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A test of adaptive hypotheses for rapid nest construction in a swarm-founding wasp

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Abstract. Most social insect species enlarge their nests gradually and in close correlation with the growing need for space for brood and/or stored food. In contrast, some species of swarm-founding eusocial wasps construct the nest rapidly to a final size in the first two to three weeks of the founding stage. We considered four hypotheses on the functions of rapid nest construction in the wasp *Polybia occidentalis* and directly tested two of them. The first hypothesis is that rapid construction maximizes output of the worker force when there are few other work demands; it predicts that construction rate remains high until the first eggs begin to hatch, following which it declines as increasing amounts of worker effort are allocated to the feeding of larvae. The second says that rapid nest construction minimizes the time the adults in the swarm are exposed to predation and the elements; it predicts that nest-construction rate should drop steeply after the nest is large enough to house all the adults in the swarm. We measured pulp-foraging rates for the first 12 days of the founding stage in control colonies and in colonies whose nests we manipulated to prevent housing of the swarm. The treatment and control groups did not differ in construction rate for several days following the housing event, contradicting the adult-protection hypothesis. Late in nest construction, treatment colonies were building at significantly higher rates than were control colonies. If demand for brood care were a major factor in determining construction rate, both groups would have responded to the eclosion of larvae in the same way and shown a parallel decline in construction rate, but this did not happen. Instead, the patterns of nest construction rate we observed provided indirect support for the two remaining hypotheses. The first of these is that rapid construction minimizes exposure of the brood to natural enemies and desiccation. The second is that rapid construction promotes competition among queens by providing empty cells for oviposition, thereby facilitating the selecting out of the less fecund of the multiple reproductive females. Also consistent with this hypothesis is the apparent absence of explosive nest construction in monogynous, eusocial bees.

Keywords: Nest construction rate, swarm-founding wasps, reproductive competition, cost-benefit, resource allocation, *Polybia occidentalis,* Vespidae, Epiponini.

Introduction

The eusocial Hymenoptera fall into two groups according to how they initiate new nests (Hölldobler and Wilson, 1977). In independent-founding species, one or a small group of queens begins construction on a new nest without the aid of workers. In swarm-founding species, a new colony is initiated by a large group of workers and one or more queens.

In the social wasps (Vespidae) the two groups differ markedly in how they allocate effort to nest construction (Jeanne and Bouwma, 2004). Independent-founding species engage in *continuous nest construction*, adding new brood cells steadily throughout the nesting cycle as they are needed to receive eggs. That is, the rate of cell construction is intimately linked to oviposition rate (Richards and Richards, 1951; Wenzel 1991, 1993). In contrast, many, but not all swarm-founding species engage in *explosive nest construction*, constructing the nest rapidly at the beginning of the founding stage. Swarms of *Polybia occidentalis* (Olivier) (Polistinae:

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Epiponini), for example, complete the initial nest in two to three weeks; expansion may occur several weeks or months later (Forsyth, 1978; Jeanne and Bouwma, 2004).

The nest of *P. occidentalis* is built as a series of several enclosed modules, one below the other. Each module consists of a single comb of cells covered by a protective envelope. The envelope of the previous module serves as the base for the next module's comb. Swarms are polygynous, and the multiple queens begin laying eggs as soon as the first cells are available. Unlike in the independent founders, however, they do not keep up with the cell construction rate (Richards and Richards, 1951; Jeanne, 1991; Wenzel, 1991, 1993). Thus, the construction of new cells is not tightly linked to oviposition by the queens, freeing it to respond to other selective factors. In this study we asked what these factors might be.

Jeanne and Bouwma (2004: Fig. 4) discerned two patterns in the rate of construction in *P. occidentalis*. First, construction rates are typically higher in the morning than in the afternoon. Second, the overall rate decreases during the 2–3 weeks of construction. These two patterns are superimposed; that is, the reduction in construction rate as the nest approaches completion is manifested largely as a reduction in afternoon construction rate.

The daily pattern is likely a function of increasing cost during the day due to extrinsic factors. As air temperature increases toward mid-day, relative humidity decreases. This has the effect of increasing the amount of water the foragers must collect to process a given amount of wood pulp (R.L. Jeanne, unpubl. data). As this cost rises, the ratio of benefit to cost decreases, and construction rate drops.

It is the second pattern that is of interest here, since it must be caused by factors intrinsic to the developing colony. The fact that construction rate is not constant through completion of the nest may provide clues about what factors influence it. If natural selection optimizes behavior at the colony level, then the rate at which a colony engages in any social activity can be thought of as a function of the ratio of the benefit to the cost of carrying out the activity (Oster and Wilson, 1978; Perrin and Sibly, 1993). The decline in the rate of nest construction as the nest nears completion suggests that the ratio of benefit to cost of engaging in this activity decreases. This could be due to a decrease in the benefit, as would occur if the primary benefit of constructing the nest came early in the process. It could also be due to an increase in the cost of nest construction, which could come, for example, in the form of the cost of not completing other tasks that are becoming more pressing.

