

Defending the nest: variation in the alarm aggression response and nest mound damage in the harvester ant *Pogonomyrmex occidentalis*

D. C. Wiernasz · B. A. Cole · B. J. Cole

Received: 24 January 2014 / Revised: 13 May 2014 / Accepted: 16 May 2014 / Published online: 7 June 2014
© International Union for the Study of Social Insects (IUSI) 2014

Abstract A number of studies have found that ant colonies vary in many colony-level phenotypes, including the level of aggression towards non-nestmates. The extent of a colony's aggression and defense of the nest in response to attacks by predators is likely to affect its survival and reproduction, but the degree to which colonies vary in their defensive response is poorly known. We documented considerable variation in damage to the external nest mound of *Pogonomyrmex occidentalis* (Cresson) at our long-term study site in 2012. Heavily damaged colonies formed several spatial clusters, consistent with predation within a home range. We tested two competing hypotheses for the variation in nest damage: (1) colonies vary in their level of aggression, those with stronger defensive responses are better protected, and suffer less damage, versus (2) colonies have similar levels of aggression, but those that suffer predator-induced damage subsequently display a stronger defense response. We measured the alarm/aggression response in colonies exposed to a standardized stimulus and determined whether the level of aggression was correlated to the level of damage. Colonies with strong defensive responses were significantly less likely to exhibit damage than those with weak responses, suggesting that aggression level is a colony phenotype.

Keywords Aggression · Alarm · Colony defense · Colony phenotype · *Pogonomyrmex*

Introduction

Social insect colonies, which store food and rear young at high density, represent a concentrated food source for other organisms. Predators include mammals (anteaters, pangolins, aardvarks) and lizards (*Phrynosoma* spp.) that specialize on ant colonies, as well as more opportunistic mammals, birds and reptiles (Hölldobler and Wilson, 1990; Taber, 1984). Workers defend the nest from predators through a variety of behaviors that include stinging, biting, and spraying with formic acid, mediated by the production of alarm pheromones (Wilson, 1971; Buschinger and Maschwitz, 1984; Hölldobler and Wilson, 1990). Soil dwelling species may also retreat deep underground. Successful defense of the colony's resources may contribute to colony fitness, in terms of increased longevity and greater reproductive output, through retention of reproductive brood and food stores.

The degree to which colonies vary in their level of aggression and the consequences of that variation are not well known. In honeybees, colonies differ dramatically in the extent of the defensive response (Wray et al., 2011). Most work in ants has focused on aggression toward conspecific non-nestmates or heterospecifics. Argentine ants display geographic variation in the level of intercolonial aggression based in part upon cuticular hydrocarbon profiles (Tsutsui et al., 2003; Buczkowski and Silverman, 2006). Colonies of *Rhytidoponera confusa* varied in their aggressive response to non-nestmates, and the level of response was consistent over several months (Crosland, 1990). Workers of *Temnothorax longispinosus* respond more aggressively to workers of a brood-raiding species than to non-nestmates (Scharf et al., 2011). Colonies of *Messor pergandei* differed in how aggressively they responded to a disturbance (Pinter-Wollman et al., 2012). Variation in aggression may be mediated by responsiveness to alarm

D. C. Wiernasz (✉) · B. A. Cole · B. J. Cole
Department of Biology and Biochemistry, Biology of Behavior
Institute, University of Houston, Houston, TX 77204-5001, USA
e-mail: dwiernasz@uh.edu

