pupae in a discovered host nest can affect raiding decisions, but to a lesser extent than the number of workers.

As the acquisition of host worker pupae is the single purpose of a raid, it can be expected that the number of pupae influences host colony choice. Although in the 'different numbers of pupae' trials slavemaker colonies showed no preferences, we found that a higher number of host pupae increased the probability of a successful raid when only one host colony was discovered. Slavemaker colonies might be more willing to raid a host colony that contains more pupae, after having judged this colony to be a suitable raiding target. Yet, when they evaluated whether host colonies qualify as potential raiding targets, *P. americanus* colonies only showed a preference for colonies with more host workers, whereas differences in number of host worker pupae alone did not lead to raiding preferences. We can think of the following explanations for why slavemaker workers rely more on host worker numbers than on pupae numbers during the evaluation process.

Host Colony Choice: Proximate Explanations

The number of workers present in a host colony is easier and more reliable to detect for slavemaker scouts. Host pupae are usually located in the rear part of the host nest, so are more difficult for the scouts to reach, whereas one or more *T. longispinosus* workers are often present at the entrance to the host colony. Additionally, the body surface of workers possesses more, and more diverse, cuticular hydrocarbons than that of worker pupae (Brandt et al. 2005b; Achenbach et al. 2010), which could ease the detection of host workers compared to host pupae.

Scouts of *P. americanus* might assess host colony size by measuring the encounter rate with both adult *T. longispinosus* workers and *T. longispinosus* pupae. Assessing encounter rates has been shown theoretically and experimentally to be a method of nest density evaluation in ant colonies (Gordon et al. 1993; Gordon 1996; Nicolis et al. 2005). By this method, ants can regulate task allocation and nest-moving behaviour. Using encounter rates in target locations as decision cues is known to occur during nest site selection in *T. albipennis* (Pratt 2005), albeit in this case encounters with nestmates lead to the final, collective decision via quorum sensing. In our model system, *P. americanus* scouts potentially make use of the same cue, the encounter rate with *T. longispinosus* workers, for deciding whether or not to raid a host colony. Such reliance on simple decision rules has already been discovered in ant foraging processes (Detrain & Deneubourg 2002) and honeybee, *Apis mellifera*, swarming (Visscher & Camazine 1999), allowing an increased efficiency without the need for complex evaluation mechanisms.

Host Colony Choice: Ultimate Explanations

A possible explanation for the preference of host colonies with more host workers may be found in host colony demography. The analysis of the available field data on the demographic composition of *T. longispinosus* colonies showed a strong correlation between worker and pupae numbers inside host colonies. So slavemaker scouts could use a 'rule of thumb' that under natural conditions they can find more pupae in host colonies comprising more host workers, taking the occurrence of many host workers to indicate many host pupae. Nest site choice experiments have demonstrated that colonies of *T. albipennis* choose to move to more attractive nest sites even if the moving distance is up to nine times greater than the distance to less suitable ones (Franks et al. 2008), showing that favourable targets are sometimes chosen despite increasing costs. This might also be the case for *P. americanus* colonies, which preferred larger, better defended, but potentially more profitable host colonies.

The risk is probably higher for solitary scouts than for slavemaker workers of a raiding party, as they face the *Temnothorax* host colonies alone, which can consist of up to 100 workers. This situation resembles that of founding social parasite queens, which are often killed by host workers (Wesson 1939). Indeed, field data from the New York population indicate that less than 7% of the *P. americanus* queens successfully establish a new colony (Foitzik et al. 2009).

It can be advantageous for slavemaker colonies to prefer larger host colonies over smaller ones. Although the risk during a specific raid might be higher when attacking a large host colony, they could thereby reduce the total number of raids that have to be completed successfully to replenish the slave workforce. As a consequence, they decrease the total costs, that is, the number of nestmates killed or injured over the entire raiding season, as fewer scouts, which are more vulnerable to attacks by defending host workers, have to leave the colony to search for host colonies.

Internal Parameters Influencing Raiding Decisions

We have shown that the total number of slavemaker workers or slaves had no effect on the decision whether or not to raid a discovered host colony. However, slavemaker colonies showed increased raiding activity when the slave:slavemaker ratio inside the slavemaker colony was low. The onset of slave raids may thus be triggered by the absence of a sufficient slave workforce to satisfy the colony's needs. To increase their raiding performance, slavemaker colonies should initiate their raiding activities only when there is actual need for new slaves, since slavemaker scouts risk being injured or killed during host colony explorations.

There are two conceivable ways by which the slavemakers could assess their own number strength in relation to the numbers of slaves in the colony. First, slavemaker workers again might use the encounter rate with enslaved host workers as a measure to quantify the number of slaves in the colony or to estimate the relative slave workforce. Second, slavemaker workers might use internal states such as their own food supply or satiety or the larval provisioning to perceive the colony's need for new slaves. As slavemaker workers are fed by the slaves via trophallaxis (Sturtevant 1927) and almost never forage themselves (Stuart & Alloway 1985), their own need for food may be used as a surrogate measure for the supply situation of the whole colony. They could use this as a trigger for host colony searching. Internal conditions of the colony, such as the need for food, often cause behavioural changes in social insects. Ants can alter their foraging activity and preferences depending on the colony's nutritional needs (Portha et al. 2002; Mailleux et al. 2010). In honeybees, regulation of pollen foraging activities is based on supply and demand (Page & Erber 2002; Fewell 2003). In previous studies, information flow to foragers has been shown to be mediated by pollen distributors (Camazine 1993), but there is also direct information assessment by the foragers via pollen storage levels in the cells (Fewell 2003).

Studying decision making in social insects provides an insight into collective processes. In *P. americanus*, individual decisions of scouts play a major role in the collective decision to carry out a raid. Thus, we have the possibility to shed light on the interface between individual and collective decision making. As the raiding behaviour represents a particular condition, with an additional risk component not present in other situations such as nest site choice, the study of slave-making social parasites offers new opportunities and the chance to address unique problems in the investigation of the decision-making processes in social insects.

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Article 2

Division of labor and slave raid initiation in slave-making ants

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Division of labor and slave raid initiation in slave-making ants

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Abstract In social insect societies, division of labor, i.e., workers of a colony specializing in different tasks, is thought to improve colony performance. Workers of social parasitic slave-making ants focus on a single task, searching for and raiding host colonies to replenish their slave workforce. However, in the North American slavemaker *Protomognathus americanus*, some workers do not partake in raids but remain inside the colony. We analyzed raid participation, fertility, and cuticular hydrocarbon profiles of slavemaker workers and slaves to understand these behavioral differences and the regulation of division of labor in slavemaker colonies. Raid observations showed that some workers were repeatedly involved in raiding activities (exterior workers), whereas others stayed inside the nest (interior workers). Exterior workers were always infertile, while half of the interior workers were fertile. Analysis of cuticular hydrocarbons demonstrated differences between the groups. We also detected chemical differences between interior and exterior slaves, indicating an influence of the individuals' tasks on their cuticular profiles. Task- and fertility-related profiles may allow selective nestmate recruiting. Division of labor should also adapt to varying conditions. Since slave raids are dangerous, they should only be initiated when the colony needs additional slaves. Exclusively fed by their slaves, slavemaker workers could determine this need via their nutritional status. In an experiment with various feeding regimes, colonies subjected to a lower food provisioning rate showed increased proportions of slavemaker workers searching for host colonies. Division of labor in slave-making ants, therefore, might be flexible and can change depending on the colonies' needs.

Keywords Brood parasite · Cuticular hydrocarbons · *Protomognathus americanus* · Slave raid · Social parasite · Task allocation

Introduction

Division of labor is a characteristic trait of social insect societies and greatly contributes to their ecological success (Wilson 1985, 1987). The most fundamental division of labor in social Hymenoptera is that between the reproductive caste—the queen—and the usually non-reproductive worker caste. Caste development is influenced in most social insects by nutrition in the larval stage, while in other species, genetic factors are predominant (Schwander et al. 2010; Wiernasz and Cole 2010). Next to the queen–worker division of labor, tasks are further subdivided among the workers, often resulting in morphological or temporal castes (Hölldobler and Wilson 1990; Johnson 2010). Division of labor among workers is commonly thought to increase colony performance because workers become more efficient in the tasks they specialize in, for example, in foraging, brood care, or colony defense (Porter and Tschinkel 1985; Robinson 1992). However, some recent studies did not find an association between task specialization and efficiency (Dornhaus 2008; Muscedere et al. 2009).

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Usually, a colony has to cope simultaneously with a variety of tasks, and a number of previous studies investigated the regulation of task allocation and the division of labor (Beshers and Fewell 2001; Gordon 1996; Robinson 1992). Social insect workers are thought to exhibit different thresholds for various tasks, and these thresholds are influenced by age, fertility, nutritional status, and experience (Robinson et al. 2009). On a proximate level, chemical signals regulate interactions between workers and, consequently, task allocation. The behavioral castes are also reflected in differing cuticular hydrocarbon profiles of workers (Ferreira-Caliman et al. 2010; Greene and Gordon 2003; Lengyel et al. 2007).

Social parasites differ from non-parasitic social insects in that they have a clear-cut division of labor between the enslaved heterospecific workers, which take over routine tasks such as brood care and foraging, and the social parasite workers, which refrain from performing these essential tasks. Instead, workers of the social parasitic slave-making ants specialize in one single task: They search for and raid host colonies in order to supply their colony with a slave workforce. In addition to this fundamental division of labor between slavemakers and slaves, previous studies on the North American slave-making ant *Protomognathus americanus* revealed an inequality in the fertility and behavior among slavemaker workers of a given colony. *Protomognathus* colonies are very small, comprising on average four to five slavemaker workers and approximately 30 *Temnothorax* slaves (Herbers and Foitzik 2002). These few slave-making workers often interact aggressively with each other and were observed to establish dominance hierarchies (Franks and Scovell 1983). Dominant individuals become fertile and genetic studies showed that worker reproduction accounts for more than 70% of the males produced in both queenright and queenless nests (Foitzik and Herbers 2001). If slavemaker colonies are given the opportunity to raid a host colony in the laboratory, these dominant, fertile slavemaker workers will generally not participate in the subsequent slave raids (Blatrix and Herbers 2004; Franks and Scovell 1983). A similar pattern with only the less fertile workers participating in slave raids exists in the European slave-making ant *Harpagoxenus sublaevis* (Bourke 1988), which shows a lifestyle comparable to that of *P. americanus*, although it is of independent evolutionary origin (Beibl et al. 2005).

Division of labor was demonstrated to occur among workers in unparasitized *Temnothorax longispinosus* colonies (Herbers and Cunningham 1983). We expected a similar distribution of tasks among enslaved *T. longispinosus* workers. Additionally, slaves in a single *P. americanus* colony originate from many different host colonies, and the resulting genetic diversity could contribute to the division of labor among slaves with regard to tasks such as foraging and brood care. Among slaves, there is no task allocation in terms of fertility, as genetic studies revealed that slave workers are generally unable to reproduce in slavemaker colonies (Foitzik and Herbers 2001). Slave workers that specialize in different tasks will probably differ in their cuticular hydrocarbon profiles, especially if these tasks require the ants to work inside versus outside of the colony, as has been shown in harvester ants (Greene and Gordon 2003).

To further improve overall colony performance, slave raids should only be initiated when there is an actual need for more slaves, as slave raids are dangerous for the raiders; an average of 19% of the slavemaker workers that participate in a raid are killed by workers of the attacked *Temnothorax* host colony (Foitzik et al. 2001). In a recent study, it was shown that more slave raids take place when the slave/slavemaker ratio inside the slavemaker colony is low (Pohl and Foitzik 2011), indicating that a shortage of slave workforce can lead to increased raiding activities. A simple mechanism to assess the current strength and efficiency of the slave workforce may be to analyze the food supply. Indeed, nutritional status has been shown to influence task division in *Temnothorax* ants (Robinson et al. 2009), and in the fire ant *Solenopsis invicta*, the motivation for individual ants to forage is based on their own nutritional status, thereby indirectly reacting to the need of the colony as a whole (Howard and Tschinkel 1980). Because *P. americanus* workers do not feed themselves, but rely on trophallaxis from their slaves (Sturtevant 1927), they might easily use their own need for food to estimate the colony's need for additional slaves.

In the present study, we extended the current body of work on the division of labor in slave-making ants, focusing on slave raid participation. We analyzed fertility and cuticular hydrocarbon profiles of slavemaker workers that repeatedly did or did not take part in slave raids and compared them with their slaves to shed further light on the division of labor in slavemaker colonies. We expected to find differences between the profiles of slavemaker workers according to their tasks, which might play a role during recruiting. Additionally, we tested the influence of food supply on raid initiation by observing the colonies' activity under two different feeding regimes. We hypothesize that starvation is sufficient to induce an increase in the scouting behavior, thereby allowing the slavemaker colonies to discover more host colonies to replenish their slave work force.

Materials and methods

Study species

The myrmicine ant *P. americanus* is an obligate slave-making ant that lives in hollow acorns, hickory nuts, and twigs on the floor of mixed deciduous forests in the northeastern USA. It is closely related to its three *Temnothorax* host species (Beibl et al. 2005). At our study site (see below), *T. longispinosus* is the main host, while *T. ambiguus* occurs only rarely and *T. curvispinosus* is absent.

Collection and maintenance of ant colonies

In May and June 2009, we collected colonies of *P. americanus* and its main host species *T. longispinosus* at the Edmund Niles Huyck Preserve, Rensselaerville, NY, USA (42°31′32.7″ N, 74°09′22.5″W). Together with some leaf litter, the ants were kept in their opened nest sites in resealable plastic bags at 7°C until their transportation to the University of Munich, Germany. In the laboratory, we kept the ants in artificial nest sites placed in three-chambered plastic boxes (9.5×9.5×2.7 cm) with a moistened plaster floor to ensure humidity. The day/night cycle was 14 h light at 20°C/10 h dark at 15°C. We fed the colonies twice weekly ad libitum with honey and pieces of crickets. Behavioral experiments were performed at 27°C under a natural light regime to stimulate raiding activities (Buschinger et al. 1980).