In this study we sought to determine what these costs and benefits might be. We considered the following four hypotheses on the adaptive significance of explosive nest construction in *P. occidentalis* (Jeanne and Bouwma, 2004). None of these alternative explanations are mutually exclusive. However, the hypothesized factors may vary in their relative importance in maintaining the behavior, and the effect of more influential factors may be detectable in the details of the pattern of nest-construction rates during the initial construction period.

1. Maximization of productivity. As the larvae start to hatch (after 6–7 days: Machado, 1977), workers begin to forage for prey (insects and spiders) to feed them (Hunt et al., 1987). Colonies may maximize their reproductive output by fully engaging in construction during the first week, when there are no larvae to feed, and thereafter allocating increasing proportions of their effort to the rearing of brood as the larvae grow in number and size. This hypothesis predicts that nest construction should continue at a high and steady rate for the first week, then gradually diminish as workers increase their food-foraging efforts in response to the growing population of larvae. In benefit/cost terms, the cost of maintaining a high rate of construction increases as the competing demands of the larvae increase.

2. Protection of adults. During the first few days of construction, the nest is too small for the wasps in the swarm to fit inside, so they remain tightly clustered on adjacent twigs and leaves until the nest has two or three combs with their covering envelopes (Forsyth, 1978). While unprotected, the wasps are vulnerable to mantids, reduviids, asilids and other predators (Richards, 1978; Bouwma et al., 2003; R.L. Jeanne, unpubl. data), as well as exposure to the elements. By maximizing the rate of construction, the swarm minimizes the time of exposure to these threats and therefore minimizes its risk of losses. Once the nest is large enough to house the swarm, the benefit of maintaining a high rate of construction is much reduced, predicting a significant drop in construction rate.

3. Protection of the brood. Building each module of the nest rapidly covers the brood in that module as quickly as possible, thereby minimizing exposure of the brood to parasites and predators (London and Jeanne, 1998) and to desiccation. If this were the main function of rapid nest construction, we would expect that construction of new nest modules would be maintained at a pace that would enclose brood-containing cells quickly.

4. Promotion of reproductive competition. Colonies of swarm-founders are cyclically oligogynous; that is, the numerous queens present early in the nesting cycle are reduced to one or a few by the time the reproductive phase of colony development is reached. The reduction comes about via interactions among queens and between workers and queens (West-Eberhard, 1978). Most of the reduction in queen numbers occurs in the founding stage of colony development (West-Eberhard, 1978). The availability of a large number of empty cells in the nest may create a context that encourages scramble competition among queens, which in turn could amplify differences in fecundity among them, facilitating the selecting out of the weaker queens. If the promotion of reproductive competition were the primary benefit driving rapid nest construction, then we would expect that construction of new cells would keep ahead of oviposition by some unspecified margin. This would predict that as construction proceeds and number of empty cells gains on the

number of egg-filled cells, rate of construction should gradually diminish.

We tested these predictions by tracking the rate of nest construction during the first 12 days of colony growth. In addition, we tested the protection-of-adults hypothesis by experimentally manipulating a set of colonies to prevent housing of the swarm. If protection of the adults is a major driver of rapid nest construction, we predicted that the rate in control colonies would drop following housing of the adults, whereas the manipulated colonies would continue constructing at high rates.

Methods

The study was conducted on private property 5 km west of Cañas, Guanacaste, Costa Rica (10°25′N, 85°7′W). For a description of the study site, see Bouwma et al. (2003). We observed nest construction between 4 June and 16 July 2006. This was after the onset of the wet season, when food had become available and colonies were actively growing.

We induced colonies to swarm and subsequently initiate new nests by destroying their old nests and brood. This was usually done just before sunrise, and the absconding swarms were monitored throughout the day and followed to their new nest sites. In some cases, active nests were moved in plastic bags from distant locations to a site near the center of the study area, where they were induced to swarm the following morning. Most swarms emigrated to a new nest site within a few hours of evacuating the old nest. Swarms that emigrated to sites out of our study area were allowed to construct for several days, then were moved to sites low in trees within the study area. To minimize losses of workers, moves were done at night, when foragers were likely to be in the nest. Nests initiated high in trees within the study area were moved to lower, more observable positions in the tree in steps of a meter or so during the first day of construction. Two colonies that suffered more than a few worker losses or did not return to normal nest construction immediately after a move were not included in this study. All nests in the study were protected from ant predation (Bouwma et al., 2007) with Tanglefoot® applied to branches supporting the nest.

