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Original Article

Social dynamics drive selection in cooperative associations of ant queens

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Social dynamics, the emergent effects of interactions within structured groups, play a key role in shaping social phenotypes and fitness. We examined the potential positive and negative effects of social dynamics in simple groups, by creating social groups of harvester ant queens with 2 alternate nest-founding strategies, solitary versus cooperative. We compared social interactions, survival, and nest productivity of pairs containing queens from the cooperative founding population, the normally solitary founding population, or mixed pairs of the 2 types. Expressed social phenotypes of queens in pairs depended strongly on the lineage of the other queen. Two behaviors, aggression and brood care, showed simple social dynamical effects. Aggression escalated in pairs of normally solitary queens, whereas queens in cooperative pairs coordinated brood output, leading to more efficient worker production. These dynamics had context-based fitness consequences, such that cooperative queens gained a survival advantage in cooperative pairs, but neither type of queen experienced an advantage or disadvantage in “mixed” associations. The interplay between social dynamics and fitness in these associations provides an empirical example of social selection. It captures a likely scenario of the transition to and the early evolution of cooperative living, in which cooperative individuals interact with solitary individuals who lack a priori strategies for cooperation or cheating.

Key words: ant foundress associations, cooperation, interacting phenotypes, pleometrosis, social dynamics, social phenotype, social selection.

INTRODUCTION

The phenotypes of both animals in social groups and the groups in which they live are shaped by the interactions of individuals within the group (Moore et al. 1997; Wolf et al. 1998; Agrawal et al. 2001; Fewell 2003; Bijma et al. 2007; McGlothlin et al. 2010). *Social dynamics* are nonlinear or self-organizational effects that amplify (or in some cases, dampen) the expression of social phenotypes (Camazine et al. 2001; Fewell 2003). Population evolution models designed to capture relationships between phenotype and selection rarely consider that social dynamics can generate emergent effects on social phenotype, with potentially profound effects on fitness. This has produced a mismatch between theoretical expectations for the evolution of cooperation and empirical data, especially for social systems such as communal groups, where relatedness cannot be used as an explanatory basis for the evolution of cooperation. A series of discussions on social selection have emphasized that social dynamics should be incorporated into models of social environment effects on phenotype and fitness, for example, as indirect genetic effects (West-Eberhard 1979; Moore et al. 1997; Wolf et al.

1998; Agrawal et al. 2001; Bijma et al. 2007; Bleakley and Brodie 2009; McGlothlin et al. 2010). However, doing so requires proximate analyses of how social environment can influence individual phenotype (Linksvayer 2006; Danielson-François et al. 2009; Wilson et al. 2009; Chenoweth et al. 2010; Teplitsky et al. 2010). In this study, we demonstrate that simple social dynamics within cooperative groups generate predictable nonlinear (nonadditive) effects on social phenotype, with outcomes for both individual- and group-level fitness, thus influencing social evolution.

Individual and group behaviors become a product of social dynamics when 1) the behavior of one individual changes the likelihood of performance by others and 2) these interactions generate feedback loops in which social effects on behavioral phenotypes are amplified (Moore et al. 1997; Wolf et al. 1998; Fewell and Page 1999; Camazine et al. 2001). Such effects can be quite simple algorithmically but with potentially large impacts on behavioral outcomes. These types of nonlinear interaction effects have been considered primarily in the context of escalated social conflict, including aggression, competition, and dominance (Agrawal et al. 2001; Danielson-François et al. 2009; Wilson et al. 2009), but more recently, these have been examined in the context of social cooperation, group coordination, and cohesion (Fewell 2003; Linksvayer 2006; Bleakley and Brodie 2009; Linksvayer et al. 2012), suggesting

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that they have the potential to influence social relationships more broadly. If so, social dynamics could inform evolutionary models of cooperation by increasing the expected likelihood of individual and group success for cooperative behavior, even in groups of unrelated individuals (Santos and Pacheco 2006; Bleakley and Brodie 2009; McGlothlin et al 2010).

The present study provides empirical evidence of both positive and negative effects from social dynamics on individual behavior and fitness, by comparing the effects of different social environments on the behavior, survival, and group productivity of queens from 2 different populations of harvester ants (*Pogonomyrmex californicus*). In 1 population, newly mated queens form cooperative associations to initiate nests (pleometrosis), whereas in the other, queens found nests solitarily (haplometrosis). Pleometrotic associations in this species comprise simple groups of unrelated individuals (Bernasconi and Strassmann 1999; Johnson 2004). Selection based on survival during early nest formation is intense; such a small proportion of foundresses survive that variation in survival for this phase of their life cycle represents a critical component of lifetime fitness (Hölldobler and Wilson 1990; Cole 2009). Unlike for most ant species (Bernasconi and Strassmann 1999; but see Helms and Helms Cahan 2012), the cooperative associations formed by pleometrotic *P. californicus* queens continue into colony adulthood and production of reproductive offspring (Johnson 2004); thus, they represent stable social associations that persist across the life of the resulting colony. The 2 populations are contiguous, with low levels of gene flow (Overson 2011).

