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Research article

Patterns of buzz running, a pre-swarming behavior, in the Neotropical wasp *Parachartergus colobopterus*

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Summary

Knowing whether workers or queens control reproduction is vital for understanding social evolution in insects. Among epiponine wasps, a significant part of reproduction is the production of daughter swarms. One of the first behaviors indicative of swarming is the buzzing run – a behavior in which a wasp runs rapidly back and forth on the natal nest, bumping into nestmates while traversing a significant portion of the nest. In this study we investigated whether the buzz runners in *Parachartergus colobopterus* were queens who were not reproducing on the current nest (reproductive losers), or workers, as evidence from other species indicates. We suspected that loser queens, who may be anxious to swarm in order to increase reproductive output, could be the buzz runners because *P. colobopterus* swarms are primarily composed of queens who are not the mothers of the accompanying workers. Our results show that workers are the buzz runners, and that queen number does not influence the level of buzz running on a colony. We also found that buzz running is more common on large colonies with low worker relatedness, the sort that are likely to produce swarms. However, buzzing runs also occurred sporadically on smaller nests. The small nests had more nest parasites (mostly flies) than the large nests, and the parasite dance, which is very similar to the buzzing run, was seen only on these nests.

Introduction

Social insect colonies are more likely to fit the superorganism paradigm if collective worker interests control key features of colony reproduction (Queller and Strassmann, 1998). Here we focus on one key stage of reproduction: new colony production. Successful reproduction in social wasps requires the production of new colonies in addition to the production of males and queens. In the subfamily Polistinae,

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there are two main strategies by which new colonies are founded – independent founding and swarm founding (Jeanne, 1980). In independent-founding species, one or more inseminated queens initiate the colony without the aid of workers. In swarm-founding wasps the colony is started by a swarm composed of both workers and queens, and workers outnumber queens (Richards and Richards, 1951; Forsyth, 1978; Richards, 1978; Jeanne, 1980; West-Eberhard, 1982). Swarming is a coordinated and synchronous migration of individuals in which the swarm follows chemical trails laid down by scouts to the new site (Naumann, 1975; Jeanne, 1981). The swarm-founding wasps include all of the nearly 200 species of the tribe Epiponini, the dominant eusocial wasps in the neotropics (Jeanne, 1991a and references therein).

Large, multiple-queen colonies produce swarms (Richards and Richards, 1951; Solís et al., 1998; Strassmann et al., in press). The colony cycle begins when many workers and queens form a swarm and relocate to a new nest site. The queens in the swarm are rarely the mothers of the accompanying workers (Strassmann et al., 1998). This is either because they did not reproduce on the original colony (i.e, they were reproductive losers) or because the original colonies had such large numbers of queens that workers were unlikely to be daughters of the few queens joining the swarm. On the new nest the queens begin to produce workers and the nest grows. New queen production does not usually occur, however, until queen number is subsequently reduced to one (West-Eberhard, 1978; Strassmann et al., 1991; Queller et al., 1993). New swarm production is independent of queen production and occurs when colonies have many workers (Strassmann et al., 1998). This separation allows for new colony production to occur when it is most ecologically advantageous (Strassmann et al., 1997; Strassmann et al., 1998).

The independence of new colony production and queen production allows for a certain flexibility in colony initiation, making it difficult to predict which group on the nest sets the timing of swarming. The workers in the colony, who possess information on prey abundance, nest site availability, and worker-to-larvae ratios can use environmental and social cues to determine the optimal time for swarming. Also, if there are queens who are reproductive losers in the original colony they may have an interest in provoking swarming in order to increase their chances of reproducing. However, worker and queen interests in swarming will not necessarily be in conflict since neither party is likely to seek to initiate a swarm that contributes to either the new or the original colony's failure.

