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Not too big, not too small

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ORIGINAL ARTICLE

Not too big, not too small: raids at moderately sized hosts lead to optimal outcomes for a slave-making ant

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Abstract

Understanding the trajectory of host-parasite co-evolution requires knowledge of how hosts and parasites impact one another's fitness, especially among the avian and insect social parasites. Host choice is an important first step in this process, but the principles guiding host choice are unresolved, especially for specialist parasites choosing among individual hosts with multiple traits. To determine how parasites weigh various host traits relative to others, we need to identify their costs and benefits. Here I use the slave-making ant, *Temnothorax americanus*, to investigate the payoffs from different host trait combinations. I measured the costs and benefits of raids at hosts that varied in their value (# brood), defensive power (# workers), or their ratios. Additionally, I investigated whether slave-maker fighting power influences which host trait combinations were optimal. Slave-makers performed best when hosts contained more brood but fewer workers. However, the ability to maximize this ratio is constrained by the correlation of brood and worker numbers in natural nests, making the optimal host moderately sized. Measures of costs reinforce this conclusion, since slave-maker mortality increased with the number of host workers. Additionally, I found that larger slave-maker colonies have higher payoffs at larger hosts, suggesting their optimal host trait profile differs from smaller colonies. This study shows that social parasites exercising force ought to balance a trade-off between host value and defensibility, rather than maximizing only value. Furthermore, the results highlight that host demography could play a larger role in insect social parasite arms races than previously appreciated.

Significance statement

A key to understanding the outcome of co-evolutionary arms races in social parasites is identifying the traits that contribute to the success of parasites and hosts. Host choice determines which traits experience selection, but the relative costs and benefits associated with different host traits, and how parasites ought to weigh them, remains unclear. I measure parasite success in relation to host and parasite demographic traits to distinguish the relative impacts of each using a slave-making ant. Maximizing host brood-to-worker ratio leads to higher payoffs, while the most populous hosts are impenetrable. These findings provide evidence that social parasites attacking by force seek a balance between a host's value and defensibility, even if it means forgoing hosts with higher potential value. This in turn highlights colony demography and life history as important host traits under selection in co-evolutionary arms races in social insect parasites.

Keywords Slave-making ants · Social parasite · Host · Choice · Colony size

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Introduction

Host-parasite interactions are an important arena for the study of behavioral evolution, as the strategies of one party necessarily impact the fitness of the other. Host-parasite interactions are known to lead to a cycle of defensive responses, or Red Queen dynamics, that have served as a stage for the study of co-evolutionary arms races (Dawkins and Krebs 1979). Brood parasites and insect social parasites in particular have been especially fruitful case studies, revealing multiple lines of defenses by the hosts and counter adaptations by the parasites

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(Brandt et al. 2005; Feeney et al. 2014; Grüter et al. 2018). Much of this work has been compared across taxa to determine whether co-evolutionary arms races proceed along predictable trajectories and result in convergent outcomes (Davies et al. 1989; Kilner and Langmore 2011).

A first step to understanding the outcome of co-evolutionary arms races is identifying the traits that contribute to the success of either parasite or host. From the perspective of the parasite, host traits that enhance their ability to attack or extract the greatest payoffs are likely to be preferentially targeted. Regardless of whether host choice involves deciding between species or between individuals within a species, a parasite's host preference will consequently determine which hosts experience the greatest selection from parasites. As a result, parasites exercise a disproportionate power in these co-evolutionary arms races by deciding which hosts become targets in the first place.

What distinguishes a superior host from an inferior one depends on several different factors. For example, generalist parasites tend to favor familiar host species (Schumann and Buschinger 1995; Teuschl et al. 1998), while others favor hosts that are easier targets because they are the least aggressive or vigilant (Banks and Martin 2001; Brandt and Foitzik 2004). Parasites may also use indicators of host value, such as nest or territory size (Soler et al. 1995; Smith and Schwarz 2009; Louder et al. 2015). However, these different axes of preference are usually investigated in isolation rather than in combination (for exceptions, see Pohl and Foitzik 2011; Soler et al. 2014). In order to gain a more realistic view of how parasites select their hosts, we need to understand the interplay of different host trait combinations as experienced by the parasite.

To understand how parasites ought to weigh different host traits relative to others requires measuring how such traits translate into costs and benefits for the parasite. This can be achieved by measuring payoffs to the parasite in relation to specific host traits in a controlled manner, thereby distinguishing the relative impacts of each trait. While this payoff-based approach has been adopted in a number of studies (Grim 2006; Pohl and Foitzik 2011; Kleeberg et al. 2014; Louder et al. 2015), they tend to measure payoffs of only one trait at a time. Only rarely are the costs and benefits associated with different host traits measured in combination (Remeš 2010; Grim et al. 2011). Therefore, it is not always clear what the impact of different host trait combinations will be or how parasites ought to weigh different host traits relative to others.

This process of weighing different host traits against each other is made more complex by differences among individual parasites. Parasites may differ in their optimal weighting of multiple host traits when additionally considering their own condition or status. Parasite traits such as size, skill, and age will likely have an impact on its own success rates, as is the case for other decisions, like foraging (Stephens and Krebs 1986) or finding mates (Hunt et al. 2005). However, this additional consideration of how parasites ought to weigh multiple host traits in relation to their own is also under explored.

To build a clearer understanding of how parasites experience and weigh a variety of factors, I use a social insect brood parasite to measure the payoffs in response to different host traits. I focus on social insect brood parasites, specifically, the slave-making ants, for various reasons. First, social insect parasites are ideal systems for these questions due to the ease and precision with which host quality, i.e., worker and brood numbers, can be quantified and manipulated. Second, features of host quality have been less extensively studied in the social insect parasites than in the avian brood parasites, which are likely to provide somewhat different answers because of their differences in attack mode (i.e., stealth vs force) (Kilner and Langmore 2011). Furthermore, the few existing studies on slave-making ant host-preferences provide an incomplete understanding of how parasites ought to weigh different attributes. For example, a study in the slave-maker *Polyergus breviceps* showed a preference based on the body-size of the workers in the host colony (Savolainen and Deslippe 1996), but it is unclear if the advantages arise during the raids themselves or when host workers labor for slave-makers. Another study offers a more nuanced analysis, showing that *T. americanus* slave-makers prefer larger host colonies, even if they contained fewer brood (Pohl and Foitzik 2011). Echoing the latter study, I aim to build a more complete understanding of how different combinations of demographic traits, specifically colony size and brood number, balance relative to each other to yield optimal outcomes for social insect parasites.