Population differences in nest-founding behavior persist even when adult queens are placed together in a common environment, suggesting that the differences between the 2 populations have a genetic component (Helms Cahan and Fewell 2004; Johnson 2004; Jeanson and Fewell 2008; Overson et al. 2013). The potential genetic basis allows us to consider the interacting effects of genotype (as lineage or population of origin) and social environment in shaping the expression of social phenotypes. Haplometrosis is the most common nest-founding strategy within the genus and is probably the ancestral state (Johnson 2004). Classic models of social evolution consider noncooperation as a “social” strategy in which “defecting” individuals gain advantage (as per Maynard Smith 1964, 1982). However, we do not expect haplometrotic queens, as solitary and in the ancestral state, to have any a priori social strategy. Thus, our experimental context reflects conditions of early social evolution in which cooperative individuals enter a population of noncooperative individuals, but wherein noncooperators have not necessarily evolved mechanisms for social manipulation or cheating.

MATERIALS AND METHODS

Queen collection

Two sets of experiments were conducted in 2 successive years to observe queen behavior and survival in pleometrotic, haplometrotic, and mixed associations. All queens for both years were collected from San Diego County, CA, USA, immediately following mating flights in July. Collected queens had shed their wings and were walking on the ground or had just begun nest excavation. At the collection sites, queens were placed into individual ventilated 1.5-ml Eppendorf tubes and remained cool and moist during transfer to Arizona State University for experiments; queens were introduced into laboratory nests within 5 days from collection. In the laboratory, queens were weighed to the nearest 0.1 mg and

marked on the abdomen with paint (hot fuel-proof dope; Midwest AeroGloss) before placement into vertical observation nests. Nests consisted of 2 panes of glass (12.5 × 17.5 cm) separated by thin (0.32 cm) nylon strips and were filled with moist soil from one of the collection sites (Cibbet Flats, see below). Nest temperatures were maintained at approximately 28 °C, and fresh seeds (Kentucky blue grass) and dead *Drosophila melanogaster* were provided ad libitum.

On 1 July 2005, 278 pleometrotic queens were collected from the Cibbet Flats campground (Rissing et al. 2000), located 4 km north of the Cameron Fire Station (32°46′45″N, 116°26′56″W). Haplometrotic queens were collected from 3 areas within a contiguous haplometrotic population: Lake Henshaw, 4 km north of Morettis Junction, on 3 July (36 queens; 33°14′22″N, 116°45′46″W); Warner Springs, at the entrance to the Cleveland National Forest, on 1 and 2 July (16 queens; 33°17′07″N, 116°39′42″W); and the Oak Grove campground, on 2 July (4 queens; 33°23′16″N, 116°47′21″W). Queens from these 3 areas have not been observed to form foundress associations (Johnson 2004; Clark RM and Fewell JH, personal observation). The centers of the haplometrotic and pleometrotic populations are approximately 50 km apart, with patchy distributions in between. Nest site mapping and genetic analyses indicate a likelihood of low levels of gene flow between populations ($F_{ST} = 0.144$ based on 5 microsatellite loci; Overson 2011). In 2005, laboratory nests were created by pairing queens with another queen of similar mass from either the same population (pleometrotic–pleometrotic or haplometrotic–haplometrotic pairs, termed PP or HH, respectively; 51 and 17 nests, respectively) or the 2 different populations (pleometrotic–haplometrotic or “mixed” pairs, termed HP; 23 nests).

In the period 1–3 July 2006, 140 pleometrotic queens from Cibbet Flats and 140 haplometrotic queens from Lake Henshaw were collected. Queens were randomly assigned to 1 of 3 nest types: paired nests containing queens from the same population (PP pairs, 39 nests; and HH pairs, 40 nests) or paired nests containing queens from the 2 different populations (HP or “mixed” pairs; 39 nests). In this set of replicates, a subset of queens was also placed solitarily into nests (P or H; 20 nests of each). Queens were not paired by mass in 2006 to allow for a direct test of how size differences influence survival probability.

Survival, behavior, and nest productivity

Behavioral observations began immediately after introduction of queens into nests. Queen survival was noted daily up to the end of the observation period (20 days in 2005, and 45 days in 2006). Queen behavior was observed 8 times per day for 20 days in 2005 and for 5 days in 2006, with a minimum of 45 min between successive observations. During each observation, each nest was briefly scanned to note the occurrence of social interactions between queens (2006 only), all task-related behaviors, or inactivity. Types of social interactions included 1) nonantagonistic interactions, such as antennation of the other individual, allogrooming, or other contact (maintaining a distance of less than 1 body length away) and 2) antagonistic interactions, such as biting or dragging (grasping the other individual and walking or carrying her). Task-related behaviors consisted of 1) foraging (grasping or manipulating a seed or fly in the mandibles), 2) excavation (using mandibles to loosen or carry soil to the nest surface), and 3) brood care (laying an egg, manipulating brood, or standing over the brood pile). In 2006, nest productivity was additionally estimated by monitoring egg production and worker emergence up to day 50. Queens began to lay eggs on the second to third day after placement in nests. Beginning on the

fourth to the sixth day, all eggs present in each nest were counted, every 2 days, up to day 14, after which the eggs began hatching into larvae.

