Original Article

Colony personality and plant health in the *Azteca-Cecropia* mutualism

Peter R. Marting,[a,b] William T. Wcislo,[b] and Stephen C. Pratt[a]

[a]School of Life Sciences, Arizona State University, ISTB1 353, 427 East Tyler Mall, Tempe, AZ 85287, USA and [b]Smithsonian Tropical Research Institute, Luis Clement Avenue, Building. 401 Tupper, Apartado Postal 0843-03092 Balboa Ancon, Panama, Republic of Panama

For interspecific mutualisms, the behavior of one partner can influence the fitness of the other, especially in the case of symbiotic mutualisms where partners live in close physical association for much of their lives. Behavioral effects on fitness may be particularly important if either species in these long-term relationships displays personality. We conducted a field study on collective personality in *Azteca constructor* colonies that live in *Cecropia* trees, one of the most successful and prominent mutualisms of the neotropics. These pioneer plants provide hollow internodes for nesting and nutrient-rich food bodies; in return, the ants provide protection from herbivores and encroaching vines. We tested the consistency and correlation of 5 colony-level behavioral traits, censused colonies, and measured the amount of leaf damage for each plant. Four of five traits were both consistent within colonies and correlated among colonies. This reveals a behavioral syndrome along a docile-aggressive axis, with higher-scoring colonies showing greater activity, aggression, and responsiveness. Scores varied substantially between colonies and were independent of colony size and age. Host plants of more active, aggressive colonies had less leaf damage, suggesting a link between a colony's personality and effective defense of its host, though the directionality of this link remains uncertain. Our field study shows that colony personality is an ecologically relevant phenomenon and sheds light on the importance of behavioral differences within mutualism dynamics.

Key words: **ant-plant symbiosis, behavioral syndromes, collective behavior, personality, mutualism, social insect.**

INTRODUCTION

Behavioral syndromes of individuals are well-known in a wide range of taxa (Sih et al. 2010), and recent studies have further shown collective behavioral syndromes emerging from groups of highly social individuals, such as social insect colonies (Chapman et al. 2011; Wray et al. 2011; Modlmeier et al. 2012; Pinter-Wollman et al. 2012; Pinter-Wollman et al. 2012; Scharf et al. 2012; Bengston and Dornhaus 2014; Keiser et al. 2014; Modlmeier, Keiser, Watters, et al. 2014; Modlmeier, Keiser, Shearer, et al. 2014; Blight et al. 2015). Conceptualizing insect societies as singular functioning superorganisms can be useful because natural selection acts at multiple levels (Wilson and Sober 1989; Korb and Heinze 2004; Hölldobler and Wilson 2009), highlighting the impact that collective behavior can have on fitness. Studying behavioral syndromes in social insects enables us to test mechanisms controlling behavioral types, because they allow for behavioral characterization and manipulation at different levels of biological organization—both the individual worker and the colony. With myriad factors affecting behavior in the wild, inherent behavioral

consistency or variation could be masked in laboratory studies, thus limiting their ecological relevance (Niemelä and Dingemanse 2014). More field-based studies are needed on collective personality and their interactions with other species and the environment.

Ants have an affinity for interspecific mutualisms (Holldobler and Wilson 1991), which raises interesting questions about how colony personality interacts with the biology of the ants' partners. Well-studied mutualisms include species that facultatively tend and protect hemipterans in return for honeydew (Styrsky and Eubanks 2007), fungus-growing ants that obligately farm nutritious fungi (Chapela et al. 1994), and species that protect plants in return for food and/or shelter (Heil and McKey 2003). The existence of differing colony behavioral types has important implications for understanding mutualistic relationships (Sih et al. 2012), and is a poorly explored topic in mutualism ecology (but see Schmiege et al. 2017). Different types may be associated with different life-history strategies, which in turn affect the strength of the mutualism. Thus, the behavioral syndrome of a colony can affect the fitness of its partner. In turn, the life-history strategy of the colony's partner may influence the behavioral syndrome.

