Original Article

Brood as booty: the effect of colony size and resource value in social insect contests

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Animals engage in contests for access to resources like food, mates, and space. Intergroup contests between groups of organisms have received little attention, and it remains unresolved what information groups might use collectively to make contest decisions. We staged whole-colony contests using ant colonies (*Temnothorax rugatulus*), which perceive conspecific colonies as both a threat and resource from which to steal brood. We recorded individual behaviors and used demographic characteristics as proxies for resource value (number of brood items) and fighting ability (number of workers). We found that ants altered their fighting effort depending on the relative number of workers of their opponent. Although the proximate mechanism for this ability remains uncertain, we found that colonies increased fighting when their opponent had relatively more brood, but not if opposing colonies had relatively many more workers. This suggests that ant colonies can use information about opposing colonies that shapes contest strategies. Further, the behavior of opposing colonies was strongly correlated with each other despite colony size differences ranging from 4% to 51%, consistent with the hypothesis that colonies can use opponent information. The behavior of a distributed, collective system of many individuals, like a eusocial insect colony, thus fits several predictions of contest models designed for individuals if we consider the gain and loss of worker ants analogous to energetic costs accrued during typical dyadic contests.

Key words: assessment strategy, brood-stealing, collective behavior, contests, slave-making, *Temnothorax*.

BACKGROUND

Many animals contest with conspecific for resources like food, space, and mates, the access to which is a key driver of reproductive fitness (Hölldobler 1976; Parr and Gibb 2010; Hardy and Briffa 2013; Chuang et al. 2017). There has been renewed interest in understanding how organisms make decisions in such contests, particularly when to give up or continue contesting (Taylor and Elwood 2003; Briffa 2007; Arnott and Elwood 2009; Chapin and Hill-Lindsay 2016; Chapin and Reed-Guy 2017; Chapin et al. 2019; Pinto et al. 2019). Despite this work, we still have no general model for understanding the circumstances under which using information may be adaptive (or not) in resolving animal contests (Chapin et al. 2019). It would seem that learning about both the fighting ability of opponents and value of contested resources should improve contest giving-up decisions, but this isn't always the case: although more information can reduce contest durations (i.e., the decision to give up can be made sooner), this doesn't necessarily mean that individuals will win more contests by using any particular combination of information sources, if any and acquiring

information may be costly (Elwood and Arnott 2012; Reichert and Quinn 2017; Chapin et al. 2019).

Contests for resources involving social groups are poorly understood, but have received a recent increase in interest, both empirically and theoretically (Chapin et al. 2019; Green et al. 2020; Rusch and Gavrilets 2017). Theoretical research on intergroup contests is largely limited to triadic (opposed to just dyadic) contests (Sherratt and Mesterton-Gibbons 2013). For example, individuals may change contest strategies after eavesdropping on other contests (Johnstone 2001), and some contest winners advertise their victory to third-party neighbors (Bower 2005). An exception is Lanchester's Laws, which are used to predict contest outcome (winner and loser) of two waring groups that engage one-on-one (Lanchester's Law) or one-on-many (Lanchester's Square Law; Lanchester 1916). In other cases, organisms may form coalitions—a group (two or more organisms) joining sides to win against a common opponent (Mesterton-Gibbons et al. 2011). However, in all these examples, agents are acting as independent organisms with their own selfish interests. Social groups with high reproductive skew (e.g., the eusocial insects), however, have a shared evolutionary trajectory (Bourke 2011), such that the fitness of most group members is contingent on the reproductive output of one or a few individuals. In this sense, eusocial

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animals are largely not contesting for access to resources that directly improve their own fitness, but instead work to increase the fitness of the colony via the queen. Group members might also share information about opponents and resources, which could make information acquisition less costly (Grüter and Leadbeater 2014; Evans et al. 2015; Chapin et al. 2019; Green et al. 2020). How this might change information use during contests remains unexplored.

