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The energetic cost of reproductive conflicts in the ant *Pachycondyla obscuricornis*

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Abstract

In a variety of social animals, individuals can secure reproductive rights through aggressive dominance. Direct individual benefits of aggression are widely recognized, but underlying costs affecting group productivity, and thus indirect benefits, are less clear. Costs of aggressive regulation of reproduction are especially important in small social insect colonies, where individual workers could potentially dominate male production. We estimated the energetic costs associated with the regulation of worker reproduction in the ponerine ant *Pachycondyla obscuricornis*, using the total CO₂ emission of a colony as a measure. The level of CO₂ emission of 12 experimental colonies varied significantly during five periods with varying levels of aggression and egg-laying. Overall, CO₂ emission increased with the degree of fighting in a colony, but was not associated with differences in egg-laying. Aggressive regulation of reproduction and the formation of a dominance hierarchy thus pose an energetic cost to the colony. Furthermore, workers reduce their work-activities immediately after experimental orphaning, giving a further cost to the colony. These costs might influence the outcome of conflicts over male production in ants. This paper presents the first quantification of energetic costs of aggressive behavior regulating reproduction in ants.

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1. Introduction

Social insects display a distinct reproductive division of labor, in which only one or a few individuals reproduce (queens), while the majority of nestmates perform helping tasks (workers) (Wilson, 1971). This division of labor is often founded on a morphological specialization of queens and workers for their respective tasks. Recent studies have shown, however, that behavioral interactions may also play an important role in the regulation of reproduction and in the resolution of conflicts over reproduction (Heinze, 1990; Ortius and Heinze, 1995; Visscher and Dukas, 1995; Gobin et al., 1999; Foster and Ratnieks, 2001; Foster et al., 2002; Monnin et al., 2002; Whitfield, 2002).

This is especially true in species with a limited queen-worker dimorphism, enhancing potential conflict over access to reproduction, and small colony sizes, where a single individual can behaviorally control all its nestmates (Heinze et al., 1994; Peeters, 1997). Here, ritualized or overtly aggressive interactions lead to the formation of dominance hierarchies, in which dominant females acquire a disproportionately high share of reproduction. Such hierarchies are known from queens and mated workers (gamergates) of several ant species (Medeiros et al., 1992; Sommer and Hölldobler, 1992; Ito, 1993; Sommer and Hölldobler, 1995; Liebig et al., 2000; Gobin et al., 2001), but may also occur among unmated workers (Bourke, 1988a; Peeters and Tsuji, 1993; Heinze et al., 1997; Monnin and Peeters, 1999). Here, workers compete to produce males from unfertilized eggs.

Unmated workers typically do not lay eggs in the presence of a queen and in most species worker hierarchies are only formed after the queen's death (Bourke,

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1988a; Heinze, 1996; Heinze et al., 1997). Only in a few cases has worker aggression (and egg laying) been regularly observed in colonies still having a queen (Cole, 1981; Franks and Scovell, 1983; Gobin and Ito, 2003).

Clear dominance relationships among workers in the presence of a reproductive queen might be advantageous in that they ensure a quick start of egg-laying after orphaning. The widespread restriction of worker aggression to orphaned colonies suggests, however, that in most cases aggression is suppressed in the presence of the queen because it is associated with high costs. Dominant individuals tend to spend less time on brood care or other essential tasks in the colony (Cole, 1986; Monnin and Ratnieks, 1999). Furthermore, aggression often interrupts brood care by subordinate workers, effectively reducing the number of brood tended per unit of time (Cole, 1986). Apart from its effect on time-budgets, the aggressive formation and maintenance of hierarchies requires extra energy investment, either from dominants to ensure their status or from subordinates trying to avoid attacks by dominants (Franks and Scovell, 1983; Senar et al., 2000). If such costs significantly lower colony efficiency, we expect to find no aggression in the presence of a queen.

We propose to estimate costs associated with worker aggression by comparing energy expenditure and work investment between queenright and artificially orphaned colonies. CO₂ emission rate is a reliable measure of metabolic rate (Eckert et al., 1988) and frequently used to measure energetic costs of specific behaviors in individual insects (Nielsen, 1986; Roces and Lighton, 1995). This technique can be expanded to measure CO₂ emission of entire colonies or experimental groups (Kleineidam and Roces, 2000).