Data analysis

Queen survival was analyzed in SAS (version 9.1.3) by generating Kaplan–Meier survival curves, using a log-rank test to check for an overall treatment effect. Posthoc pairwise comparisons between treatments used Bonferroni-corrected log-rank tests. The influences of body size and excavation frequency on survival were assessed via *t*-tests in R (version 2.15.3; R Core Team 2013), by comparing the mean initial masses or excavation frequencies of surviving queens to queens that died by the end of the observation period (day 20 in 2005; day 45 in 2006). The excavation comparison used total excavation frequencies across the first 5 days of the observation period and excluded queens that died during the first 5 days. Within-treatment comparisons were subjected to Bonferroni correction.

Aggressive behavior, characterized by overt biting and stinging, was observed infrequently; therefore, the nests were classified according to whether any aggression had been observed, and the incidences of aggressive versus nonaggressive nests were compared across the 3 paired treatments (HH, HP, and PP) in 2006 by chi-square analysis. The remaining nonagonistic behavioral observations were converted to arcsine square-root-transformed proportions and compared across treatments with analysis of variance (Anova) in R. Egg and worker production levels were compared across social contexts with Anova in R.

RESULTS

Social context and survival

Survival curves for queens in haplometrotic (HH), pleometrotic (PP), and mixed pairs (HP) were compared for 20 days in 2005 and 45 days in 2006. Social environment significantly influenced queen survival in both years (Figure 1; for 2005, overall log-rank $\chi^2 = 1.56$, $P < 0.0001$; for 2006, log-rank $\chi^2 = 35.24$, $P < 0.001$; see Table 1 for Bonferroni-corrected pairwise comparisons). Individual queens in PP associations consistently had the highest individual survival rates, whereas queens in HH associations had the highest mortality. Individual queen survival in mixed (HP) pairs was not significantly different from that in pleometrotic pairs for 2005 and was intermediate between PP and HH in 2006. Individual haplometrotic and pleometrotic queens within HP pairs had similar survival rates. In the 2006 experiment, haplometrotic and pleometrotic queens were also placed alone in nests; survival rates for these queens were similar to each other and to survival of queens in HP pairs (Figure 1).

Differences in queen survival across social contexts were not explained by body size. In 2005, queens from the haplometrotic population were heavier than the pleometrotic queens ($\bar{x}_{\text{Hap}} \pm \text{standard error of the mean} = 14.5 \pm 0.2 \text{ mg}$; $\bar{x}_{\text{Pleo}} = 12.5 \pm 0.1 \text{ mg}$; $t = 7.71$, $N = 450$, $P < 0.0001$). However, initial mass did not predict survival ($t = 0.621$, $P = 0.536$). In 2006, haplometrotic and pleometrotic queens were similar in initial mass ($\bar{x} = 13.77 \pm 0.13$; $t = 1.75$, $N = 274$, $P = 0.081$). Although the surviving queens across treatments were heavier than the queens who died by day 45 ($\bar{x}_{\text{surv}} = 14.2 \pm 0.2 \text{ mg}$, $N = 105$; $\bar{x}_{\text{died}} = 13.5 \pm 0.2 \text{ mg}$, $N = 169$; $t = 2.49$, $P = 0.014$), survival rates did not differ by body mass within treatment groups and, in particular, did not predict which queen survived in mixed pairs (Table 2).

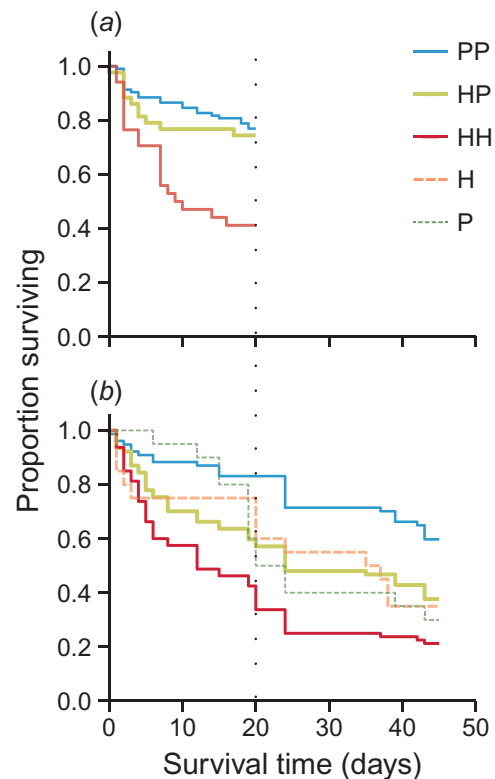


Figure 1

Queen survival patterns. Survival curves for queens paired with other queens from the same population (HH or PP), queens paired with others from an alternate population (HP), or queens maintained by themselves (H, P). (a) Survival across the first 20 days of colony founding in 2005. (b) Survival across the first 45 days of colony founding in 2006. Survival differed across different treatment groups (refer to text and Table 1 for full statistical comparisons).