We studied collective behavioral syndromes in colonies of the neotropical arboreal ant *Azteca constructor*, an obligate mutualist

Address correspondence to P.R. Marting. E-mail: pmarting@asu.edu.

with *Cecropia* trees. The symbiosis between *Azteca* ants and *Cecropia* trees is one of the most successful and prominent mutualisms of the neotropics (Davidson and Mckey 1993), abundant in disturbed areas and forest gaps ranging from southern Mexico to northern Argentina. These pioneer plants provide ants with hollow internodes as shelter and nutrient-rich food bodies; in return, the ants provide protection from herbivores and encroaching vines (Schupp 1986). The mutualism is a rich system for the study of behavior and ecology because ants have robust, measurable behavior, and discrete territories and resources within each fast-growing host plant (Heil and McKey 2003). These features allow us to investigate interesting questions about the causes and consequences of behavioral variation. The ants' defensive and exploratory behaviors are of particular relevance to the mutualism. These behaviors include patrolling activity and aggression similar to that seen in non-mutualist ants, but *Azteca* also have specialized behaviors adapted to their symbiosis, such as responding directly to leaf damage (Agrawal and Dubin-Thaler 1999). How these different traits relate to one another is important when assessing behavioral consistency and correlations. In particular, if some colonies have consistently stronger defensive behavior, their host plants potentially suffer less leaf damage and potentially benefit from faster growth rates, which in turn may feed back into colony fitness through growth and reproductive output.

If colonies do show evidence of personality, there are many possible drivers of behavioral difference that must be considered. These include intrinsic factors such as colony age and size, but also environmental factors, such as resource availability, that are intertwined with their *Cecropia* host. Colony nesting space depends on the host tree's internode size, and the ants' nutrition is derived from food body production, which is influenced by light environment (Folgarait and Davidson 1994) and soil nutrients (Folgarait and Davidson 1995). How might canopy cover affect colony behavior? A single *Azteca* species can colonize several *Cecropia* species. Might there be differences in colony behavior depending on the *Cecropia* species they occupy?

We tested the hypothesis that *A. constructor* colonies living in *Cecropia* trees display a collective behavioral syndrome under natural conditions in the field. We measured consistency and correlation in 5 distinct colony-level behavioral traits related to activity, boldness, exploratory behavior, and response to threats against the ants and their host. We then measured the relationship between colony behavior and host plant leaf damage, canopy cover, *Cecropia* species, colony age, and colony size.

METHODS

Study site and colony selection

We located *Azteca constructor* colonies along a 12 km stretch of Pipeline Road in and around the lowland tropical rainforests of Soberania National Park, Colón, Panama between March and May 2013. Based on the correlation between tree height and colony size in related species (Vasconcelos and Casimiro 1997), we limited the variation in colony size by choosing colonies inhabiting similar-sized *Cecropia peltata*, *C. obtusifolia*, and *C. insignis* trees (height ± SD = 3.43 m ± 0.83 m, $n = 14$). Trees in these species can reach over 20 m in height and have many branching points, but we used smaller trees with single stems for assay standardization and ease of access. Each tree contained a single colony, which we confirmed by collecting the colony and locating the queen after the behavioral trials. We identified the queens as *Azteca constructor* using keys in Longino (2007). Queen and worker voucher specimens were deposited in the

Arizona State University Natural History Collections. We identified the host *Cecropia* species using keys in Berg et al. (2005).

Behavioral traits

To characterize colony-level behavior, colonies were subjected to 5 bioassays: patrolling behavior, vibrational disturbance, response to intruder, response to leaf damage, and exploratory tendency (detailed below). Colonies received each assay at least 2 times to assess behavioral consistency (the patrolling behavior assay was repeated 4 times per colony). Colonies received only one manipulation per day, and repeated assays were separated by at least 24 h. *Cecropia* trees have thin, distinct septa lines that segment the stem into discrete internodes. To standardize behavioral measurements across different tree sizes, we focused on the central stem at the lowest leaf's internode (henceforth, the "focal internode"), which we estimated to be the location of median colony distribution based on 4 preliminary tree dissections. For patrolling behavior, vibrational disturbance, and response to intruder, we scored activity by counting the number of times we saw a worker completely traverse the lower septum line of the focal internode, regardless of direction or ant identity. For leaf damage assays, we focused on an entire leaf instead of the stem, and counted the number of workers on that leaf every minute. Trials were recorded with an HD camcorder (Panasonic HC-X900M) between May and August of 2013.

Patrolling behavior

Azteca ants constantly patrol stems and leaves of their host plant (Longino 1991). Patrolling behavior is most closely synonymous with "activity level" measured in similar studies (Bengston and Dornhaus 2014) and can be indicative of a number of colony traits that are not mutually exclusive, including food-body foraging effort and threat detection effort. In addition, the likelihood of a colony detecting and responding quickly to a potential threat increases with the number workers that traverse the stem (Rocha and Bergallo 1992).