The strategies used in contests by eusocial insect colonies remain poorly understood (Chapin et al. 2019; Green et al. 2020; Rusch and Gavrilets 2017), despite intraspecific competition being a major driver of social insect ecology and spatial dynamics (Hölldobler 1979; Hölldobler and Lumsden 1980; Gordon 1992; Ryti and Case 1992; Parr and Gibb 2010; Cerdá et al. 2013). For example, *Oecophylla longinoda* weaver ants exhibit residency effects in contests (i.e., where the "home team" has the advantage), mediated by pheromone cues; and dulotic (i.e., "slave-making") *Protomagnathus americanus* and *Polyergus rufescens* ants have shown increased recruitment to colonies with more brood available to steal (Visichio et al. 2003; Pohl and Foitzik 2011). At least some ants use ritualized displays to decide contest outcomes. In meat ants (*Iridomyrmex purpureus*), for example, such displays typically decide contests, which only rarely escalate to lethal fights (Wilgenburg et al. 2005). Honeypot ants (*Myrmecocystus mimicus*) use whole-colony ritualized displays to decide contest outcomes, with workers of the losing colony being enslaved by the winning colony (Hölldobler 1976; Lumsden and Hölldobler 1983). That being said, other species appear to engage in direct, individual fights that often end in injury or death (Whitehouse and Jaffee 1996) highlighting the variation in contest strategies that social insects might employ (Rusch and Ravrilets 2017; Green et al. 2020).

In this study, we investigate the outcomes and the behavior of ant colony contests, with a focus on what information colonies use to make giving-up decisions. Studies of how social groups decide contests are rare (Sherratt and Mesterton-Gibbons 2013). In general, organisms can use three types of information to make contest decisions: information about themselves, their opponents, or the contested resource (Taylor and Elwood 2003; Chapin et al. 2019). Surprisingly, some organisms do not use opponent information (Crabs: Prenter et al. 2006; reptiles: Stuart-Fox 2006; Smallegange et al. 2007; insects: Briffa 2007; Dietemann et al. 2008; spiders: Elias et al. 2008; Brandt and Swallow 2009; Constant et al. 2011; fish: Copeland et al. 2011; frogs: Reichert and Herhardt 2011; anemones: Rudin and Briffa 2011; McLean and Stuart-Fox 2014; Pinto et al. 2019). Researchers can test for the use of these information sources by observing changes in behavior in staged contests against opponents of different sizes, where size is a proxy for RHP (Arnott and Elwood 2003, 2009; Chapin et al. 2019). Note that research on assessment strategies typically does not address the proximate mechanism(s) for information transfera. Instead, this work concerns the question of *which* information is transferred and *why*, if information transfer is occurring at all. Here we also do not study these mechanisms, but what information is used by colonies.

Ant colonies might assess their own colony-wide resource holding potential (RHP, the absolute fighting ability of an individual, or, in this case, of a colony; Parker 1974). For example, workers of the species *Formica xerophila* are less aggressive when they sense they have been separated from their colony (Tanner 2006) and small colonies of the wood ant *Formica rufa* escalate to riskier contest behavior relative to large colonies (Batchelor and Briffa 2011). Although the proximate mechanism for how individual ants or colonies gain this information remains largely unresolved, assessing opponent

group RHP also seems to occur in some species. For example, *Azteca trigona* groups flee or attack based on the ratio of nest mates to intruders (Adams 1990). Further, some ants assess the quality of the resource they defend (Arnott and Elwood 2008). For example, some *Formica* ants show increased aggression in contests with higher territory resource value (Tanner and Adler 2009). It remains unclear if social groups, in general, rely more on one source of information than others, or how information use in contests might vary across taxa. There is evidence, however, that contest strategies can vary among individuals in a colony. For example, minor workers of the polymorphic *Cataglyphis niger* always flee from opponents, whereas majors base their response on the fighting ability of their opponent (Nowbahari et al. 1999).

We staged paired whole-colony contests using the ant *Temnothorax rugatulus* to test what information eusocial insects use to make collective contest decisions. These ants are known "slave-making" ants that steal brood from other colonies to raise as workers (D'Ettorre and Heinze 2001). As such, colonies are motivated both to acquire opponent resources (i.e., brood) and defend their own. We investigated whether and how colonies use information about themselves, their opponent, and the contested resources, to make collective, colony-wide contest decisions by measuring variation in investment of colonies in offense (number of workers physically fighting opponents) and defense (number of workers allocated to guarding). Only a small proportion of ants engage in these behaviors in *Temnothorax* ants, so colony investment in fighting or guarding is not a zero-sum game—in all cases, most ants remained inactive in the nest away from the entrance, such that the number of guards did not directly limit the number of fighters. Further, fights could occur among more than two individuals, so the number of fighting individuals of each colony need not match. We hypothesize that colonies compare their own number of workers and brood to that of their opponents, and use this information to adjust fighting and guarding behavior in response. In the framework of assessment strategies, we consider the number of workers as a proxy of RHP and use the number of brood as a measure of resource value. Alternatively, colonies may use only a subset of these information sources, or none at all.