Treatment groups

We studied 19 nests, 9 in a treatment group and 10 in a control group. Nests were observed for 12 full days of construction (hereafter "colony days"), beginning the day after emigration. As colonies approached 12 days of observation, new colonies were swarmed to maintain seven colonies under observation at all times. To control for seasonal effects, we assigned colonies evenly to treatment and control groups throughout the study period. We also assigned nests so as to keep the range of colony sizes similar in the two groups.

For the treatment group, when colonies began to build the envelope that would allow the remaining unhoused workers to move inside the nest, we prevented housing by cutting away this envelope with a penknife, trimming it several times daily for the remainder of the observation days. We let control colonies build undisturbed for the 12 days of observation, noting when all the adults in the swarm were first fully accommodated within the nest.

Observations

Observations began the day after a colony moved to a new nest site (colony day 1). On each of the 12 observation days, data were recorded from each nest for 10 minutes in each of four observation periods (OP 1–4): 0600–0800 h, 0900–1100 h, 1200–1400 h, and 1430–1630 h. On each day we randomized the order in which the nests were observed within each observation period. The number of foragers returning with pulp loads during the 10-minute period was recorded and used as a measure of construction rate. If a comb was exposed and cells were visible, the number and approximate position of eggs were recorded.

We made 773 ten-minute observations over the course of 43 days: 201, 202, 197, and 173 in OPs 1–4, respectively. The low total for OP 4 was due to interruptions caused by rain, which was more frequent later in the day. Observations were not taken during periods when rain was heavy enough to affect building; anything more than a light rain usually caused construction to stop. The difficulty of observing construction before new nests were moved to a more accessible position reduced the number of observations on the first colony day to 44 on 14 colonies.

On the evening of colony day 12, we collected each nest and sacrificed the adults and brood. We counted the adults and dissected 50 randomly selected from each nest to determine the degree of infection by a gregarine parasite known to affect foraging behavior (Bouwma et al., 2005). Each comb was measured and larvae were classed into instars. The relative locations of groups of instars within combs were recorded for comparison with data on egg location taken during construction. From this information, the ages, in days, of groups of brood were calculated.

Because adult colony members experience high mortality rates in the founding stage, we calculated an estimate of the adult population for each colony on each day of construction, using the adult count on day 12 and applying the mean daily hazard rate (the average daily probability that a colony member will die) of 0.023, estimated for post-emigration swarms in a previous study at the same site (Bouwma et al., 2003). These population estimates were then used to calculate the per-capita foraging rate for each observation. We plotted the average foraging rate of each treatment group against colony day to see how construction rate changed over the 12 days, and to test for an effect of brood eclosion. Averages include all colonies observed, even if they stopped building (rate = 0) late in the day or after the nest was completed.

To assess the effect of the housing of the swarm, we plotted per-capita foraging rate by colony day relative to the housing event. To do this, we shifted the colonies' temporal records so as to align them all on their respective dates of housing, allowing us to compare the effect of the housing event across colonies that were housed on different colony days. This had the effect of revealing any housing-correlated step change in rate that would be blurred by the cross-colony variation in colony day on which housing occurred.

To test for a significant difference between treatment and control colonies following the housing event, we used independent-sample t-tests for each colony day and each time of day, with the colony as the observation unit. Although it would be possible to perform a mixed-model analysis incorporating all of the nesting in this study, such an analysis would be very complicated; to perform it properly would require a model with two levels of repeated measures: day and time of day. Despite being fully cognizant of the risks of multiple comparisons, we felt that use of multiple t-tests leads to the most straightforward interpretation (E.V. Nordheim, pers. comm.). For this data set, it is doubtful that a nested-model analysis would reveal much more. However, because the t-test approach results in many tests, it is important to include the caveat that the reported p-values not be overinterpreted.

Results

The two treatment groups did not differ in mean number of adults per colony (two-tailed t-test: $t_{17} = 0.72$, $p = 0.42$) (Table 1). The frequency of adults infected by the gregarine parasite had a negative effect on the maximum observed per-capita pulp-foraging rate ($R^2 = 0.23$, $p = 0.036$) (Table 1). However, treatment and control colonies did not differ in average level of infection (two-tailed t-test: $t_{17} = -0.0947$; $p = 0.92$). We can be reason-

Table 1. Description of colonies. *Move date* is the date of swarm emigration to the new nest site (colony day 0). *Housing module* is the module under construction when the swarm was housed in control nests, or the module under construction when envelope removal began for treatment colonies. *Number of adults* was adjusted with a published hazard rate for colonies that were collected before or after the end of the 12th colony day. *Last constructing* is the comb or envelope (e.g. E3 is the third envelope) that was last under construction before collection. *Maximum observed P arrivals* is the greatest number of pulp foragers arriving in a 10-minute observation period. *Maximum P rate per capita* is the maximum observed pulp arrivals per 100 adults per 10 minutes.