We measured energetic costs related to the formation of worker hierarchies in colonies of the ponerine ant *Pachycondyla obscuricornis*. This species has various features that facilitate direct recording of energy consumption and activity: their large body size allows an easy observation of behavioral interactions and assessment of respiration, while at the same time small natural colony size allows for realistic experimental groups. After orphaning, fights over reproductive dominance start quickly, with a few workers dominating reproduction after a few weeks (Oliveira and Hölldobler, 1991). We aimed to estimate costs related to the aggressive establishment of worker reproduction by comparing metabolic rates, levels of aggression, and general activity in colonies at various periods before and after queen removal.

2. Methods

Colonies of *Pachycondyla obscuricornis* were collected from their nests in October 1999 at La Selva Bio-

logical Station in Costa Rica. Colonies contained median 38 workers (quartiles 19 and 59, $n = 27$). Stock colonies were housed in plaster nests (about $10 \times 15 \times 2$ cm³) in plastic containers, connected to a 20×20 cm² foraging area. Live crickets and sugar water were provided as food three times per week, while the plaster was moistened once a week. For our measurements, we created 19 experimental colonies by reducing the number of workers in stock colonies so that they finally contained one dealate queen and 20 workers each. Experimental colonies were kept in a climatized room at 25 °C and 50% relative air humidity. For CO₂ measurements, 12 experimental colonies were housed in Plexiglas nest chambers ($7 \times 10 \times 2$ cm³). Each nest chamber had an inlet and outlet tube for airflow and two entrance holes (diameter 13 mm), which could be sealed airtight with rubber stoppers. Moist cotton was provided in the chamber through one entrance, while the other entrance connected the chamber to a 10×10 cm² foraging arena. For CO₂ measurements, we chose not to include brood to avoid variations in colony metabolism due to larval growth. All eggs laid during the duration of the experiment were removed. The remaining seven experimental colonies, with 10 eggs and 10 larvae each, were housed in plaster nests covered with glass plates to allow observation of changes in activity of the workers.

We performed one main manipulation on the experimental colonies, the removal of the queen, and allowed a natural development of worker aggression and egg-laying. Preliminary experiments led us to expect a peak in aggression around day 3 after queen removal, while egg-laying started two weeks later (Table 1). CO₂ measurements and activity observations were planned to reflect diverse patterns in aggression and egg-laying. On day 0, we observed twice (Table 1) to detect the direct effects of queen removal.

CO₂ emission rates were measured over 10 min bouts at each observation point (Table 1). Bout duration was chosen to avoid effects of the discontinuous gas exchange cycle of individual ants, which lasts 1–2 mins (Vogt and Appel, 1999; Duncan and Newton, 2000). Any inter-individual aggression (antennal boxing or

Table 1

Expected fighting and egg-laying activity as a function of the presence (+Q) or absence (–Q) of the queen, over different time periods at which both the metabolic rate measurements and activity records were performed, i.e., just before and after queen removal, as well as 1, 3 and 21 days later

	Day 0	Day 0	Day 1	Day 3	Day 21
condition	+Q	–Q	–Q	–Q	–Q
Expected:					
Fighting	–	–	±	+	–
Egg-laying	–	–	–	–	+

jerking) occurring during our measurement was recorded. Before the start of CO₂ measurements, the moist cotton was removed from the nest chamber and both entrances were sealed airtight. The nest chamber was then connected to a CO₂ analyzer and a pump. Open-flow respirometry was used to measure CO₂ production of experimental colonies. CO₂-free air was drawn through the chamber at a flow rate of 300 ml/min⁻¹. For details on the high-resolution respirometry system used (Sable System TR-3, resolution 0.01 ppm CO₂), including temperature control and correction to S.T.P.D. conditions see (Lighton, 1990). After thirty minutes of airflow, measurements started. Nest boxes were weighed with ants before and empty after each measurement, so total mass of workers could be determined. CO₂ production was calculated per total worker mass for each colony.