Raiding experiment setup

We set up a total of 45 raids in Y-shaped experimental arenas (2.7 cm wide and 2.5 cm high, 15 cm arm length, all angles 120°). We allowed a slavemaker colony simultaneous access to two host colonies. All ant colonies remained in their artificial nest sites. We recorded the behavior of slavemaker workers and slaves using the software Observer XT 9 (Noldus Information Technology, Wageningen, The Netherlands). This software was developed to facilitate behavioral observations. It allows noting down the behaviors of a number of different individuals over time and then compiles the data of one or more observations to calculate frequencies and time spans of certain behaviors performed by selected individuals. We noted whether the ants walked around in the experimental arena, stayed inside the slavemaker nest or entered one of the host nests, as well as the occurrence of a subsequent raid. We defined a host nest as being chosen when the scout fiercely attacked the hosts, causing confusion and excitement, when the scout brought brood items to its own colony, or when the scout recruited nestmates to the respective host colony.

Following a successful raid, we marked all active scouts by tying a piece of fine wire (20 µm diameter) around the petiole or postpetiole. On a separate day (range of interval between trials, 1–19 days), we set up a second raiding trial with the same colony. A total of 16 slavemaker colonies successfully performed a second raid, and we checked for *P. americanus* workers that participated in both raids (exterior workers) or in neither of the two raids (interior workers). We then separately froze one exterior and one interior slavemaker worker as well as one *T. longispinosus* slave found outside the nest before the trial (exterior slave) and one that remained inside the slavemaker nest during the raid (interior slave).

Fertility and size assessments

After extracting the ants for chemical analyses (see below), we measured and dissected all studied individuals. We used head width as a standard measure of body size (Hölldobler and Wilson 1990) since the workers of both study species are monomorphic. During dissection, we counted and measured all ovarioles, counted the number of eggs, and checked for the presence of yellow bodies (corpora lutea). These are remnants of nurse cells necessary for egg production and hence indicate that an individual has already laid eggs (Billen 1985). We defined an individual as being fertile when we found developing eggs inside the ovarioles. The presence of yellow bodies served as an additional, stricter criterion as all individuals with yellow bodies present also showed developing eggs.

Chemical analyses

We analyzed the cuticular hydrocarbon profiles of exterior and interior workers to search for differences between their profiles by means of gas chromatography with coupled mass spectrometry. We tested exterior and interior individuals of both slavemaker workers and slaves from 16 *P. americanus* colonies (64 individuals in total). Individuals were extracted for 10 min in 100 µl hexane. After evaporation of the solvent, we dissolved the cuticular hydrocarbons in 20 µl hexane containing methylstearate (concentration, 2 mg/100 ml; FLUKA Analytics, Sigma-Aldrich) as an internal standard.

Using an autosampler (Agilent Technologies, 7683 Series), 1 µl of each sample was then injected in the gas chromatograph (Agilent Technologies 6890N GC, equipped with a Restek Rxi-5MS column, 30 m length, 0.25 mm i.d., 0.25 µm film thickness). Injection was splitless over 1.0 min at 280°C under a pressure pulse of 16 psi for 0.5 min, followed by an automatic flow control of 1.0 ml/min with helium as carrier gas. The oven program started isothermal at 120°C for 1 min and then increased rapidly by 25°C/min for 4 min, followed by a gentle temperature ramp of 4°C/min until 300°C, and finally stayed isothermal for 5 min.

Since our study species are very small (both species are about 2–3 mm long) and total cuticular hydrocarbon amounts are therefore small as well, we used selected ion monitoring for subsequent analyses with the mass spectrometer (Agilent Technologies GC 5975 MSD). We scanned only selected mass units that are typical for hydrocarbons (55, 57, 69, 71, 83, 85, 97, and 99 amu) to increase sensitivity. The transfer line was held constant at 310°C. The initial solvent delay was 3.8 min.

Peak areas were determined with the software MSD ChemStation, version E.02.00.493 (Agilent Technologies, Inc.).

Starvation experiment

We divided 22 *P. americanus* nests into two groups of 11 colonies each. We provisioned the control group with half a cricket and honey ad libitum twice a week, whereas we fed the treatment group once a week with half a *Drosophila* fly and a small droplet of honey (approximately 1 µl). We established this feeding regime 3 weeks before observations began and continued it until the end of the experiment 21 days later. In two colonies of the control treatment, all slavemaker workers died during the establishment of the feeding regime. We replaced them with two new colonies that were kept under control conditions at the beginning of the observations.

When we started the feeding regime, slavemaker worker numbers did not differ markedly between treatments (Mann–Whitney *U* test, U=39.5, N_1=11, N_2=9, P=0.45). Slave worker numbers were reduced in some colonies to obtain similar slave/slavemaker ratios (Mann–Whitney *U* test, U=38.5, N_1=11, N_2=9, P=0.40), and slave worker numbers subsequently did not differ between treatments (Mann–Whitney *U* test, U=48.5, N_1=11, N_2=9, P=0.94). Incorporation of the two replacement colonies and eclosion of slavemaker worker pupae prior to the observations led to variation between colonies in both treatment groups, but we could not find any differences in slavemaker worker numbers (Mann–Whitney *U* test, U=59, N_1=11, N_2=11, P=0.92), slave worker numbers (Mann–Whitney *U* test, U=43, N_1=11, N_2=11, P=0.25) or slave/slavemaker ratios (Mann–Whitney *U* test, U=51, N_1=11, N_2=11, P=0.53) between the two treatments.

We recorded the colonies' activity, counting the number of slavemakers and slaves both inside and outside the artificial nest site once per working day (total of 15 recordings per colony). Slavemaker presence outside the nest site indicates the willingness to search for host nests, and slaves outside the nest presumably search for food. Additionally, we performed raiding experiments during the observational period as described above to reveal the potential influences of the nutritional status on the raiding behavior.

Statistics

For the statistical analyses, we used the computer program Statistica 6.0 (StatSoft, Inc., Tulsa, OK, USA). Boxplots were generated using PAST version 2.03 (Hammer et al. 2001). For all tests, we selected an alpha value for the significance level of α=0.05.

Chemical data were evaluated with the program PRIMER 6, version 6.1.13, with the PERMANOVA+ add-in, version 1.0.3 (PRIMER-E Ltd). We analysed slavemakers and slaves separately. We omitted all peaks that were smaller than 5% of the maximum peak of each run to normalize between the different runs. The data were standardized by the maximum peak area to detect differences in the relative proportions of cuticular hydrocarbons. We ran non-parametric, permutational MANOVAs (PERMANOVAs) (Anderson et al. 2008) with 9,999 permutations using Canberra metric as resemblance measure. We tested for differences caused by the location of workers using colony as a random factor and location (exterior/interior) as a fixed factor. To find potential differences in the total amount of cuticular hydrocarbons, we calculated real concentrations for each sample using the internal standard and ran a PERMANOVA with the same design. According to the results of the fertility analyses (see below), we regrouped all *P. americanus* individuals into three groups and ran two PERMANOVAs with 9,999 permutations using Canberra metric as resemblance measure, testing for differences in the relative proportions and in the total amount of cuticular hydrocarbons using groups as a fixed factor. In the case of differences between groups, we ran an additional PERMANOVA to locate these differences using a pair-wise test.

We calculated a colony's activity in the starvation experiment as the proportion of slavemaker workers outside the nest for every observation day. For every colony, we calculated the median activity and then compared median values of all colonies, as not all colonies survived during the entire observation period.

Results

Fertility and size assessments

All analyzed *P. americanus* workers outside the nest were infertile (16 out of 16), whereas half of the tested interior workers (eight out of 16) had eggs in their ovarioles (Fisher's exact test, N_1=16, N_2=16, P=0.0024). Moreover, five out of the 16 interior workers showed yellow bodies, a sign of recent egg-laying (Fisher's exact test, N_1=16, N_2=16, P=0.0434). We found no differences in the number of ovarioles (Mann–Whitney *U* test, U=124.5, N_1=16, N_2=16, P=0.91) and in mean ovariole length (Mann–Whitney *U* test, U=88, N_1=16, N_2=16, P=0.14).

Fertile slavemaker workers were larger than infertile workers (Mann–Whitney *U* tests; fertility based on the presence of yellow bodies, U=21, N_1=5, N_2=27, P=0.017,

Fig. 1; fertility based on the presence of eggs, $U=55$, $N_1=8$, $N_2=24$, $P=0.078$).

We did not find fertility differences between exterior and interior *T. longispinosus* slaves, neither based on the presence of eggs or yellow bodies (Fisher's exact tests, $N_1=16$, $N_2=16$, all $P>0.48$) nor in ovariole number or length (Mann–Whitney *U* tests, $N_1=16$, $N_2=16$, all $P>0.77$). Overall, *T. longispinosus* slaves exhibited less developed ovaries and fewer developing eggs compared to the slavemakers. Even slaves that were classified as fertile had fewer eggs present in their ovarioles than fertile slavemaker workers (Mann–Whitney *U* test, $U=3$, $N_1=18$, $N_2=8$, $P=0.0001$).

Chemical analyses

We detected differences in the relative proportions (PERMANOVA, $P=0.0001$) and in the total amount (PERMANOVA, $P=0.0026$) of cuticular hydrocarbons between colonies for slavemaker workers. Beyond that, we found differences between interior and exterior workers regarding the relative proportions of detected components (PERMANOVA, $P=0.0385$), but not in total amounts (PERMANOVA, $P=0.52$). As we found fertile individuals only among interior workers, we regrouped the slavemaker workers into fertile interior workers ($N=8$), infertile interior workers ($N=8$), and infertile exterior workers ($N=16$) to reveal the potential influence of fertility on the cuticular profile. We found no differences between the three groups in the relative proportions of cuticular hydrocarbons (PERMANOVA, $P=0.23$). We have to note that due to regrouping, sample sizes for these comparisons were quite small. However, the groups differed in the total amounts of cuticular hydrocarbons (PERMANOVA, $P=0.0165$). Subsequent pair-wise tests revealed differences in the total amounts of cuticular hydrocarbons between fertile and infertile interior workers (PERMANOVA, $P=0.006$). Infertile interior and exterior workers (PERMANOVA, $P=0.074$) as well as infertile exterior workers and fertile interior workers (PERMANOVA, $P=0.091$) differed, though not significantly, in the total amount of cuticular hydrocarbons (Fig. 2). Fertile interior workers carried the highest amount of cuticular hydrocarbons (median=1.95 µg), while infertile interior workers had the lowest amount (median=0.76 µg), and infertile exterior workers were in the middle (median=1.44 µg).

Slave workers differed between colonies in the relative proportions of cuticular hydrocarbons (PERMANOVA, $P=0.0004$) and also, though not significantly, in their total amounts (PERMANOVA, $P=0.091$). Moreover, exterior and interior slave workers differed in the relative proportions (PERMANOVA, $P=0.0147$), but not in the total amounts of cuticular hydrocarbons (PERMANOVA, $P=0.46$).

Starvation experiment

Limited food supply led to increased proportions of *P. americanus* workers leaving the nest site (Mann–Whitney *U* test, $U=24.5$, $N_1=11$, $N_2=11$, $P=0.020$; Fig. 3). *Temnothorax longispinosus* slaves in the starvation treatment also left the nest more often (Mann–Whitney *U* test, $U=32.5$, $N_1=11$, $N_2=11$, $P=0.066$; Fig. 3), although this difference was not significant. However, during raiding experiments, we could not find any differences between treatments in the time needed to discover the first host nest (starved: median, 2,087 s; range, 41–9,732 s; unstarved: median, 1,319 s; range, 65–10,360 s; Mann–Whitney *U* test, $U=35$, $N_{\text{starved}}=9$, $N_{\text{unstarved}}=10$, $P=0.41$) or in the time elapsed until they chose a host nest (starved: median, 4,629 s; range, 1,196–10,051 s; unstarved: median, 1,548 s; range, 86–10,408 s; Mann–Whitney *U* test, $U=26$, $N_{\text{starved}}=9$, $N_{\text{unstarved}}=10$, $P=0.12$).

Discussion

We can show a division of labor even among the few slavemaker workers in *P. americanus* colonies. Albeit these workers are specialized in one main task, we found

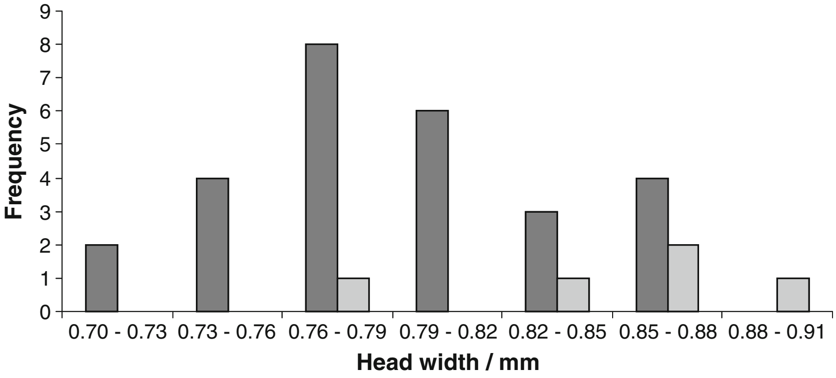

Fig. 1 Frequency distribution of the head width of fertile (*light bars*) and infertile (*dark bars*) slavemaker workers. Fertility assignment is based on the presence or absence of yellow bodies

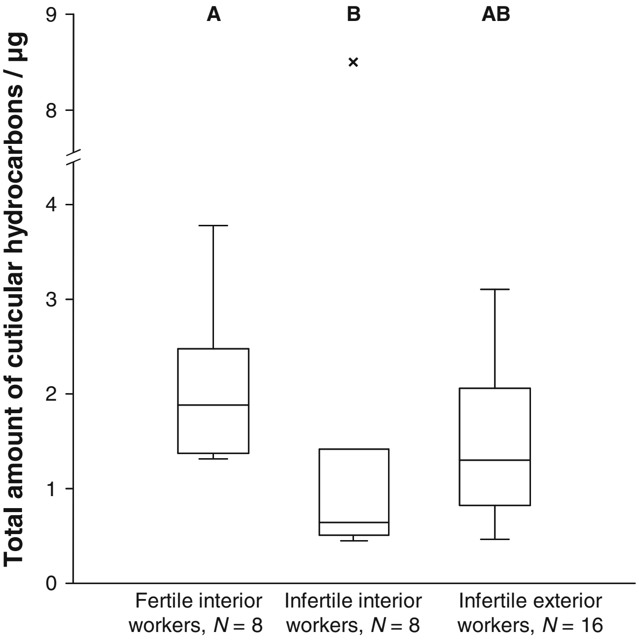

Fig. 2 Total amounts of hydrocarbons on the surface of slavemaker workers, depending on their location and fertility. *Boxes* show medians and lower and upper quartiles; *whiskers* represent the lowest datum still within 1.5 interquartile ranges (IQR) of the lower quartile and the highest datum still within 1.5 IQR of the upper quartile, respectively. An outlier (*ex symbol*, value further than 3 IQR) is additionally marked. PERMANOVA, $P=0.0124$. *Different capital letters* depict differences in PERMANOVA pair-wise tests

consistent differences in behavior, which were connected to ovary development and body size. Fertile *P. americanus* workers were found only among interior workers, whereas variation in fertility was not associated with task in *T. longispinosus* slave workers. Analyses of cuticular hydrocarbons showed differences in the profiles of the infertile exterior, infertile interior, and fertile interior slavemaker workers. Moreover, the profiles of exterior and interior *Temnothorax* slave workers differed, and these differences were unconnected to fertility. We can show that slavemaker workers perceive the need for new slaves over the food supply since starving led to increased searching activity in *P. americanus* scouts.