	Nest	Move date	Housing module	Colony day housed	Colony size on day 12	Last constructing	Maximum observed P arrivals	Maximum P rate per capita	Fraction of adults with parasites
Control	21	4-Jun	2	2	433	E3	46	8.27	0.14
	77	3-Jul	3	4	594	C4	25	3.76	0.66
	30	2-Jul	3	4	726	E4	27	3.20	0.7
	43	13-Jun	3	3	732	C6	83	10.60	0.08
	66	18-Jun	3	2	761	E5	66	8.10	0.46
	64	20-Jun	3	5	866	E4	28	2.89	0.8
	11	3-Jun	2	2	930	E4	75	7.04	0.38
	70	20-Jun	3	3	1235	E5	82	6.20	0.36
	9	7-Jun	4	3	1350	E6	98	6.05	0.12
	80b	5-Jul	4	3	1624	E6	70	3.44	0.64
Treatment	20	7-Jun	2	2	205	E2	29	12.08	0.58
	72	22-Jun	2	2	614	E2	37	6.03	0.26
	78	3-Jul	3	5	637	E3	29	4.35	0.58
	80a	4-Jul	3	4	879	E3	55	5.33	0.44
	25	25-Jun	3	4	935	E3	39	3.48	0.88
	10	17-Jun	3	3	1301	E3	66	4.88	0.18
	5	3-Jun	4	3	1453	E4	109	6.42	0.3
	23	4-Jun	3	2	1760	E3	96	4.87	0.28
	67	19-Jun	4	3	1983	E4	80	3.68	0.5

ably confident, therefore, that differences in colony size and parasite infection are not responsible for any differences seen between the groups.

Removing the envelope on treatment nests occasionally disturbed nest construction, especially in larger nests, but construction usually resumed within a few minutes. For five of the treatment colonies, this manipulation effectively left a large majority of the workers unhoused; for the remaining four colonies only a few workers were unhoused, and in periods of high activity there were occasionally no unhoused inactive workers visible at the nest.

Timing of housing and eclosion

The housing event (or the start of envelope removal for treatment nests) took place on colony day 2 (4 colonies), 3 (11 colonies), or 4 (4 colonies) (Table 1). The treatment and control groups did not differ in this respect; each had two colonies housed on colony days 2 and 4. Housing was a gradual process, because wasps in the swarm would crowd into space created by construction as soon as it became available. Thus, many individuals were housed by the first few modules, sometimes a day or two before the remainder of the swarm was housed. However, the module that accommodated the last of the unhoused adults was usually larger than previous modules and typically accommodated the largest portion of the swarm. Every control colony built at least one more module after completing the module that housed the swarm, and two colonies built three additional modules (Table 1).

We saw no groups of eggs more than 8 days old. Of the 32 groups of 1st-instar larvae for which we knew the age at collection, none were younger than 7 days old, five were 7 days old, and 20 were 8 days old. This suggests that eggs hatch 7–8 days after being laid, slightly longer than the 6–7 days reported for this species by Machado (1977). Queens began laying in cells within a few hours of comb initiation, so the first eggs in a nest were typically laid on colony day 0 or 1. However, the first module contained very few eggs; most brood were raised in subsequent, larger modules.

Number of colonies constructing

With two exceptions, control colonies engaged in construction during OP 1 throughout the 12-day period (Fig. 1). In late morning (OP 2) the number of colonies building dropped slightly in the last three days. By early afternoon (OP 3), cessation of construction occurred in about half the control colonies by day 7. This pattern was even more pronounced in OP 4, with construction stopping even earlier in the period and among more colonies. Treatment colonies showed a similar pattern, both during the day and during the 12-day period, but this was much less pronounced than in the controls.