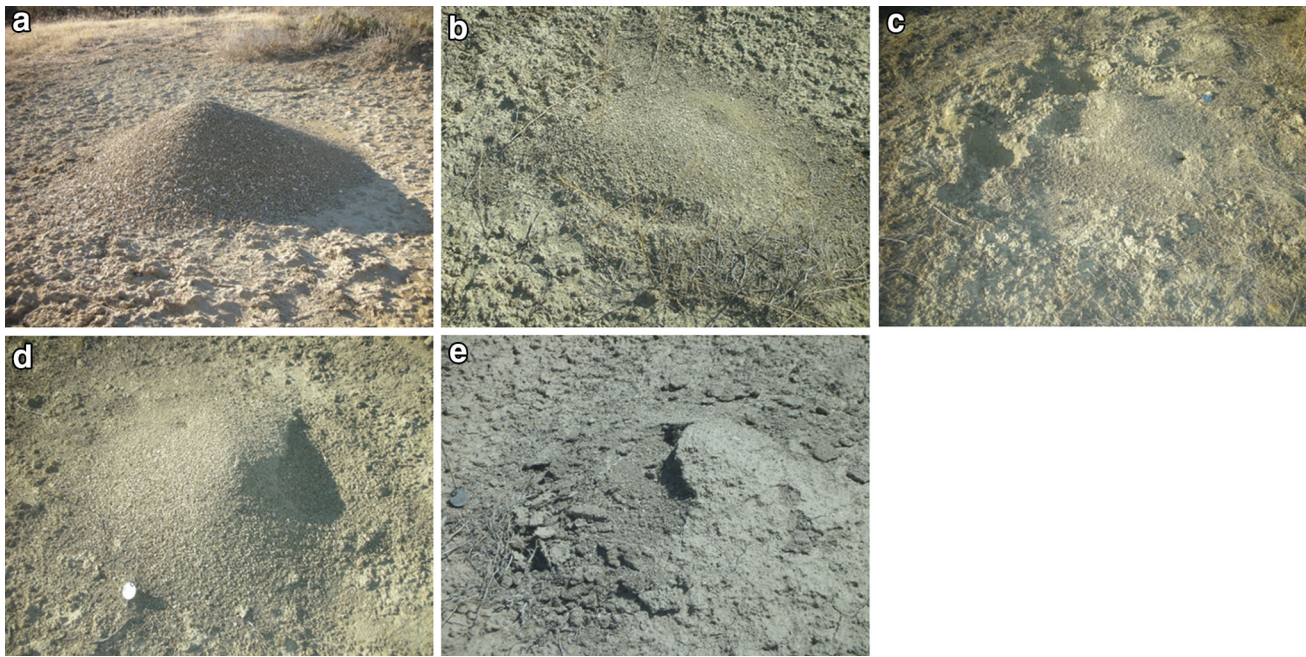


Fig. 1 Levels of damage sustained by colonies in 2012. **a** No damage (level 0), **b** small digs (level 1), **c** large holes (level 2), **d** hole into the interior (level 3), **e** substantial destruction of the mound (level 4) (for detailed descriptions, see the text)

pheromone. Several species display among-caste variation in their response to alarm pheromone (Hughes et al., 2001; Francelino et al., 2008).

The western harvester ant, *Pogonomyrmex occidentalis* (Cresson), is a seed-harvesting ant that is common through much of the western United States. Although most of the colony is underground, the nest entrance is surrounded by an area of worked dirt and gravel. As the colony grows, this is gradually built into an external nest mound with a diameter that can exceed 1.5 m and a height that can exceed 30 cm, although most mounds are smaller. The mound is used as a granary (Lavigne, 1969; Eddy, 1970), and also as a brood incubator (Cole, 1994). Thus mounds of *P. occidentalis* contain two sources of protein, brood and seeds that would make them attractive to predators. Kangaroo rats (*Dipodomys* spp.) have been reported digging into *P. occidentalis* mounds in Nevada to obtain stored seeds (Clark and Comanor, 1973).

In our long-term study population, colonies typically display no or minimal damage to the external nest mound—the sides of the mounds are smooth and pebble covered (see Fig. 1a). Nests can be damaged by abiotic factors such as heavy rains, which results in a “plastered-over” appearance, but never produces holes in the mound surface. Substantive damage (holes: for examples, see Fig. 1b–e) occurs only during dry springs when a lack of rain reduces germination by annual species and seed set by both annuals and perennials. During the summers of 2002 and 2012, damage to colonies was especially widespread. In these years, the

precipitation at our study site was <50 % of normal (1.7 cm in 2002; 0.5 cm in 2012 relative to a mean of 4.0 cm). Not all nest mounds suffered equal damage—some were ripped open, while others remained untouched. The species responsible is not known, but the type of damage suggests a species of small mammal, which are known to cause similar damage in other areas (Clark and Comanor, 1973). Such variation could have many causes—some nests may not have had sufficient food stores, may not have been located within the predator’s foraging area or may have varied in their ability to repel the predator. Disturbance of a *P. occidentalis* nest (by tapping on the mound) causes additional workers to emerge and attempt to sting any foreign objects on the nest surface. The venom in the sting of *Pogonomyrmex* harvester ants is extremely toxic (Schmidt and Blum, 1978; Schmidt, 1990). Because this venom is ineffective against other insects as well as the main specialist predator on foragers, *Phrynosoma* lizards (Schmidt et al., 1989), it is thought to have evolved as a deterrent to mammalian predators.