Prior to reproductive swarming there are definitive changes in wasp behavior which can be used as indicators that a colony is about to produce a swarm. The most widely observed of these behaviors is the buzzing run (Naumann, 1970; Jeanne, 1975; Forsyth, 1978; West-Eberhard, 1982). A buzzing run is characterized by frantic, jerky running by one to many wasps on the nest. It resembles the parasite alarm behavior (Naumann, 1970; West-Eberhard, 1982) which can trigger nest evacuation. The parasite alarm is a jerky movement performed in response to parasitoids such as flies, moths or wasps that lay eggs in the nest, producing young that devour the nest brood (West-Eberhard, 1969; Strassmann, 1981). This behavior occurs in many social wasps including non-swarming genera such as *Polistes* (West-Eberhard, 1969; Strassmann, 1981). Buzz running is also similar in form and function to the "Schwirrlauf" of *Apis* honeybees (Naumann, 1970; West-Eberhard, 1982), which is performed by scouts and incites the colony to swarm (Wilson, 1971). These similarities and other indicators suggest that the buzz runners on a wasp colony are associated with the induction of swarming.

West-Eberhard (1982) described buzz running as the most widespread and characteristic pre-swarming behavior described by observers. The behavior has been observed occurring from at least a week before swarming up to the actual day of the event (Naumann, 1970; Forsyth, 1981). Naumann (1970) assigned buzzing run activity to the worker caste in *Protopolybia acutiscutis*. Forsyth (1978) marked wasps from *Polybia occidentalis* nests and found that active foragers were the individuals exhibiting the buzzing run (breaking run) behavior. Observations by West-Eberhard (1982) also demonstrated that in *Metapolybia aztecoides* and *Synoeca surinama* the majority of wasps seen buzz running were old foragers. In *M. aztecoides* some of the buzz runners were younger workers, but none were queens. Although the evidence indicates that workers, specifically foragers, are the individuals performing buzz running, queens may also display the behavior in an attempt to facilitate swarming, particularly if they might reproduce more on a new colony then they did on the original one.

In this study, we determined whether workers or queens are the buzz runners in *Parachartergus colobopterus* in order to shed light on who initiates pre-swarming behaviors in this species. Also, in order to learn more about when buzz running occurs on a colony and to further investigate the relationship between buzz running and swarming, we compared the frequency with which the behavior occurred on large, potentially swarming colonies to that on small colonies where swarming was unlikely. Finally, to examine the effects of buzz running on colonies, we studied the responses of other colony members to buzz runners. We conducted all of our studies in the rainy season when swarming is most frequent in this species (Strassmann et al., 1997 and unpublished observations).

Materials and methods

Videotaping and collection

We studied 10 *Parachartergus colobopterus* colonies in Maracay, Venezuela (10° 16′ N 67° 36′ W, altitude 445 m) at the Universidad Central de Venezuela in the middle of the wet seasons of 1993 and 1995. We studied the 5 small colonies (<250 wasps: V20-8, V20-12, V20-14, V20-38, V20-42) from 29 July to 6 August 1993, and studied the 5 large colonies (>340 wasps: V21-1, V21-2, V21-8, V21-13, V21-18) from 29 July to 6 August 1995. First, we marked as many individuals as possible on all 10 nests with dots of Testors© enamel over two mornings. Then, to videotape each nest we pulled back the nest envelope in order to expose the combs. We videotaped each colony over two days so our samples of behavior provide a detailed picture of a brief period of time. Upon completion of videotaping, we collected all of the colonies (the nests and the wasps) and stored the wasps in liquid nitrogen or dry ice for transport back to the lab for photographing, dissection, and genetic analysis.

Behavioral observations

In order to facilitate the identification of specific individuals on tape, we photographed and numbered each wasp collected. We watched videotapes from all nests for instances of the buzzing run behavior, as well as instances of the parasite alarm/dance because of its similarity to the buzzing run. We identified as many of the actors as possible by their marks. We watched a total of 137 hours of tape; hours of tape per nest ranged from 10 to 18 hours, with an average of 13.7 hours per nest. We also determined the number of individual buzz runners and parasite dancers on each nest, as well as the frequency of the two behaviors. Unmarked wasps were included in the behavior counts. A single buzzing run or parasite dance event was classified as each instance in which a wasp exhibiting either behavior appeared in view of the camera. If the wasp stopped and then resumed the behavior on screen, we recorded the behavior as two separate episodes.