METHODS
Study species, collection, and maintenance

We collected 18 queenright colonies of *T. rugatulus* in 2017 and 2018 from the Catalina Mountains in Coronado National Forest near Tucson, Arizona. This species is a small brown ant that lacks morphological castes, although body size variation occurs, with larger individuals more likely to leave the nest (Westling et al. 2014). In nature, *T. rugatulus* usually occur in colonies of 50–400 workers, which can be polydomous, polygynous, and dulotic (i.e., colonies may include multiple nests, multiple queens, and enslaved ants from other nests; Bengston and Dornhaus 2013, 2015). Colonies commonly nest in crevices and cracks of rocks, where they can be easily collected and transplanted to artificial nests for study. Most *T. rugatulus* stay inactive in the nest, whereas a small proportion forage outside (Charbonneau and Dornhaus 2015). As such, it is not clear that activity in one task limits colony investment in another task.

We housed colonies in separate polypropylene containers measuring 11 × 11 cm with an open top and sides coated in Fluon (polytetrafluoroethylene, Bioquip Products Inc., Compton, California) to prevent escape. We added an artificial nest to each container, which we made by sandwiching a 50 mm × 75 mm rectangle of 1.8 mm thick cardboard with a 35 × 25 mm die-cut cavity and 4 × 3 mm

entrance between two 1 mm thick glass slides of the same dimensions (Figure 1). We provided colonies ad libitum water, sucrose solution (2 mmol/mL), and either dead (fresh-frozen) fruit flies (*Drosophila melanogaster*) or cockroaches' pieces (*Nauphoeta cinerea*). We counted the number of queens, workers, and brood (eggs, larvae, and pupae) in each nest. We painted (Pactra Racing Finish, Testor Corporation, USA) each ant to track individual identity and colony affiliation sensu Charbonneau et al. (2017).

Contest trials

Our goal was to test if the number of workers (i.e., the colony's fighting ability) or brood (i.e., the colony's resource value) of the opposing colony influenced the fighting or guarding behavior of the focal colony during contests. We identified the focal colony of each dyad as the colony with the lower number of workers. Animal contest theory is predicated on the assumption that contests are decided when losers give up whereas winners persist. As such, we can only elucidate contest strategies of losing opponents (reviewed in Chapin et. al 2019): the end of the contest is the point at which the losing contestant gave up, which can be used to study which factors determine this decision.

We recorded nine paired, whole-colony interaction trials (18 colonies total) in a rectangular borosilicate glass dish (Pyrex, Greencastle, Pennsylvania) lined with Fluon (Insect-a-Slip, BioQuip) and measuring 38.6 × 25.7 cm. We loosely size-matched colonies to avoid extreme differences in colony size and annihilation of the losing colony, resulting in relative size differences of 4–51%. We started each trial by simultaneously placing the artificial nests with the two colonies on opposite ends of the arena and equidistant from the midline, with entrances facing the arena center (Figure 1). Any workers outside the nest at the time of transfer were moved to the arena with a fine paint brush. We performed trials for 3 h, after which we returned colonies to their home containers.

We recorded two main behavioral measures via instantaneous sampling at 15 min intervals (from 0 to 180 min, by 15 min; 12 samples per contest): the number of ants engaged in physical fights (i.e., where two opposing ants have stopped other behaviors and are in physical contact at the time of sampling), and the number of ants defending the entrances of each nest (i.e., stationarily positioned within the 4 × 3 × 1 mm nest entrance). Additionally, we examined two trials in complete detail by recording all major behaviors (Supplementary Table S1) at any time point, with the goal of generally describing the contest behavior of this species.