We hypothesized that colonies may vary in their level of aggression, which influences their ability to deter mammalian predators. The Protective Aggression hypothesis assumes that the defensive response is a colony-specific trait that is independent of the colony’s experience. If some colonies are more aggressive or have a more efficient alarm response they will suffer less damage than colonies that are only mildly aggressive or have a weak alarm response. An alternative, the Induced Aggression hypothesis, assumes

that all colonies have a similar intrinsic aggression level, which changes as a function of recent experience. In this case, the damage caused by a predator attack induces an aggressive response among the workers. The two hypotheses make opposite predictions about the relationship between nest damage and colony response. The Protective Aggression hypothesis predicts a negative correlation between the level of defensive response and the amount of nest damage. Colonies that have a highly aggressive nest defense succeed in protecting their nest from predation. The Induced Aggression hypothesis predicts that those colonies that have suffered the most damage are induced to show the greatest defensive response, leading to a positive correlation between damage and response.

The spatial patterns of damage and defensive response should also be revealing. Significant spatial clustering of damaged colonies would suggest that the predator is foraging within a home range, consistent with it being a heteromyid rodent. The Induced Aggression hypothesis predicts that the level of aggression will be highly spatially correlated with the level of colony damage, because damage to the nest induces the response. The Protective Aggression hypothesis predicts that the spatial distribution of aggression level should be independent of the spatial distribution of damage. Colonies that have a low defensive response may or may not be damaged, depending on their proximity to a predator, but colonies with a strong defensive response are less likely to be damaged. We did not have a clear prediction about the size of the nest mound and the extent of damage. Larger mounds represent a larger amount of concentrated resources, making them more attractive to predators, which would produce a positive correlation between damage and mound size. However, large mounds have a larger worker force and might be better defended, leading to a negative correlation between size and extent of damage.

We address these hypotheses by documenting variation in the alarm/aggression response of colonies to a standardized stimulus and comparing these responses to the amount of damage suffered by the colony from potential predators. We also examine how these two traits are affected by the local density of colonies, and the degree to which damage and aggression level were spatially correlated.

Materials and methods

The study was conducted during June–July 2012 on the site of our long-term harvester ant population study area ~15 km northwest of Fruita (Mesa Co.), Colorado (see Wiernasz and Cole, 1995 for a detailed description). The habitat is dominated by saltbush (*Atriplex* spp.), greasewood (*Sarcobatus*) and perennial grasses (*Hilaria*, *Oryzopsis*).

Much of the vegetation consists of primarily native species, with a few patches characterized by invasive species such as cheatgrass (*Bromus tectorum*).

Colony size

All colonies were measured in late July. Size of the colony is estimated by measuring the size of the external nest cone along the North–South and East–West axes as well as the height of the nest cone. The size of the colony is calculated as: $\text{Ln}(\text{NS} \times \text{EW} \times (\text{HT} + 1)) \text{ cm}^3$ which is highly correlated with the estimated worker force of the colony (Wiernasz and Cole, 1995). When the top of the nest cone was damaged severely enough to make the height measurement uncertain, we used the height from the previous year. In 2012, the size of colonies ranged from 3.40 to 14.55. Colonies with a size of 7.0 or smaller are typically 1-year-old colonies. Colonies of size 10.0 or higher have a well-developed nest cone and are considered reproductively mature, although these colonies may not reproduce every year (Cole and Wiernasz, 2000). Colonies of size 12.0 and greater are fully mature, represent the largest 15 % of the population, and are responsible for the greatest amount of ‘worker activity’ and reproduction.