Theory developed from classic studies on ecto-parasites offers some guidance as to which host features are expected to indicate the most profitable host targets. Some researchers have hypothesized that parasites ought to target hosts in the best condition, from which a maximum quantity or value of resources can be exploited (Valera et al. 2004). If resource value, or the number of brood in the host nest, has the greatest influence over the payoffs from host choice, then slave-makers ought to gain the most brood from nests containing the most brood.

Alternative theory posits that parasites ought to target hosts that can least effectively resist attack, such as hosts that are immuno-compromised (Christe et al. 1998). The intensity of host defenses can be shaped by local host-parasite co-evolution and lead to among-population differences in host colony aggression (e.g., *Rossomyrmex minuchae–Proformica longiseta*: Zamora-Muñoz et al. 2003; *T. americanus–T. longispinosus:* Brandt and Foitzik 2004; Pamminger et al. 2011; Jongepier et al. 2014; Kleeberg et al. 2015). However, within a population, colony size may be a better indicator of host defensiveness. Indeed, host aggression and defensibility are positively related to host colony size in some species (e.g., *T. americanus–T. longispinosus*; Pohl and Foitzik 2013), although this is not always the case (e.g., *Harpagoxenus sublaevis–Leptothorax* sp.;

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Foitzik et al. 2003). When host colony size and aggression are indeed linked, larger host colonies can cause higher rates of slave-maker mortality during raids (Pohl and Foitzik 2011). The net payoff to slave-makers in relation to host colony size, however, has never been quantified. If overall host defensibility increases with colony size, then we should expect slave-maker colonies to gain less from colonies with the most workers.

The expectations outlined above, however, fail to take into account that value and defensibility tend to be inextricably linked, such that hosts in good condition also tend to mount strong defenses (Sheldon and Verhulst 1996). Parasites may then be constrained to make a compromise between the above two factors in a way that optimizes net profitability (Stephens and Krebs 1986; Theron et al. 1998). It is likely that slave-makers face the same constraint, since host colonies containing high numbers of brood also have a higher number of workers (Hölldobler and Wilson 1990; Pohl and Foitzik 2011). To illustrate, it might be easier to steal brood from host colonies with few workers, but such colonies may also have fewer brood; conversely, hosts with large quantities of brood may also be better guarded. Slave-makers should then be expected to perform best at hosts of intermediate size. I test these predictions to identify what balance of workers and brood lead to the best outcomes for slave-makers.

Finally, the optimal compromise between a host colony's brood number and defensibility may not have a "one-size-fits-all" solution for slave-maker colonies. The optimal host choice may depend on the size of the slave-maker colony itself. First, larger slave-maker colonies are expected to require a larger host work-force to maintain and care for the larger colony, particularly in obligate parasites. Therefore, larger slave-maker colonies may meet those needs by preferentially raiding colonies with the greatest potential value. Second, larger slave-maker colonies may also be better at infiltrating better defended host colonies. Slave-maker colonies are almost always smaller than the hosts they raid, so asymmetry in group size is to be expected; but the extent of this asymmetry can vary substantially. Prior work on combat in slave-making ants and other ant species has shown that colonies can overcome their numerical disadvantage by being stronger individual fighters (Whitehouse and Jaffe 1996; McGlynn 2000; Plowes and Adams 2005) or by releasing a chemical called a "propaganda" pheromone known to disrupt the host's ability to fight back (Regnier and Wilson 1971; Franks and Partridge 1993; Brandt et al. 2006; Jongepier et al. 2015). Given these tactics, it remains unclear what the impact of relative fighting sizes will be on overall raiding success.

Here, I investigate these hypotheses in a slave-making ant with the aim of measuring the relative importance of several key host traits on the parasite's success. I use the obligate slave-making ant, *T. americanus*, which collectively attacks heterospecific ant colonies in coordinated raids to steal host brood (Wesson 1939). As obligate social parasites, colonies of *T. americanus* depend on host workers to perform all colony tasks, including foraging, brood care, and other nest maintenance (Alloway and Del Rio Pesado 1983). Raids begin after one of the scouting slave-maker workers finds a host colony and recruits a group of nest-mates through physical agitation, which follow her to the host nest (Alloway 1979). In addition to biting and stinging the slave-maker workers (Alloway 1979), defending host workers protectively carry their brood out of the nest to hide in the leaf-litter, functionally reducing the quantity of available brood (Kleeberg et al. 2014), implicating both host colony size and worker-to-brood ratios in this system. The importance of colony demography during raids in this system has already been illustrated in numerous studies that pave the way for this study. For instance, larger host colonies are known to be more aggressive (Pohl and Foitzik 2013; Jongepier et al. 2014) and cause a greater number of slave-maker deaths (Pohl and Foitzik 2011). On the other hand, larger slave-maker colonies may be more successful at quickly locating the best hosts because they send out more scouts than smaller colonies (Pohl and Foitzik 2013). In addition, host choice in the context of host demography has also been studied and found a preference for hosts with more workers, even when the number of brood is similar (Pohl and Foitzik 2011). In spite of this work, it remains undetermined what weighting of host workers relative to brood is advantageous and whether this preference depends on parasite size.

To investigate what balance of colony attributes make an optimal raiding site for the *T. americanus*, I observed the outcomes of experimental lab raids at their host, *T. longispinosus*. In no-choice tests, I presented slave-maker colonies with host colonies that differed in their number of workers, brood, and the ratio between the two. I measured the outcomes of those raids in terms of their benefits (number of host brood stolen) and their costs (number of slave-maker workers killed). Additionally, I examined the role of the slave-maker's colony size on raiding outcomes. The findings here will provide a novel perspective on how multiple traits, both from the host and the parasite, combine to shape parasite fitness. By identifying the weighting of traits related to defense and value, we can ultimately better predict which host traits experience the strongest selection in these co-evolutionary arms races.

Methods

Colony collection and census

Slave-making ants of the species *Temnothorax americanus* raid colonies of three host species: *T. longispinosus*, *T. ambiguus*, and *T. curvispinosus*, but the populations

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measured in this study consisted almost exclusively of *T. longispinosus* hosts, and were the only species used in experimental host colonies. Colonies of *T. americanus* and *T. longispinosus* were collected from their natural nest sites, hollowed acorns, hickory nuts and rotted sticks, in New York state at the Huyck Preserve (42° 30′ 53.7876″, − 74° 8′ 27.7836″), Cornell Plantations Land (42° 27′ 55.2738″, − 76° 26′ 34.299″), Black Rock Forest (41° 25′ 11.64″, − 74° 0′ 33.48 ″), and at Bear Mountain State Park (41° 18′ 33.9768″, − 74° 0′ 14.6808″) between May and July, 2013–2016. Colonies were transported back to Liddell Field Station in Ithaca, NY, in Ziploc bags and stored in a refrigerator (4 °C) for up to 3 weeks before censusing queens, workers, mature sexuals, larvae, and pupae (worker and sexual). In the trials below, mean slave-maker (*T. americanus*) colony size was 6.31 ± 0.39 slave-maker workers (min 2, max 17). Mean host colony size was 79.34 ± 15.53 workers (min 21, max 536).