For our measure of patrolling behavior, we counted the absolute worker number, a distinct measure from colony response effort to a given stimulus. We recorded undisturbed patrolling behavior for 5 min and scored activity as the number of worker crossings of the focal internode.

Vibrational disturbance

Azteca are notorious for their aggressive response to vibrational disturbance caused by vertebrate attacks on their host tree (Longino 1991). Vibrational disturbance is caused when a vertebrate threatens the colony (e.g., anteaters: Hirsch et al. 2014; woodpeckers: Calderon 2011) or the tree (e.g., sloths: Wheeler 1942; monkeys: Silver et al. 1998). Colonies likely require a large response to deter this type of threat because workers do not have stingers and rely on their mandibles to dissuade attacking vertebrates. Deterring vertebrates is probably costly because defending workers that mount the attacker likely die during the attack, though this has not been measured. Therefore, the response to vibrational disturbance indicates colony defensive aggressiveness and risk-taking boldness.

We simulated a large herbivore attack by flicking the tree 10 times 1m below the focal internode with a custom-built flicking machine (Supplementary Figure S1) that produced 10 flicks at a constant rate and force over 30 s. Vibrational disturbance was scored as the number of times workers crossed the focal internode during the first minute after the first flick, subtracted by the baseline (the average number of times workers crossed per minute during the 3 min immediately preceding the first flick).

Response to intruder

Azteca ants often protect their trees from the threat of herbivory by *Atta* leafcutter ants and other herbivores (Vasconcelos and Casimiro 1997). In contrast to responding to large-scale vibrations, deterring a leafcutter scout is an easier, less risky task. After only a few bites from responding workers, the leafcutter ant often jumps off the tree and is unlikely to recruit her nestmates. If the leafcutter scout is permitted to recruit, the *Cecropia* tree could suffer major defoliation (Vasconcelos and Casimiro 1997). Additionally, leafcutter ants likely do not offer much nutritional value and are not captured for consumption. Response to leafcutter ants likely indicates colony aggressiveness as it pertains to host plant defense.

To assess the colony's response to scouting leafcutters, we gently introduced a single *Atta colombica* worker to the focal internode. We scored response to intruder as the number of times workers crossed the focal internode during the first minute after the leafcutter made contact with the stem, subtracted by the baseline. All *A. colombica* workers were of similar size and collected from a foraging trail of a single colony.

Response to leaf damage

Azteca ants are known to recruit to fresh damage to the leaves of their host plant (Agrawal and Dubin-Thaler 1999). Free-living species of *Azteca* are among the most carnivorous arboreal ants (Davidson et al. 2003), and thus incidentally benefit plants by consuming insect herbivores. *Cecropia* leaf damage is caused by a variety of insects (Schupp 1986) and *Azteca* workers responding to the damage are occasionally able to immobilize, dismember, and consume palatable herbivores as an additional source of protein (Dejean et al. 2009; Mayer et al. 2014). Many parasitoid wasps use volatile chemicals released by leaf damage as cues to find their caterpillar hosts (Pare and Tumlinson 1999). It is possible that chemicals released by the leaf damage serve as a cue for potential prey, and thus a colony's response may indicate motivation to capture prey.

To assess the colonies' response to leaf damage, we used a standard hole-puncher to make 6 holes in the distal tip of the largest lobe of one of the host plants' leaves. Response to leaf damage was scored as the maximum number of workers on the damaged leaf within 10 minutes after the damage was discovered. Colonies that did not discover the leaf damage in one or both trials ($n = 3$) were excluded from the consistency analysis.

Exploratory tendency

Colonies may gain new potential territories when branches from surrounding *Cecropia* plants come in contact with their host tree (P.R.M., personal observation). To measure colony exploratory behavior, we provided a new territory by gently placing a dowel rod 1 cm × 85 cm in length in contact with the host tree at the focal internode. We scored exploratory tendency as the total number of times workers ventured past the first 2 cm of the dowel rod in 10 min.

Colony demography and leaf damage

After completing the behavioral trials, we harvested the host trees and extracted entire colonies in August of 2013. To subdue and collect the ants, we used internal and external insecticides. The ants chew through most of the internode septa (Longino 1991), providing a path for the insecticide to traverse the internal height of the tree. We drilled a hole into the base of each tree and inserted the nozzle of a propane-powered insecticide fogger (active ingredient:

resmethrin), and discharged the insecticide for several minutes. The tree was then cut at the base, laid on a plastic tarp, and sprayed with a liquid insecticide externally (active ingredients: pyrethrins, piperonyl butoxide, and permethrin). Stems were cut in meter-long segments and split vertically to access the internal workers, brood, and queen. We collected all workers from the stems, leaves, tarps, and bags and immediately placed them in 95% ethanol. To survey colony size, workers were spread out on grid paper, photographed, and counted using ImageJ software.