Damage assessment

The condition of external nest mounds was evaluated during the annual demographic census of the study population in June. Damage was rated on a qualitative scale: 0 = no damage; 1 = small digs into the mound surface, ≤ 1 cm deep; 2 = larger holes in the mound surface, 1–3 cm deep; 3 = large holes in the mound, exposing some of the inner structure; 4 = a minimum of a quarter of the mound destroyed; 5 = virtually none of the mound remains (see Fig. 1). Colonies that were intermediate between two categories were scored as the average (e.g., 2.5 indicated large holes that were deeper than 3 cm, but not exposing inner structure). All damage was assessed by one observer (DCW), and was conducted independently of information on nest alarm response. Completing the census for the entire study site requires ~4 weeks, so some nests were re-scored during August when the size of all colonies was measured. August scores were identical to June scores ($N = 116$), indicating both that the scoring systems are consistent, and that 4 weeks was insufficient for colonies to repair damage.

Alarm/aggression response

The intensity of the alarm/aggression response was measured in late June and early July. We agitated colonies by blowing into the nest entrance, using a procedure similar to the one used when we collect random worker samples

(Wiernasz and Cole, 2010). Once most colonies in an area were actively foraging, they were agitated individually by placing the tip of an aspirator at the nest entrance and then exhaling for 30 s. The colony was observed for the next 30 s; alarmed or aggressive ants were those that emerged with flared mandibles. Alarm/aggression was scored on a qualitative scale: 0 = no response; 1 = five or fewer ants; 2 = up to ten ants, but the response diminished within the 30-s observation period; 3 = up to 30 ants, the response plateaued by the end of the 30-s observation period; 4 = >30 ants, the number continued to increase during the observation period. Colonies that were intermediate between two categories were scored as the average (e.g., a score of 2.5 would represent a colony where more than ten ants initially responded, but the response diminished within the 30-s observation period). Once the rate of foraging began to slow (mid-late morning), we ceased measuring colonies. To assess whether colonies were consistent in their responses, colonies measured on the first 3 days of the study were agitated and their alarm response scored twice on the same day, once when they were actively foraging, and again as foraging was ending for the morning. All aggression and alarm scoring were conducted by one observer (BAC). While this observer was unaware of the damage score assigned to a colony, he did know whether a nest had some degree of damage. Colonies that were not active on a particular day were skipped, and sometimes rechecked. Because many colonies were less active during this period due to the circumstances of the drought, we obtained behavioral data from a total of 668 colonies, fewer than the number scored for damage. Of these, 645 had size measurements.

Spatial analysis

We tested whether nest damage or the response to disturbance was influenced by local colony density using two approaches. We calculated the nearest neighbor distances among colonies, and the number of colonies that were within a local neighborhood of 20 m. Colonies that were within 20 m of the edge of the study site were not used, which reduced the sample sizes (for damage, 779 and 241 colonies of size ≥ 10.0 and 12.0 respectively; for alarm/aggression response, 503 and 172 colonies). We calculated the results separately for colonies that were larger than size 10 and colonies that were larger than size 12. Thus, the local density would be the number of colonies of size 10 (or 12) or greater within 20 m of the focal colony and the nearest neighbor distance would be the distance to the nearest colony of size 10 (or 12) or greater. These two measures were correlated (-0.64 and -0.66 for colonies of size 10 and 12 respectively).

All *P. occidentalis* colonies on our study site are permanently marked and mapped. To address whether damage to colonies or the intensity of their response to disturbance varied spatially, we measured the spatial autocorrelation in the pattern of damage or in the response to disturbance using data from colonies of size class 10 or larger. We measured the correlation in these measures between colonies that are separated by increasing distances. We used a step size of 5 m out to a maximum of 100 m (beyond 100 m the spatial autocorrelation declined to insignificance). Measurements in all directions were weighted equally, thus the correlogram is non-directional. Because the number of colonies that are a given distance apart varies with distance, so do the confidence limits. We estimate the 95 % confidence limits of the spatial autocorrelation as: $\rho = \pm 2/\sqrt{N}$, where N is the number of pairs of colonies in the given distance interval (Chatfield, 1984).