To quantify general activity, 7 experimental colonies with brood were videotaped for 30 mins at each observation point (Table 1). The time budgets, accurate at one-second intervals, for all behavioral acts were recorded for one randomly selected worker per colony. As we did not know the metabolic cost of specific behaviors, we analyzed only the difference between activity and inactivity. Ants were considered inactive only when they remained totally motionless. The period of activity was then divided by 3 to get an estimate of activity per 10 min bout, as in CO₂ measurements. Activity-corrected metabolic rate for a 10 min bout was then calculated by dividing CO₂ emission with median activity.

3. Results

No aggressive interactions, neither antennal boxing nor jerking, occurred among workers in the presence of the queen. Aggression, at first mostly antennal boxing, started one day after orphaning (Fig. 1(A)). The frequency of boxing and jerking differed significantly between observation periods (Friedman ANOVA, $\chi^2_1 = 60$, $p < 0.05$, $N = 12$). Three days after orphaning, jerking and boxing occurred significantly more frequently than on the other days (Tukey HSD, $p < 0.01$). At this point, no eggs were seen in the colonies. Generally, aggression decreased after a few weeks, so, as expected, jerking and boxing occurred only at low frequencies on day 21 after orphaning.

The metabolic rate of the colony, measured as its specific CO₂ production, showed a more peculiar pattern (Fig. 1(B)), but again with a significant effect of observation period (Friedman ANOVA, $\chi^2_1 = 17.06$, $p < 0.05$, $N = 12$). CO₂ emission did not change significantly from queen presence to a few hours after queen removal (LSD posthoc comparison, NS), but all subsequent changes were significant (LSD posthoc, $p < 0.05$). One

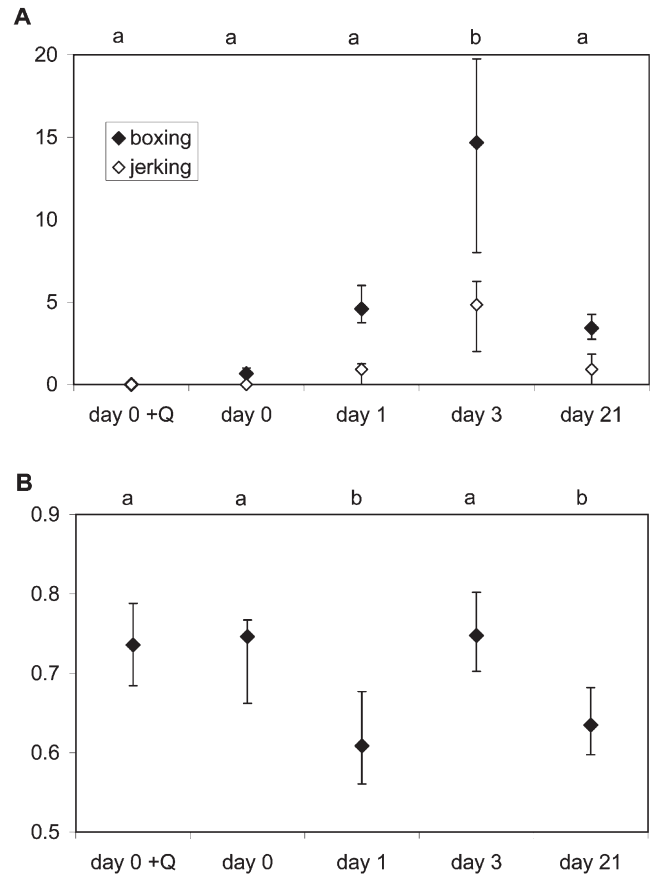


Fig. 1. Aggressive interactions and metabolic rate in 12 experimental colonies containing 20 workers of the ant, *Pachycondyla obscuricornis* at various periods, just before and on specific days after experimental queen removal (see text for details). Values are medians with bars representing upper and lower quartiles. Different lettering above data-points indicates significant differences in both variables boxing and jerking. (A) average occurrence of antennal boxing and jerking per 10 minutes per experimental colony of 20 workers. (B) average CO₂ emission in ml CO₂ per hr per mg ant mass.

day after orphaning, CO₂ emission was at its minimal level. A significant increase followed on day 3 after orphaning. This value did not differ from queenright CO₂ production (LSD posthoc, NS). Three weeks after orphaning, the metabolic rate dropped again to the level of day 1. The peak in metabolic rate on day 3 corresponds to the peak in aggression, but the low value on day 1 was puzzling. This decrease could not be caused by a reduction in total respiration by removing the queen, as we did not find a significant difference on day 0, before and after orphaning. Longer absence of the queen apparently modified worker behavior in such a way that the colony's metabolic rate dropped.