Statistical analysis

We developed two pairs of linear models to address the question, *does opposing colony resource holding potential or resource value affect focal colony behavior in contests?* The first pair tested if focal colony contest behaviors were predicted by the demographics of both the focal and opponent colonies via ridge regression. We chose ridge regression because of collinearity among some predictor variables (Imdad and Aslam 2018). We included either the number of focal colony workers engaged in physical fights with opponents or guarding the nest entrance as response variables. We used four measures of colony demography as predictor variables: the number of workers and brood in the focal and opponent colony. We included trial time to account for repeated sampling and to investigate how the effects changed across the trial. A significant effect of opponent worker or brood number on the behavior of the focal colony indicates that the focal colony is using opponent information to increase or decrease fighting or guarding behavior.

The last pair of models tested if the number of focal colony workers engaged in fights or guarding the nest entrance could be predicted by those measures of the opposing colony via generalized linear regression. Focal and opposing colony behavior might not correlate, because physical fights can occur among more than two individuals (i.e., need not be dyadic), the relative difference between colonies in number of workers varied by as much as 51%, and brood varied by up to 185%. We used a Poisson distribution to accomodate count data. We used R 3.5.1 (R Core Team 2018) with the package lmridge (Imdad and Aslam 2018) for analysis and figures. All analyses can be reproduced with data and code archived in Chapin et al. (2022) via Dryad (https://doi.org/10.5061/dryad.98sf7m0kp).

RESULTS

Overall contest behavior and time course

Generally, colonies explored the new environment, detected opponents, and engaged in both physical fighting and attempts to steal brood by entering the opposing colony's nest. Contests continued to escalate for the duration of the 3 h trial. We recorded all major behaviors that occurred in two trials by continuous observation to generally describe colony-wide contests in this species. We saw similar behavioral patterns in both colony pairs (Supplementary Figure S2). Antennation was the most common behavior and occurred most often inside the nest (Supplementary Figure S2a). Opposing colonies seem to track each other's movements for several behaviors, and especially movements into and out of the nest appear to increase or decrease in parallel (Supplementary Figure S2b and c). Barrier-building tended to occur early in trials (Supplementary Figure S2d). Stinging was quite rare and occurred only a total of 25 times and in only one of the two trials examined in detail. Successful brood stealing (removing brood from the opposing colony) occurred but was also rare (2 or 3 times per trial).

Contest assessment strategies

Relative differences in the number of workers and brood between opponents varied from 4% to 51% and − 185% to 87%, respectively. Ridge regression models showed that the number of fighting focal workers was predicted by the number of brood and workers in the opposing colony (Table 1; Figure 2). The number of guarding workers was only predicted by the number of brood in
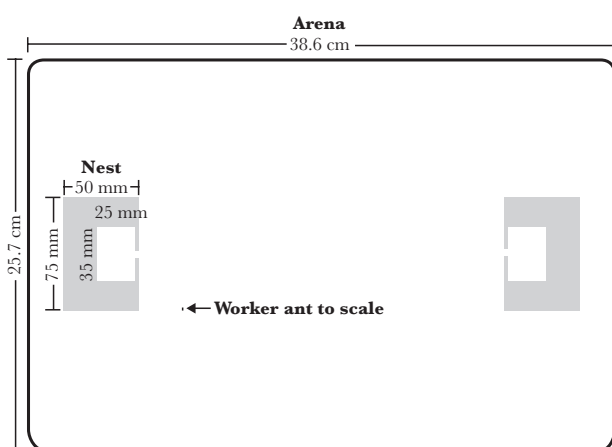

Figure 1
Arena design for colony-wide contests. We placed two artificial nests into a common arena and videographed subsequent behaviors and interactions.

the focal colonies ($t = 3.11$, $P = 0.002$, Table 1). This suggests that the fighting effort of the focal colony changed depending on how much larger the colony is relative to its opponent, indicating an opponent assessment strategy. In particular, colonies became more offensive (i.e., more fighting workers) when opposing colonies were large, when their own colony was large, and when there was a large number of brood to steal from the opposing colony. Colony defense, however, seems to be a function of the colonies own resource value, not the opponents, suggesting self-assessment for resource value. The number of fighting workers in opposing colonies predicted the number of fighting workers in focal colonies ($t = 16.00$, $P < 0.001$; Table 2).