Statistical analysis

Only one measurement of damage and of aggression/alarm response from a colony was used in the analyses. When a colony was scored more than once, only the first measurement was used. It is difficult to compare the aggression/alarm response of colonies that differ dramatically in the number of workers. As a consequence, we limited the comparison of colony damage and behavioral response to colonies that have reached reproductive size (size ≥ 10.0 , $N = 522$) or to the fully mature colonies (size ≥ 12.0 , $N = 185$). We calculated the Spearman rank-correlation coefficient between damage and behavioral response because both variables were measured on a categorical scale. For the spatial analyses, we calculated the Spearman rank-correlation between density or nearest neighbor distance and damage or response to disturbance. All tests were two-tailed. We inferred significant spatial autocorrelation when the autocorrelation fell outside of the 95 % confidence limits.

Results

The amount of damage varied considerably among colonies (Fig. 2). Larger colonies were more likely to be damaged compared to smaller ones ($\rho = 0.333$, $N = 1,272$, $p \ll 0.0001$). If pre-reproductive colonies (nest size < 10.0) are excluded, the relationship is still significant ($\rho = 0.101$, $N = 856$, $p = 0.003$). For those colonies that were measured twice, the second aggression score was typically slightly lower, but highly positively correlated with the first measure ($\rho = 0.681$, $p < 0.001$, $N = 246$). The intensity of the alarm/aggression response was significantly positively correlated with colony size, indicating that larger colonies

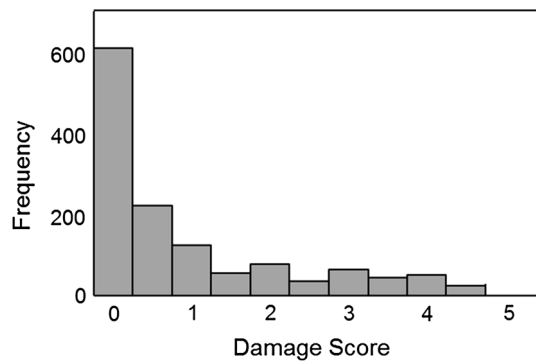


Fig. 2 The distribution of damage levels in 2012

responded more strongly compared to smaller colonies ($\rho = 0.276$, $N = 645$, $p < 0.001$).

In reproductively mature colonies (size ≥ 10.0 or greater), we found a significant negative correlation between damage score and aggression level ($\rho = -0.106$, $N = 522$, $p = 0.017$). Colonies with higher damage scores were less aggressive in response to disturbance. For colonies that were fully mature (size ≥ 12.0), the negative correlation between damage and aggression was stronger ($\rho = -0.237$, $N = 185$, $p = 0.003$).

The alarm/aggression response of colonies did not show a clear-cut relationship to measures of colony density. The level of aggression was positively correlated with colony density for reproductively mature colonies (size ≥ 10.0 , $\rho = 0.09$, $N = 503$), but negatively correlated with local density for fully mature colonies (size ≥ 12.0 , $\rho = -0.09$, $N = 172$). Nearest neighbor distance was not correlated with the alarm/aggression response. Colony damage levels

were more consistent. Damage was significantly correlated with density ($\rho = 0.15$, $N = 778$, $p < 0.001$) and nearest neighbor distance ($\rho = -0.12$, $p < 0.01$, $N = 778$) for reproductively mature colonies (size ≥ 10.0), but not for fully mature colonies (size ≥ 12.0 , $p > 0.3$, $N = 241$ for both measures).

The magnitude of the alarm/aggression response did not display spatial autocorrelation, a single point was outside the confidence limits. However, the extent of colony damage was non-randomly distributed (Fig. 3). The correlation coefficient for damage was outside the 95 % confidence interval until ~ 50 m, indicating significant spatial autocorrelation (Chatfield, 1984).

Discussion

Our results do not support the hypothesis that the intensity of response is induced by prior attacks on the colony. The induced aggression hypothesis predicted a positive correlation between damage and aggression, which we did not find. The significant negative correlation between damage and response is consistent with the protective aggression hypothesis: colonies that respond more aggressively to attacks on the nest cone are less likely to suffer damage. A negative correlation would also result if colonies that were severely damaged suffered the loss of much of their worker force, and were unable to respond as they might have previously. However, the majority of the colony is underground when attacks occur, and no colony in the study suffered subsurface damage. Consequently, it seems unlikely that damaged colonies suffered the loss of large