Fig. 3 The proportion of slavemaker workers and slaves outside their nest site for the treatment with limited food supply (starved) and the control treatment (unstarved). *Boxes* show medians and lower and upper quartiles; *whiskers* represent the lowest datum still within 1.5 interquartile ranges (IQR) of the lower quartile and the highest datum still within 1.5 IQR of the upper quartile, respectively. Outliers are additionally marked: *circle*= values between 1.5 and 3 IQR, *ex symbol*=values further than 3 IQR. Mann–Whitney *U* tests, all $N=11$, $^*P=0.020$

Slave raid participation served as our main criterion to unravel task allocation between *P. americanus* workers. We combined behavioral observations and data on size and fertility of slavemaker workers with analyses of their cuticular hydrocarbon profiles to document potential factors that could affect division of labor among ant workers with a limited task repertoire. We included only those individuals in subsequent analyses of fertility, size, and chemical profiles that repeatedly showed the same behavior, either staying inactively inside the nest or participating in scouting and raiding activities.

Previous studies on colony organization in *P. americanus* by Franks and Scovell (1983) and Blatrix and Herbers (2004) focused on dominance hierarchies between slavemaker workers and their implications on provisioning, fertility, and, to a lesser extent, raiding activity. They showed that behaviorally dominant slavemaker workers are fertile and do not take an active part during scouting or single raiding events. In accordance with these studies, we found fertile *P. americanus* workers only among those workers that stayed inside the nest during both trials.

In queenless *P. americanus* colonies, top-ranking individuals reproduce (Blatrix and Herbers 2004), and for the New York population studied here, it is known that slavemaker workers can also become fertile in the presence of the queen (Foitzik and Herbers 2001). Male production by workers has been demonstrated in other slave-making ant species as well (Bourke et al. 1988; Brunner et al. 2005). Hence, by staying inside the colony and producing male offspring, fertile workers increase their direct fitness.

Subordinate workers, in turn, have two possibilities to increase their inclusive fitness. Usually they raid host colonies to replenish the slave workforce of their mother colony, leading to a higher production of sexuals and to an increase in their indirect fitness. However, they can also opt to stay in an attacked host nest to produce their own male offspring (Wesson 1939). Both options, however, require leaving the nest site for a raid. Thus, the division of labor between fertile workers staying at home and infertile workers leaving the colony for a raid can ultimately increase the fitness for all individuals.

Interestingly, fertile slavemaker workers were larger than infertile workers. Body size variation is due to differences in larval nutrition and does not depend on adult nourishment. In slavemaker colonies, slavemaker larvae are fed by slave workers, which may cause the variation in slavemaker body size. Since social hierarchies are established via dominance behaviors such as antennal boxing (Blatrix and Herbers 2004), our results suggest that larger individuals may have advantages when competing for dominance. The connection between body size and fighting success was shown in red wood ants, in which groups with larger ants were more successful in fights than ants of smaller size (Batchelor and Briffa 2010).

Task allocation was also reflected in the chemical profiles of slavemaker workers. The relative proportions, but not the total amount, of cuticular hydrocarbons varied between exterior and interior slavemaker workers. Hence, exterior and interior slavemaker workers are probably distinguishable by their chemical profile. However, exterior *P. americanus* workers were invariably infertile, so that fertility differences might be responsible for the variation in chemical profiles, as in many ant species cuticular hydrocarbon profiles of fertile individuals differ from those of their infertile nestmates (Moore and Liebig 2010; Peeters et al. 1999; Smith et al. 2009).

When we classified the *P. americanus* workers on the basis of both location and fertility, we found differences in the total amount of cuticular hydrocarbons. Since fertile interior workers bear the highest amount of cuticular hydrocarbons and infertile interior workers the lowest amount, while infertile exterior workers lay in between (Fig. 2), we suppose these differences remained undetected in the analyses considering only fertility or task.

Assigning the analyzed individuals to these three groups, we did not find differences in the relative proportions of the cuticular hydrocarbons, but this might be due to the resulting smaller sample sizes. Altogether, fertility as well as location and thereby potentially the actual task of an individual are reflected in its cuticular hydrocarbon profile. Differences between profiles of different task groups were previously found in harvester ants, especially between exterior (foragers/patrollers) and interior (nest maintenance) workers, and these differences are caused by the task-related environment (Wagner et al. 1998, 2001). Slavemaker workers might be able to discriminate between nestmates through chemical cues indicating task or fertility. Recognition of their nestmates' preferred tasks could allow returning scouts to direct their recruitment effort toward potential exterior workers, which are more likely to accompany them on a raid.

The results obtained from the slave workers support our conclusions. Interior and exterior slaves differed in the relative proportions of their cuticular hydrocarbons, pointing toward a strong influence of the individuals' tasks on their chemical profile. Slave workers are not able to reproduce within slavemaker colonies (Foitzik and Herbers 2001), and indeed, their ovaries were only weakly developed. Additionally, individuals classified as fertile were equally distributed among exterior and interior workers. We therefore ruled out a substantial influence of fertility on the composition of the cuticular hydrocarbons of slaves, leaving location and task as influential factors for slave profiles.

Division of labor should not be rigid, but has to be flexible to respond to the colonies' needs. Food deprivation led to increased scouting activities of slavemaker workers, but did not alter the course of a raid. Since *P. americanus* workers do not forage (Sturtevant 1927), we suggest that searching for food cannot be the cause for their increased activity. Slaves also were more active, though not significantly, in colonies with a limited food supply, presumably because they increased their foraging activity.

Although starved slavemakers were in general more active, we found strong variation in activity patterns between and within colonies of the same treatment group, which can be explained as follows. First, slavemaker workers may vary in their starvation tolerance, so that they start searching for host colonies at different starvation levels. Variability in individual thresholds for specific tasks is known to occur in social insects and is recognized to account for flexibility in colony response (Bonabeau et al. 1996; Detrain and Pasteels 1991; Robinson 1992). Second, individual slavemaker workers may differ in their actual nutritional status. Dominant slavemaker workers are fed more often by slave workers than subordinates (Blatrix and Herbers 2004; Franks and Scovell 1983). Hence, they should reach a threshold leading to the search for host colonies later or not at all, which further solidifies the division of labor between fertile interior workers and infertile exterior workers.

If individual slavemaker workers used their nutritional status as a measure to determine the colony's need for new slaves, it should allow slavemaker colonies to respond flexibly to changing conditions. Slavemaker workers that stay inside the colony under good conditions probably start to search for host nests when the circumstances become unfavorable, meaning that the division of labor between exterior and interior workers is not fixed, but can be adjusted depending on the colony's need. Flexible task allocation after manipulating colony need or experimental removal of foragers has been previously demonstrated in various groups of social insects (Cartar 1992; Gordon 2002; O'Donnell 1998).

In social insect societies, division of labor and the evaluation of colony need can lead to increased colony performance. Due to the specialization of slavemaker workers in a single task, the study of slave-making ants allows detailed insights into the mechanisms that lead to division of labor.

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Article 3

Parasite scouting behaviour and host defence are regulated by colony size in a social parasite system

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Parasite scouting behaviour and host defence are regulated by colony size in a social parasite system

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Running title: Scouting behaviour in slave-making ants

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ABSTRACT

Most animals encounter individuals of other species, and the course of these encounters can be variable. During these interspecific interactions, individuals can benefit from behavioural flexibility, i.e. the ability to choose between different behavioural tactics. In the North American slave-making ant *Protomognathus americanus* scout workers search for colonies of their *Temnothorax* hosts to initiate raids, during which host pupae are stolen in order to replenish the workforce of the slavemaker colony. We observed the behaviour of *P. americanus* scouts in the laboratory to investigate the flexibility of their searching behaviour. The number of actively searching scouts increased with increasing slavemaker worker numbers, but was unaffected by the slave to slavemaker ratio, indicating that the number of slavemaker workers can be used as a measure to determine the strength of the scouting worker force. Additionally, colonies with fewer slave workers discovered host colonies faster, suggesting that scouts adjust their searching behaviour to the strength of their colony's slave workforce. The more scouts were active, the faster a host colony was discovered, but the time span between host colony discovery and trial completion did not vary with slavemaker colony demography. Host colonies were successfully attacked in nearly 80% of all trials, and hosts could fight off an intruding scout only once. Yet host aggression towards slavemaker scouts increased with host colony size, and higher aggression rates increased the time lag before an attack, which might offer the hosts the possibility to escape. We show here that colony size influences the behaviour of both parasites and hosts in a social parasite system during crucial interspecific interactions.

INTRODUCTION

During their lives, almost all animals are regularly confronted with other animals. Besides frequent intraspecific interactions with rivals or potential mates, interactions with other species are also widespread. Several interspecific encounters might be of particular interest for an individual, e.g. when they face competitors or cooperators (Schoener 1983; Herre et al. 1999), predators or prey organisms (Lima 1998; Abrams 2000; Peckarsky et al. 2008), hosts or parasites (Bush et al. 2001). In particular antagonistic relationships often show an evolutionary sequence of adaptations and counter-adaptations, i.e. these interacting species are engaged in so-called arms races (Dawkins & Krebs 1979). As a consequence of co-evolutionary arms races, both partners may develop morphological or behavioural adaptations that enable them to gain a temporary advantage over their counterparts. In host-parasite relationships, such modifications can lead to highly derived phenotypes and behavioural strategies in the parasites, which improve host detection, infiltration and exploitation, whereas the hosts continually enhance their abilities to detect, avoid and/or reject the parasites (Moore 2002; Combes 2005). While morphological adaptations are often fixed, the behavioural repertoire of a species is frequently flexible, and individuals might choose between various options. Flexible behaviours occur especially in parasites that exploit the behaviour of their hosts such as avian brood parasites and insect social parasites. Here, both host and parasite individuals can utilize alternative behavioural tactics (Foitzik et al. 2001; D'Ettorre et al. 2004; Svennungsen & Holen 2010). Moreover, in social parasite systems many individuals are involved in host defence and often also in parasite attacks, which increases the potential for flexibility in both defensive and offensive behaviour.

Social parasitism is defined as the exploitation of the social system of a eusocial species through another eusocial species (Hölldobler & Wilson 1990). These specific host-parasite systems allow studying inter- and intraspecific interactions between several protagonists, because simultaneous confrontations of multiple host and parasite individuals take place. For example, the demography of both the host and the parasite colony could influence the behaviour of both parties and ultimately the parasites’ impact on the host.

To address the influence of demography on behavioural flexibility in a social parasite system, we studied the interactions between parasites and hosts during the host searching behaviour of slave-making ants. Comparable to the well-known and extensively studied examples of avian brood parasitism (Payne 1977; Rothstein & Robinson 1998; Davies 2000), slave-making ants exploit the brood care behaviour of their hosts (Buschinger 2009), and despite their phylogenetic distance, both systems show remarkable similarities in the type and outcome of the respective arms races between parasites and hosts (Kilner & Langmore 2011).

The North American myrmicine ant *Protomognathus americanus* is an obligate slavemaker that completely relies on the work force of its enslaved *Temnothorax* host workers. Slavemaker workers do not take part in tasks like foraging or brood care, which are performed by the slaves, and they are even fed by slave workers via trophallaxis (Sturtevant 1927). However, they are specialized in replenishing the slave work force of their colony by stealing host worker pupae, which will imprint on the parasite's colony odour once they have emerged in the slavemaker colony (Goodloe & Topoff 1987; Le Moli & Mori 1987). Inactive during most of the year, slavemaker workers leave their nest site on summer days to search for suitable host colonies (Wesson 1939). Walking around on the forest floor, these so-called scouts eventually encounter a host colony. After a short exploration phase during which a scout often enters the host nest, the scout decides whether or not the host colony is worth raiding. At that point, the subsequent course of a raid is not determined by a linear sequence of slavemaker actions and host reactions, but both parties can choose between various behavioural options. For example, a slavemaker scout might return to its mother colony and recruit nestmates to the host colony, or it could begin an attack on its own (Alloway 1979; Alloway & Del Rio Pesado 1983). Hosts that have detected a slavemaker scout can either try to fight off the intruder, or they might start to evacuate the nest site, trying to save the queen and as much brood and nestmates as possible (Wesson 1939; Alloway 1979).

In order to understand the flexibility in the behavioural repertoire of parasites and hosts, we set up trials in the laboratory during which we focused on the initial scouting and exploration phase and observed the behaviour of both slavemaker and host workers. Detailed recordings of their actions combined with data on the demographic composition of the colonies involved allowed us to determine potential influences of relevant factors on the course of the trials. In particular, our study had three main objectives:

First, we questioned whether the beginning of the scouting activity is associated with the number of slavemaker and slave workers in the parasite colony. We expected that more scouts would be active in colonies with more slavemaker workers, as well as in colonies with a higher need for new slaves, i.e. with a lower slave to slavemaker ratio. We also investigated whether the proportion of slavemaker workers that leave as scouts depends on the demographic composition of the slavemaker colony.

Second, we were interested in how the course of the scouting behaviour is influenced by the parasites' demography, i.e. the number of slavemaker workers and slaves inside the slavemaker colony. The presence of more slavemaker scouts could lead to a shorter duration, i.e. a faster discovery of the host colony. On the other hand, increased slave presence could result in longer search times, due to lower pressure to strengthen the slave workforce. Furthermore, the time span between host colony discovery and trial completion might be influenced by both parasite and host numbers.

Third, we asked how the effectiveness and strength of the host defence depends on the number of host workers, and how the defensive behaviour influenced the course of the trial. We expected that larger host colonies would show a stronger defensive behaviour, which, in turn, might delay the parasites' attack. We also investigated a possible correlation between scout and host aggression and potential factors that influenced the duration of aggressive behaviours.