Table 1

Pairwise comparisons of survival rates between social contexts

Year	Comparison	Log-rank χ^2	<i>P</i>
2005 ^a	Overall	19.56	<i>P</i> < 0.0001
	HH versus HP	7.42	<i>P</i> = 0.0064
	PP versus HP	0.4874	<i>P</i> = 0.4851
	HH versus PP	19.6508	<i>P</i> < 0.0001
	Within HP, H versus P	0.6582	<i>P</i> = 0.4172
	HH versus H within HP	2.9028	<i>P</i> = 0.0884
	PP versus P within HP	0.0002	<i>P</i> = 0.9898
2006 ^b	Overall	35.24	<i>P</i> < 0.0001
	HH versus HP	8.16	<i>P</i> = 0.0043
	PP versus HP	9.0639	<i>P</i> = 0.0026
	HH versus PP	34.0824	<i>P</i> < 0.0001
	Within HP, H versus P	1.8952	<i>P</i> = 0.1686
	HH versus H in HP	8.3892	<i>P</i> = 0.0038
	PP versus P in HP	12.5997	<i>P</i> = 0.0004
	Solitary P versus P in HP	0.1882	<i>P</i> = 0.6644
	Solitary H versus H in HP	0.7296	<i>P</i> = 0.3930
	HH versus Solitary H	2.5304	<i>P</i> = 0.1117
PP versus Solitary P	7.1182	<i>P</i> = 0.0076	

Comparisons that are significant after Bonferroni correction are in bold (<0.01).

^aSurvival comparisons across days 1–20.

^bSurvival comparisons across days 1–45.

Table 2

Pairwise comparisons of initial masses of queens that survived versus queens that died in different social contexts during the early stages of nest founding (up to day 45 of nest establishment)

Treatment group	Mass (mg) \pm standard error (sample size)		<i>t</i>	df	<i>P</i>
	Died	Survived			
HH	13.3 \pm 0.3 (63)	14.1 \pm 0.68 (17)	1.13	20.7	0.27
HP	13.7 \pm 0.3 (48)	14.6 \pm 0.4 (29)	1.67	53.5	0.10
PP	13.7 \pm 0.4 (31)	13.9 \pm 0.2 (46)	0.58	49.3	0.56
H	12.3 \pm 0.6 (13)	13.6 \pm 0.9 (7)	1.17	11.6	0.27
P	14.6 \pm 0.5 (14)	14.8 \pm 1.5 (6)	0.15	6.3	0.89

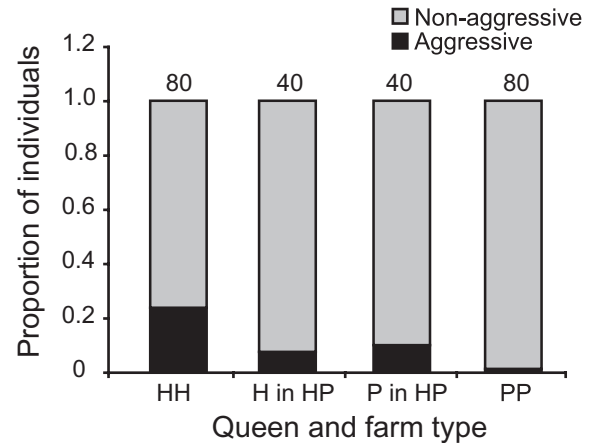
Agonistic interactions and survival

Social interactions were monitored in the 2006 replicates to determine whether agonistic or cooperative behaviors were influenced by social context and whether social phenotype was related to survival. Although overt aggression was infrequent (a total of 27 queens in 21 nests), it was not randomly distributed (Figure 2; $\chi^2 = 21.03$, $P < 0.0001$): the majority of aggressive incidents occurred in HH nests (19 queens in 14 nests). We observed only 7 queens behaving aggressively among the mixed pairs (4 pleometrotic and 3 haplo-metrotic queens in 6 nests) and only 1 aggressive event in a PP pair. Almost all cases of overt aggression were followed by the death of at least 1 queen (20 of 21 nests).

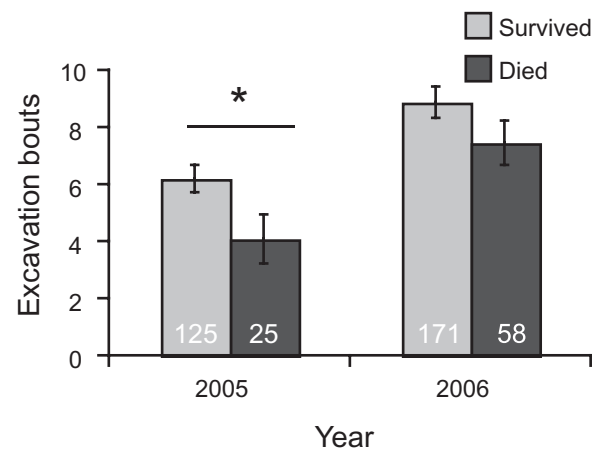
Potential nonagonistic effects on survival

Nonagonistic social contact rates were similar across the 3 pair types (2006 data only; Anova on arcsine square-root-transformed proportions of observations: $F = 1.25$, degrees of freedom [df] = 2, 231, $P = 0.29$). Queens spent an average of $32 \pm 1\%$ of all observations in contact with each other (allogrooming, antennating, or in close proximity), and in all nests, they maintained a single, shared brood pile. Differential mortality was not explained by differences in task performance. In previous experiments, excavation had been associated with increased mortality (Fewell and Page 1999; Helms Cahan and Fewell 2004; Jeanson and Fewell 2008). However, queens from both years who survived up to day 20 actually performed more excavation bouts in the first 5 days (when almost all excavation occurs) than queens who died during this time, although this trend was not significant for 2006 (Figure 3; for 2005, $t = 2.15$, $P = 0.037$; for 2006, $t = 1.50$, $P = 0.14$).