Azteca ants colonize *Cecropia* trees as saplings (Perlman 1992), so plant and colony age are likely tightly correlated; hence, we used estimated plant age as a proxy for colony age. *Cecropia* internodes have a consistent growth-periodicity internode branching pattern that allows for accurate estimates of plant age (Zalamea et al. 2012). We counted the number of internodes between branching points of larger, mature trees to estimate an average annual internode output for each *Cecropia* species. We divided the number of internodes from our focal plants by the annual output to estimate plant age.

To assess leaf damage, all leaves were separated and photographed against a light background. Damaged leaf edges were reconstructed using Adobe Photoshop CS6 software. We analyzed leaf damage using ImageJ software (adapted from O'Neal et al. 2002) by calculating the total defoliated area: leaf area without damage (holes filled in via software) subtracted by the leaf area with damage (holes not filled in). When assessing leaf damage, we did not include holes punched for the leaf damage behavioral assay, because we aimed to measure only damage due to natural causes. We presume the majority of missing leaf area is due to defoliating herbivores.

To assess canopy closure, we took photos with a circular fish-eye lens aimed vertically 1.3 m above each plant stump after plants were cleared. We converted images to black and white and used MATLAB to calculate the percentage of black pixels (methods in Korhonen and Heikkinen 2009).

Statistical analyses

Colony consistency for each behavioral trait was analyzed by regressing the scores from the first and second trial and calculating repeatability using the intraclass correlation coefficient (ICC) (Lessells and Boag 1987). The ICC gives the proportion of total variation due to differences among subjects and therefore the degree of subject consistency. For patrolling behavior, where we attained 4 replicates per colony, we analyzed repeatability using a repeated measures ANOVA. Relationships among traits were analyzed by entering the average scores for significantly consistent traits into an un-rotated principal component analysis (PCA). For the leaf damage assay, 3 colonies required special handling. Two discovered the leaf damage on only one trial, hence we used each colony's single observation rather than the average of 2 observations. One colony discovered the damage on neither trial. To avoid missing data in the PCA, we assigned this colony the mean leaf damage response value of all the other colonies (as in Manson and Perry 2013). We also performed a PCA without this colony to assess its role in the overall model. To select which components to retain, we used the Kaiser-Guttman stopping rule, which drops components with eigenvalues less than the mean eigenvalue (Jackson et al. 1993). As we describe in the results, this left us with only the first principal component (PC1), which we defined as the colony "behavioral type." To examine possible drivers of behavioral difference, we tested for linear correlations of behavioral type with

colony age and size. To assess the relationship between ant behavior and host plant health, we tested for linear correlation between leaf damage and each consistent behavioral trait, as well as overall colony behavioral type. Given the distinct contexts of the behavioral traits (detailed above), we treated these correlations as distinct a priori hypotheses and therefore did not correct for false discovery rates (Ruxton and Beauchamp 2008). We also used the behavioral type scores to split the colonies into 2 categories; "aggressive" (those with positive scores) and "docile" (those with negative scores). We compared the defoliated area between these groups with a Mann–Whitney U-test. We tested for effects of *Cecropia* species on colony behavioral type using an ANOVA. All statistical analyses were completed using Stata 12.1.

RESULTS

Behavioral consistency

Colonies differed substantially in their response to all assays (range of colony averages for patrolling: 36–493 crossings; disturbance: 0–633 crossings (Supplementary Video S1); intruder: 0–123 crossings; leaf damage: 12–133 ants; exploration: 0–39 crossings). Colony responses also differed consistently in all behavioral traits except exploratory tendency (patrolling activity: Figure 1, $n = 14$, $P < 0.001$, ICC = 0.52; vibrational disturbance: Figure 2a, $n = 14$, $P < 0.0001$, $r^2 = 0.75$, ICC = 0.86; response to intruder: Figure 2b, $n = 14$, $P < 0.05$, $r^2 = 0.34$, ICC = 0.48; response to leaf damage: Figure 2c, $n = 11$, $P < 0.01$, $r^2 = 0.59$, ICC = 0.72; exploratory tendency: Figure 2d, $n = 14$, $P = 0.71$, $r^2 = 0.01$, ICC = −0.19).