To determine the naturally occurring colony sizes and worker-to-brood ratios of the host species, I measured the mean and standard error of the number of workers and brood from all *T. longispinosus* nests collected between 2014 and 2016. I compared the number of adult workers with the number of worker brood (larvae and pupae) with a linear regression, using the "lm" function in the "stats" R package. Two outliers with high Cook's distance and leverage were removed. This and all other analyses were performed in R version 3.4.3.

Additionally, to confirm that slave-maker nests with more host workers tend to produce a higher number of sexual offspring, I fit the number of reproductives per slave-maker nest (male and female alates + mature sexual pupae) to the number of host workers using a linear regression. While *T. americanus* colonies are known to occupy multiple nests (Alloway and Del Rio Pesado 1983) and transport both workers and brood between nests, we can only estimate nest productivity as a proxy for overall colony fitness.

Colony maintenance and preparation

Immediately following its census, a colony was placed inside a nest box containing an artificial nest consisting of a balsa wood or Plexiglas U-shaped structure (2.5 mm thick) placed between 2 glass microscope slides (7.5 × 5.0 cm). Each nest was then wrapped in a foil sleeve to exclude light and housed in a plastic Ziploc box (10 × 10 × 6 cm) with a plaster floor, which was moistened twice per week to maintain humidity. Colonies were fed a teaspoon of Bhatkar diet twice per week (Bhatkar and Whitcomb 1970) and housed in a room at 26 °C, with a 14L:10D light cycle.

To prepare colonies for raids, I removed all brood and some adult host workers from every slave-maker colony up to the point that the number of host workers matched the number of slave-maker individuals (including the queen), so that there was a 1:1 ratio of slave-makers to host workers. Slave-maker colonies with fewer host workers than slave-makers were not used. All removals occurred 2 days before trial initiation. This was done to standardize any sense of urgency for host workers that might influence raiding behaviors. One day before trial initiation, host nests were prepared by randomly selecting a set number of workers and brood (pupae and larvae) from an existing lab colony (see *Experimental Conditions* below for specific numbers of worker and brood). When colonies contained insufficient brood for the treatment, I added brood from other lab colonies, but always from colonies from the same population. These size-engineered colonies were then given a naturally emptied acorn or hickory nut to move in to; each nut had one naturally formed entry hole no larger than 2 mm in diameter. This size limit was based on the size of the entryway for nests of collected colonies, which the ants sometimes narrowed with detritus when the pre-formed hole exceeded this diameter.

Raid set-up

Raiding trials took place in 45 × 25-cm rectangular glass arenas, unless otherwise noted below, and the inner rims of the arena walls (10 cm high) were coated with Vaseline to prevent escape. On the morning of a raiding trial, I positioned a prepared slave-maker colony at one end of the arena and a target host colony on the opposite end between the hours of 8:00 and 11:00. In all trials, the room temperature was elevated to 30 °C the morning of the raid to increase overall activity levels, and a plastic dish of food and a dish of wet cotton were placed in the center of the arena to prevent dehydration or starvation during the trials.

The nest entrances of the target and the slave-maker colonies were filmed using a webcam (Logitech C920 HD Pro), pointed through the transparent arena wall or positioned above the arena. If by 16:00, there were no slave-makers recruiting to or attacking the target nest, both colonies were removed from the glass arena and returned to their boxes until the next day, when they were re-introduced to the same arena. The colonies were given 5 days to initiate a raid before the trial was aborted. If there was evidence of recruitment or a raid (i.e., the target nest was vacated, there was a raiding party in the arena, or slave-maker workers were entering or exiting the target nest), I left both colonies in the arena overnight and collected both colonies the next morning, so that colonies stayed in the arena for 24 (± 4) h. The raiding room was set to the same lighting regime as the room housing the colonies, and I lowered the temperature back to 26 °C to coincide with darkness. After completion of a trial, I confirmed that a raid had been attempted or initiated by watching videos of the trials. Any instances where a scout had discovered a nest but refrained from recruitment would therefore have been excluded from this analysis. Using these videos, I also counted the number of

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slave-maker workers in each raiding party, and included only those that arrived at the host nest.

The morning after each raid, I retrieved both nests and collected any remaining ants from within the arena and counted the contents of both nests. At this time, I counted the total number of brood the slave-makers possessed since all slave-maker colonies started each raid with zero brood. A slave-maker colony could take possession of brood by returning it to their own nest or by moving in to the host colony's nest, adopting the brood within. After each raid, I also counted the number of dead slave-maker workers to quantify the costs.

Experimental conditions

To test which host colony demographic traits influence the costs and benefits for slave-maker colonies, I conducted no-choice raiding trials using target colonies that differed in their worker and brood combinations. All results were analyzed using GLMMs with either count or proportion response data and were checked for overdispersion and multi-collinearity. All the models here and further below have slave-maker colony ID and queen presence as random effects, with colony ID nested within queen presence.

Colony size

To compare the outcome of raids at large versus small hosts, I compared brood gained at host nests containing either 25w:25b or 100w:100b. Brood and worker numbers were equivalent to recreate conditions that mimic the correlation between worker and brood number found in natural nests. These options therefore had the same worker-to-brood ratio (1:1), but differed in their potential value and defensibility. All host brood consisted entirely of pupae. Colonies were housed in balsa wood nests described above. The slave-maker colony and its target were placed 100 cm apart by connecting two glass arenas (each 45 × 25 cm) with a paper bridge 10 cm in length. This arena lay-out differed from the other trials below because slave-maker scouts rarely discovered the host nest before being attacked by the higher density of host workers in the smaller arenas.

The brood stolen in this experiment was analyzed using two GLMMs: (1) one model for the total number of brood gained and (2) another for brood gained as a proportion of brood available. Thirteen *T. americanus* colonies were used in 14 raiding trials. All trials were conducted in 2015 using colonies from Ithaca, Bear Mountain, and Black Rock Forest. I did not control for source location in the parasite and host pair, and therefore included this effect in the model. Therefore, the fixed effects in the models were the size treatment (i.e., number of brood and workers in each nest) and whether the source population of the host and parasite were the same. The count model used a Poisson distribution with log link function, and the proportion model used a binomial distribution with a logit link function (Zuur, Ieno, Walker, Saveliev, and Smith 2009).