During a buzzing run a wasp typically runs around rapidly on the nest buzzing its wings and bumping into other wasps. The wasp runs from comb to comb, going from either the top of the nest to the bottom, or from one side of the nest to the other. In the case of the parasite dance, however, the wasp flaps its wings and pivots from side-to-side on the comb which harbored the parasite. Often the buzzing run and parasite dance are indistinguishable. In the most distinct cases, buzzing run movements are more expansive; the wasp circles the entire nest, bumping into nest mates. On the other hand, the movements of the parasite dance are more restricted. After the wasp attacks and expels the nest parasite, or the parasite leaves on its own, the wasp circles the affected cells. In many cases however, the movements of the wasp are not as clear cut. Often the behavior starts out on a single comb, suggestive of parasite dancing, but over time the wasp expands its movements until the behavior coincides with that expected of the buzzing run. Also, we observed some cases of buzzing runs in which activity was concentrated on a single comb similar to parasite dancing.

To obtain an unambiguous means of separating at least some parasite dancing from buzz running, we classified as parasite dancing all jerky runs performed with a nest parasite present on the nest. These parasites were usually flies that lay eggs in the nest, but included parasitic wasps. A beetle, which is not a nest parasite, also elicited the parasite alarm response. This method of distinguishing between the two behaviors probably led to some behaviors that were actually parasite dancing being classified as buzz running. The reverse is improbable.

Caste determination and colony characteristics

We dissected all adults collected on each nest. We differentiated between males and females by using the presence of either ovaries or testes and then dissected all females further to determine caste. Dissections evaluate age, ovarian development of females, and insemination status. We determined relative age from the degree of sclerotization of the gastral sternite (Gastreich et al., 1993). Older wasps are more heavily sclerotized and therefore darker than younger workers. We assessed ovarian development by counting the number of mature eggs, the number of nearly mature eggs, and the length of the longest oocyte. Females with sperm in their spermatheca were classified as queens, and females lacking sperm were classified as workers (Strassmann et al., 1991; Gastreich et al., 1993). We were not able to dissect all of the wasps for which there were behavioral data because some had disappeared by the time the nest was collected. Also, to determine colony size characteristics we counted the number of cells, combs, and pupae on the collected nests (see Table 1).

Relatedness estimation

We estimated the genetic relatedness among workers on each colony using polymorphic DNA microsatellites (Strassmann et al., 1996a). We genotyped 24 workers from nests V21-1, V21-2, V21-8, and V21-18, and 40 workers from nest V21-13 at the following 7 trinucleotide microsatellite loci: Paco3107TAG, Paco3155TAG, Paco3304CAT, Paco3305CAT, Paco3417AAT, Paco3436AAT, and Paco3457AAT (Strassmann et al., 1996b). Fifty-seven workers from nest V20-8 were genotyped at all but one (Paco3436AAT) of the loci listed above and 20 workers from nest V20-14 were genotyped at all but 2 (Paco3304CAT and Paco3305CAT) of these loci. For nest V20-38 we genotyped 68 workers at 10 loci: the 7 listed above in addition to Paco41TAG, Paco3117TAG, and Paco3434AAT (Strassmann et al., 1996b). The methods used were standard for our laboratory (Strassmann et al., 1996a).

For estimating relatedness we used the Macintosh computer program Relatedness 4.2c (Goodnight and Queller, 1996). Single individuals from 36 different colonies from the same study site were included in the calculations to obtain a more precise estimate of background allele frequencies. Colonies were weighted equally in the estimations and standard errors were determined by jackknifing over loci.

Table 1. Summary of nest characteristics for 10 *Parachartergus colobopterus*

Nest	#wasps	#queens	#workers	#males	#combs	#cells	#pupae	R ± S.E. (N)*
V21-1	444	55	389	0	13	1400	444	0.23 ± 0.10 (24)
V21-2	889	54	835	0	14	2158	621	0.14 ± 0.08 (24)
V21-8	614	80	522	12	12	1523	590	0.21 ± 0.07 (24)
V21-13	345	6	313	26	15	1248	476	0.14 ± 0.05 (40)
V21-18	634	79	554	1	9	2030	431	0.31 ± 0.07 (24)
V20-8	64	5	59	0	9	314	90	0.32 ± 0.08 (57)
V20-12	104	4	99	1	6	597	90	
V20-14	71	1	70	0	6	317	73	0.45 ± 0.06 (20)
V20-38	69	1	68	0	4	164	64	0.31 ± 0.06 (68)
V20-42	205	0	205	0	10	503	97	

* Worker relatedness ± standard error (sample size).