Foraging occurred infrequently and was not associated with individual survival probability. There were no differences in foraging rates across treatments in 2005 (Anova on arcsine square-root-transformed observations: $F = 1.55$; df = 4, 147; $P = 0.19$). In 2006, however, foraging rates did vary, but posthoc analyses showed only weak differences between treatments ($F = 3.33$; df = 4, 224; $P = 0.011$). Solitary pleometrotic queens foraged the least (0.9 ± 0.3 times), whereas solitary haplo-metrotic queens foraged the most (2.7 ± 0.9 times); paired queens in all 3 treatments foraged at intermediate levels (1.9 ± 0.2 for HH, 2.0 ± 0.3 for HP, and 1.3 ± 0.2 for PP). Initial foraging frequencies did not predict who survived and who died by the end of 20 days in either year (for 2005, $t = 0.208$, df = 28, $P = 0.84$; for 2006, $t = 1.09$, df = 114, $P = 0.28$).

**Figure 2**

Frequency of observed aggression. Proportion of individuals in each pair type for which at least 1 aggressive behavior was observed. Sample sizes are given by numbers above the columns.

**Figure 3**

Frequency of excavation behavior. Mean number (\pm standard error of the mean) of excavation bouts observed across the first 5 days of colony founding for queens that survived up to at least the twentieth day of the experiment compared with queens that died before day 20. Significant differences ($P < 0.05$) are indicated by asterisks, and sample sizes are noted inside the bars.

Nest productivity and social context

In 2006, initial worker production and egg production (number of eggs produced in days 1–14) were compared across social contexts. Worker production per nest across social treatments was compared only for those cases in which at least 1 of the 2 queens survived ($n = 25$, 21, and 14 for PP, HP, and HH, respectively). Although worker numbers varied, there was no significant effect of nest type on the number of workers produced by day 50 (Figure 4b; $F = 1.57$, df = 2, 57, $P = 0.217$). Note, however, that sample sizes were too small by day 50 for sufficient power to definitively test this question. Time from nest initiation to the emergence of the first workers was constant across nests, including pairs and single queens, suggesting this component of productivity is not socially flexible ($F = 1.746$, df = 4, 71, $P = 0.1494$, $n = 76$, mean = 40 days).

To measure group investment in worker production, initial egg production was compared across treatments for pairs in which both

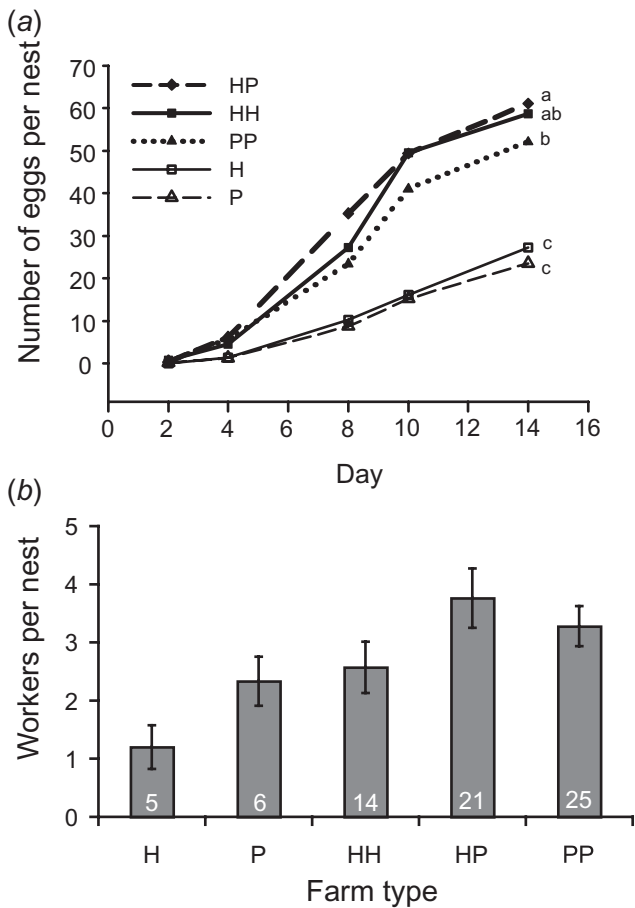


Figure 4 Brood and worker production during nest development. (a) Number of eggs present in different nest types across the early stages of nest founding, before larval development began. Numbers that were significantly different between nest types ($P < 0.05$ using Tukey’s honestly significant difference test) are indicated by different letters to the right of the lines. Sample sizes were 20 (HP), 6 (HH), 32 (PP), 15 (H), and 18 (P). (b) Mean number of workers per nest (\pm standard error of the mean) on Day 50, which were produced by paired queens (HH, HP, and PP) or queens by themselves (H and P). Sample sizes are indicated inside the bars.

queens survived the full 14-day egg-laying period ($n = 33, 20,$ and 6 for PP, HP, and HH, respectively). Despite similarities in the timing and number of workers produced, initial egg production varied across treatments (Figure 4; randomized block Anova, social treatment with time as blocking factor, $F = 7.789, df = 2, 288, P < 0.001$). As perhaps expected, pairs laid approximately twice as many eggs per nest as solitary queens. However, PP pairs produced fewer eggs than HP pairs, with HH pairs producing intermediate number of eggs. This affected the efficiency of worker production. Surviving haplo-metrotic associations reared approximately 0.04 workers for each egg observed at day 14, versus 0.06 for pleometrotic associations.