Worker-to-brood ratio—variable workers

To test the effect of host worker-to-brood ratios on raiding success, I compared brood gained in raids at hosts containing constant brood number but a variable worker number. Hosts both contained 25 brood items, but either 25 or 50 workers, such that brood-to-worker ratios were 1:1 or 2:1. Twelve *T. americanus* colonies were used in 19 trials conducted in 2014 or 2016 using colonies from Ithaca, Bear Mountain, Black Rock Mountain, and the Huyck Preserve.

Counts of stolen brood were examined using a poisson GLMM, but due to overdispersion (c-hat = 1.651), I used a quaisi-Poisson distribution with the "glmmPQL" function in the "MASS" package version 7.3–51.1 (Ripley et al. 2018). The number of workers in the host nest (25 or 50) was the primary fixed effect of interest. However, the relative proportion of pupae to larvae within each nest was not held constant across trials, and was also included as a fixed effect. As above, I did not control for source population in my host-parasite pairs but include it as a fixed effect. Year was included as a random effect, nested within queen presence.

Brood-to-worker ratios—variable brood

I conducted a second set of trials in which worker-to-brood ratios varied, but this time keeping worker number constant while varying the number of brood. Hosts both contained 20 workers, but 20 or 60 brood items, such that brood-to-worker ratios were 1:1 or 1:3. Thirteen *T. americanus* colonies were used in 19 trials conducted in 2014, such that 6 colonies were run twice, once for each ratio. All host and parasite colonies were collected from the Huyck Preserve and contained equal parts pupae and larvae (10 larvae + 10 pupae or 30 larvae + 30 pupae).

Brood stolen were analyzed using GLMMs, with number of brood in each nest as the fixed effect. Raiding success was analyzed using two different approaches: First, to test whether hosts with more brood yield more stolen brood, I modeled brood gained as a count. I ran the GLMM using a negative binomial distribution for count data using the "glmer.nb" function in the "lme4" package (Bates et al. 2018). I then tested the effect of brood-to-worker ratios on the proportion of brood stolen as a function of brood available. To model proportion data, I ran the GLMM using a quasi-binominal distribution to correct for overdispersion (Ripley et al. 2018).

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Pooled trials

To separately examine the role of slave-maker colony size, as well as mortality rates, I pooled the data from the above trials. Additionally, I added data from other trials that used hosts containing 50w:30b ($n = 2$) and 30w:10b ($n = 10$) using nine slave-maker colonies that were from other non-invasive behavioral experiments. These trials were identical in set-up except that trials took place in glass arenas of different size and shape (square, 75 × 75 × 13 cm). This gave rise to a larger data set (64 raiding trials with 41 *T. americanus* colonies: 19 trials of 20v60, 19 trials of 25v50, 14 trials of 100v25, 12 additional trials). Every GLMM in this section therefore contained the random effects: queen presence, year, and slave-maker colony ID, and the following fixed effects: arena size, whether the source population was the same and the proportion of host brood that were pupae. Both brood and worker number were not included as fixed effects in a single model to avoid collinearity between these experimentally correlated factors. However, to check for collinearity between the fixed effects in each model, I checked the variance inflation factor for each variable, and excluded those with a value greater than 3.

Slave-maker colony size: relative fighting power

Here I ask two questions about the role of slave-maker colony size in raiding outcomes: (1) Do larger slave-maker colonies have a raiding advantage due to their greater size? And (2) how does relative fighting power, i.e., the ratio of host to slave-maker worker numbers, affect raiding success? Relative fighting power was represented as a ratio, with the number of host workers divided by the number of slave-maker workers in the arriving raiding party. Nine trials were missing data on raiding party size, so 55 trials were used in this analysis and the one below. I modeled the proportion of brood stolen in a binomial GLMM in response to the following fixed effects: relative fighting power, slave-maker colony size, host's brood-to-worker ratio, arena size, whether the source population of the host and parasite were the same and the proportion of host brood that were pupae. I checked both the correlation coefficient between fixed effects and the variance inflation factor of each to eliminate collinearity among factors. As a result, I excluded host colony size from the model due to a high correlation coefficient with relative fighting power ($r = 0.8059$). To determine how influential relative fighting power was in comparison to other host traits, I performed multi-model averaging. Models were ranked using QAIC due to overdispersion in the global model (c-hat = 2.289). I report model averaged effect sizes, significance, and relative importance of each factor, and do the same for each of the model averaged analyses detailed below. A factor's relative importance is the proportion of the candidate models that included that factor; a relative importance of 1 indicates the factor was in every candidate model, and a measure of 0.5 indicates it was only in half of the candidate models.

Slave-maker colony size: per capita success

Here I ask whether larger slave-maker colonies have a sufficient advantage in raiding to compensate for their greater need for host workers. Since larger slave-maker colonies are expected to require more host workers than smaller slave-maker colonies, I examined raiding success as per capita brood gained. If larger slave-maker colonies cannot achieve the same per capita success as small colonies despite their greater fighting power, then slave-maker colony size will have a negative effect on per capita raiding success.

Per capita success was modeled using a GLMM and calculated as the brood gained divided by slave-maker's colony size. Per capita data were not normal and non-integer, so I used a Gamma distribution and log link function. I added 1 × 10–8 to each value to make the data non-zero. The model's fixed effects included host colony size, the brood-to-worker ratio, the size of the raiding party, slave-maker colony size, arena size, whether the source population of the host and parasite were the same, and the proportion of host brood that were pupae. Assumptions of non-collinearity of variables were checked, and I dropped host brood from the model due to high correlation coefficients (host brood cor coef = 0.607; brood-to-worker ratio cor coef = 0.562). To determine how influential slave-maker colony size was relative to other host traits, I performed multi-model averaging. Models were ranked using QAIC due to overdispersion in the global model (c-hat = 4.528).

Mortality

To quantify the costs from raiding hosts with different worker-brood combinations, I analyzed slave-maker mortality rates in this pooled data set. Mortality was analyzed in GLMMs using two different approaches: First, as a total count of slave-maker deaths and then as a proportion of slave-maker colony size, i.e., per capita mortality. In both cases, the model's fixed effects included the size of the slave-maker colony, the size of the host colony, arena size, whether the source population of the host and parasite were the same, and the proportion of host brood that were pupae. Raiding party size was not included in the model due to a high variance inflation factor (VIF = 21.5).

To determine which factor(s) contribute most strongly to mortality rates in slave-makers, I performed multi-model averaging with model selection criteria of AICc < 4 (Bolker et al. 2009; Burnham, Anderson, and Huyvaert 2011). The count model for mortality used a Poisson distribution with a log link function. The proportion model used a binominal distribution and logit link function, and corrected for overdispersion in the global model (c-hat = 1.482) by used QAIC < 4 in model selection.