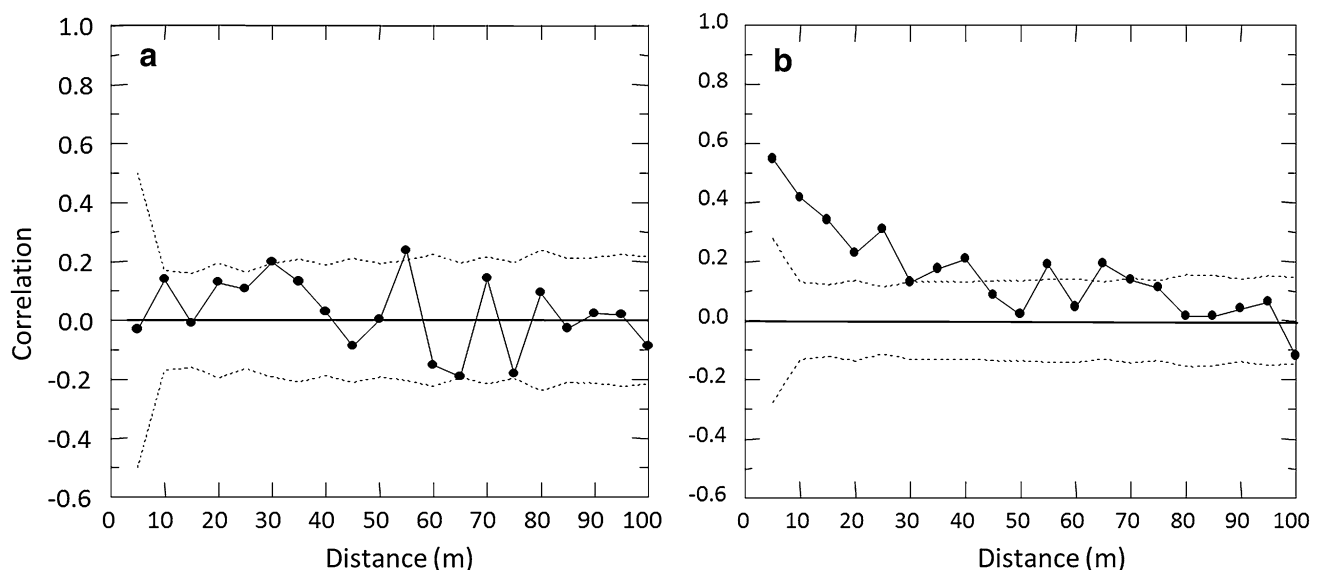


Fig. 3 Correlograms showing the level of spatial autocorrelation for alarm/aggression response (a) and the damage (b)

numbers of the worker force, although they may have lost considerable resources. Although our results are consistent with the Protective Aggression hypothesis, they could also result from another, unmeasured factor. Establishing a definitive causal relationship between aggression level and predator deterrence will require experimental work. Although damage to colonies showed strong spatial structure, the absence of spatial patterning in the defensive response is a prediction of the Protective Aggression hypothesis. Our findings suggest that aggression level is a colony phenotype which varies among colonies.

Why do colonies differ in their aggressive response level? The pattern we have observed suggests that intrinsic differences among colonies lead to differences in the intensity of their defensive behavior. Alternatively, the cause of these differences could be environmental, perhaps due to variation in diet. In some populations of *Linepithema humile*, prey-derived cuticular hydrocarbons mediate nestmate recognition (Buczkowski and Silverman, 2006). In *Temnothorax longispinosus* colony aggression level covaried with colony productivity and nest density in the field, a pattern that might be generated by variation in environmental quality (Modlmeier and Foitzik, 2011). In the laboratory, more aggressive colonies of *T. nylanderi* were less likely to move their nest in response to the presence of microparasites (Scharf et al., 2012), which could contribute to spatial patterns in the field. Patrollers of *Pogonomyrmex barbatus* are more aggressive to non-nestmates than other types of workers (i.e., foragers, Sturgis and Gordon, 2013), suggesting that variation in the numbers of a temporal caste could lead to among colony variation in behavioral response. Variation in foraging behavior and alarm response differed among colonies of *Messor andrei* (Pinter-Wollman et al., 2012), and was correlated with nest location, suggestive of an environmental component.