Mean rates of nest construction

The average per-capita pulp-foraging rate showed a similar pattern (Fig. 2). That is, rates of construction in control colonies over the 12-day period were highest and
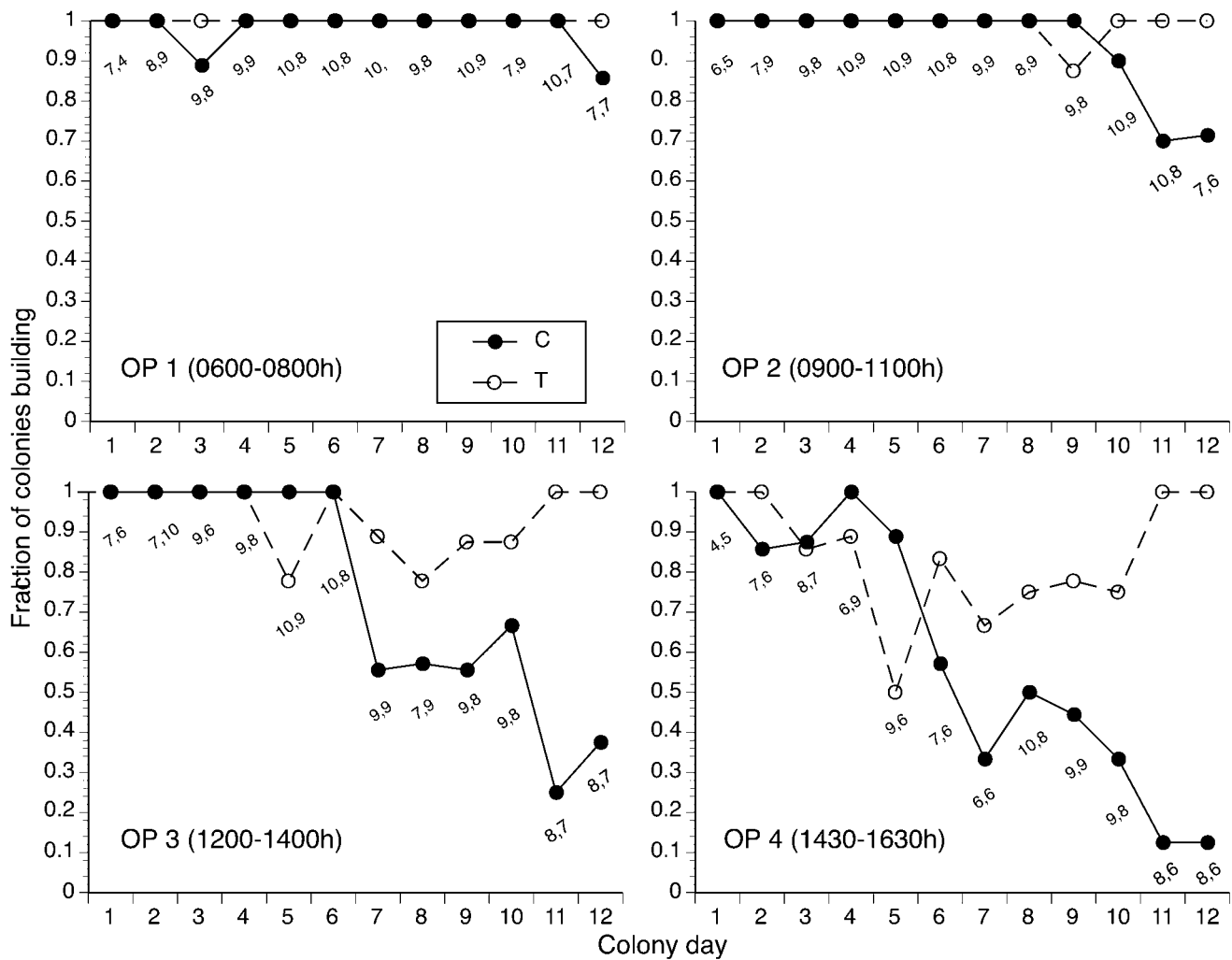
Figure 1. Frequency of building. OP 1–4 are four daily observation periods, 0600–0800 h, 0900–1100 h, 1200–1400 h, and 1430–1630 h, respectively. Filled circles are control colonies, open circles are treatment colonies. Colonies were considered to be building if any pulp foragers arrived at the nest during the 10-minute observation period. Observation periods skipped because of rain are not included. Numbers below data points for each day are the number of control and treatment colonies observed.

most consistent during OP 1. Rates decreased during the course of any given day, and with each progressive day during the 12-day period. These two patterns combined to yield ever more steeply decreasing within-day construction rates as colony days increased.

A similar but less pronounced pattern was seen in treatment colonies. That is, treatment colonies tended to build at higher rates than controls. The differences in rate between treatments and controls tended to increase both during the day and toward the end of the 12-day period (Fig. 2). Nine (19%) of the 48 t-tests performed were significant at $\alpha = 0.05$ or greater. If all of these 48 tests could be viewed as independent, then by chance alone one would expect 2.4 (48*.05) of them to be significant. Although the tests are not independent, the fact that 19% of the tests were found to be significant is strongly suggestive of the conclusion that the observed significances are real and not just due to chance. Also, eight of

the nine significant differences were in the last three days, and in every case the difference was in the same direction. Thus, the stated significances are solidly supported.

When the average per-capita pulp-foraging rate is plotted against colony day relative to housing day, no significant differences between treatments and controls occurred until four days after the housing event (Fig. 3). Significant differences between treatments and controls occurred in a few of the later days, especially in the afternoon OPs. Ten (19%) of the 52 t-tests performed were significant at $\alpha = 0.05$, again many more than the number expected from false positives alone, and all in the same direction.