To correct for these possible changes in worker behavior, we measured the activity of a worker each in seven additional experimental groups, at the same periods used for CO₂ measurements. Activity level, measured as the proportion of time a worker moved, dropped significantly after queen removal (Friedman ANOVA,

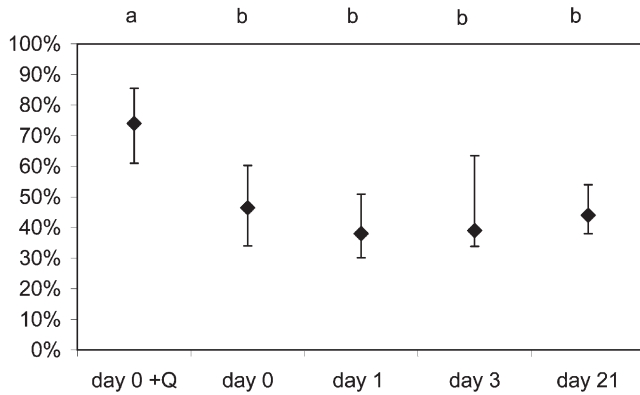


Fig. 2. Activity of workers in 7 experimental colonies at various periods before and after queen removal. The percentage of time that a worker is active per 10 min bout is plotted (median with upper and lower quartiles). Different lettering above datapoints indicate significant differences.

$\chi^2_1 = 12.69$, $p < 0.05$, $N = 7$, LSD post hoc comparison ($p < 0.05$), reaching its lowest value on day 1 (less than 4 mins per 10 mins, Fig. 2). Workers were immobile most of the time even during periods of aggressive fights. Division of CO_2 measurements by activity gave activity-corrected metabolic rates that peaked on the same day as the frequency of aggressive interactions (Fig. 1(A), Fig. 3). Activity-corrected metabolic rates had a significantly positive correlation with the frequency of antennal boxing (GLM MANOVA, $SS = 74.8$, $F_1 = 8.5$, $p < 0.05$), but not with jerking ($F_1 = 0.09$, NS), while there was no linear effect for period (days of measurement, $F_1 = 0.0001$, NS). Jerking might have a large metabolic cost, but the behavior is too erratic to find an effect in our measurements. The presence of egg-layers had no measurable effect on the colony's metabolic rate, since both effective CO_2 production and activity-corrected CO_2 production decreased on day 21.

In sum, we identified two costs associated with con-

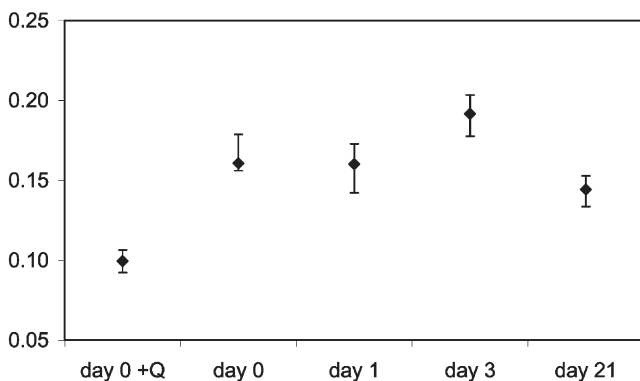


Fig. 3. Activity-corrected metabolic rate in 12 colonies of *P. obscuricornis*, representing CO_2 emission in ml CO_2 per hour per mg ant mass divided by activity per 10 min bout for each period before and after queen removal.

licts over reproduction in *P. obscuricornis*. High levels of aggression in the colony are associated with higher total energy expenses. Simultaneously, workers spend more time immobile and thus less time working for the colony. Intuitively, both factors are likely to affect colony productivity in the long term.