Alternatively, colony differences could be due to the genotype of the queen or the workers. In the laboratory, colonies of *P. occidentalis* show consistent differences in aggressive behavior that are correlated with matriline (Wiernasz et al. unpubl. data). Although a number of studies have documented differences among workers within a colony in their propensity to perform specific tasks or in other traits (see Jandt et al., 2014 for a review), the basis for these differences and the extent to which they are heritable are unknown. However, if highly responsive colonies are better able to deter predators, and suffer fewer losses of stored seeds and/or brood, they may have higher reproductive success in a given year, leading to higher fitness. In honeybees, consistent differences in a number of colony-level performance metrics, including colony defense, were posi-

tively associated with correlates of colony fitness (Wray et al., 2011).

The severity of damage was correlated with colony size, suggesting that large nests may be attacked preferentially because of their larger stores of resources (brood and seeds). Lubin et al., (1977) found that larger termite mounds were more prone to attack by anteaters than smaller mounds. Large nests may be easier to see and locate in the habitat, and it is possible that larger nests provide olfactory cues that enable predators to find them more easily. It is also possible that larger colonies, with their greater resource stores, represent a reward that is sufficiently large to offset the cost of being stung.

If the differences among colonies in their defensive responses result from intrinsic differences, there should be no spatial relationship to differences in disturbance, which was what we observed. However, the spatial pattern of damage suggests that the underlying cause has spatial structure. We did not observe any attacks on colonies; many were damaged earlier in the spring. Potential candidates for the destruction are two rodent species, kangaroo rats (*Dipodomys ordii*) and white-tailed prairie dogs (*Cynomys leucurus*), which are both resident at the study site. An ecologically equivalent species (*D. merriami*) has been shown to inflict damage to *P. occidentalis* mounds at least to damage category 3 in Northern Nevada (Clark and Comanor, 1973). Whether they are capable of more severe damage is unknown. Prairie dogs seeking protein could produce all the levels of damage that we observed. Both species are spatially localized, but in 2012, prairie dogs occurred at much lower densities than in the recent past because of an episode of plague in 2010. Identifying the specific cause of damage will require further work.

Although colonies varied in the strength of the defensive response, relatively few colonies were strongly aggressive. Widespread severe damage to nest mounds at our site only occurs during times of drought and food scarcity, when both ants and predators are likely to be food stressed. In typical years, rodents either may not attack colonies as frequently, or perhaps they attack less intensively, and are successfully repulsed. If the advantage of a strong defensive response is episodic, and if there is a cost to aggression otherwise, balancing selection may favor colonies that are less reactive to disturbance.

Acknowledgments We thank Lara Appleby, Drew Russey, and two anonymous reviewers for comments on an earlier version of the manuscript. We thank the Bureau of Land Management for protection of the harvester ant study area. Our long-term study of *P. occidentalis*, which provides the context for this work, has been supported by National Science Foundation Grants IOS-0344896 and IOS-1147418 to BJC and DCW.