For control colonies, construction rate of the housing module did not differ from that of the modules built before or after it (two-tailed, paired t-tests, paired within OP and colony: module H-1 and H, $t_{22} = -0.55$, $p = 0.587$; module H and H+1, $t_{33} = 1.12$, $p = 0.272$).
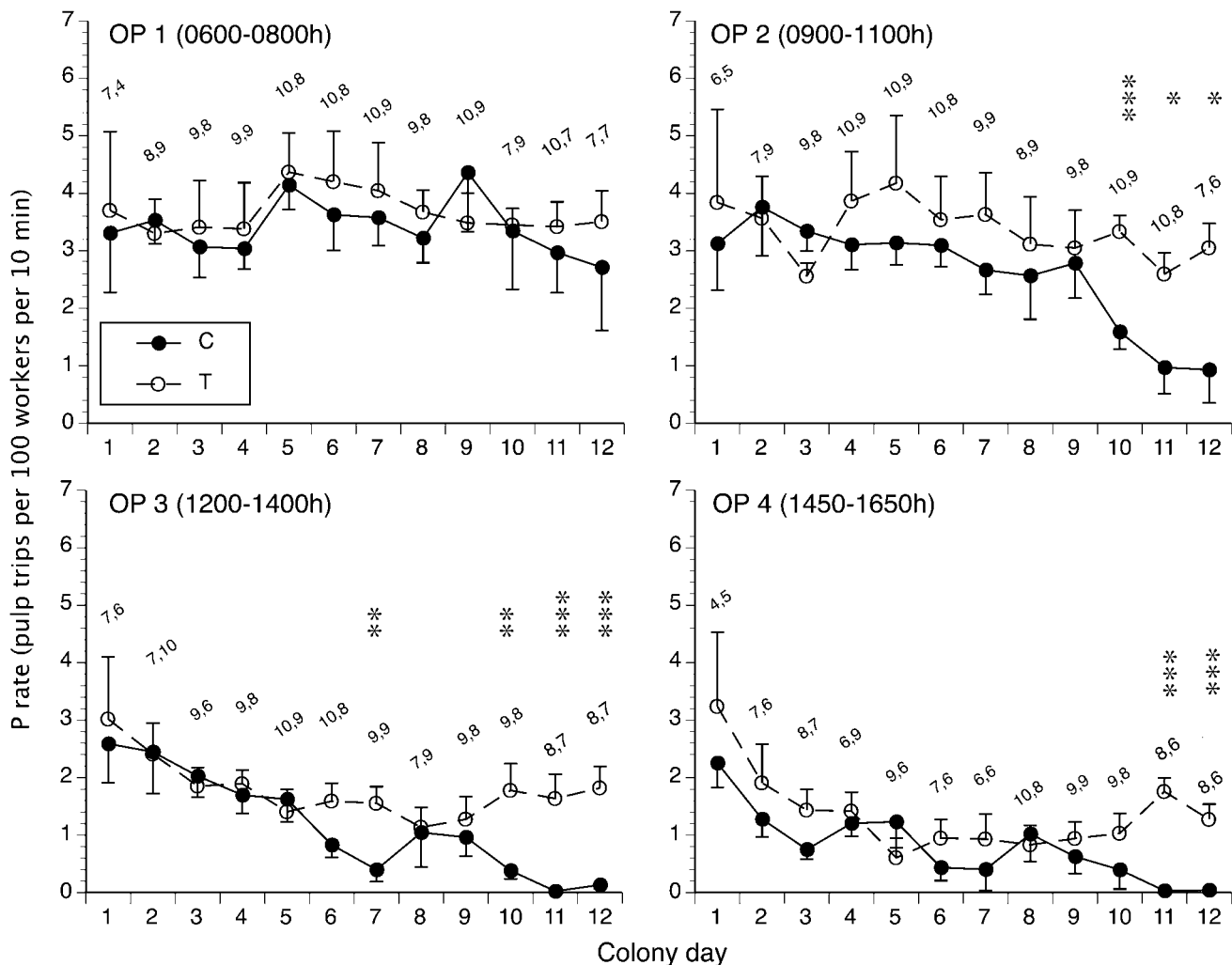
Figure 2. Per-capita pulp-foraging rate. This rate was measured as the number of pulp foragers arriving at the nest during a 10-minute observation period per 100 adults. OP 1–4 are four daily observation periods, 0600–0800 h, 0900–1100 h, 1200–1400 h, and 1430–1630 h, respectively. Filled circles are means of control colonies, open circles are means of treatment colonies. Error bars are 1 SE. Numbers above data points for each day are the number of control and treatment colonies observed for each mean. Significant differences in two-tailed t-tests between controls and treatments: *p < 0.05, **p < 0.01, ***p < 0.001.