MATERIALS AND METHODS

Collection and maintenance of ant colonies

In this study we were interested in how colony demography influences the scouting behaviour, and therefore used host and parasite colonies that varied in size. Since population of origin has been shown before to influence the outcome of slave raids, we focused on a single host-parasite community. Here we studied a population from New York with strong parasite pressure, in which the coevolutionary arms race is advanced (Foitzik et al. 2001; Brandt & Foitzik 2004). We collected colonies of the social parasite *P. americanus* and of its main host species *T. longispinosus* (Herbers & Foitzik 2002) at the Edmund Niles Huyck Preserve, Rensselaerville, NY, USA (N 42°31'32.7", W 74°09'22.5"), in May and June 2009. Note that some of the nests we collected may have been subunits of the same colony, since both parasite and host colonies can be polydomous (Alloway et al. 1982; Alloway & Del Rio Pesado 1983; Foitzik & Herbers 2001a). However, genetic analyses of slave workers suggest that subunits of slavemaker colonies engage in raids independently of each other (Foitzik & Herbers 2001b). Brought to the laboratory, we kept all colonies in artificial nest sites in three-chambered plastic boxes (9.5 cm × 9.5 cm, 2.7 cm high), which had a moistened plaster floor to prevent desiccation. We provisioned the ants *ad libitum* with cricket pieces and honey twice a week. We stored the colonies in a climate chamber with a day / night cycle of 14 h light at 20 °C / 10 h dark at 15 °C until the beginning of the trials, which took place at 27 °C under a natural light regime to stimulate raiding activities (Buschinger et al. 1980).

Experimental setup

We set up a total of 48 trials during the raiding season in August 2009. We used a total number of 27 slavemaker colonies, hence some colonies were tested more than once (10 colonies were tested once, 14 colonies were tested twice, two colonies were tested three times and one colony was tested four times). Since *P. americanus* colonies in the field perform about six raids per season (Foitzik & Herbers 2001b), setting up several trials with the same colony was within natural behavioural ranges. Slavemaker colony demography varied between trials, and we accounted for re-using some colonies during statistical analyses (see below). The trials took place in Y-shaped experimental arenas (2.7 cm wide and 2.5 cm high, 15 cm arm length, all angles 120°). We placed a slavemaker colony inside their artificial nest sites at the end of one arm of the arena. Simultaneously, we confronted the slavemaker colony with two host colonies placed at the end of the other arms of the arena, thereby offering potential targets that varied in size to ensure that an adequate host colony was presented to each slavemaker colony. Prior to each trial, we determined colony demography of both the parasites and the hosts, counting all individuals. We observed the ants' behaviour from the beginning of a trial, which started with the introduction of the ant colonies into the experimental arena, until trial completion. We defined a trial as being completed when one of the following four behavioural patterns occurred: A *P. americanus* scout discovered a host colony and (1) started to attack the host colony, i.e. the scout ran around, bit host workers and stimulated alarm reactions from them; (2) recruited nestmates back in the slavemaker colony and led them to the host colony via tandem running, during which the following ant stays in contact by repeatedly touching the leader's gaster with her antennae; (3) brought host pupae to the slavemaker colony; (4) the host workers started to evacuate the nest site, carrying their brood with them, presumably after detecting the intruder. The first three outcomes were defined as successful for the slavemakers, since (1) and (2) were regularly followed by a colony takeover by the slavemakers (personal observation), and (3) resulted in the gain of host brood. We stopped the experiment before trial completion when all slavemaker workers stayed inactively inside their own nest site for more than 90 minutes, which occurred, however, only in three trials. Note that we observed only the scouting behaviour until trial completion as defined above and did not analyse entire raiding events.

Data recording and evaluation

We recorded in detail the behavioural patterns of both the slavemakers and the discovered hosts, using the software Observer XT 9 (Noldus Information Technology, Wageningen, The Netherlands). This software, developed to facilitate behavioural observations, allows noting down simultaneously for different individuals when and where a specific behaviour occurred, how long it lasted, and towards whom it was directed. It subsequently facilitates data analyses by combining the records of selected individuals or behaviours (e.g. scouts or aggression behaviour) over all trials according to the particular question. We distinguished between the behaviours presented in table 1 and defined them as either aggressive or neutral, depending on the direct impact on the individual to whom the behaviour was directed. We assigned each behavioural action to the individual (scout or host worker) that displayed it and noted down the location where it occurred (inside the slavemaker nest / inside the host nest / in the arena). For each behavioural action, we recorded the point in time when it started and ended. In particular, we noted the discovery (= entering) of the first host colony and the time of trial completion (see above). During the time span between the discovery of a host colony and the decision of a scout for a host colony or the escape of the hosts (= contact time), we recorded the total time during which a scout was subject to an aggressive behaviour of at least one host worker (= aggression time). We merged time periods during which aggressive behaviours against two scouts in the same host colony overlapped, since we used this measure in order to investigate general host defence behaviour. Similarly, we calculated the aggression time for scouts that showed aggressive behaviours against host workers.

Statistics

We analyzed our data with the program PRIMER 6, version 6.1.12, with the PERMANOVA+ add-in, version 1.0.2 (PRIMER-E Ltd). We ran non-parametric, permutational MANOVAs (PERMANOVAs) (Anderson et al. 2008) with 9,999 permutations and type III sum of squares, using Euclidian distances as resemblance measure. We tested for influences on the respective response variables using colony as a random factor and potential explanatory variables as covariables. All covariables tested in a specific analysis are mentioned in the respective section of the results. Since the course of the scouting and raid initiation behaviour was very variable between trials, total sample sizes vary between analyses. In particular, sample sizes related to host colonies can be larger than 45 (the number of completed trials), since in some trials slavemaker scouts discovered more than one host colony. Due to the course of the trials, not all variable values could be determined in every case. Hence for particular analyses, sample sizes may be smaller than 45. For sample sizes of specific PERMANOVA analyses, please refer to table 2.

A Spearman rank correlation between the aggression time of scouts and hosts, Mann-Whitney *U* tests and Fisher's exact tests were calculated using the computer program PAST version 2.10 (Hammer et al. 2001).

RESULTS

Out of 48 attempts, we observed 45 completed trials. The slavemaker scouts did not discover a host colony in two trials, and in a single trial the host workers were able to fend off the slavemakers by dragging the intruding scout out of the nest site. Of the 45 completed trials, seven ended with the evacuation of the nest site by the hosts, i.e. the hosts fled with their brood onto the top of their nest site and in small crevices between the nest site and the walls of the experimental arena. The remaining 38 trials ended mostly with the attack of a single scout ($N = 24$), whereas in ten trials the scouts recruited nestmates via tandem running, and in four trials the scout carried host pupae to its own colony without further attacking or recruiting. The number of discovered host colonies did not affect the type of trial completion (χ^2-test, $df = 1$, $\chi^2 = 5.60$, $P = 0.13$).

Parasite demography

First we analyzed the demographic composition of the slavemaker colonies (number of slavemaker workers, number of slaves, slave to slavemaker ratio) and its influence on host colony searching. Slave to slavemaker ratios decreased with increasing slavemaker worker numbers (PERMANOVA, $P = 0.001$; Fig. 1a), but did not depend on slave worker numbers (PERMANOVA, $P = 0.43$).

The number of scouts that left their colony to search for host colonies in the experimental arena increased with increasing total slavemaker worker numbers (PERMANOVA, $P = 0.011$; Fig. 1b), but did not vary with slave numbers or the slave to slavemaker ratio (PERMANOVA, all $P > 0.26$).

The number of scouts per slavemaker worker neither varied with slavemaker worker numbers, nor with slave numbers or the slave to slavemaker ratio (PERMANOVA, all $P > 0.33$).

Temporal course of the scouting behaviour

The time span from the beginning of the trial until the discovery of a host colony varied between 26.62 s and 9198.37 s (median: 482.32 s). It decreased with increasing numbers of slavemaker scouts (PERMANOVA, $P = 0.038$; Fig. 2a). In contrast, increasing slave worker numbers led to an increase of the time until host discovery (PERMANOVA, $P = 0.006$; Fig. 2b). The number of scouts was higher in trials in which both host colonies were discovered ($N_{\text{one host discovered}} = 30$, $N_{\text{two hosts discovered}} = 16$; one host discovered:

median = 2 scouts, range = 1 – 10 scouts; two hosts discovered: median = 4 scouts, range = 1 – 9 scouts; Mann-Whitney *U* test, $U = 139.5$, $P = 0.019$).

The time span from the discovery of a host colony to the completion of the trial varied between 1.27 s and 6422.12 s (median: 127.45 s), but it was neither influenced by the slavemaker colonies' demography (number of slavemaker workers, number of slaves, number of scouts) nor by the number of host workers in the attacked host colony (PERMANOVA, all $P > 0.49$).

Host defence

Workers of discovered host colonies sometimes displayed aggressive behaviours towards slavemaker scouts. Colonies showing aggressive responses comprised more host workers than colonies that did not show any aggressive behaviours ($N_{\text{aggressive}} = 11$, $N_{\text{non-aggressive}} = 37$; aggressive colonies: median = 27 workers, range = 14 – 41 workers; non-aggressive colonies: median = 16 workers, range = 4 – 36 workers; Mann-Whitney *U* test, $U = 79$, $P = 0.002$). The length of time during which host workers showed aggressive behaviours against at least one scout (= host aggression time) correlated positively with the scout aggression time, i.e. the time during which scouts showed aggressive behaviours against at least one host worker (Spearman rank correlation, $r_S = 0.47$, $P < 0.001$; Fig. 3). A subsequent analysis revealed that the observed pattern of scout and host aggression was influenced by the number of scouts that entered the host colony (PERMANOVA, $P = 0.013$), with more intruders leading to longer aggression times, as well as by the number of host workers (PERMANOVA, $P = 0.013$), which also with increasing numbers led to increased aggression times.

To determine the influence of the hosts' aggressiveness on the course of the scouting behaviour, we focused on the trials in which slavemaker scouts discovered only one host colony, to eliminate the delays caused by the discovery of the second host colony. The values for aggression time and for the time span from the discovery of the host colony to the completion of the trial are not completely independent, since longer subjection to host aggression could lead to longer total contact times before the scouts could indicate their decision. We hence standardized the duration of aggressive behaviours of host workers against scouts by determining the proportion of the contact time during which scouts received aggressive interactions. The higher this proportion, the longer the time span from the discovery of the host colony until the completion of the trial (PERMANOVA, $P = 0.013$), whereas this time span was neither influenced by the number of host workers nor by the number of intruding scouts (PERMANOVA, all $P > 0.26$).

Nestmate recruitment

In 22 out of 45 completed trials, slavemaker scouts returned back to their mother colony after the discovery of a host colony. In 7 trials, additional *P. americanus* workers were active besides the returning scouts. Recruitment of additional slavemakers occurred more often in trials in which *P. americanus* scouts antennated with nestmates back in the slavemaker colony ($\mathrm{N}_{\mathrm{recruitment}} = 6$, $\mathrm{N}_{\mathrm{no\ recruitment}} = 7$) than in trials in which scouts did not antennate with nestmates ($\mathrm{N}_{\mathrm{recruitment}} = 1$, $\mathrm{N}_{\mathrm{no\ recruitment}} = 31$; Fisher's exact test, $P = 0.001$), but did not depend on the number of discovered host colonies (Fisher's exact test, $P > 0.99$). The number of recruited slavemaker workers was also higher in trials during which nestmate antennation was observed (Mann-Whitney U test, $U = 121.5$, $N_{\mathrm{antennation}} = 13$, $N_{\mathrm{no\ antennation}} = 32$, $P < 0.001$). Additionally, on two occasions returning scouts performed vibrating movements with their gaster inside their nest site, once during and once before they antennated with nestmates. In both cases this behaviour was followed by a tandem run to the host colony.

DISCUSSION

The detailed observation of *P. americanus* scouting behaviour demonstrated that parasite and host behaviour is strongly influenced by both the parasites' and the hosts' group size. Larger parasite colonies sent out more scouts, but the number of scouts per slavemaker worker did not vary with colony size. Discovery time decreased with the number of slavemaker scouts, whereas it increased with the number of slaves. Larger host colonies showed aggressive behaviour more often and in higher rates, and host aggression correlated positively with scout aggression. Though defending host workers did not drive away slavemaker workers permanently, increased host aggression delayed the completion of the trial.

Before the scouting behaviour of *P. americanus* takes place, a slavemaker colony has to determine when the search for new slaves is necessary, and which individuals will leave the nest as scouts. For this purpose, especially two demographic parameters may play an important role, the number of slavemaker workers and the slave to slavemaker ratio. Colonies with more slavemaker workers showed a lower slave to slavemaker ratio, which should impair the slavemaker workers' provisioning and thereby could provide information about the colony's need for new slaves, resulting in differences in the searching behaviour. Indeed, a previous study demonstrated that in starved slavemaker colonies, increased proportions of slavemaker workers showed scouting activity outside their nest, suggesting that they use their own nutritional status to estimate the overall colony need (Pohl et al. 2011). Here, however, the number of scouts per slavemaker worker did not vary with slavemaker worker numbers or with the slave to slavemaker ratio, and the slave to slavemaker ratio did not affect the number of scouts. We suppose that the *ad libitum* feeding regime in this study ensured sufficient provisioning of slavemaker workers independent of their number, so that the nutritional status of slavemaker individuals and hence their probability to scout did not depend on the slave to slavemaker ratio. Yet more slavemaker individuals were found scouting in colonies with higher numbers of slavemaker workers, indicating that slavemaker workers might also use other mechanisms to assess the strength of their own workforce. For these larger colonies, the potential costs of losing a scout might be smaller, especially when compared with the benefits of a quicker discovery of a host colony due to the activity of more scouts. The number of slavemaker workers thus influenced the strength of the scouting worker force during the scouting behaviour. The probability for an entire raid to be successfully completed, however, has been shown before to increase with a lower slave to slavemaker ratio and to be unaffected by the total number of slavemaker workers (Pohl & Foitzik 2011). This implies that different factors exert influence on the slavemakers' behaviour during different stages of the scouting and raiding behaviour.

Higher scout numbers reduced the time span until host nest discovery, possibly due to an increase in the probability to encounter a host colony. Higher slave worker numbers in turn slowed down the scouts' searching behaviour, i.e. the time until host discovery increased. We suppose that slavemaker workers which live in colonies with many slave workers and get in contact with them regularly are used to encounters with *Temnothorax* workers. Therefore they might be less likely to intensify their searching efforts after contact with workers of a host colony. Such a mechanism would provide a method of fine-tuning the slavemakers' activity towards the colony's need of additional slaves.