Statistical analyses

We performed regression analyses to determine the relationship between buzzing run frequency (buzzing runs/hour) and six different colony characteristics. In a second set of regressions we looked at the relationship between per capita buzz running (buzzing runs/hour/wasp) and the same six colony characteristics. For all of these analyses, both the small and the large colonies were analyzed together although they were collected in different years. We did this because there were not enough points to separate the colonies by year. Both sets of colonies were collected at the exact same time of year, and because these data were originally collected for another study we specifically selected small colonies in one year and large colonies in the other, although both types of colonies were present in both years.

Results

We observed a total of 128 buzz runners on 10 colonies, and 18 of these were identified and dissected. Unidentifiable wasps were either not marked distinctively enough for precise identification with photographs, unmarked, or not collected. Although some markings could not be used for identification with the photographs, they were sufficient to distinguish among the buzz runners on videotape. Only two nests (V21-2 and V20-42) had more than one unmarked buzz runner (see Table 2), and these wasps were each classified as separate individuals. Of the 18 buzz runners identified, 17 (94%) were old workers and 1 was a young worker. None of these workers were inseminated and none had any ovarian development. Since queens make up a significant proportion of the females on each nest it is unlikely that this result is due to sampling error. Thus, it is the workers and not loser queens who perform buzzing runs. A regression analysis of queen number and buzz running frequency (Fig. 1 A) showed that colonies with more queens do not have more buzz running ($p = 0.19$), further validating this point.

Table 2. Number of buzz runners and parasite dancers, the frequencies of the two behaviors, and the per capita frequency of buzz running on 10 colonies

Nest	#buzzing runners (# unmarked)	#buzzing runs/hour	#buzzing runs/hour/ worker	#parasite dancers (max. # seen simultaneously)	parasite dances/hour
V21-1	14 (0)	9.64	0.025	0	0
V21-2	30 (3)	23.60	0.028	0	0
V21-8	6 (0)	6.90	0.013	0	0
V21-13	7 (0)	10.90	0.035	0	0
V21-18	15 (1)	5.06	0.009	0	0
V20-8	2 (1)	5.03	0.085	0	0
V20-12	1 (0)	1.15	0.012	3	3.85
V20-14	1 (0)	0.38	0.006	10 (6)	1.61
V20-38	0	0.00	0.000	1	0.33
V20-42	9 (5)	3.28	0.016	29 (12)	4.16