4. Discussion

After the queen is removed from colonies of the ant, *Pachycondyla obscuricornis*, workers start to aggressively compete for egg laying. The number of aggressive encounters increased on day 1 after queen removal, had a maximum on day 3, and decreased again once the dominance relations among workers had become stable and egg-laying had started (day 21 in Fig. 1(A)). This is a typical pattern for aggressive establishment of dominant egg-layers in ants (Cole, 1981; Franks and Scovell, 1983; Peeters and Tsuji, 1993; Gobin et al., 2001). The rise and fall in frequency of aggressive behavior appears to be reflected in colony-level CO_2 emissions between day 1 and day 21 after orphaning and therefore also with metabolic rate.

In general, higher metabolic rates during hierarchy formation can be associated with dominant individuals actively searching for competitors and frequently participating in agonistic encounters (Roskaft et al., 1986) and subordinates being stressed by aggression and attempting to escape (Senar et al., 2000). In addition, altered metabolic rates may result from behavioral changes related to differences in colony organization before and after queen removal. We cannot distinguish between these causes, as we measured CO_2 production of entire experimental colonies. Ideally, the CO_2 emission of interacting pairs should be measured to determine the costs of certain types of behavior and interactions. However, to do so was impossible, as isolated pairs of individuals never interacted—the social context of the colony is obviously needed for the behavioral expression of conflict. Nevertheless, regardless of the exact cause for high CO_2 emission, our results show that the colony as a whole consumes more energy during periods of fighting than during periods with minimal aggression, giving an extra cost to the colony. Egg development had no apparent colony-level energetic cost, as CO_2 levels were still low three weeks after orphaning. It is however possible that a slow process such as oocyte development remains undetected in our measurements, especially when egg-laying rates are low at the start of worker reproduction.

One peculiar aspect of our data, the drop in colony-level CO_2 emission just after queen removal, suggested that overall activity of workers lowered quickly after orphaning. Indeed, activity rates of randomly chosen workers decreased significantly just 3 hs after orphaning

and remained low throughout the observation period (Fig. 2). Removing the queen thus has a clear effect on worker behavior, apparently reducing their inclination to work for the colony. Cole (1986) demonstrated that dominant workers work indeed less than they potentially could, but our results show that workers change their activity even before dominance ranks are established. Individual workers could potentially trade-off available metabolic reserves between working and fighting. A reduction in work performance is a cost to the colony in itself and might account for the observed reduction in energy consumption. If we correct our CO₂ emission data with the observed activity rates, we still find an overall correlation with aggression levels, and the maximum for the entire observation period now coincides with maximal aggression (Fig. 3).

In sum, fighting to gain dominance is thus costly to the colony, both in energetics, as the colony spends more energy overall, as in work performance, as workers carry out less work. These costs decrease once dominance relationships stabilize and egg-laying starts.

Costs of aggression at the colony level may ultimately explain why hierarchies are typically formed only after queen removal. Because young individuals tend to become dominant over older nestmates (Higashi et al., 1994; Monnin and Peeters, 1999), the emergence of young workers in queenright, perennial colonies would constantly disrupt the stability of the worker hierarchy and lead to a constant expression of high levels of aggression. Costs inflicted by such worker fighting would presumably decrease offspring production of the colony and considerably reduce the inclusive fitness of workers (Bourke, 1999). Worker hierarchy formation and worker reproduction should be counter-selected when the costs to colony productivity outweigh direct benefits (Kikuta and Tsuji, 1999; Monnin and Ratnieks, 2001; Foster et al., 2002). Only when the colony's queen dies and the entire colony is therefore doomed, workers should maximize their fitness by attempting to raise sons (Bourke, 1988b). Physical aggression of workers in the queen's presence is consequently relatively rare in ants. Only in *Leptothorax allardycei*, the costs associated with worker fighting appear to be too low to inhibit worker reproduction (Cole, 1986). When workers can mate, however, dominant workers can replace gamergates, thus gaining increased benefits of parentage of both female and male offspring. Consequently, we expect expression of aggression at a wider range of costs. Indeed, physical aggression of workers in the presence of gamergates is common in ponerine ants with worker mating (Ito and Higashi, 1991; Ito, 1993; Monnin and Peeters, 1999; Monnin and Ratnieks, 1999).

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