Behavioral correlations

A principal component analysis including the 4 consistent traits showed that the first component (PC1) explains 48.3% of the variation with an eigenvalue of 1.93 and that all the traits' loading scores are strongly positive (Figure 3, Supplementary Table S1). Omitting the colony with missing leaf damage response data did not alter the structure of the model (Supplementary Table S2). The second component's eigenvalue was barely greater than the mean (1.06) and was therefore excluded from further analysis. We used colony score on PC1 to characterize each colony's behavioral type along a docile-aggressive axis, with higher values indicating greater activity, aggression, and responsiveness. Colony behavioral type was not correlated with colony size (Figure 4a, correlation, $n = 14$,

$P = 0.18$, range: 1,880–13,534 workers) or estimated colony age (Figure 4b, correlation, $n = 14$, $P = 0.80$, range: 1–4.5 years). Host plant defoliation showed no significant correlation with patrolling ($n = 14$, $P = 0.26$), vibrational disturbance ($n = 14$, $P = 0.06$), or leaf damage response ($n = 14$, $P = 0.31$), but it was negatively correlated with response to intruder ($n = 14$, $P < 0.05$, $r^2 = 0.30$). Defoliation was also negatively correlated with overall colony behavioral type ($n = 14$, $P < 0.05$, $r^2 = 0.33$). We split colonies into docile (negative values, $n = 8$) and aggressive (positive values, $n = 6$) categories (Figure 5). The total area of host plant defoliation was significantly lower for aggressive colonies (Figure 5, Mann–Whitney U-test, $n = 14$, $P < 0.05$). Colony behavioral type was not correlated with *Cecropia* species (ANOVA, $n = 14$, $P = 0.46$) or canopy closure (correlation, $n = 14$, $P = 0.35$).

DISCUSSION

Our results support the existence of a collective behavioral syndrome for colonies of *Azteca constructor*. We found that colonies differ substantially and repeatably in 4 distinct behavioral traits, all of which were positively related. Thus, each colony could be characterized by a behavioral type score along a docile-aggressive axis, with higher scoring colonies being more active, responsive, and aggressive than those with lower scores. Furthermore, colony behavioral types were correlated with their host plants' health such that trees containing more aggressive colonies also exhibited less leaf damage.

Exploratory behavior was not consistent, which suggests colonies display flexibility under certain conditions. Furthermore, colonies tend to have a higher exploratory score in the first trial (Supplementary Figure S2), which may indicate colony desensitization, habituation, or another form of learning. Under certain conditions, a single *Azteca* colony can occupy multiple *Cecropia* trees that have adjacent stems or overlapping leaves and reap the benefits of both plants (P.R.M., personal observation). New potential territories, such as overlapping *Cecropia* leaves, are often already occupied by other *Azteca* colonies and encounters among non-nestmates result in a fight to the death (P.R.M., personal observation; Adams 1990). Colonies with high rates of exploration risk losing workers to gain potential resources, but this trade-off remains to be investigated. The fact that exploration behavior was not consistent over time highlights the importance of assessing a range of colony traits because some behaviors have more plasticity than others.

What causes this behavioral syndrome? Our data discount 2 obvious explanatory factors: colony age and size. As colonies mature, changes in the resources they need might be reflected in their collective behavior (Bengston and Jandt 2014), but we found no correlation between estimated colony age and behavioral type. This may reflect the purposefully narrow age range of our colonies, and it remains possible that age affects behavioral differences over larger age differences. Nonetheless, age does not appear to explain the behavioral variation that we observed. Another potential explanation for this variation is that more active colonies have more workers (as in seed-harvester ants; Waters et al. 2010). However, we show that total colony size is independent of colony behavioral type, suggesting that colonies invest differently in the number of workers afforded to a given stimulus. Other studies documenting collective behavioral syndromes in social insect colonies either control for colony size (Wray et al. 2011; Blight et al. 2015) or find colony size independent of behavioral type as well (Bengston and Dornhaus 2014), suggesting that there is a general need for an
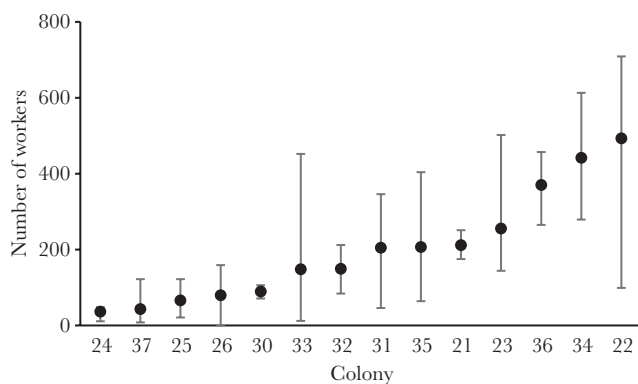