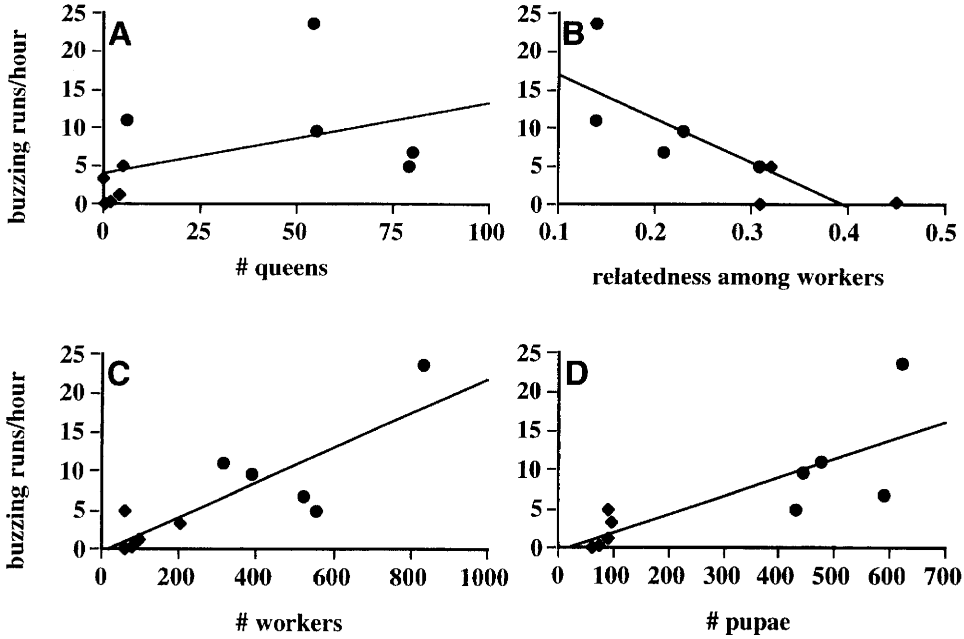

Figure 1. Diamonds represent small nests with n < 250 individuals and circles represent large nets with > 340 individuals. (A) Regression plot showing no relationship between queen number and buzzing run frequency; $Y = 3.965 + 0.092X$; $R^2 = 0.202$. (B) Regression plot showing a negative relationship between buzzing run frequency and worker-worker relatedness; $Y = 22.62 - 56.393X$; $R^2 = 0.634$. (C–D) Regression plots showing a positive correlation between buzz running frequency and two indicators of colony size; (C) # workers: $Y = -0.348 + 0.022X$; $R^2 = 0.694$; (D) # pupae: $Y = -0.445 + 0.024X$; $R^2 = 0.620$

We were not able to determine the caste of the parasite dancers because many wasps usually performed the behavior simultaneously making individual identification difficult. This was particularly true on nests V20-14 and V20-42, so in Table 2 we include the maximum number of parasite dancers seen at one time on these 2 nests as a more conservative estimate of their respective numbers of parasite dancers.

We observed buzzing runs on all 10 nests, but saw parasite dancing only on the 5 small colonies (Table 2). There were more buzz runners on the large nests. The large colonies had between 7 and 30 buzz runners, while four of the five small colonies had between 0 and 2 buzz runners (Table 2). The one small colony with 9 buzz runners was the largest of the small colonies (n = 205). This colony had 29 parasite dancers, which made us think that some of the cases recorded as buzz running on this nest could have actually been parasite dancing (i.e., responses to parasites that were not visible on videotape).

A minority of workers participated in buzz running, ranging from 1% to 4% per colony. On the four small colonies where we observed parasite dancing behavior, more parasite dancers were seen than buzz runners. On the small colonies 1%–14% of the workers engaged in parasite dancing. We found no evidence that buzz runners successfully incited other wasps on the nest to take up the behavior.

No buzz runner ever induced nestmates to buzz run; the females the buzz runners contacted did not start to buzz run. Two wasps were seen buzz running simultaneously on only 5 occasions. And although they were buzz running at the same time, there was no indication that one was induced to start buzz running by the other, or that the behavior was cooperative. The two wasps were never in direct contact and were often on opposite sides of the nest. In contrast, responses to parasites were often cooperative with as many as 12 individuals either responding directly to a single parasite or responding to other parasite dancers.

Although buzz runners did not incite actual swarming during the 2 to 4 day course of our observations of each colony, our findings do corroborate the idea that buzz running is a pre-swarming behavior. One of the nests examined (V21-2) exhibited other pre-swarming behaviors such as brood removal and occasional cannibalism (West-Eberhard, 1982), which suggested that swarming was imminent. This nest also had the most buzz runners and the highest frequency of buzz running (see Table 2). This result supports the possibility that the buzzing run behavior increases as a colony prepares to swarm.

Using four different indicators of colony size – numbers of workers, pupae, combs, and cells (see Table 1), we found that the number of buzzing runs per hour increased with increasing colony size ($p<0.02$), and that colony size explained 57% to 69% of the variance in buzz running (Fig. 1C–F). There was no clear relationship between buzzing runs/hour/worker and colony size. Buzzing runs/hour is probably the more important measure, however, because buzz running is a colony-level phenomenon and each worker may sense and respond to the level of buzz running on its particular nest. We also found that genetic relatedness among workers was negatively correlated with the frequency of buzzing runs ($p<0.02$), and that relatedness among workers explained 63% of the variance in buzz running (Fig. 1B). Low worker relatedness is indicative of multiple queens (Hamilton, 1972; Queller et al., 1988) so again these results indicate that buzz running is more common on nests that are likely to swarm, i.e., large nests with multiple queens. In general, the nests with the higher values for worker relatedness had lower queen numbers, which was expected. Some of the colonies, including all of the small ones, seem to have already gone through some queen reduction so the number of queens that produced the workers on these nests is higher than the number of queens present when we collected the colonies.