DISCUSSION

The question of how social context shapes individual phenotype and fitness is critical to, but often unanswered in, models of social evolution (West-Eberhard 1979, 2003; Agrawal et al 2001; Nowak et al. 2010; Wade et al. 2010). In this study, we measured the influence of social dynamics on survival and productivity of harvester

ant queens that employ 2 distinct social strategies, forming cooperative associations of unrelated individuals versus initiating nests solitary (Rissing et al. 2000; Johnson 2004; Helms Cahan and Fewell 2004). Our results demonstrate that social context can act as an important driver of social phenotype and fitness and that self-organizational social dynamics can mediate such effects at both the individual and the group levels.

Foundational game theoretical models of social evolution make the explicit assumption that noncooperation provides an individual fitness advantage, whereas cooperation benefits the group as a whole (Axelrod and Hamilton 1981; Maynard Smith 1982). The behavioral outcomes and consequent fitness advantages in our groups deviate from these fitness payoffs, especially in the mixed associations. Models of cooperation (even when incorporating contingent strategies) generally assume that individual payoffs for cooperators will decrease below those of noncooperators in mixed associations (Taylor and Nowak 2007; Brown and Vincent 2008; Antal et al. 2009). However, the survival payoffs for queens in our mixed associations were neutral relative to other pairs—lower than those for pleometrotic pairs, equivalent to the solitary condition, for both queen types. Queens in groups where both members had a cooperative evolutionary history (PP) had survival rates 2 times higher than those in normally noncooperative pairs (HH). The high survival in pleometrotic groups was also coupled with more efficient brood production, such that individual and group payoffs were maximized when both group members cooperated. Because the 2 queen types survived equally well alone, we suggest that in pairs, the differential survival outcomes were driven primarily by the social partner.

Why do our results deviate from such a key expectation of social evolution? Most models of the evolution of cooperation treat both cooperation and noncooperation as social strategies, by assuming that noncooperators have the social tools in place to evaluate and respond to social contingencies. However, at the transition from solitary to social living, normally solitary individuals are unlikely to have a priori mechanisms in place to cheat or win in a social context. If so, this changes our theoretical consideration of noncooperation from a scenario in which noncooperation is an advantage to one in which nonsocial individuals can be taken advantage of.

Amplification of social phenotype: conflict escalation

The survival and productivity outcomes for foundresses across social contexts were driven proximately by self-organizing social dynamics. Self-organizational effects on social behavior have usually been considered as they relate to group-level behavior in complex societies (Camazine et al. 2001; Jeanson and Deneubourg 2009). However, nonlinear effects of social interactions also shaped individual behavior in these simple groups. Aggression, in particular, manifested as conflict escalation and was dependent on the behavior of social partners. Conflict escalation is a good fit with simple self-organizational models of reinforcement by positive feedback (Camazine et al. 2001; Jeanson and Deneubourg 2009) and is similar in interaction effects to social selection models of dominance (Agrawal et al 2001; Moore et al. 2002).

Social regulatory mechanisms for behavioral coordination and cheating

Social selection can also act to enhance behavioral coordination, and thus cooperation, if social interactions generate individual and/or group benefits. This seems to have occurred for brood

production, where queens in pleometrotic pairs were able to produce the same number of workers while investing in fewer eggs. This suggests that pleometrotic queens have evolved some mechanism for social regulation or policing, in which they adjust production and/or consumption of brood relative to production by other queens (Holman et al. 2010).

If so, this adjustment could provide a critical benefit to both the queen and the group. Brood production in ants is metabolically expensive (Wheeler and Buck 1995), and *P. californicus* queens have low fat stores relative to other *Pogonomyrmex* species (Hahn et al. 2004). Queens only produce sterile workers during colony initiation and early development, so brood production at this stage represents a cost for individual queens and a benefit to the group as a whole. We know from direct observation (across multiple experimental contexts and video capture) and from genetic data (Fewell JH, in preparation) that both queens in *P. californicus* associations produce eggs and that eggs are consumed by their own mothers, other queens, and their sibling larvae, allowing opportunities to socially regulate brood production.