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Results

Natural colonies

There were 34.3 ± 1.7 (SE) workers (median = 28, range = 2–167) and 50.5 ± 2.7 worker brood (larvae and pupae; median = 38, range = 1–266) in the 241 *T. longispinosus* nests censused. Brood number was significantly positively related to worker number ($p < 0.0001$, $R^2 = 0.16$, $F_{(1,239)} = 48.05$; Fig. 1a), and the mean ratio of workers-to-brood was 1.34 ± 0.19 (median = 0.67, range = 0.06–36.33). The slave-maker nests ($n = 191$) contained a mean of 8.3 ± 0.7 slave-maker workers (median = 6, range = 0–82) and a mean of 60.2 ± 3.9 host workers (*T. longispinosus*; median = 43, range = 0–294), with 45.5% of nests containing a queen. Slave-maker productivity was positively related to the number of slave workers in a given nest ($p < 0.0001$, $R^2 = 0.18$, $\beta = 0.28$; Fig. 1b).

Experimental conditions

Colony size

When faced with large (100w:100b) or small (25w:25b) host nests, slave-maker colonies performed better at smaller nests, even though those nests contained fewer brood (Fig. 2). Slave-maker colonies stole more total brood ($n = 14$, $\beta = -0.036 \pm 0.013$ (SE), $p = 0.006$) and a higher proportion of available brood ($\beta = -0.089 \pm 0.026$, $p = 0.001$) from smaller nests (Table 1). In the count model, source location was a significant factor in how much brood was stolen ($\beta = 2.149 \pm 0.933$, $p = 0.021$), with parasites stealing more brood when matched with hosts from the same population. A similar result for source location was found in the proportion model ($\beta = 3.181 \pm 1.886$), but it was not significant ($p = 0.092$).

Worker-to-brood ratio—variable workers

As predicted, slave-maker colonies stole more brood from nests with lower worker-to-brood ratios (Fig. 2). When host colonies were matched for number of brood, slave-makers stole more brood from nests with fewer workers (25w:25b) than from those with more (50w:25b); however, the difference was not significant ($n = 19$, $\beta = -0.024 \pm 0.014$, $p = 0.154$; Table 1). The strongest effect on the number of brood stolen was instead the proportion of brood that were pupae ($\beta = 0.824 \pm 0.628$, $p = 0.260$). Whether the source populations were different between host and parasite was not significantly related to number stolen ($\beta = -0.489 \pm 0.373$, $p = 0.261$).

Brood-to-worker ratios—variable brood

When host colonies were instead matched for number of workers but differed in their number of brood (20w:20b versus 20w:60b), slave-maker colonies gained more total brood from the nests with more brood ($n = 19$, $\beta = 0.033 \pm 0.009$, $p > 0.001$; Table 1). In contrast, slave-maker colonies did not gain a higher proportion of brood at nests with the higher brood-to-worker ratio (20w:60b; $\beta = 0.011 \pm 0.012$, $p = 0.396$).

Pooled trials

Slave-maker colony size: relative fighting power

Relative fighting power was a significant predictor of the proportion of brood stolen, with a larger proportion stolen when

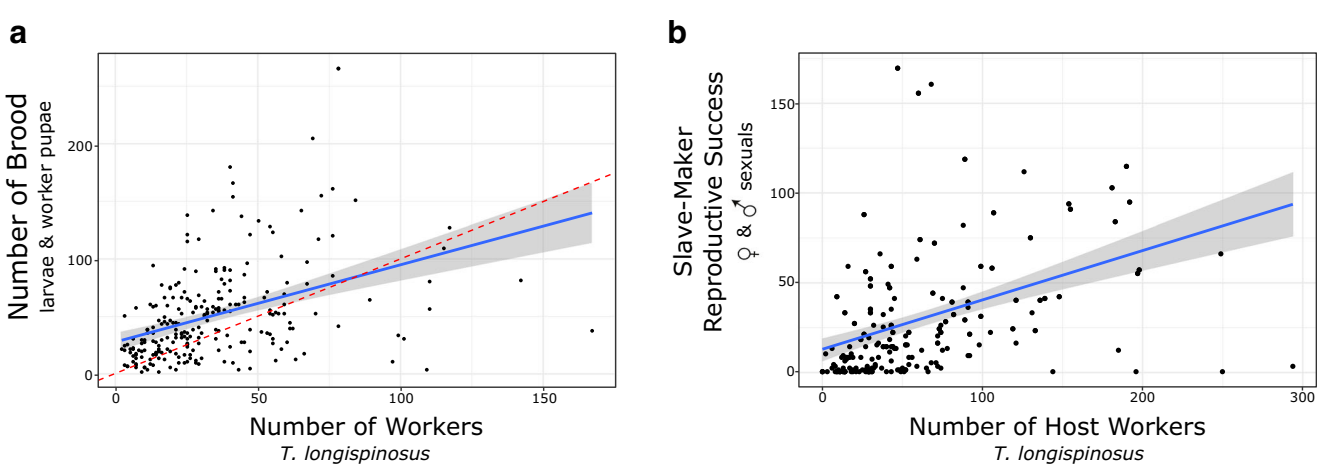


Fig. 1 Plots of natural colony contents: **a** The number of brood scales with the number of workers in natural *T. longispinosus* nests ($R^2 = 0.15$). Brood counts consist of larvae and worker pupae, and does not include reproductive pupae. The solid line depicts a regression, with the shaded region as the 95% CI. The dotted-line depicts a one-to-one ratio of workers-to-brood. **b** Slave-make colony reproductive success is predicted by its number of host workers. Reproductive success includes male and female sexuals. Each point represents a different *T. americanus* colony. The solid line depicts a regression and the shaded region is the 95% CI