DISCUSSION

This study indicates that colonies of the ant *T. rugatulus* in contests change fighting effort depending on the number of both workers and brood in the opposing colony (Figure 2). This indicates that, regardless of how it is acquired, ants use information about themselves, their opponent, and the contested resource to inform contest offensive behaviors, suggesting a opponent assessment strategy that incorporates resource value (Chapin et al. 2019).

Colonies with more workers were more offensive in the same way that individuals with more energy stores engaged in more energetically expensive displays (Mesterton-Gibbons et al. 1996) or can withstand more physical costs (Payne 1998). If we consider

worker death analogous to energetic cost, then colony-level contests fit models designed for individual-level contests like wars of attrition (Maynard Smith 1974; Parker and Rubenstein 1981; Payne and Pagel 1996, 1997; Mesterton-Gibbons et al. 1996), but with colony level information exchange. As is predicted by these models, colony contests escalated with time, and resource holding potential—measured as number of workers—predicted contest offensive and defensive behaviors (Hardy and Briffa 2013).

Group size in eusocial insects appears analogous to body size, such that it drives several life-history traits (Dornhaus et al. 2012). Slave-making ants like *T. rugatulus* are particularly interesting in this regard, as the contested resource is brood (eggs, larvae, and pupa), most of which mature into workers, which directly contribute to colony RHP. Like adult workers, brood might be valued as the net calories they could provide the colony. Brood are necessarily younger, and thus have, on average, more opportunity to collect resources for the colony. This being the case, we predict that eusocial colonies should value the cost of losing brood more than workers, and lethal fights should be more common among eusocial species that defend brood compared with species without brood-stealing. Larger colonies in some eusocial species communicate more effectively than small colonies (Dornhaus et al. 2012; Donaldson-Matasci et al. 2013). Larger colonies also tend to have more structured division of labor, and more regulated interaction networks (Holbrook et al. 2011; Ferguson-Gow et al. 2014; Ulrich et al. 2018). Intraspecific or ontogenetic variation in colony size can also

Table 1

Parameter estimates and significance for a linear ridge regression predicting the number of fighting or guarding workers in the focal colony by the number of brood and workers in the focal and opposing across time (T; 0–180 min by 15 min). Relative workers and brood significantly predicted the number of fighting workers, and the number of guards was predicted by the brood in both colonies and the number of workers in the opposing colony

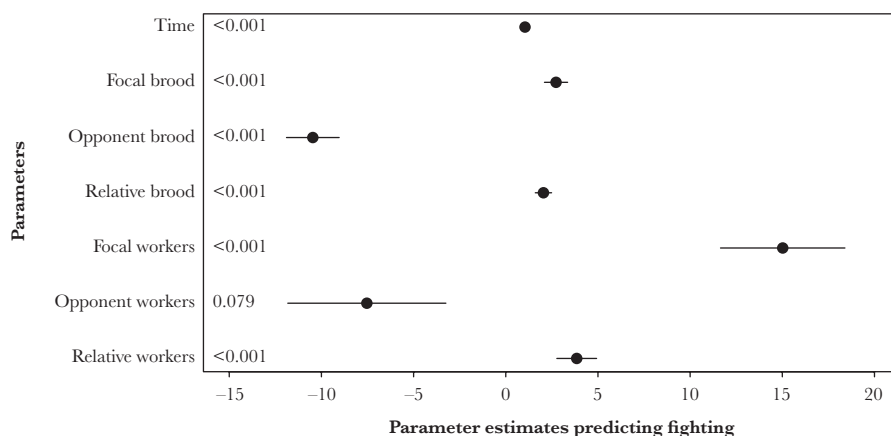| Variable	Response: fighting workers			Response: guarding workers		
	Slope ± SEM	t	P	Slope ± SEM	t	P
Focal workers	24.56 ± 14.77	1.66	0.099	−2.42 ± 44.78	0.51	0.614
Opponent workers	87.46 ± 12.20	7.17	<0.001	−4.89 ± 3.95	1.24	0.218
Focal brood	−6.17 ± 5.26	1.17	0.244	5.30 ± 1.70	3.11	0.002
Opponent brood	−109.54 ± 17.47	6.2689	<0.001	7.34 ± 5.65	11.30	0.200
Time	12.97 ± 2.62	4.95	<0.001	−0.94 ± 0.85	1.11	0.268