Altogether, parasite colony size influences the search for host colonies, which can be described as foraging for new slaves. Group size-dependent foraging behaviour has been described for various other animals as well. For example, foraging techniques depend on group size not only in ants (Beckers et al. 1989), but also in white ibises (Petit & Bildstein 1987), and capuchin monkeys that foraged in larger groups were able to exploit additional food sources (Miller 2002). The main demographic factor of parasite colonies that affected the scouting behaviour was the number of slavemaker workers. In this context, it is interesting to mention the recently described slave rebellion behaviour of enslaved host workers (Achenbach & Foitzik 2009). Slave workers kill parasite worker pupae, and by reducing the number of slavemaker workers, they hence directly influence the course of the scouting behaviour.

Another important point during the scouting events is the transfer of information from slavemaker workers to their nestmates about the discovery of a host colony in order to recruit them for an attack. Antennation was previously described to play a role in the invitation and recruitment behaviour in ants (Lenoir & Jaisson 1982; Hölldobler 1985). Our results support the view that antennation with nestmates back in the slavemaker colony is a possible recruitment mechanism in *P. americanus*, although the antennation behaviour is possibly not mandatory to evoke subsequent tandem running, since we recorded one tandem run without prior observation of nestmate antennation. The initiation of a tandem run may further be triggered by the vibrating gaster movements, which potentially are associated with the release of gland secretions.

Slave raids are a crucial component in the slavemakers' life cycle, but they also profoundly impair the fitness of a raided host colony (Foitzik & Herbers 2001b; Fischer-Blass et al. 2006). To prevent severe fitness losses, the hosts evolved several strategies to oppose the parasites' attacks, including detection and elimination of slavemaker scouts (Alloway & Del Rio Pesado 1983) and the evacuation of their colony which allows them to save a considerable amount of their brood (Wesson 1939; Alloway 1979). Yet, *P. americanus* workers were successful in 38 out of 48 trials observed. However, also among these trials the hosts' reaction towards intruding slavemakers was variable. Besides the escape behaviour, a first line of host defence against slave-making ants is the aggression against intruders. Recently, it could be demonstrated that *T. longispinosus* workers show different levels of aggression when confronted with intruders of various species, depending on the respective risk the intruder poses to the colony (Scharf et al. 2011). Hence *T. longispinosus* workers might also modulate their level of aggression during encounters with the same species, but under varying conditions. Indeed, scout and host aggression correlated positively, and increased numbers of opponents led to longer periods of aggression. Furthermore, smaller host colonies, i.e. colonies with less workers, were less likely to show aggressive behaviour at all. Proximately, the more host workers, the more likely is the detection of non-nestmates, and an increase in aggressive behaviour can then be reached by higher alarm pheromone concentrations and the extension of the active space of the pheromone (Wilson 1958; Hölldobler & Wilson 1990). Ultimately, these differences in the hosts' level of aggression might be an adaptation to the slavemakers' preference for larger host colonies (Pohl & Foitzik 2011) in the ongoing co-evolutionary arms race between *P. americanus* and its *Temnothorax* hosts (Foitzik et al. 2001; Brandt & Foitzik 2004). Behavioural patterns such as vigilance and defensive behaviour are also influenced by group size in many prey species (Lima & Dill 1990). In pied flycatchers, for example, individuals that live in larger groups show higher mobbing intensity against potential predators (Krams et al. 2009), comparable to the stronger aggression displayed by larger *Temnothorax* colonies.

Since in almost all trials the *P. americanus* scouts succeeded to initiate an attack against the *Temnothorax* host colonies, it seems that resistance is futile. But extended host aggression eventually delayed the further course of the trial, which possibly gives the host workers additional time to evacuate their nest. This could allow the hosts to increase the number of nestmates that succeed to escape, and thereby to salvage a considerable part of their brood, especially when considering that in the field the hosts are not confined to a bordered experimental arena that prevents them to get out of reach of the attacking slavemaker workers. Average distances between parasite and host colonies are probably larger in the field than in our experimental set-up, and more hiding places can be found in the well-structured leaf litter habitat of these ants. Consequently, the time gained from attacking slavemakers might increase host colony survival in the field and could increase host fitness.

Our detailed behavioural observations of the scouting behaviour in *P. americanus* demonstrated variable behavioural patterns in both the slavemaker workers and their *Temnothorax* hosts. *Protomognathus americanus* adjusts its behaviour according to the demographic composition of its colonies, and *T. longispinosus* host colonies respond flexibly according to their own colony size. We show here that interspecific interactions between parasites and hosts in a social parasite system strongly depend on colony sizes as well as on the number of individuals that are directly involved.

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Figure 1. Influence of the number of slavemaker workers in the slavemaker colony (a) on the slave to slavemaker ratio in the slavemaker colony and (b) on the number of scouts that search for host colonies. A linear regression line was added to visualize the direction of the relationship. Unfilled circles represent a single occurrence of a specific x-value/y-value combination. Combinations depicted by grey dots occurred twice, and those that occurred three to five times are marked with black dots. *N*: sample size.

Figure 2. Influence of (a) the number of slavemaker scouts and (b) the number of slave workers in the slavemaker colony on the time until the discovery of a host colony. Y-values were $\log_{10}$-transformed for better data visualization. A linear regression line was added to visualize the direction of the relationship. *N*: sample size.

Figure 3. Correlation between the aggression time of scouts and the aggression time of host workers. All values were $\log_{10}(x+1)$-transformed for better data visualization. A linear regression line was added to visualize the direction of the correlation. All x-value/y-value combinations that occurred once are indicated by unfilled circles, and a single combination (0/0) that occurred ten times is marked by a black dot. *N*: sample size.

Table 1. Behavioural actions recorded during the raiding experiments.

Behaviour	**Description**	**Category**
Biting	One ant bites another ant with its mandibles.	Aggressive
Dragging	One ant grabs another ant with its mandibles and drags it around.	Aggressive
Stinging	One ant bends its gaster towards another ant and attempts to sting it. The attempt does not need to be successful.	Aggressive
Carrying away	One ant grabs another ant or a brood item and walks away with it.	Aggressive if one ant carries away a worker of another colony; otherwise neutral
Antennating	One ant touches another ant repeatedly with its antennae.	Neutral
Tandem running	One slavemaker worker leads one or more nestmates to a host colony.	Neutral

All behaviours were observed for both *P. americanus* and *T. longispinosus* workers, except for tandem running, which was an exclusive behaviour of *P. americanus*.

Table 2. Sample sizes for the PERMANOVA analyses.

PERMANOVA analysis	**Parasite demography**	**Time span until host discovery**	**Time span between host discovery and trial completion**	**Aggression time**	**Host aggression time vs. time span between host discovery and trial completion**
Number of parasite colonies that were used once	10	8	10	12	24
Number of parasite colonies that were used twice	14	14	14	10	2
Number of parasite colonies that were used three times	2	2	0	2	0
Number of parasite colonies that were used four times	1	1	1	0	0
Total number of trials (= sample size)	48	46	42	38*	28

*: In ten trials, two host colonies were discovered by slavemaker scouts, resulting in a sample size of $N = 48$.

Fig. 1

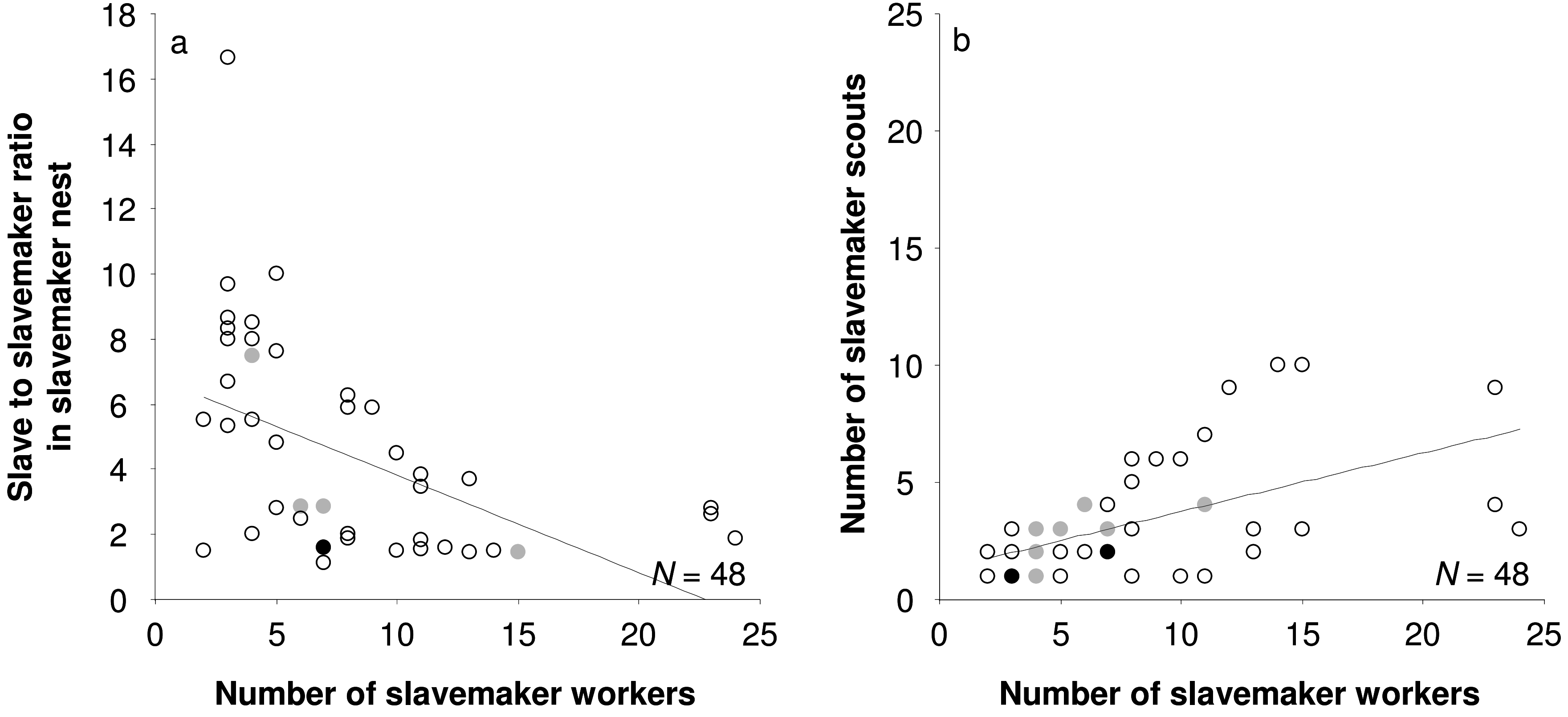

a
Slave to slavemaker ratio in slavemaker nest
0
2
4
6
8
10
12
14
16
18
0
5
10
15
20
25
Number of slavemaker workers
N = 48
b
Number of slavemaker scouts
0
5
10
15
20
25
0
5
10
15
20
25
Number of slavemaker workers
N = 48

Fig. 2

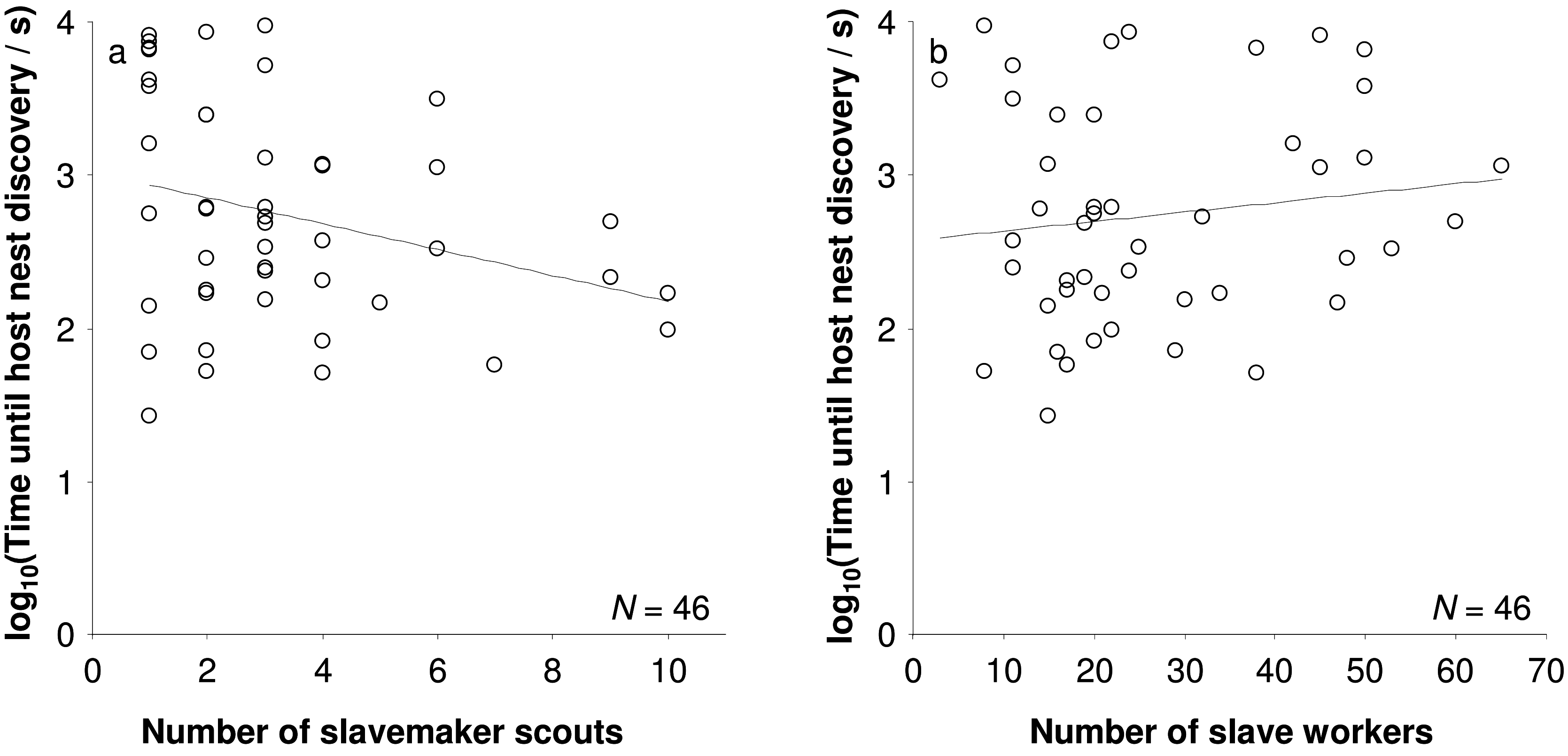
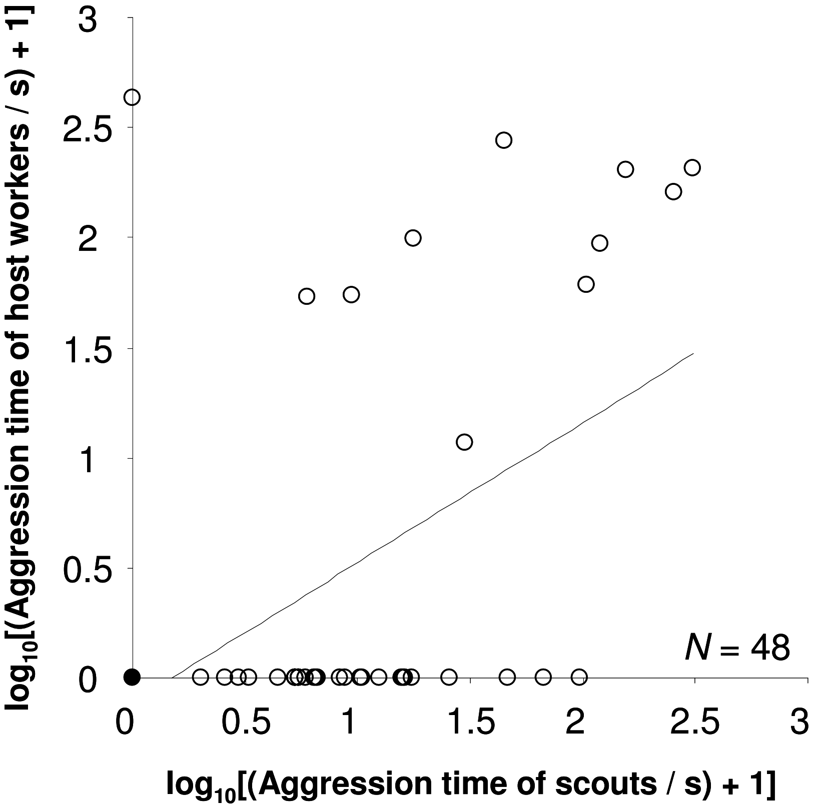