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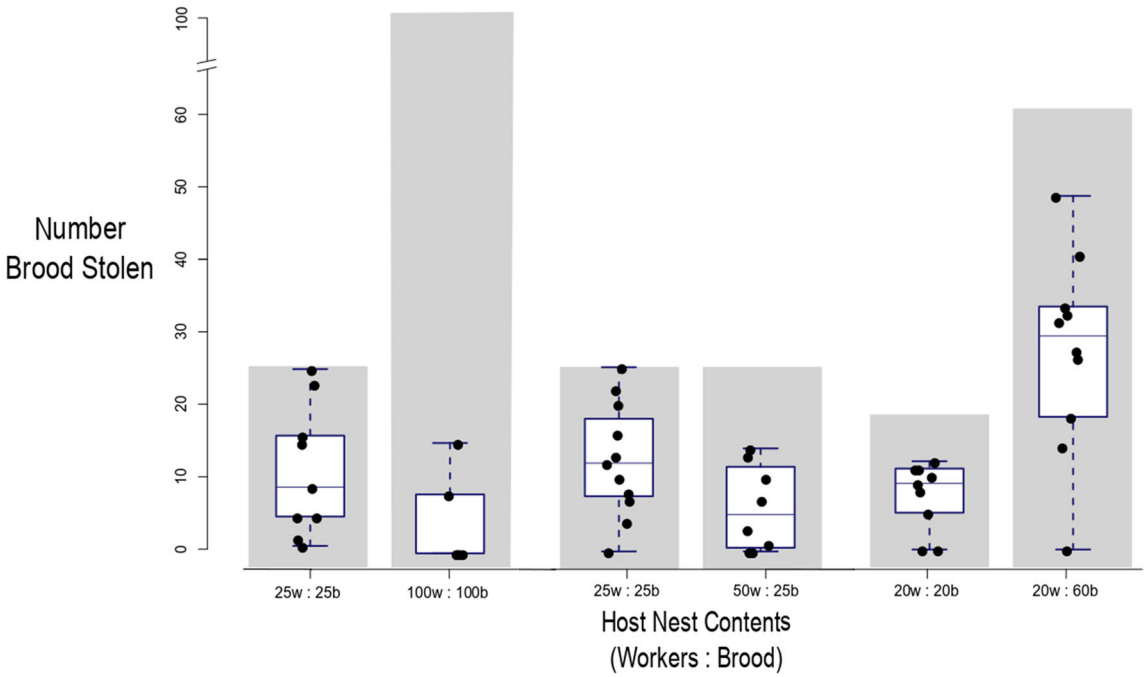


Fig. 2 Total number of brood stolen by slave-makers at host nests containing one of six different worker-brood combinations. Gray bars behind boxplots represent the total number of brood inside the host and the maximum possible that could have been stolen. Boxplots display the median and 25% and 75% quartiles of total number of brood stolen during raids at each nest size. Results are shown in the pairs for which they are statistically compared

the two colonies were more closely matched in size, i.e., when the ratio of host colony to raiding party size was smaller ($n = 55$, $\beta = -0.046 \pm 0.008$, relative importance = 1.0, $p > 0.0001$; Table 2A). Slave-making colony size was a similarly strong and significant positive predictor of the proportion of brood stolen ($\beta = 0.050 \pm 0.007$, rel. imp = 1.0, $p > 0.0001$). Source population and brood-to-worker ratio were also significant predictors of the proportion of brood stolen, but had weaker effects and lower relative importance (Source: $\beta = -0.029 \pm 0.010$, rel. imp. = 0.78, $p = 0.006$; B-W ratio: $\beta = 0.008 \pm 0.004$, rel. imp. = 0.45, $p = 0.047$).

Slave-maker colony size: per capita success

Larger slave-maker colonies tend to have lower per capita success in their raids, as slave-maker colony size was a negative predictor of per capita raiding success ($n = 55$, $\beta = -0.134 \pm 0.050$, rel. imp. = 0.217, $p = 0.008$; Table 2B). Consistent with results from the individual experiments, brood-to-worker ratio was also a strong positive predictor of per capita success ($\beta = 0.199 \pm 0.051$, rel. imp. = 0.273, $p = 0.0001$) while the number of host workers was a strong negative predictor ($\beta = -0.168 \pm 0.057$, rel. imp. = 0.217, $p = 0.004$). In spite of the significant results from this model, model averaging did not attribute high values of relative importance to any of the fixed effects.

Mortality

Both the size of the slave-maker and host colonies positively predicted slave-maker mortality. In the count model, both had a similarly strong and significant effect on mortality ($n = 64$, # Host Workers: $\beta = 0.285 \pm 0.097$, rel. imp. = 1.00, $p = 0.004$; # S-M Workers: $\beta = 0.295 \pm 0.103$, rel. imp. = 0.92, $p = 0.005$; Table 3A). However, in the proportion model, the strongest predictor of slave-maker mortality rate was the host colony size ($\beta = 0.130 \pm 0.041$, rel. imp. = 0.94, $p = 0.002$; Table 3B). Larger slave-maker colonies did not lose a larger proportion of their slave-maker workers to raids ($\beta = -0.040 \pm 0.042$, rel. imp. = 0.26, $p = 0.357$), an indication that the per capita costs are proportional for large and small colonies.

Discussion

This study aimed to determine which suite of demographic characteristics in host nests lead to the best raiding outcomes for the slave-making ant *T. americanus*. Colonies tend to gain more brood from hosts that contain more brood. Stolen host brood, which eventually matures into adult workers, is positively linked to the parasite's reproductive success in a single nest. Slave-makers gained more brood from raids at nests containing more brood, with 20w:60b nests yielding more brood than 20w:20b nests (Fig. 2). However, this tendency

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Table 1 Results of the GLMMs for number or proportion of brood stolen for each experimental trial. Significant fixed effects are in italics

Variables	Effect size (β)	± standard error	z value or t value	p value
Colony size—100 vs 25 trials				
A)Count				
Intercept	2.723	0.543	5.013	5.37e−7
# Host brood	*− 0.036*	*0.013*	*− 2.731*	*0.006*
Source Loc.	*2.149*	*0.933*	*2.303*	*0.021*
Random effects (Std. dev.): S-M colony ID = 0.998				
Queen = 0				
B) Proportion				
Intercept	1.678	1.158	1.449	0.147
# Host brood	*− 0.089*	*0.026*	*− 3.424*	*0.001*
Source Loc.	3.181	1.886	1.687	0.092
Random effects (Std. dev.): S-M colony ID = 2.172				
Queen, Std. dev. = 0				
Brood-to-worker ratios—25:25 vs 25:50 trials				
Intercept	2.636	0.813	3.243	0.012
# Host workers	− 0.024	0.014	− 1.754	0.154
Prop. pupae	0.824	0.628	1.311	0.260
Source Loc.	− 0.489	0.373	− 1.309	0.261
Random effects (Std. dev.): S-M colony ID = 1.316e−6				
Year = 8.085e−6				
Queen = 5.711e−6				
Brood-to-worker ratios—20:20 vs 60:20				
A) Count				
Intercept	1.336	0.431	3.100	0.002
# Host brood	*0.033*	*0.009*	*3.555*	*0.0004*
Random effects (Std. dev.): S-M colony ID = 4.043e−7				
Queen = 5.194e−7				
B) Proportion				
Intercept	− 0.651	0.721	− 0.903	0.386
# Host brood	0.011	0.012	0.927	0.396
Random effects (Std. dev.): S-M colony ID = 0.276				
Queen = 0.410				

breaks-down when high brood hosts are also defended by a high number of workers. In the trials comparing raids at nests of 100w:100b versus 25w:25b, slave-makers instead gained more brood from the smaller of the two nests (Fig. 2). High worker number in the 100w:100b nests negated the benefit of high brood numbers because the brood in these well-defended colonies was essentially inaccessible.