Figure 2
Parameter estimates for a generalized linear model predicting the number of workers fighting in a paired colony-wide contest by the number of workers and brood in both colonies, their relative differences (calculated as [opponent—focal]/opponent), and trial time (T; 0−180 min by 15 min). All estimates are significant except for opponent workers. The relative number of workers and brood in the colony predict the number of workers engaged in fighting.

change the value of resources and costs of contesting, as we have shown here. Many eusocial insect colonies show exponential initial growth (Macevicz and Oster 1976; Tschinkel 1988). From this, we can expect that existing workers will be valued most when colonies are young, and thus small colonies should be more risk-averse to limit worker mortality. In our study, colonies with fewer brood were both more defensive and more offensive (Figure 3). It remains unclear, however, if this is a general trend for eusocial groups.

It remains unclear how colonies estimate resource value. Our study showed that colonies use information about the opponents' resource value when making offensive decisions, but only assess their own resources when making defensive decisions. Ants may glean this information from opponent workers, perhaps by behavioral changes or chemical cues that indicate resource quality. Indeed, the present study showed that colonies use information about their own resources to make contest decisions so it seems logical that opposing ants might be able to interpret changes in worker behavior or brood chemical cues as indicators of resources within the nest. Research on the proximate mechanisms for estimating brood among slave-making ants may be fruitful. At least one other species of ant has been shown to use worker number to assess resources in the nest: the slave-making ant *Protomognathus americanus*, which

Table 2

Parameter estimates and significance for a generalized linear model with Poisson error distribution predicting the number of fighting or guarding workers in the focal colony by that of the opposing colony across time (0−180 min by 15 min), with all interactions. The interaction of the number of fighting opponent workers and time predicted the number of fighting focal workers

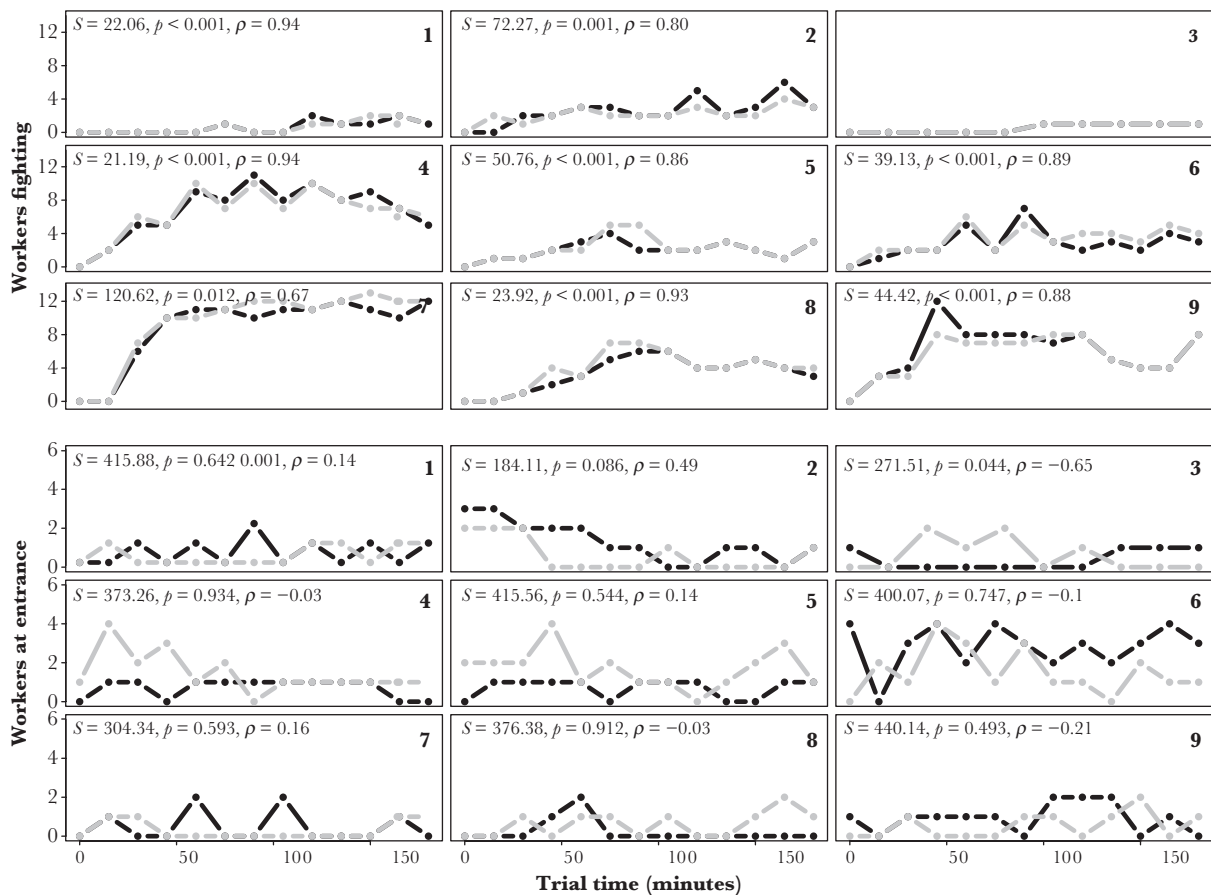| Variable	Response: fighting workers			Response: guarding workers		
	Slope ± SEM	z	P	Slope ± SEM	z	P
Opponent behavior	0.26 ± 0.027	9.80	<0.001	0.23 ± 0.14	1.72	0.085
Time	0.006 ± 0.001	6.68	<0.001	0.002 ± 0.001	0.25	0.806
Interaction	−0.0006 ± 0.0002	2.65	0.007	−0.0008 ± 0.0015	0.57	0.572