Discussion

We assume that natural selection favors behavioral strategies that apportion colony effort among tasks so as to maximize the overall benefit/cost ratio, while minimizing risk of colony failure. We suggest that the pattern of reduction in nest construction rate during the course of the day, repeated throughout our 12-day observation period, is a direct function of increasing cost of construction as the air warms and relative humidity drops. Given that the cost of nest construction is higher in the afternoon than in the morning (R.L. Jeanne, unpubl. data), it makes sense that the reduction in nest construction would be most pronounced during these drier times of day.

In contrast, the second pattern – the decrease in overall construction rate during the 12-day period – must have other causes. Although attrition in worker numbers during the colony-founding stage is significant in this species (Bouwma et al., 2003), we controlled for this effect by converting all building rates to per-capita rates based on hazard-rate-adjusted colony population numbers. Attrition of workers, therefore, cannot explain the observed changes in building rate. Thus it appears that the pattern is the manifestation of a shift in allocation of worker effort in response to changes in benefit and/or cost that are intrinsic to the colony.

The maximization-of-productivity hypothesis (hypothesis 1) predicts that nest-construction rates would remain high until larvae hatch, after day 7–8, then gradually decline as increasing numbers of larvae demand feeding. Instead, our control colonies showed the steepest rate declines in the first few days (afternoons), followed by another steep decrease (late morn-
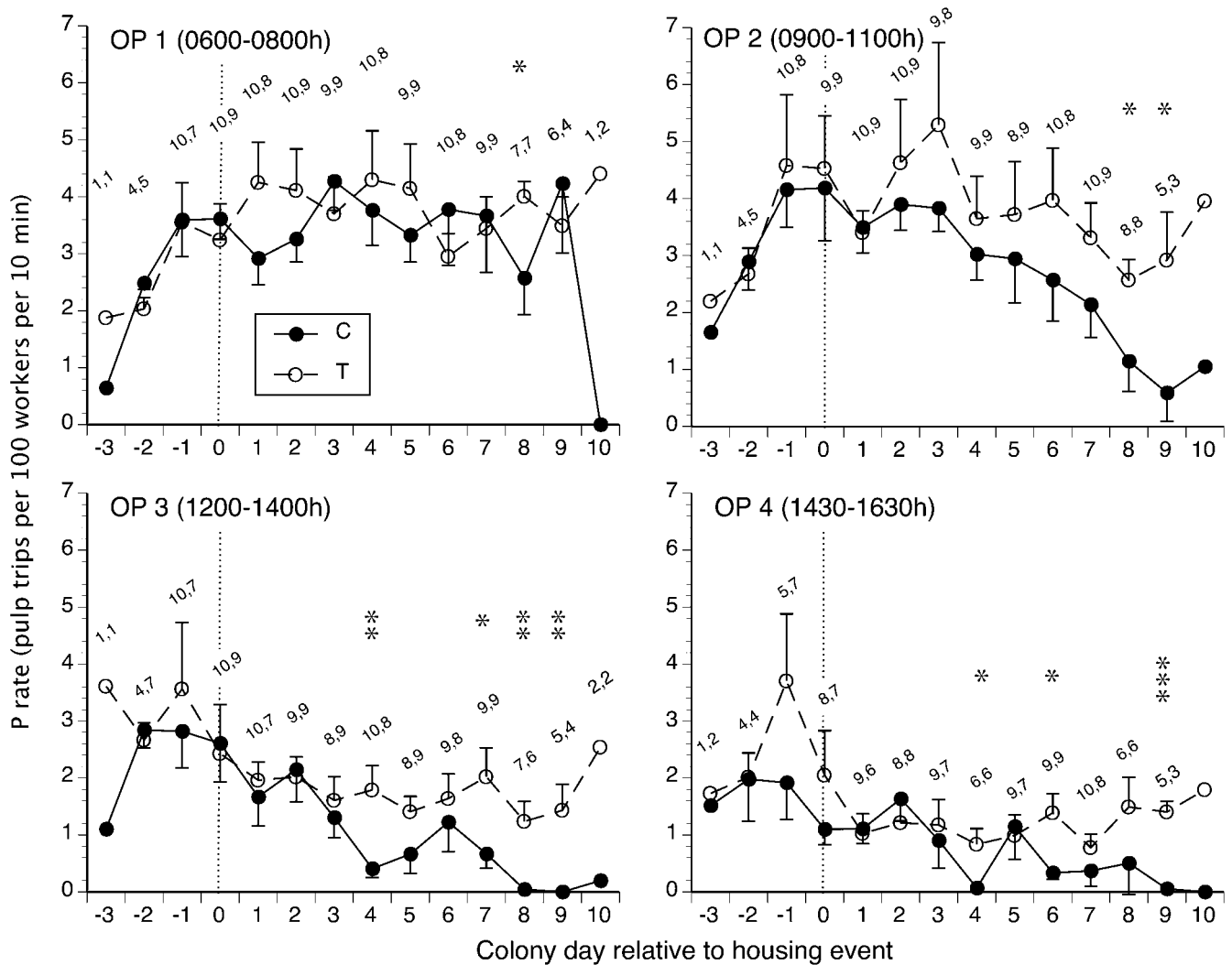
Figure 3. Per-capita pulp-foraging rate relative to housing event. The rate of nest construction was measured as the number of pulp foragers arriving at the nest during a 10-minute observation period per 100 adults. OP 1–4 are four daily observation periods, 0600–0800 h, 0900–1100 h, 1200–1400 h, and 1430–1630 h, respectively. Colony day relative to housing event is the day of construction relative to the day in which the swarm was housed within the nest (or the day envelope removal began for treatment colonies). Filled circles are means of control colonies, open circles are means of treatment colonies. Error bars are 1SE. Numbers above data points for each day are the number of control and treatment colonies observed for each mean. Significant differences in two-tailed t-tests between controls and treatments: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