As suggested above, slave-maker colonies do worse at hosts with more workers, where they gain fewer brood and suffer higher mortality. Colonies tended to steal fewer brood items at nests with 25w:25b than with 50w:25b (Fig. 2), although this result was not significant due to the small sample size relative to the number of factors. In spite of this, the model of per capita raiding success supports this same pattern with higher confidence that greater host worker numbers reduces the proportion of brood that slave-makers gain. In addition to the numerical advantage larger host colonies have during an attack, prior work shows that they also tend to be more aggressive (Pohl and Foitzik 2013; Jongepier et al. 2014), which protect more of their brood and cause more harm to slave-maker workers. While the results here likely reflect differences in aggressiveness related to colony size, host colony aggression may also vary both between and within populations (Brandt and Foitzik 2004; Jongepier et al. 2014; Kleeberg et al. 2015; Pamminger et al. 2011) and according to the aggressiveness of individual ants (Modlmeier et al. 2012). Even though host aggression was not measured here, its effect will undoubtedly impact the outcome of raids and could be an additional consideration for a slave-maker colony should they be capable of this assessment.

Taking into account the above results, it is also apparent that the brood-to-worker ratio was a strong and consistent

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Table 2 Results of GLMM model selection for colony size effects from the pooled data set. Highly significant fixed effects are in italics. (A) In the relative fighting power model, the response variable was the proportion of available brood stolen. See Supp. Table S1 for list of candidate models. (B) In the per capita success model, the response variable was the number of brood stolen divided by the slave-maker colony size. See Supp. Table S2 for list of candidate models

Variables	Effect size (β)	± standard error	95% confidence interval (2.5, 97.5)	z value	p value	Relative importance
A) Relative fighting power						
# S-M workers	*0.050*	*0.007*	*0.036, 0.064*	*6.976*	*< 2e−16*	*1.000*
Rel. fight	*− 0.046*	*0.008*	*− 0.061, − 0.030*	*5.810*	*1.0e−08*	*1.000*
Source Loc.	*− 0.029*	*0.010*	*− 0.050, − 0.008*	*2.731*	*0.006*	*0.780*
B-W ratio	0.008	0.004	0.000, 0.017	1.986	0.047	0.450
Prop. pupae	0.017	0.011	− 0.004, 0.040	1.566	0.117	0.440
Arena size (40 cm)	0.030	0.018	− 0.007, 0.066	1.573	0.115	0.210
Arena size (75 cm)	0.035	0.018	− 0.001, 0.071	1.915	0.056	0.210
B) Per capita success						
B-W ratio	*0.199*	*0.051*	*0.097, 0.300*	*3.839*	*0.0001*	*0.273*
# Host workers	*− 0.168*	*0.057*	*− 0.282, − 0.053*	*2.876*	*0.004*	*0.225*
# S-M workers	*− 0.134*	*0.050*	*− 0.233, − 0.034*	*2.636*	*0.008*	*0.217*
Raiding party	0.097	0.066	− 0.034, 0.229	1.449	0.147	0.194
Prop. pupae	− 0.032	0.086	− 0.202, 0.139	0.365	0.715	0.184
Source Loc.	− 0.019	0.066	− 0.151, 0.113	0.279	0.781	0.180
Arena size (40 cm)	0.145	0.064	0.018, 0.273	2.230	0.026	0.027
Arena size (75 cm)	− 0.051	0.064	− 0.178, 0.080	0.776	0.438	0.027

predictor of raiding success, with high ratios leading to more brood stolen in all trials. Yet, despite the apparent benefit from maximizing brood-to-worker ratios, the census data revealed that the range of brood-to-worker ratios in natural host colonies are constrained. Although natural host colonies exhibited substantial variation in their worker-to-brood ratios (range = 0.06–36.33), the number of workers and brood within a nest were correlated on average (mean worker-to-brood ratio = 1.34 ± 0.19; Fig. 1a), a result consistent with the findings in Pohl and Foitzik (2011) for pupal counts. This suggests there

Table 3 Results of GLMM model selection for slave-maker mortality rates from the pooled data set. Significant fixed effects with high relative importance are in italics. (A) Count model: response variable is slave-maker mortality as a total count. See Supp Table 3 for list of candidate models. (B) Proportion model: response variable is the slave-maker colony's mortality as a proportion of its colony size just prior to the raid. See Supp Table 4 for list of candidate models

Variables	Effect size (β)	± standard error	95% confidence interval (2.5, 97.5)	z value	p value	Relative importance
A) Mortality—count model						
# S-M workers	*0.295*	*0.103*	*0.089, 0.501*	*2.802*	*0.005*	*0.92*
# Host workers	*0.285*	*0.097*	*0.090, 0.479*	*2.868*	*0.004*	*1.00*
Source Loc.	− 0.042	0.127	− 0.296, 0.213	0.320	0.749	0.16
Prop. pupae	− 0.025	0.138	− 0.295, 0.245	0.182	0.856	0.15
Arena size (40 cm)	− 0.059	0.175	− 0.409, 0.291	0.331	0.741	0.08
Arena size (75 cm)	− 0.179	0.174	− 0.529, 0.170	1.007	0.314	0.08
B) Mortality—proportion model						
# Host workers	*0.130*	*0.041*	*0.049, 0.211*	*3.138*	*0.002*	*0.94*
# S-M workers	− 0.040	0.042	− 0.124, 0.045	0.921	0.357	0.26
Source Loc.	− 0.042	0.049	− 0.141, 0.056	0.842	0.400	0.25
Prop. pupae	− 0.016	0.052	− 0.119, 0.088	0.295	0.768	0.22
Arena size (40 cm)	− 0.019	0.062	− 0.144, 0.106	0.300	0.764	0.07
Arena size (75 cm)	− 0.079	0.061	− 0.202, 0.044	1.261	0.207	0.07

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is a constraint on the range of possible brood-to-worker ratios a slave-maker colony is likely to encounter, and that host colonies with extreme ratio values are unlikely to be found. Hence, slave-maker colonies could benefit from discriminating hosts based on this ratio, but the margin of benefit may be small given the observed correlation. This constraint on brood-to-worker ratios is important because it places upper and lower bounds on optimal host size. Slave-maker colonies will do best to avoid the best defended nests even though they are also likely to contain the most brood, while also avoiding the smallest hosts because they are likely to contain very few brood. Furthermore, the largest nests may be especially unfavorable, since Pohl and Foitzik (2011) found that brood-to-worker ratio begins to decline in very large colonies. In light of these factors, raids at moderately sized hosts should theoretically maximize benefits to slave-makers.