Discussion

Most of the females who performed buzzing runs in this study were old workers. It is highly unlikely that queens buzz run in *Parachartergus colobopterus.* Age polyethism in the worker caste is prevalent in social wasps with large colony sizes (Wilson, 1971), and particularly defined among the swarm-founding Polistinae (Jeanne, 1991b). Temporal division of labor among workers in which young workers carry out tasks on the nest and old workers forage, has been described in several swarm-founding species including *Protopolybia acutiscutis* (Naumann, 1970), *Protopolybia exigua*, *Agelaia pallipes* (Simões, 1977), and *Polybia occidentalis* (Forsyth, 1978; Jeanne et al., 1988). Since the evidence indicates that buzz runners in *P. colobopterus* are foragers, which in other species are the individuals that select new nest sites (Jeanne, 1991 a), they are probably associated with swarm induction. Numbers of queens have no influence on the level of buzz running on a colony, further supporting the view that buzz running is controlled by the worker caste.

Foragers are sensitive to local changes in food availability, hence they are susceptible to ecological pressures resulting from environmental variability in abundance of prey, water, and nectar. As a result, environmental change may trigger pre-swarming behaviors. Swarming peaks during the rainy season (Strassmann et al., 1997, 1998) when pressures to swarm are highest due to an increase in local resources. Although all of our observations were conducted over a month into the rainy season and we saw buzz running on most of our nests, we did not see the behavior escalate into swarming. This could have been a consequence of the short period of time over which the nests were observed.

The colonies which produce swarms are larger than average and they have multiple queens (Strassmann et al., in press); worker-to-larvae ratios are high and as a result the loss of workers to a swarm is not a large detriment to the parental colony. Low relatedness among workers is another characteristic of colonies producing swarms (Solís et al., 1998; Strassmann et al., 1998). Our results show that buzz running occurred more often on large nests with low worker relatedness, supporting a possible link between buzz running and swarming.

We did, however, observe some buzz running on small colonies and suggest that these buzzing runs may have been a response to parasitism and thus better classified as parasite dancing. Our results show a clear difference in the number of nest parasites on large versus small nests. Since the method we used to distinguish between buzzing running and parasite dancing was so conservative (parasite dancing reported only in instances where a parasite was seen) it is likely that the parasite dancing on the small nests was higher than reported. Parasite dancing could have been directed toward flies and parasitic wasps in the act of approaching the nest. Our observations indicate that several behaviors formally recorded as buzzing runs on the small nests because of the absence of a parasite, would have been more suitably classed as parasite dancing. It is also possible that the large nests had some parasite dancing even though parasites were never seen. In any case, the results imply that the parasite load of small nests is greater. This apparent asymmetry is important because nest parasitism can induce absconding swarming (Richards and Richards, 1951; Naumann, 1975; Chadab, 1980), which is the evacuation of a nest by the entire colony. Naumann (1975) studied absconding swarms exclusively and observed the buzzing run behavior, indicating that this behavior precedes both types of swarming.

The unusually high parasite load of smaller colonies suggests that large group size is advantageous. Alexander (1974) hypothesized that aggressive group defense is one of the primary benefits of group living, which suggests reasons why the smaller *P. colobopterus* nests may be more sensitive to parasitism. One of the reasons is that smaller colonies have fewer individuals to defend the nest, resulting in parasites preferentially attacking smaller nests. It is also possible that the same number of parasites visit both nest types, but the larger colonies are more successful at deterring these parasites before they alight on the nest. Since the small and large nests were taped in different years, however, year-to-year variation may be a confounding variable in determining relative parasite load. There is also the possibility that removing the nest envelope in order to videotape the nests made the colonies more susceptible to parasites. However, this does not explain the variability observed between the two nest types.

We have previously shown that worker interests control male and queen production (Queller et al., 1993). New queens are produced when there are few queens on the colony, and males are produced when there are more queens, in accord with worker split sex ratio interests (Boomsma and Grafen, 1991; Pamilo, 1991). Collective worker interests favor male production by queens and not by workers, and these interests are met; queens produce the males (Henshaw, Strassmann and Queller, unpubl.). Our finding in this study, that buzz running is performed by workers, implies that swarming, the third aspect of colony reproduction, may also be under worker control.

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