Figure 3
Correlations of the proportion of workers in each contesting colony that engage in (a) physical fights and (b) nest entrance guarding across trial time. Each plot is accompanied by Spearman rank correlations between focal (black) and opponent (grey) workers fighting (top 9 panels) or at the nest entrance (bottom 9 panels) sampled at 15 min intervals across trial time (0−180 min) are provided, except trial 3, where contestants matched exactly. Numbers in top right are trial number consistent with Supplementary Table S3 and Supplementary Figure S1.

enslaves *Temnothorax* ants (Pohl and Foitzik 2011). This species preferentially raids nests with more workers even if brood have been experimentally removed, presumably because colonies use worker number to estimate brood number instead of assessing brood number directly (Pohl and Foitzik 2011). It seems that *T. rugatulus* received information about brood from workers, but further research is needed to understand both the proximate mechanisms for resource quality assessment in *T. rugatulus*, and the pervasiveness of this ability in brood-stealing ants in general. Research on a congeneric showed that quorum sensing was cued by encounter rates (Pratt 2005). At least some eusocial insects flee or attack based on the relative number of nest mates to intruders (Adams 1990). Our research, however, suggests that workers use encounter rates, plus the behavior of individuals, to make contest decisions.

It remains unknown what individual-level strategy, if any, workers might use to gather information or make contest decisions; typical contest assessment strategies may only be applicable at the colony level. Similarly, it remains unknown if all workers contest following the same or different rules. For example, in the polymorphic ant *Cataglyphis niger*, minors always flee from opponents, but majors base their response on the RHP of their opponent (Nowbahari et al. 1999). How ants with less obvious division of labor allocate workers to contests remains poorly understood. Future research on individual-level assessment in eusocial insect workers could elucidate this.

Temnothorax rugatulus colonies in contests can assess the fighting ability and resources of their own colony and their opponents. Contest strategies using this information are implemented at the colony level, where contest decisions are made in the collective. Entire colonies contesting followed patterns predicted from contest theory developed for pairs of individuals. This is consistent with the superorganism hypothesis—that groups of individuals perform in much the same way as cells in a body (Wilson and Sober 1989; Hölldobler and Wilson 2009). Further, we posit that colony-level contest assessment strategies may not mirror dyadic contests in all regards. Indeed, the colony-level contest strategy we describe here is elaborate, information rich, dynamic, and warrants further investigation. Further, colonies seem to have the ability to indirectly assess resource quality. It remains unclear if this ability is common among brood-stealing ants and investigating the proximate mechanism of this phenomenon could elucidate how colony-wide strategies of social groups manifest among individual workers.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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