References

- Buczowski G. and Silverman J. 2006. Geographical variation in Argentine ant aggression behaviour is mediated by environmentally derived nestmate cues. *Anim. Behav.* **71**: 327–335
- Buschinger A. and Maschwitz U. 1984. Defensive behavior and defensive mechanisms in ants. In: *Defensive Mechanisms in Social Insects* (Hermann H.R., Ed). Praeger Publishers, New York. pp 95–150
- Chatfield C. 1984. *The Analysis of Time Series*, 3rd ed. Chapman and Hall, New York
- Clark W.H. and Comanor P.C. 1973. The use of western harvester ant, *Pogonomyrmex occidentalis* (Cresson), seed stores by heteromyid rodents. *Biol. Soc. Nev. Occas. Pap.* **34**: 1–6
- Cole B.J. 1994. Nest architecture in the western harvester ant, *Pogonomyrmex occidentalis* (Cresson). *Insect. Soc.* **41**: 401–410
- Cole B.J. and Wiernasz D.C. 2000. Size and reproduction in the western harvester ant, *Pogonomyrmex occidentalis*. *Insect. Soc.* **47**: 249–255
- Crosland M.J.W. 1990. The influence of the queen, colony size and worker ovarian development on nestmate recognition in the ant *Rhytidoponera confusa*. *Anim. Behav.* **39**: 413–425
- Eddy T.A. 1970. Foraging behavior of the western harvester ant, *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae) in Kansas. Ph.D. dissertation, Kansas State University
- Francelino M.V., Mendonca A.A., do Nascimento R.R., de Mendonca F.C., da Silva E.L., de Freitas M.R.T., Cabral Jr C.R., da Silva C.E., Ribeiro J.H.S. and Santana A.E.G. 2008. Polyethism and nestmate recognition in the alarm reaction of *Atta* leaf-cutting ants. *Physiol. Ecol.* **33**: 37–42
- Hölldobler B. and Wilson E.O. 1990. *The Ants*. The Belknap Press of Harvard University Press, Cambridge.
- Hughes W.O.H., Howse P.E. and Goulson D. 2001. Mandibular gland chemistry of grass-cutting ants: species, caste and colony variation. *J. Chem. Ecol.* **27**: 109–124
- Jandt J., Bengston S., Pinter-Wollman N., Pruitt J., Raine N., Dornhaus A. and Sih A. 2014. Behavioral syndromes and social insects: personality at multiple levels. *Biol. Rev.* **89**: 48–67
- Lavigne R.J. 1969. Bionomics and nest structure of *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Amer.* **62**: 1166–1175
- Lubin Y.D., Montgomery G.G. and Young O.P. 1977. Food resources of anteaters (Edentata: Myrmecophagidae). I. A year's census of arboreal nests of ants and termites on Barro Colorado Island, Panama Canal Zone. *Biotropica* **9**: 26–34
- Modlmeier A.P. and Foitzik S. 2011. Productivity increases with variation in aggression among group members in *Temnothorax* ants. *Behav. Ecol.* **22**: 1026–1032
- Pinter-Wollman N., Gordon D.M. and Holmes S. 2012. Nest site and weather affect the 'personality' of harvester ant colonies. *Behav. Ecol.* **23**: 1022–1027
- Scharf I., Pamminger T. and Foitzik S. 2011. Differential response of ant colonies to intruders: attack strategies correlate with potential threat. *Ethology* **117**: 731–739
- Scharf I., Modlmeier A.P., Fries S., Tirad C. and Foitzik S. 2012. Characterizing the collective personality of ant societies: aggressive colonies do not abandon their home. *PLoS One* **7**: e33314 doi:10.1371/journal.pone.0033314
- Schmidt J.O. and Blum M.S. 1978. A harvester ant venom: chemistry and pharmacology. *Science* **200**: 1064–1066
- Schmidt J.O. 1990. Hymenopteran venoms: Striving towards the ultimate defense against vertebrates. In: *Insect Defenses: Adaptive Mechanisms and Strategies of Prey and Predators* (Evans D.L. and Schmidt J.O., Eds), SUNY Press, Albany. pp 387–419
- Schmidt P.J., Sherbrooke W.C. and Schmidt J.O. 1989. The detoxification of ant (*Pogonomyrmex*) venom by a blood factor in horned lizards (*Phrynosoma*). *Copeia* **1989**: 603–607
- Sturgis S.J. and Gordon D.M. 2013. Aggression is task dependent in the red harvester ant (*Pogonomyrmex barbatus*). *Behav. Ecol.* **24**: 532–539
- Taber S.W. 1984. *World of the Harvester Ants*. Texas A&M Univ Press, College Station
- Tsutsui N.D., Suarez A.V. and Grosberg R.K. 2003. Genetic diversity, asymmetrical aggression, and recognition in a widespread invasive species. *Proc. Natl. Acad. Sci. USA* **100**: 1078–1083
- Wiernasz D.C. and Cole B.J. 1995. Spatial distribution of *Pogonomyrmex occidentalis*: recruitment, mortality and over dispersion. *J. Anim. Ecol.* **64**: 519–527
- Wiernasz D.C. and Cole B.J. 2010. Patriline shifting leads to apparent genetic caste determination in harvester ants. *Proc. Natl. Acad. Sci. USA* **107**: 12958–12962
- Wilson E.O. 1971. *The Insect Societies*. Belknap Press of Harvard Univ Press, Cambridge
- Wray M.K., Mattila H.R. and Seeley T.D. 2011. Collective personalities in honeybee colonies are linked to colony fitness. *Anim. Behav.* **81**: 559–568