a
log$_{10}$(Time until host nest discovery / s)
0
1
2
3
4
N = 46
0
2
4
6
8
10
Number of slavemaker scouts
b
log$_{10}$(Time until host nest discovery / s)
0
1
2
3
4
N = 46
0
10
20
30
40
50
60
70
Number of slave workers

Fig. 3


log$_{10}$[(Aggression time of host workers / s) + 1]
3
2.5
2
1.5
1
0.5
0
0
0.5
1
1.5
2
2.5
3
N = 48
log$_{10}$[(Aggression time of scouts / s) + 1]

Article 4

On the use of adaptive resemblance terms in chemical ecology

Christoph von Beeren, Sebastian Pohl and Volker Witte

Psyche, in press

On the use of adaptive resemblance terms in chemical ecology

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Abstract

Many organisms (mimics) show adaptive resemblance to an element of their environment (model) in order to dupe another organism (operator) for their own benefit. We noted that the terms for adaptive resemblance are used inconsistently within chemical ecology and with respect to the usage in general biology. Here we first describe how resemblance terms are used in general biology, and then comparatively examine the use in chemical ecology. As a result we suggest the following consistent terminology: “Chemical crypsis” occurs when the operator does not detect the mimic as a discrete entity (background matching). “Chemical masquerade” occurs when the operator detects the mimic but misidentifies it as an uninteresting entity, as opposed to “chemical mimicry” in which an organism is detected as an interesting entity by the operator. The additional terms “acquired” and “innate” may be used to specify the origins of mimetic cues.

1. Introduction

Social insects, especially ants and termites, dominate many terrestrial habitats in terms of abundance, biomass and energy turnover [1,2]. They accumulate considerable amounts of resources that can be of potential use for other organisms, in the form of living biomass, infrastructures (e.g. nest sites) or stored products [3]. The ecological success of social insects comes with the cost that predators and parasites may exploit their societies [4-6]. Since Wasmann's [7] extensive study on organisms that developed close relationships with ants, a multitude of so-called myrmecophiles has been found to exploit ant colonies and their social resources in a variety of ways [5,8]. Parasitic relationships may escalate in an evolutionary arms race where the hosts adapt towards protecting themselves from exploitation, while parasites adapt towards avoiding expulsion from the host [9].

In this context it is crucial that members of a society can be recognized reliably and distinguished from aliens, which can thus be aggressively expelled [10]. An efficient social recognition system is essential for a colony to function as a closed unit. The better such recognition works, the more effectively social exploitation can be prevented. Complex profiles of cuticular hydrocarbons (CHCs) are known to carry information necessary for recognition of colony members in ants, bees and wasps [10].

Macroparasites of ants have evolved a variety of strategies to cope with their hosts' elaborate recognition system [5]. Potential strategies for avoiding or resisting the hosts' defense behavior include the use of morphological, acoustical and behavioral adaptations or the use of chemical repellents or attractants [1,5,11-13]. Particularly widespread and important are chemical strategies for avoiding recognition, either by not expressing relevant recognition cues or by matching host recognition cues [11,14,15]. For simplicity, we use the term "cue" referring to any chemical information that is potentially perceivable, irrespective of whether the information transfer is "intentional" or "unintentional" sensu Steiger et al. [16].

Chemical resemblances work analogously to other biological resemblances, such as acoustic or visual mimicry [17]. Unfortunately, different definitions exist in chemical ecology (see below), and thus different authors may describe different forms of chemical resemblances with identical terms or the same type of resemblance with different terms.

The aim of this article is threefold: First, we identify how definitions of resemblances are generally used in biology. Second, we analyze the terminology that is used in chemical ecology. Finally, we attempt a synthesis and suggest a terminology that agrees best with the general biological definitions and with the chemical strategies observed in nature.

2. General definitions of biological resemblances

Since the resemblance of organisms to elements of their environment (e.g., other organisms or background) is often not coincidental, but rather evolved for the benefit of the mimic, the term adaptive resemblance was coined [18]. In adaptive resemblance one organism (the mimic) modifies its appearance, pretending to be something different (the model), in order to dupe another organism (the operator) [19,20]. Many different terms have been used to describe adaptive resemblance, including mimicry, camouflage, crypsis, masquerade, and mimesis. These terms have been debated intensively and defined repeatedly according to different criteria (see Tab. 1).

Table 1. Summarized table of adaptive resemblance terms in general biology as used in important reviews. Systems can either be considered according to what a mimic pretends to be or according to what an operator perceives. We adopted the latter view.

By an operator, the mimic is…			
not detected as a discrete entity (causing no reaction)	detected as an uninteresting entity (causing no reaction)	detected as an interesting entity (causing a reaction beneficial to the mimic)	Reference(s)
Crypsis	Masquerade	Mimicry	Endler 1981 [21], 1988 [22]
Eucrypsis	Mimesis	Homotypy	Pasteur 1982[a] [23]
Eucrypsis	Plant-part mimicry	Mimicry	Robinson 1981 [24]
Crypsis	Masquerade	Mimicry	Ruxton et al. 2004 [25], Ruxton 2009 [17]
Cryptic resemblance	Cryptic resemblance	Sematic resemblance	Starrett 1993 [18]
Crypsis	Masquerade	---	Stevens & Merilaita 2009[b] [26]
Crypsis	Crypsis	Mimicry[c]	Vane-Wright 1976 [27], 1980 [20]
Camouflage or mimesis	Camouflage or mimesis	Mimicry	Wickler 1968 [19]

--- not considered

[a] Pasteur [23] uses the term ‘camouflage’ as generic term for both eucrypsis and mimesis.

[b] The term ‘camouflage’ is used by Stevens & Merilaita [26] to describe all forms of concealment, including crypsis and masquerade.

[c] For the imitation of inanimate objects, Vane-Wright [27] uses the expressions ‘decoys’ or ‘deflective marks’.

For the purpose of this article, we adopted an operator’s view to narrow down the existing definitions of adaptive resemblance into a unified system. This means that we distinguish the cues of a mimic with respect to whether and how they are perceived by the operator. The resulting categories are only valid within a given perceptive channel between mimic and operator, and they can differ in other channels or if other organisms are considered. The first column of table 1 defines resemblances in which a mimic is not perceived as a discrete entity by the operator and consequently causes no reaction in the operator. In such cases the mimic frequently blends with the background. We adopt the term “*crypsis*” for this phenomenon according to Endler [21], who first distinguished this type of resemblance from “*masquerade*”. In the latter a mimic is perceived by an operator as a discrete entity, which is however misidentified as uninteresting so that the operator also shows no reaction to the mimic. Accordingly, crypsis relies on the relationship between the organism and the background, whereas the benefit of masquerade is thought to be independent of the background [28]. A stick insect, for example, is likely to be recognized as a stick by a potential predator independent of its surroundings (e.g., when lying on grass). A cryptic organism, however, depends strongly on the background. This fact allows testable predictions to be made. For example, a mimic performing masquerade should be treated similarly by the operator independent of its background. On the other hand a mimic that performs crypsis should be treated differently (e.g., recognized and attacked) by the operator when the background changes.

The third column of table 1 defines adaptive resemblances in which a mimic is perceived by the operator as an entity of interest. This category was first described in a biological context by Bates [29] as "*mimicry*" and this term is currently most frequently used, hence we adopt it here.

Finally, another mechanism exists to avoid detection by an operator, which is however not based on resemblance. The term "*hiding*" has been applied to cases in which the absence of informative cues is achieved by behavioral adaptations, making detection by an operator impossible [17]. In visual systems, for example, a rabbit is hiding if it stays in its burrow in the presence of a predator (operator), thereby avoiding detection [17]. If a hiding organism was removed from the environment, the perceptive input of the operator would not change in the concerning channel. Hiding is not included in table 1 because it does not fall into categories of resemblance; nevertheless this term will be of importance in our discussion on chemical interactions below.

3. The use of adaptive resemblance terms in chemical ecology

Compared to visual adaptive resemblances, chemical adaptive resemblances had initially been paid less attention to in scientific literature, despite the fact that chemical communication is the most widespread form of communication among organisms [16,30,31]. However, more recent reviews on this topic show that understanding of chemical adaptive resemblance has increased markedly [11,15,32,33].

According to this special issue on ants and their parasites, we focus here particularly on important reviews about parasites of social insects, and on reviews about adaptive chemical resemblance. Reviews are suitable for analyzing how the terminology is used, since they provide overviews about specific fields, summarize the literature and therefore mirror common practices.

We used the same categorization as in table 1, adopting an operator's point of view. Note that two resemblance types were combined, i.e. resemblances in which a mimic is not detected as discrete entity and resemblances in which a mimic is detected as an uninteresting entity (Tab. 2). We combined these two types of resemblances because none of the reviews distinguished them. Additionally, we included the origins of mimetic compounds in the table, since this is an interesting point regarding chemical resemblances and several authors based their terminology upon it.

Table 2. Summarized table of the main terms used for chemical adaptive resemblances in reviews about parasites of social insects and in reviews about adaptive chemical resemblance. Systems can either be considered according to what a mimic pretends to be or according to what an operator perceives. We adopted the latter view. Furthermore, the terminology based on the origins of mimetic compounds is shown.

By an operator, the mimic is…		Origin of mimetic compounds in cases where the mimic is detected as interesting entity by the operator		
not detected as discrete entity or detected as an uninteresting entity[a]	detected as an interesting entity	Innate biosynthesis	Acquisition from host	Reference
Chemical mimesis[b]	Chemical mimicry or camouflage	Chemical mimicry	Chemical camouflage	Akino 2008[c] [14]
---	Chemical mimicry	No distinction		Bagnères & Lorenzi 2010[d] [33]
Chemical camouflage	Chemical mimicry	No distinction		Dettner & Liepert 1994 [15]
Chemical camouflage	Chemical mimicry	No distinction		Geiselhardt et al. 2007[e] [34]
---	Chemical mimicry	No distinction		Howard & Blomquist 2005 [32]
---	Chemical mimicry	No distinction		Keeling et al. 2004 [35]
---	Chemical mimicry	Chemical mimicry by biosynthesis	Chemical mimicry by camouflage	Lenoir et al. 2001 [11]
---	Chemical mimicry or camouflage	Chemical mimicry	Chemical camouflage	Nash & Boomsma 2008[c] [3]
---	Chemical mimicry	---		Pierce et al. 2002 [36]
---	Chemical mimicry	Not specified	Chemical mimicry	Singer 1998[f] [37]
Chemical crypsis[g]	Chemical mimicry	No distinction		Stowe 1988 [31]
----	Chemical mimicry	Not specified	Chemical camouflage[h]	Thomas et al. 2005[e] [8]

--- not considered in the article

No distinction: the term chemical mimicry was used irrespective of the origin of mimetic cues.

[a] According to the first two columns in Tab. 1.

[b] Defined as being invisible through background matching.

[c] Authors follow the definition of Howard et al. [38].

[d] Authors use the term mimicry irrespective of the origin of mimetic compounds but point out that different definitions exist depending on their origin.

[e] Authors follow Dettner & Liepert [15].

[f] The term camouflage was used once to describe invading predators that biosynthesize CHCs of social insects.

[g] Defined as resemblance of the background or of an entity in the background.

[h] Inconsistent to the definitions of Dettner & Liepert [15].

Table 2 shows that the terms chemical mimicry and chemical camouflage are not used consistently. Some authors used the terms according to criteria similar to those used in general biology (see Tab. 1). They distinguished between chemical mimicry as the imitation of an interesting entity, and chemical camouflage either as the imitation of an uninteresting entity or as the resemblance of background cues (sensu Dettner and Liepert [15]). This use of terms did not include the origins of mimetic compounds. In contrast, other authors focused primarily on the origin of mimetic cues. According to their terminology, chemical mimicry implies that mimetic cues are biosynthesized by the mimic, while chemical camouflage implies that the mimic acquires mimetic cues from the model (first defined by Howard et al. [38]). Additional definitions specifically focused on a mimic's avoidance of being detected as a discrete entity (Tab. 2). Chemical resemblances that allow mimics to avoid detection by background matching were defined as chemical mimesis by Akino [14] or as chemical crypsis by Stowe [31].