Figure 1
Colonies differed repeatably in their patrolling behavior, shown as the number of workers crossing the lowest leaf internode in 5 min. Points indicate the colony mean and error bars indicate the range.
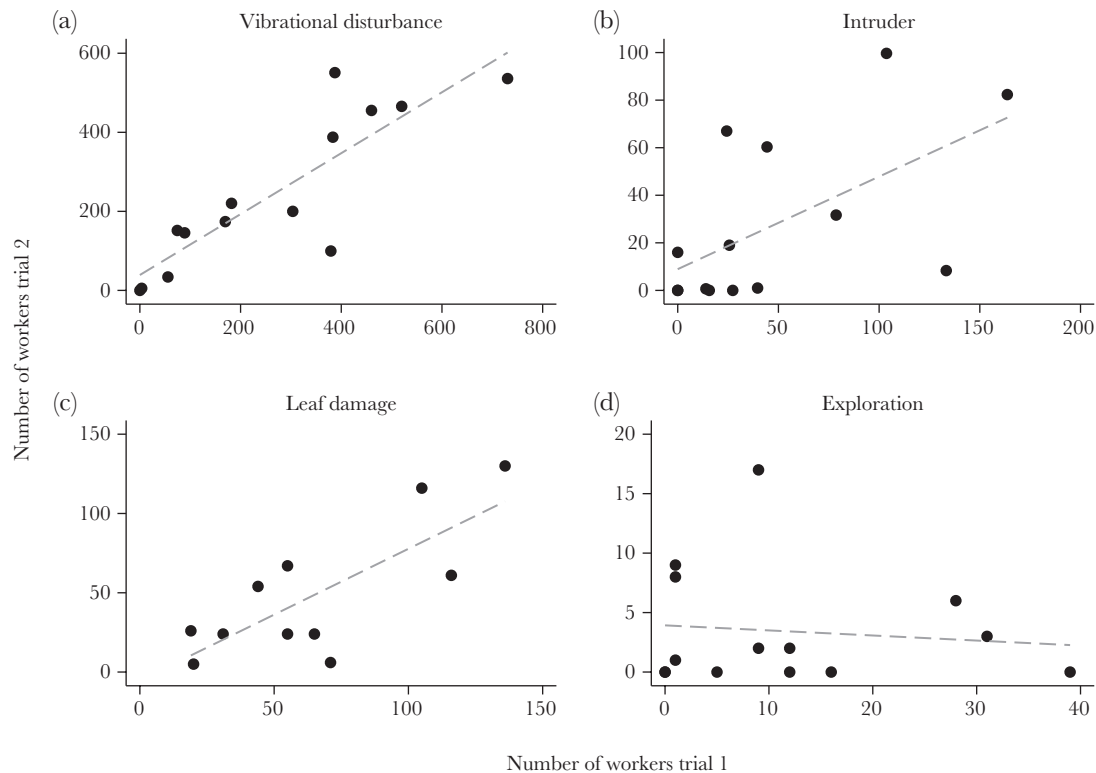
Figure 2

An overview of colony consistency for 4 traits shows significant regressions of the first trial on the second trial. Colonies differed repeatably in (a) vibrational disturbance, (b) intruder response, and (c) leaf damage response, but not in (d) exploratory tendency.
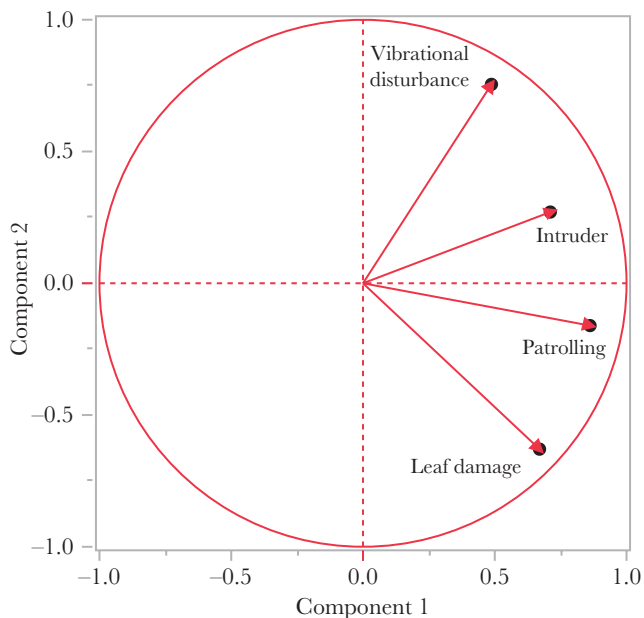