This sets up the somewhat ironic situation in which “cooperative” behaviors can become “cheating” with different social partners. Pleometrotic queens who regulate brood output can potentially take advantage of haplometrotic partners who lack similar regulatory mechanisms. In support, previous work on *P. californicus* found that pleometrotic queens in mixed pairs are more likely than haplometrotic queens to engage in brood care and to remain near the brood (Jeanson and Fewell 2008). Also consistent with this scenario, haplometrotic *Messor pergandei* queens placed in associations with pleometrotic queens have higher relative weight loss and mortality (Helms Cahan 2001). These data emphasize that if we define cooperation as behaviors with ultimate benefit for individuals and social partners, cooperation becomes dependent on social context.

The social environment as an indirect genetic effect

Our findings are compatible with recent models emphasizing the role of indirect genetic effects on selection of social traits (Wolf 2003; Linksvayer 2006; Bijma et al. 2007; Bijma and Wade 2008; McGlothlin et al. 2010). Social group composition can have a profound and heritable influence on an individual's phenotype; thus, it can be considered a source of indirect genetic effects that influence social evolution (Moore et al. 2002; Wolf 2003; Bijma and Wade 2008; McGlothlin et al. 2010). Recognition of this can enrich theoretical models of social evolution from fixed effects to contingencies that incorporate social context in more realistic ways.

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REFERENCES

- Agrawal AF, Brodie ED 3rd, Wade MJ. 2001. On indirect genetic effects in structured populations. *Am Nat.* 158:308–323. doi: 10.1086/321324
- Antal T, Ohtsuki H, Wakeley J, Taylor, PD, Nowak MA. 2009. Evolution of cooperation by phenotypic similarity. *Proc Natl Acad Sci USA.* 106:8597–8600. doi: 10.1073/pnas.0902528106
- Axelrod R, Hamilton WD. 1981. The evolution of cooperation. *Science.* 211:1390–1396. doi: 10.1126/science.7466396
- Bernasconi G, Strassmann JE. 1999. Cooperation among unrelated individuals: the ant foundress case. *TREE.* 14:477–482. doi: 10.1016/S0169-5347(99)01722-X
- Bijma P, Muir WM, Ellen ED, Wolf JB, Van Arendonk JAM. 2007. Multilevel selection 2: estimating the genetic parameters determining inheritance and response to selection. *Genetics.* 175:289–299. doi: 10.1534/genetics.106.062729
- Bijma P, Wade MJ. 2008. The joint effects of kin, multilevel selection and indirect genetic effects on response to genetic selection. *J Evol Biol.* 21:1175–1188. doi: 10.1111/j.1420-9101.2008.01550.x
- Bleakley BH, Brodie ED 3rd. 2009. Indirect genetic effects influence anti-predator behavior in guppies: estimates of the coefficient of interaction ψ and the inheritance of reciprocity. *Evol.* 63:1796–1806. doi: 10.1111/j.1558-5646.2009.00672.x
- Brown JS, Vincent TL. 2008. Evolution of cooperation with shared costs and benefits. *Proc R Soc London, Ser B.* 275:1985–1994. doi: 10.1098/rspb.2007.1685
- Camazine S, Deneubourg J-L, Franks NR, Sneyd J, Theraulaz G, Bonabeau E. 2001. Self-organization in biological systems. Princeton (NJ): Princeton University Press.
- Chenoweth SF, Rundle HD, Blows MW. 2010. Experimental evidence for the evolution of indirect genetic effects: changes in the interaction effect coefficient, ψ , due to sexual selection. *Evol.* 64:1849–1856. doi: 10.1111/j.1558-5646.2010.00952.x
- Cole B. 2009. The ecological setting of social evolution: the demography of ant populations. In: Gadau J, Fewell JH, editors. *Organization of insect societies: from genome to sociocomplexity.* Cambridge (MA): Harvard University Press. pp. 74–104.
- Danielson-François AM, Zhou Y, Greenfield MD. 2009. Indirect genetic effects and the lek paradox: inter-genotypic competition may strengthen genotype \times environment interactions and conserve genetic variance. *Genetica.* 136:27–36. doi: 10.1007/s/10709-008-9297-z
- Fewell JH. 2003. Social insect networks. *Science.* 301:1867–1870. doi: 10.1126/science.1088945
- Fewell JH, Page RE. 1999. The emergence of division of labour in forced associations of normally solitary ant queens. *Evol Ecol Res.* 1:537–548.
- Hahn DA, Johnson RA, Buck NA, Wheeler DE. 2004. Storage protein content as a functional marker for colony-founding strategies: a comparative study within the harvester ant genus *Pogonomyrmex*. *Physiol Biochem Zool.* 77:100–108. doi: 10.1086/380214
- Helms KR, Helms Cahan S. 2012. Large-scale regional variation in cooperation and conflict among queens of the desert ant *Messor pergandei*. *Anim Behav.* 84:499–507. doi: 10.1016/j.anbehav.2012.05.019
- Helms Cahan S. 2001. Cooperation and conflict in ant foundress associations: insights from geographical variation. *Anim Behav.* 61:819–825. doi: 10.1006/anbe.2000.1671
- Helms Cahan S, Fewell JH. 2004. Division of labor and the evolution of task sharing in queen associations of the harvester ant *Pogonomyrmex californicus*. *Beh Ecol Soc.* 56:9–17. doi: 10.1007/s00265-003-0746-5
- Hölldobler B, Wilson EO. 1990. *The ants.* Cambridge (MA): Belknap of Harvard University.
- Holman L, Dreier S, d’Ettorre P. 2010. Selfish strategies and honest signaling: reproductive conflicts in ant queen associations. *Proc R Soc London, Ser B.* 277:2007–2015. doi: 10.1098/rspb.2009.2311
- Jeanson R, Deneubourg J-L. 2009. Positive feedback, convergent collective patterns, and social transitions in arthropods. In: Gadau J, Fewell JH, editors. *Organization of insect societies: from genome to sociocomplexity.* Cambridge (MA): Harvard University Press. pp. 460–482.
- Jeanson R, Fewell JH. 2008. Influence of the social context on division of labor in ant foundress associations. *Beh Ecol.* 19:567–574. doi: 10.1093/beheco/am018
- Johnson RA. 2004. Colony founding by pleometrosis in the semiclaustal seed-harvester ant *Pogonomyrmex californicus* (Hymenoptera: Formicidae). *Anim Behav.* 68:1189–1200. doi: 10.1016/j.anbehav.2003.11.021
- Linksvayer TA. 2006. Direct, maternal, and sibsocial genetic effects on individual and colony traits in an ant. *Evolution.* 60:2552–2561. doi: 10.1554/06-011.1
- Linksvayer TA, Fewell JH, Gadau J, Laubichler MD. 2012. Developmental evolution in social insects: regulatory networks from genes to societies. *J Exp Zool (Mol Dev Evol).* 318:159–169.