In addition to adaptive resemblances, another mechanism exists among parasites to prevent detection by an operator. This mechanism was called "chemical insignificance" [39]. However, chemical insignificance was originally brought up to describe the status of freshly hatched ant workers (callows), which typically carry very low quantities of cuticular hydrocarbons [39]. The term insignificance referred to these weak chemical cues, which are frequently not colony or even species specific, allowing the transfer and acceptance of callows into alien colonies [11]. The term chemical insignificance was also adopted to describe a status of ant parasites, which may benefit from displaying no or only small quantities of recognition cues to sneak unnoticed into host colonies [3,11,39,40]. We discuss this point in more detail at the end of the following chapter.

Furthermore, chemical transparency was recently described as a chemical strategy in a wasp social parasite [41]. This strategy is somewhat similar to chemical insignificance, except that it refers particularly to a subset of cuticular compounds that are presumably responsible for recognition. We discuss both strategies, chemical insignificance and transparency, in more detail at the end of the following section.

4. Suggestions for a consistent terminology

As described above, adaptive resemblance terminology is used inconsistently in important reviews of chemical ecology, likely mirroring inconsistent use in this field generally. Most importantly, the terms chemical camouflage and chemical mimicry are inconsistently used by different approaches. While some authors distinguish them according to different models that are mimicked, others distinguish them according to the origin of mimetic cues (Tab. 2). To avoid confusion, we suggest a consistent terminology that is in line with the definitions used in general biology (Tab. 1). Consequently, adaptive resemblance of an entity interesting for the operator should be referred to as "*chemical mimicry*", irrespective of the origin of mimetic cues. Nevertheless, an additional distinction between biosynthesis and acquisition of mimetic cues might often be useful. Hence, we suggest using additional terms to distinguish the origins of mimetic cues: "*acquired* chemical mimicry" indicates that mimetic cues are acquired from the model, while "*innate* chemical mimicry" (as first mentioned by Lenoir et al. [11]) indicates that a mimic has an inherited ability to biosynthesize mimetic compounds. The two different mechanisms may affect coevolutionary dynamics in different ways. For example, a consequence of the acquisition of recognition cues by a parasite from its host is that the mimetic cues of model and mimic are of identical origin [3]. Coevolutionary arms races select in such cases for effective ways of acquiring chemical host cues by the mimic, e.g. through specific behaviors such as intensive physical contact to the host. In the host, selection favors counter-defenses which prevent the acquisition of chemical cues. Selection pressures are somewhat different when a parasite biosynthesizes the mimetic cues [3]. In this case, the origins of the chemical cues of mimic and model are different, which allows coevolutionary arms races to shape on the one hand the accuracy of chemical mimicry of the mimic and on the other hand the discrimination abilities of the operator.

Mimics that are not detected as discrete entities or that are detected but misidentified as uninteresting entities by an operator have rarely been addressed in chemical ecological reviews, although they are common in general biology (first two columns of Tab. 1). Since the term camouflage is not used in general biology to distinguish these two forms of resemblances (Tab. 1), and since the term chemical camouflage is used inconsistently in chemical ecology (Tab. 2), we suggest abandoning this term so as to avoid confusion. Instead, we suggest using terms consistent to general biology: Accordingly, "*chemical crypsis*" describes cases in which an operator is not able to detect a mimic as a discrete entity, while "*chemical masquerade*" describes cases in which an operator detects a mimic as an uninteresting entity. In both cases, the operator shows no reaction. The terms “acquired” and “innate” can be applied to these categories as well to add further information on the origin of the disguising cues. Note that it is challenging but logically possible to empirically separate cases of masquerade and crypsis [28], but this has yet to be done in a non-visual context. Table 3 gives an overview on our proposed terminology for chemical adaptive resemblances. Please note that in our terminology it is only important whether and how mimics are perceived by an operator. Similarities in the chemical profiles of parasites and hosts may be important diagnostic tools, but they are not part of the definitions.

Table 3. Proposed terminology for chemical adaptive resemblances. Chemical cues of a mimic can either be “*acquired*” from the environment (including the host), or they can be “*innate*”, i.e. biosynthesized. In all cases of chemical adaptive resemblance, the operator is deceived by the mimic so that the mimic benefits.

Suggested term	By an operator, the mimic is…
Chemical crypsis	… not detected as a discrete entity due to the expression of cues that blend with the environment (causing no reaction in the operator).
Chemical masquerade	… detected but misidentified as an uninteresting entity (causing no reaction in the operator).
Chemical mimicry	… detected as an entity of interest (causing a reaction in the operator).

Finally, we want to stress the special case of organisms that suppress the expression of chemical cues which can potentially be detected by the operator. Following our aim of applying a consistent biological terminology, “*chemical hiding*” is the most appropriate definition. This definition includes two slightly different scenarios, the total absence of relevant cues and the presence of cues below the operator’s perceptive threshold. In both cases chemical perception of the organism is impossible. A host’s inability to detect any chemical cues of a parasite was also referred to as “chemical insignificance” [3]. However, the term chemical insignificance is unfortunately used ambiguously regarding the important point whether there are no detectable cues [3] or small yet detectable amounts of cues are present [39]. Clearly, it should be distinguished whether an operator is able to detect an organism or not. If resemblance cues are present and perceived (irrespective of the quantitative level), the phenomenon will fall per definition into one of the categories chemical crypsis, chemical masquerade or chemical mimicry (Tab. 3). For example, if a callow’s weak chemical signature was expressed by a parasite, and adult host ants misidentified this parasite as a callow, we would follow Ruxton [17] by assigning this to chemical mimicry (since callows are certainly interesting entities). Empirical evidence for a chemical mimicry of callows could result in practice from a combination of chemical data (callow resemblance) and behavioral data (hosts treat parasite as callows). However, an exhaustive discussion about methods is beyond the scope of this conceptual article. Consequently, the original definition of chemical insignificance as a “weak signal” [39] appears not applicable to parasites without the risk of confusing it with chemical mimicry. If chemical cues are below an operator’s perceptive threshold, the definition of chemical hiding will apply. However, the term chemical insignificance may be used as a functional term describing the lack of chemical information in a certain context. For example, callows are chemically insignificant in terms of nestmate recognition due to a lack of chemical information in that context. Nevertheless, callows carry apparently sufficient information in the context of caste identity since workers show characteristic behaviors towards them; for example, they receive assistance during hatching and are transported to new nest sites in migratory ants.

The above discussion on chemical insignificance applies also to the phenomenon of chemical transparency. If no cues are expressed that are perceivable by the operator, the focal organism would show chemical hiding, regardless of the presence of any other compounds. In contrast, if perceivable cues are present, chemical crypsis, chemical masquerade or chemical mimicry applies. In the described case of chemical transparency [41], the parasite is most likely recognized and misidentified as an interesting entity (e.g. as brood), since social parasites usually exploit the brood care behavior of their hosts.

Notably, a parasite may alternatively avoid chemical detection through behavioral mechanisms by “hiding” according to the definition in general biology (see above) rather than “chemical hiding”. For example, if it avoids detection by staying in a cavity so that its chemical cues do not reach the operator, it is hiding. A parasite that performs “hiding” could potentially be detected if it was somehow confronted with the operator. In contrast, a parasite that shows “chemical hiding” cannot be detected by chemical senses of the operator at all.

5. Examples for the use of adaptive resemblance terms

In this section we want to discuss examples to clarify the use of terms regarding adaptive resemblances. The mimicking of CHC profiles of the host is widespread among ant parasites, and this is generally assumed to facilitate integration into the host colonies. Parasites are indeed frequently not recognized as alien species [11,33]. This strategy of avoiding recognition as an alien species by expression of host CHCs could potentially be referred to as chemical crypsis (if the colony odor is regarded as the background) or as chemical masquerade (if a nestmate worker is regarded as an uninteresting entity). However, we argue that the strategy is best described by chemical mimicry for the following reasons: First, workers are certainly able to detect other workers, and hence parasites that mimic them are discrete entities, excluding the term chemical crypsis. Second, workers are certainly interesting entities to other workers because social actions are shared, such as grooming or trophallaxis. Consequently, a mimic that uses a worker as model resembles an entity of potential interest to ant workers, so that chemical mimicry rather than chemical masquerade applies.

It becomes more complicated when a parasite mimics the nest odor of its host. Lenoir et al. [42] demonstrated that the nest inner walls of the ant species *Lasius niger* are coated with the same CHCs as those that occur on the cuticle of workers. However, the CHCs on the walls occurred in different proportions and showed no colony-specificity. If a mimic resembles such a chemical profile, chemical crypsis will be the most appropriate term, because the mimic represents no discrete entity and rather blends with the uniform nest odor. To our knowledge, no clear evidence exists for this case.

It is worth highlighting in this context another example, which was already pointed out by Ruxton [17]. The CHCs of *Biston robustum* caterpillars resemble the surface chemicals of twigs from its host plant [43]. *Formica japonica* and *Lasius japonicus* workers do not recognize the caterpillars on their native host plant, but when caterpillars were transferred to a different plant, the ants noticed and attacked them. In this case it depends on the operator’s perception whether the example should be considered as chemical crypsis or chemical masquerade. If the ants did not detect a twig (and hence a caterpillar) as a discrete entity, but as background, chemical crypsis would apply. If the ants detected the caterpillar as a discrete but uninteresting entity, e.g. as a twig, then chemical masquerade would apply. As Ruxton [17] emphasized, twigs are of huge dimension compared to the size of ants. Hence, it is more likely that ants do not detect caterpillars as discrete (uninteresting) entities, but rather perceive them as (uninteresting) background. Accordingly, chemical crypsis appears to be the most appropriate term for this example.

These examples may demonstrate that it can be rather difficult to assign appropriate terms to particular adaptive resemblance systems. Nevertheless, the definitions we proposed are generally straightforward, and they can be applied unambiguously if the necessary information about a system is available. We hope that this article contributes to a careful and consistent use of adaptive resemblance terminology in chemical ecology.

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Discussion

> “[…] *I could show that none of these characters of instinct are universal. A little dose* […] *of judgment or reason, often comes into play, even in animals very low in the scale of nature.”*
>
> – Charles Darwin (1859)

Decision making is a common behavioural characteristic among all animals that deal with a variable environment, helping them to increase the benefit and to decrease the costs of their actions, and so ultimately to increase their fitness. The study of decision making and the mechanisms underlying it thus provides insights into the principles that shape the diversity of behaviours. In particular, decision making in social animals allows us to gain insight into the mechanisms of collective behaviour, which is often determined by the sum of behaviours and the resulting interactions of a group of individuals (Sumpter 2006). Social insects are a famous example of cooperation and division of labour between individuals (Wilson 1971). Although the fitness benefits of the colony as a whole will be affected by the outcome of crucial decisions, often only a few individuals gather the information that is relevant for the upcoming decision. Hence the initial decision-making process will rely on the individuals that collect the information, and in a second step on the processing of this information by other colony members. While gathering as much information as possible reduces the amount of uncertainty about the environment, it comes with considerable costs in terms of time and energy spent (Dall et al. 2005). It has been suggested that a set of simple decision rules is sufficient to elicit complex behaviours in social insect colonies (Detrain & Deneubourg 2002). Particularly, the assessment of some highly informative and reliable key parameters that integrate information about various relevant factors should be enough to evoke an elaborate response. Variation in the final decision may occur depending on the environmental frame conditions (Detrain & Deneubourg 2002). In order to determine these decision rules and the crucial key parameters in a specific system, it is necessary to record the values of potential decisive factors and to study in detail the behaviours of the individuals involved during decision-making situations.

For this purpose, I studied decision making in the slave-making ant *P. americanus*. The scouting behaviour of *P. americanus* demands several decisions to be made by the slavemaker workers at various points during the search for new slaves. Most importantly, decisions have to be made about when to start searching for host colonies, who to send out as scouts and whether or not to raid a discovered host colony. These decisions can potentially be influenced by certain key parameters that provide reliable information about both the conditions in the slavemaker colony and the composition and reaction of the host colony.

Indeed, the results presented in the articles 1-3 suggest that decision making in *P. americanus* workers relies on just a few key parameters in order to achieve the replenishment of the slave work force if necessary, i.e. to evaluate the need of the slavemaker colony as well as the costs and benefits of attacking a specific host colony. The number of conspecific nestmates, i.e. slavemaker workers, represents one of these parameters. It influences the number of scouts that leave the nest to search for host colonies, and it correlates with the slave to slavemaker ratio inside the slavemaker colony (article 3). Higher scout numbers led to quicker discovery of a host colony and increased the probability of discovering additional host colonies (article 3), and a lower slave to slavemaker ratio increased the probability of a successfully completed entire raid (article 1). A correlation between the number of colony members and specific behaviours has been repeatedly demonstrated in ants before (e.g., Thomas & Framenau 2005; Holbrook et al. 2011). For example, during house-hunting experiments in the rock ant *T. albipennis*, larger colonies discovered new nest sites more quickly (Dornhaus & Franks 2006), comparable to the faster discovery of a host colony by larger slavemaker colonies.

A possible proximate mechanism of how the slavemaker workers assess the need for slaves and translate it into scouting activity is via determining the colony's demand for food. A simple mechanism to evaluate this demand is presented in article 2. Individual slavemaker workers could use the food supply they experience to gain information about the overall colony need, and the number of conspecifics can play a role here. In the presence of a given slave work force, higher slavemaker worker numbers are expected to lead to a decrease in the mean food supply, since the slavemaker workers are exclusively fed by their slaves (Sturtevant 1927). Experimentally starved colonies showed higher proportions of slavemaker workers that left their colony as scouts (article 2). The nutritional status of a slavemaker worker may thus directly serve as measure to determine the colony's need for new slaves. It can easily be determined by every individual, and it is closely linked to the current slave work force. Hence the individual nutritional status provides a slavemaker worker with a reliable cue about the strength of the slave work force and the need for additional slaves. By replenishing the slave work force, the slavemaker workers eventually improve the provisioning and thereby the nutritional situation of their colony. It is thus conceivable that the search for slave workers as a behavioural response to low food supply potentially evolved as a modification from the behaviour of non-parasitic ant workers, which search for food when their nutritional status is low (e.g., Howard & Tschinkel 1980; Blanchard et al. 2000). While starvation caused an increase in scouting activity, in article 3 the slave to slavemaker ratio, which should basically determine the provisioning of slavemaker workers, was not found to influence the number of scouts. This might be explained by the *ad libitum* feeding regime in the respective experiments, which likely led to an adequate provisioning of slavemaker workers irrespective of the strength of the slave work force. Nevertheless, the number of scouts and the course of the scouting events varied with the number of slavemaker workers, indicating that slavemaker workers may possess additional mechanisms to assess the number of conspecifics. In any case, the evaluation of the number of slavemaker workers, backed by the nutritional status of individuals, is sufficient as a parameter for the determination of the necessity and the size of a scouting event. Detailed assessments of additional parameters such as the number of slave workers or the accurate slave to slavemaker ratio are not necessary to come to an adequate decision.