Figure 3

A principal component analysis of the 4 consistent traits shows that the first component explains 48.3% of the variation and that all the traits load strongly positive. Colonies' first principal component scores were used as the colony "behavioral type" scores.

alternative explanation for behavioral variation. Environmental effects, such as local climatic conditions, colony density, or resource availability, likely play a role in selecting for one behavioral type

over another, or for variation itself (e.g., see Pinter-Wollman et al. 2012; Bengston and Dornhaus 2014; Pruitt and Goodnight 2014; Bengston and Dornhaus 2015). Personality in *Azteca* colonies may also be influenced by resource availability provided by their host plant, such as internal nesting space and food body production, a topic which merits further research.

Differences in colony personality can also be interpreted as distinct life-history strategies along the r-/K-selection continuum. In this framework, more bold, aggressive, and active individuals are associated with r-type strategies; faster resource accumulation, faster growth, earlier reproduction, and shorter life spans (Biro and Stamps 2008). In *Temnothorax* ants, colonies with risk-taking personality types are associated with r-selected life-history strategies in that they grow faster and invest more in reproduction than colonies with risk-averse personalities (Bengston et al. 2015). Risk-taking colonies are found at higher latitudes with shorter growing seasons, which likely drive the selection for a fast-paced, r-type life-history strategy (Bengston and Dornhaus 2014). In the context of the *Azteca-Cecropia* mutualism, r-type aggressive colonies may deter more threats and provide better protection for their host tree, but the maintenance of high vigilance and loss of workers may be metabolically costly (Riechert 1988). The energetic demand could be met by higher rates of prey-capture and food body production from a healthier host-plant, which could promote faster growth for both partners and reinforce the strategy. On the other hand, K-type docile colonies may conserve energy by hiding within the walls of their host plant, allowing defoliating herbivores to damage their tree, which could decrease growth rates in both partners and delay reproduction. While colony life-history strategy may reflect inherent colony differences
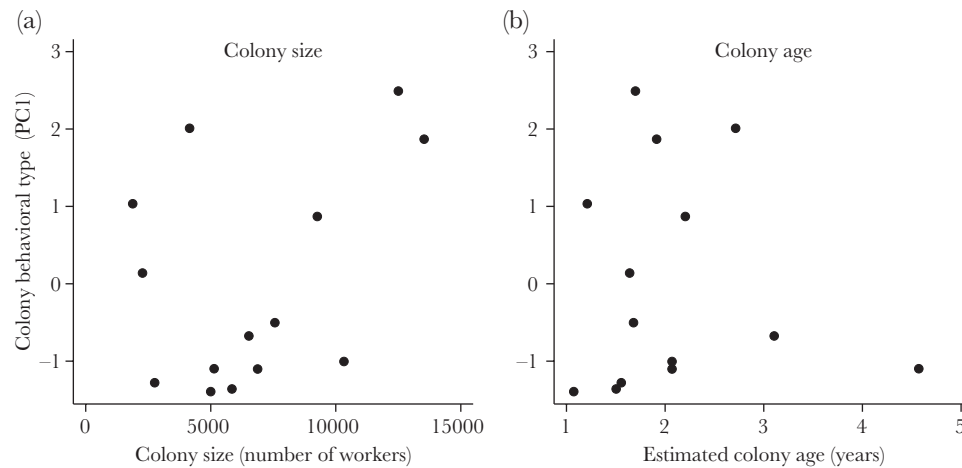
Figure 4
Colony behavioral type was not correlated with colony size (a) or age (b). Colony size was measured by harvesting the host plant, extracting the workers, photographing them, and using imageJ software to mark and count each one. Colony age estimates were determined by estimating host plant age.
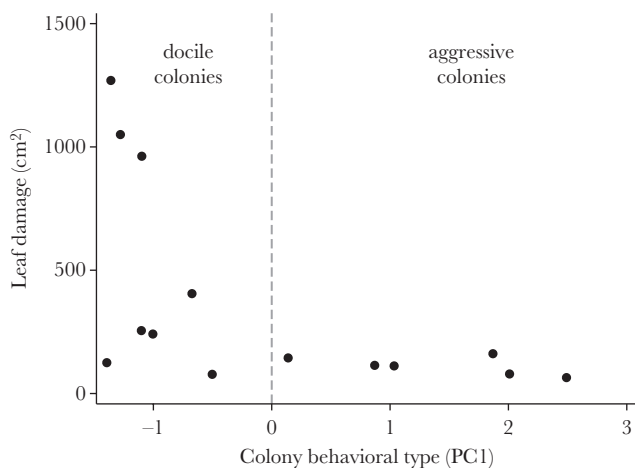