The findings here are consistent with the conclusions reached in a study that directly tested for host preference in *T. americanus*, which found that slave-maker colonies tend to choose hosts with a moderate (~40–50) number of workers (Pohl and Foitzik 2011). However, they found no preference for nests with higher brood-to-worker ratios or more pupae, even though the data here suggests these characteristics are some of the best predictors of brood stolen. Despite its advantage, slave-maker workers may not be able to detect the brood content inside of nests, and so must base their raiding choices on incomplete information, perhaps relying on worker number as a proxy for brood number. In another study of host choice in the social parasite *Polistes sulcifer*, which single-handedly take over nests of its congener, *P. dominulus*, preference was instead given to nests with the highest density of pupae, regardless of nest size (Cervo and Turillazzi 1996). In contrast to the slave-makers studied here, *Polistes* nests are open, so information about pupal and worker numbers could be obtained more easily. If information about worker-to-brood ratios are not accessible to *T. americanus* scouts, then colonies may be limited in their ability to optimize the value-defensibility trade-off common to many parasites (Schmid-Hempel 2003; Bize et al. 2008; Václav and Valera 2018).

In spite of the patterns outlined above, slave-maker colonies of all sizes do not experience the same benefits. Slave-maker colony size played a significant role in the payoffs from raids. First, larger slave-maker colonies steal a larger proportion of brood than small slave-maker colonies from equivalently sized hosts. Second, the relative fighting power between the host colony and the slave-maker raiding party was also a significant predictor of raiding success, with a larger proportion of brood stolen when the two colonies were more closely matched in size. This latter result is similar to patterns observed in an incipient and facultative slave-making ant species, *Myrmecosystus mimicus*, which only choose to raid when they outnumber their conspecific opponent (Hölldobler 1976). The tendency for larger slave-maker colonies to perform better may have been influenced by the removal of host workers to a 1:1 ratio of slave-makers to hosts before raids by reducing the number of host workers that joined in raids. Although the presence of host workers has been shown to increase the duration of aggressive interactions during attack (Pohl and Foitzik 2013), their impact on raiding outcomes has not been measured. Furthermore, the host reduction here maintained the tendency of smaller colonies to have fewer host workers, so this manipulation is also likely to represent differences that would occur naturally.

In spite of the apparent advantage for larger slave-maker colonies, the outcomes are different when per capita success is taken into account. Larger slave-maker colonies stole fewer brood per slave-maker worker than smaller colonies. As obligate slave-makers, the workers of *T. americanus* depend on the labor from their host workers for all basic functions, and thus likely require a host worker force to match their colony size. The results here, however, may be partly due to a ceiling effect brought about by the limited range of size options offered in the experiments. Larger host options between 50 and 100 worker/brood might have given larger slave-maker colonies the opportunity to surpass their smaller counterparts in terms of per capita success. Nevertheless, the per capita raiding success results here show that the advantage larger slave-maker colonies have in acquiring more total brood is not sufficient to compensate for their presumed greater need for slaves. In contrast, patterns of mortality show that large and small slave-maker colonies lose a similar proportion of their slave-maker workers to raids, suggesting that the costs are proportional to slave-maker colonies regardless of their colony size. The implications of these results are that the optimal host size will be different for small and large slave-maker colonies. Larger slave-maker colonies can therefore be expected to gain a higher net payoff from larger hosts.

One of the next steps in understanding the raiding preferences of slave-making ants will be to investigate the sensory mechanisms by which slave-maker workers can or cannot detect the relevant features of their hosts, like quantities of workers and/or brood. Given that there are benefits to this knowledge prior to initiating an attack, it is plausible that slave-maker nervous systems could have evolved sensitivity to various cues associated with workers and their brood, such as chemical cues like footprint pheromones (Wust and Menzel 2016) or intranidal CO_2 levels. Should slave-makers possess these sensitivities, it suggests there is the opportunity for selection on hosts to conceal this information, especially about their brood number. One testable prediction is that hosts in highly parasitized populations should differ qualitatively or quantitatively in the chemical evidence they leave around their nest exterior. Future work on sensory biology in slave-making ants has the potential to reveal an information-based arms race between parasites and their hosts at the nest entrance.

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A consequence of parasite pressure based on host size may be selection on host demography and social structure. As such, slave-making social parasites ought to exert the greatest pressure on moderately sized host colonies. Given that larger host colonies possess a sort of "immunity" to slave-makers, it is tempting to theorize that there is positive selection on hosts to get large quick. However, becoming a large colony is a catch-22 because colonies necessarily pass through more vulnerable sizes on their way to becoming large. Foitzik et al. (2009) found that parasite pressure can reduce average host colony size over a 2-year period, so growing large under persistent parasite pressure may be impossible. However, several authors have suggested that colonies may be able to accelerate or shorten the period of growth by being polygynous (Brandt et al. 2005; Rosengren and Pamilo 1983), since colony reproduction by budding allows colonies to skip the very small foundress stage and grow faster with more worker-producing queens. An additional, but unexpected, result from the experiments here provides evidence that the developmental stage of the host's brood also play a role in its vulnerability to raids. In the 25:25 vs 25:50 experiment, more brood was stolen when there was more pupae in the target nest, suggesting that slave-makers recognize that pupae are more valuable than larvae. The potential for social parasites to exert selection on host demography requires more experimental work, but may play an underappreciated role in shaping the social structures of many social insect hosts.

In summary, the optimal host for the slave-making ant *T. americanus* is one that reaches a compromise between maximizing a hosts' value and minimizing its defensibility. However, this compromise is constrained by the tendency for brood and worker numbers to co-vary in hosts. In addition, social parasites can benefit by adopting different preference strategies based on their own status, particularly where forceful attack depends on the size or condition of the parasite. These patterns differ from some of the stealthy brood parasites (e.g. birds, bees), for which host nest size, and thus value, is maximized instead (Soler et al. 1995; Smith and Schwarz 2009). The findings here contribute to our understanding of the ways in which social parasites that attack via force are distinct from the stealthy social parasites, and which lead to distinct and predictable patterns of host choice across taxa.

Data availability The datasets generated and analyzed during the current study will be available in the Dryad repository upon acceptance for publication.

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