A further reason for the influence of slavemaker worker numbers on the number of scouts may be the fact that slavemaker workers differ in their physiological state, causing them to perform different behavioural tasks (see article 2). *Protomognathus americanus* workers form dominance hierarchies inside their colonies, and the dominant individuals become fertile (Franks & Scovell 1983; Blatrix & Herbers 2004). In article 2 I demonstrated that only infertile individuals take part in the scouting events. Their fertile nestmates presumably benefit from their top rank positions in the dominance hierarchy by producing male offspring in the safety of the colony (Foitzik & Herbers 2001a). Since the number of top-ranking individuals inside a colony is limited due to ongoing dominance behaviours (mostly antennal boxing [Blatrix & Herbers 2004]) that establish and maintain a linear dominance hierarchy (Franks & Scovell 1983), higher numbers of slavemaker workers should consequently result in more non-reproducing individuals, which in turn can increase the colony's and thereby their own fitness by scouting and replenishing the slave work force. This division of labour was reflected in the cuticular hydrocarbon profiles of the slavemaker workers (article 2). Fertile and infertile non-scouting individuals differed in their cuticular hydrocarbon profile, with infertile scouts showing an intermediate chemical profile. Different profiles may help returning scouts to selectively approach and recruit nestmates for a slave raid. It is interesting to note here that scouting slavemaker workers can also take over a host colony and start to reproduce instead of returning to their mother colony with the raided host pupae (Wesson 1939). If the intermediate profiles of scouts indicated that they are close to becoming fertile, task allocation that results in these individuals leaving as scouts could have evolved as an adaptation to the chance of worker reproduction outside of the slavemaker colony. Having discovered a host colony, a scout finds herself in a central position, being able to decide whether to raid host pupae in order to replenish the mother colony's slave work force or to stay and start producing own male offspring. It would be interesting to clarify in future studies whether this decision is linked to a trade-off between individual and group benefits, i.e. whether scouts that reproduce in the former host colony increase their own fitness benefit at the expense of the overall colony fitness. Environmental conditions might play a role in this situation, as it is the case for the conflict over male production between the slavemaker queen and the workers. In *P. americanus*, worker reproduction inside the queenright mother colony is thought to depend on the overall density of host colonies (Blatrix & Herbers 2004). In a population with a low density of host colonies in West Virginia, male production is monopolized by the queen (Blatrix & Herbers 2004), whereas workers reproduce in equal measure in the presence and in the absence of the queen in the New York population where the host colony density is high (Foitzik & Herbers 2001a).

The number of slavemaker workers, measured either directly or indirectly via the factors that are associated with it, apparently serves as a key parameter for decision making. But since *P. americanus* is an obligate slavemaker that is completely dependent on its hosts, it seems plausible that the slavemakers' decisions are also influenced by certain host parameters. In particular, when estimating a discovered host colony's suitability for an attack, scouts should not neglect reliable information about the particular host colony. Indeed, the number of host workers of a discovered host colony played an important role in the final decision of whether to raid or not. *Protomognathus americanus* colonies preferably attacked host colonies with more host workers, which could be only partly compensated by more distinct host pupae : host worker (i.e., benefit : risk) ratios (article 1). Although slavemaker workers face a higher risk when attacking host colonies with more workers (article 1), this preference could be explained by the naturally occurring pupae : worker ratios of host colonies and by the increased risk of scouts, which are presumably more vulnerable to defending host workers than members of a raiding party. The number of host workers thus constitutes a good example of a key parameter during the decision-making process. It is directly related to the potential risk that the slavemakers will face if they attack the host colony, since host colonies with more workers were more likely to treat intruding scouts aggressively (article 3). At the same time, host worker numbers provide the scouts with reliable information about the potential benefit of an attack in terms of host pupae, due to the positive correlation that occurs in the field between host worker and pupae numbers (article 1). Hence there is no need for the scouts to collect information that is difficult to gather, such as host pupae numbers. Scouts can limit themselves to the more easily accessible host worker force to get a good estimation about potential costs and benefits of attacking a host colony.

It has been demonstrated that host colonies from the New York population studied here intensified their defence against intruders in comparison to a second population in West Virginia (Foitzik et al. 2001), apparently as an adaptation to the high prevalence of *P. americanus* and the resulting increased parasite pressure on *T. longispinosus* in the former community (Foitzik et al. 2001; Herbers & Foitzik 2002). According to the geographic mosaic theory of coevolution which predicts that species interactions differ in their characteristics depending on local selection pressure (Thompson 1999; Thompson 2005), the slavemakers' decision-making strategies could also be shaped by the local conditions of the ongoing coevolutionary arms race. The number of host workers and therefore the probability for host aggression is thus certainly a crucial parameter for the decisions of slavemaker scouts in New York. It could be promising to investigate in further, comparative studies whether the decision rules of slavemaker scouts in West Virginia (which are confronted with the less aggressive host population) also rely strongly on host worker numbers, which would mean that this dependence can be seen as a general coevolved trait on the species level irrespective of the population (Thompson 1999), or whether other factors play a more important role in the West Virginia population.

During the choice experiments in article 1, where slavemaker colonies were presented with host colonies which differed in their demographic composition, the slavemaker scouts often did not discover both host colonies. Nevertheless, an overall preference for host colonies with more host workers could be found. *Protomognathus americanus* scouts may simply judge whether the demographic composition of a discovered host colony exceeds a certain threshold and thus represents a suitable raiding target. Recently, Robinson and coworkers (2011) demonstrated that complex decisions at the colony level can arise from simple threshold rules in individual scouts, which do not require direct comparisons between different options. They could show that the house-hunting rock ant *T. albipennis* can come to elaborated nest site choices by comparing a potential new nest site with an internal threshold of acceptability, and inferior nest sites were less likely to be chosen due to recruitment latency. It must be stated that the time span between the discovery of a host colony and the final decision of *P. americanus* scouts was not influenced by the demography of the host colony (article 3). That is, it did not depend on the quality of the target, unlike in the case of *T. albipennis*. However, contrary to potential nest sites, host colonies are able to react to the presence of scouts, and their value for the slavemakers may thus alter accordingly. Indeed, increased host aggression slowed the course of the scouting behaviour (article 3), possibly influencing the final decision of the scouts via the delay in the evaluation process.

Socially parasitic ants have received increasing attention in the last decades (D'Ettorre & Heinze 2001; Buschinger 2009). They have been compared to the well-studied avian brood parasites, with which they show remarkable parallels in the way arms races between parasites and hosts take place (Davies et al. 1989; Kilner & Langmore 2011). Socially parasitic ants are becoming popular as a model system for addressing the mechanisms of coevolution between hosts and parasites (Brandt et al. 2005), not least because of their suitability for experimental manipulation, both under controlled conditions and with large sample sizes. Here I investigated decision making as another important aspect of social parasite biology. The slave-making ant *P. americanus* uses a few key parameters to gain information about current conditions in order to reach decisions during the scouting process: The number of conspecific nestmates and the nutritional status of a slavemaker colony influence the probability of beginning the search for host colonies, and the final decision of whether to raid a host colony depends on the number of host workers, with *P. americanus* scouts preferring larger host colonies. Thus the study of social parasites also allows addressing general questions in the context of decision making in social insects.

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Thesis title: "Decision making during the scouting behaviour of the slave-making ant *Protomognathus americanus*"

Supervisor: Prof. Dr. Susanne Foitzik

2006	Diploma in Biology at the University of Freiburg (grade 1.1) Topics: Evolution and ecology Neurobiology / Physiology of animals Biochemistry French Thesis title (translated): "The influence of different factors on the production of a replacement clutch in the burying beetle *Nicrophorus vespilloides* HERBST (Coleoptera: Silphidae)"; Supervisor: Prof. Dr. Josef K. Müller
2003	recommended for membership in the German National Academic Foundation
2001 – 2006	Study of Biology at the University of Freiburg

Alternative civilian service

04.10.2000 - 31.08.2001, at the residential home of the "Lebenshilfe", Idar-Oberstein

School education

07.06.2000	Graduation ("Abitur", grade 1.0) Award for excellent achievements Award of the "Fund of the Chemical Industry"
1991 - 2000	Gymnasium an der Heinzenwies, Idar-Oberstein 1996 Laureate of the 2nd round of the Federal Mathematics Competition 1995 school champion and 9th place on federal level in the competition "Lire sans frontières"
1987 - 1991	Grundschule am Markt, Idar-Oberstein

Language skills

German (native language)
English, French (fluent)
Spanish, Italian (basic)

Publications

Pohl, S. & Foitzik, S. 2011: Slave-making ants prefer larger, better defended host colonies. Animal Behaviour **81**, 61-68.

Pohl, S., Witte, V. & Foitzik, S. 2011: Division of labor and slave raid initiation in slave-making ants. Behavioral Ecology and Sociobiology **65**, 2029-2036.

Pohl, S. & Foitzik, S. Parasite scouting behaviour and host defence are regulated by colony size in a social parasite system. Submitted to Ethology.

von Beeren, C., Pohl, S. & Witte, V. On the use of adaptive resemblance terms in chemical ecology. Psyche, in press.

Presentations

Pohl, S. & Foitzik, S. 2011: Scouting behaviour and host worker response in slave-making ants. 7th Ecology & Behaviour Meeting, Rennes

Pohl, S. & Foitzik, S. 2010: Raid organisation and division of labour in slave-making ants. 13th International Behavioral Ecology Congress of the International Society for Behavioral Ecology (ISBE), Perth

Pohl, S. & Foitzik, S. 2010: Raid organisation and task allocation in slave-making ants. 15th Graduate Meeting of the Section Evolutionary Biology of the German Zoological Society, Freiburg

Pohl, S. & Foitzik, S. 2010: Raid organisation and division of labour in slave-making ants. 6th Ecology & Behaviour Meeting, Tours

Pohl, S. & Foitzik, S. 2009: Decision making and host nest choice in the slavemaking ant *Protomognathus americanus*. 1st Central European Meeting of the International Union for the Study of Social Insects, Frauenchiemsee

Pohl, S. & Foitzik, S. 2009: Risk evaluation and decision making in slavemaking ants. 5th Ecology & Behaviour Meeting, Lyon

Pohl, S. & Foitzik, S. 2009: Risk evaluation and decision making in slavemaking ants. 14th Graduate Meeting of the Section Evolutionary Biology of the German Zoological Society, Munich

Pohl, S., Konrad, M. & Foitzik, S. 2008: Behavioural and chemical changes in orphaned *Temnothorax* ant workers. 13th Graduate Meeting of the Section Evolutionary Biology of the German Zoological Society, Hamburg

Poster contributions

Pohl, S. & Foitzik, S. 2010: Raid organisation and division of labour in slave-making ants. XVI Congress of the International Union for the Study of Social Insects, Copenhagen

Pohl, S. & Foitzik, S. 2009: Cost-benefit evaluation and host nest choice in the slavemaking ant *Protomognathus americanus*. 102nd Conference of the German Zoological Society, Regensburg

Pohl, S., Steiger, S. & Müller, J. K. 2007: On the benefit of filial infanticide in burying beetles. 12th Graduate Meeting of the Section Evolutionary Biology of the German Zoological Society, Bayreuth

Pohl, S. & Müller, J. K. 2006: The effect of potential risk and potential benefit on the behaviour of widowed burying beetles. 11th International Behavioral Ecology Congress of the International Society for Behavioral Ecology (ISBE), Tours

Grants

2010 Research and travel grant IRT 3 trial of the Munich Graduate Program for Evolution, Ecology and Systematics

2009 Research Grant of the E. N. Huyck Preserve and Biological Research Station, Rensselaerville, NY, USA
Title: "Host-parasite interactions in slavemaking ants and their slaves"

Research and travel grant IRT 3 trial of the Munich Graduate Program for Evolution, Ecology and Systematics

2008 Research Grant of the E. N. Huyck Preserve and Biological Research Station, Rensselaerville, NY, USA
Title: "Different fronts in the coevolutionary arms race of slavemaking ants and their hosts"

Research and travel grant IRT 3 trial of the Munich Graduate Program for Evolution, Ecology and Systematics

2007 Research Grant of the E. N. Huyck Preserve and Biological Research Station, Rensselaerville, NY, USA
Title: “Risk evaluation and decision making in slavemaking ants”

Media coverage

Science news websites:

BBC online:
http://news.bbc.co.uk/earth/hi/earth_news/newsid_9160000/9160744.stm

Encyclopaedia Britannica Blog:
http://www.britannica.com/blogs/2010/11/science-up-front-sebastian-pohl-and-susanne-foitzik-on-the-raiding-behavior-of-the-slavemaking-ant-protomognathus/

Bayerischer Rundfunk online

Newspapers:

Süddeutsche Zeitung, November 10th, 2010, also available online:
http://www.sueddeutsche.de/wissen/verhaltensbiologie-immer-auf-die-starken-1.1021766

Radio programs:

Adelaide Breakfast, 891 ABC Adelaide

Organization experience

Member of the Organization Board of the
1st Central European Meeting of the International Union for the Study of Social Insects &
3rd Central European Workshop in Myrmecology,
Frauenchiemsee, October 8th - October 12th, 2009

Eidesstattliche Versicherung

Ich versichere hiermit an Eides statt, dass die vorgelegte Dissertation von mir selbständig und ohne unerlaubte Hilfe angefertigt ist.

München, 21. Dezember 2011

Sebastian Pohl

Erklärung

Hiermit erkläre ich, dass die Dissertation nicht ganz oder in wesentlichen Teilen einer anderen Prüfungskommission vorgelegt worden ist, und dass ich mich anderweitig einer Doktorprüfung ohne Erfolg **nicht** unterzogen habe.

München, 21. Dezember 2011

Sebastian Pohl