Figure 5
The total amount of host plant leaf damage differed between colony behavioral types. The dashed line represents where colonies were split into aggressive and docile categories.

(e.g., genetics and development), it may also depend on host-plant investment strategies (e.g., tradeoffs between food body production and vertical growth), or environmental variation (e.g., light level and soil nutrients).

It is well established that there is a significant difference in *Cecropia* leaf damage between plants with and without *Azteca* ants (Schupp 1986), but here we document a significant difference among *Azteca*-occupied plants. Colonies with positive behavioral type scores are associated with extremely and uniformly low levels of leaf damage, appearing to be very effective at controlling their host plants' exposure to herbivory. In contrast, host plants housing colonies with negative behavioral type scores have a high variation in leaf damage, suggesting the plants are subjected to greater risk. Furthermore, by comparing correlation coefficients, colony behavioral type explains leaf damage variation better than any single colony trait that we tested—including response to leaf damage. This suggests that it is important that colonies have a strong response in several distinct contexts to limit herbivory. Response to intruder also significantly correlated with host plant defoliation, highlighting that a strong, immediate response to encountering an intruder

may outweigh the response to an already damaged leaf. Defoliation can be detrimental to plant growth, competitive ability, and fitness, especially in the tropics (Coley and Barone 1996). For example, individuals of the tropical plant *Piper arieianum* that have more leaf damage suffer from a long-term decrease in growth, seed production, and seed viability (Marquis 1984). We did not measure how fitness is shaped by defoliation rates, and future studies are needed to assess how the behavioral type of the inhabiting colony influences the success of its host plant, which has implications for partner selection and fidelity (Mayer et al. 2014).

While we document the relationship between colony personality and plant health, it is important to underscore that the directionality remains uncertain—it is possible that the amount of host plant leaf damage influences colony behavioral type. In other ant-plant systems, plants can alter the output of their extrafloral nectaries in response to herbivory, but it is still poorly understood how food body production might change (Mayer et al. 2014). External factors such as intraspecific genetic variation (Marquis 1984) or variation in local herbivore abundance (Coley and Barone 1996) could give rise to differential leaf damage rates. Reduction in photosynthetic area from defoliation may decrease food body production since Müllerian food bodies are largely carbon-based (Rickson 1971). Colonies with access to fewer food bodies may have lower levels of activity and aggressiveness. This possibility gives a novel insight into mechanisms that maintain behavioral syndromes in natural populations. Colony behavior and plant health may influence each other in a feedback loop; aggressive colonies help prevent leaf damage and are rewarded with more food bodies, making them even better equipped to defend their host plant, whereas less aggressive colonies permit more defoliation and suffer lower resource availability. Behavioral differentiation in host plant defense has been documented between different plant-inhabiting species (Mayer et al. 2014), but not within species. Our results imply that partner-host dynamics, cost-benefit analyses, and conflict in ant-plant mutualisms may be more complicated than previously thought. The correlation between colony personality and leaf damage must ultimately be backed by controlled experiments, and further research is required to elucidate factors contributing to the important ecological relationship between colony behavior and host plant health.

Our study on collective behavioral syndromes of a social insect is the most comprehensive investigation conducted entirely in the

field, and the first of its kind pertaining to mutualisms. We show that colony personality is a robust, ecologically relevant phenomenon that cannot be explained by colony size or age, and that it is an important consideration for mutualism dynamics. The current study paves the way for future research on the internal and external factors contributing to the variation among colonies and its relationship within the mutualism.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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AUTHOR CONTRIBUTIONS

P.R.M. conceived the study, designed it, conducted the field work and video scoring, carried out the statistical analysis, and drafted the manuscript; W.T.W. participated in the design of the study, helped troubleshoot fieldwork, and helped to edit the manuscript; S.C.P. participated in the design of the study, helped with statistical analysis, and helped to draft the manuscript.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Marting et al. (2017).

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