- Maynard Smith J. 1964. Group selection and kin selection. *Nature*. 201:1145–1147. doi: 10.1038/2011145a0
- Maynard Smith J. 1982. *Evolution and the theory of games*. New York (NY): Cambridge University Press.
- McGlothlin JW, Moore AJ, Wolf JB, Brodie ED 3rd. 2010. Interacting phenotypes and the evolutionary process. III. Social evolution. *Evol*. 64:2558–2574. doi: 10.1111/j.1558-5646.2010.01012.x
- Moore AJ, Brodie ED 3rd, Wolf JB. 1997. Interacting phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. *Evol*. 51:1352–1362.
- Moore AJ, Haynes KF, Preziosi RF, Moore PJ. 2002. The evolution of interacting phenotypes: genetics and evolution of social dominance. *Am Nat*. 160:S186–S197. doi: 10.1086/342899
- Nowak MA, Tarnita CE, Wilson EO. 2010. The evolution of eusociality. *Nature*. 466:1057–1062. doi: 10.1038/nature/09205
- Overson RP. 2011. Causes and consequences of queen-number variation in the California harvester ant *Pogonomyrmex californicus*. Tempe (AZ): Arizona State University. p. 104.
- Overson RP, Gadau J, Clark RM, Pratt SC, Fewell JH. 2013. Behavioral transitions with the evolution of cooperative nest founding by harvester ant queens. *Beh Ecol Soc*. doi: 10.1007/s00265-013-1618-2
- R Core Team. 2013. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Rissing SW, Johnson RA, Martin JW. 2000. Colony founding behavior of some desert ants: geographic variation in metrosis. *Psyche*. 103:95–101. doi: 10.1155/2000/20135
- Santos FC, Pacheco JM. 2006. A new route to the evolution of cooperation. *J Evol Biol*. 19:726–733. doi: 10.1111/j.1420-9101.2005.01063.x
- Taylor C, Nowak MA. 2007. Transforming the dilemma. *Evolution*. 61:2281–2292. doi: 10.1111/j.1558-5646.2007.00196.x
- Teplitsky C, Mills JA, Yarrall JW, Merilä J. 2010. Indirect genetic effects in a sex-limited trait: the case of breeding time in red-billed gulls. *J Evol Biol*. 23:935–944. doi: 10.1111/j.1420-9101.2010.01959.x
- Wade MJ, Wilson DS, Goodnight C, Taylor D, Bar-Yam Y, de Aguiar MAM, Stacey B, Werfel J, Hoelzer GA, Brodie ED 3rd, et al. 2010. Multilevel and kin selection in a connected world. *Nature*. 463:E8–E9. doi: 10.1038/nature08809
- West-Eberhard MJ. 1979. Sexual selection, social competition, and evolution. *Proc Am Philos Soc*. 123:222–234.
- West-Eberhard MJ. 2003. *Developmental plasticity and evolution*. New York: Oxford University Press.
- Wheeler DE, Buck NA. 1995. Storage proteins in ants during development and colony founding. *J Insect Physiol*. 41:885–894. doi:10.1016/0022-1910(95)00028-S
- Wilson AJ, Gelin U, Perron M-C, Réale D. 2009. Indirect genetic effects and the evolution of aggression in a vertebrate system. *Proc R Soc London, Ser B*. 276:533–541. doi: 10.1098/rspb.2008.1193
- Wolf JB. 2003. Genetic architecture and evolutionary constraint when the environment contains genes. *Proc Natl Acad Sci USA*. 100:4655–4660. doi: 10.1073/pnas.0635741100
- Wolf JB, Brodie ED 3rd, Cheverud JM, Moore AJ, Wade MJ. 1998. Evolutionary consequences of indirect genetic effects. *Trends Ecol Evol*. 13:64–69.