ings) after day 9. We conclude that this hypothesis is not supported. That is, the increase in larval mouths to feed is not an influential cause of the pattern. In support of this conclusion is the observation that workers engaged in pulp and water foraging during the morning hours become idle in the afternoon if construction stops; that is, they do not switch to foraging for food (O'Donnell and Jeanne, 1990).

The adult-protection hypothesis (hypothesis 2) predicts that unmanipulated colonies should show no decline in nest-construction rate until the swarm is housed, then a more or less steep decline followed by a leveling-off. Our control colonies did not show such a pattern. For the experimental colonies, the prediction was for no decline during the 12 days, because the swarm was prevented from being fully housed. Instead, the pattern in treatment

colonies followed approximately that of the control colonies, albeit at sometimes significantly higher construction rates. Moreover, there was no significant difference between the pulp-foraging rates of the treatment and control groups for several days following the housing event, despite the fact that only control-group swarms were housed. In addition, construction rates did not differ between the module that housed the swarm and the following module. Taken together, this evidence strongly suggests that the housing of the swarm is not a proximate stimulus for a reduction in the rate of nest construction during the founding stage. False positives resulting from multiple t-tests would not affect this interpretation because we are accepting the null hypothesis. We conclude that the adult-protection hypothesis (hypothesis 2) is not supported. The case of *Apoica*,

another genus apparently exhibiting explosive construction (Jeanne and Bouwma, 2004), lends support to this conclusion. *Apoica* builds a single, uncovered comb; the adults form a cluster on the lower surface of the finished comb, and are thus exposed (Jeanne and Bouwma, 2004). Rapid construction in *Apoica* therefore cannot be driven by a rush to get the swarm into a protected nest.

Thus it appears that rate of nest construction is not closely tied to any single event, neither to the hatching of larvae nor to the housing of the swarm. On the other hand, our data are not inconsistent with the brood-protection hypothesis (hypothesis 3). This predicts that the cost of leaving a nest incomplete, exposing the eggs and larvae to parasitoids, parasites, and desiccation exceeds the cost of rapid construction, leading to selection for rapid construction at the outset. There is evidence that a completed envelope protects the brood from parasites (London and Jeanne, 1998) and ants (Jeanne, 1975; Smith et al., 2001). Because the rate of cell construction exceeds the rate of oviposition, the production of brood cells by the workers is expected to pull increasingly ahead of egg-production by the queens with the construction of each new module. Thus, as construction proceeds, brood are distributed farther behind the construction front, potentially reducing the pressure on the colony to construct rapidly. This hypothesis predicts that construction would continue as long as the brood remained exposed. This is consistent with our observation of continued construction when the envelopes of treatment-group nests were removed. Selection for envelope completion would hasten the construction of a module already under construction, and new modules would be initiated once the queens require new cells for oviposition.

Our results are also consistent with hypothesis 4: that the availability of empty cells in the nest promotes scramble competition among queens. Because rate of cell construction exceeds the rate of oviposition, as construction proceeds the number of empty cells in the nest increases and the workers could afford to pull back from their initial high rate of construction. To cut back most strongly in the late afternoon would cut the cost of nest construction by limiting it to the cheaper, more humid hours early in the day.

Another pattern supporting hypotheses 3 and 4 is that the differences in rate between treatment and control colonies are not significant for several days following the first manipulation of treatment colonies. In the treatment group, per-capita rates and the proportion of colonies that were building actually rose in the last few days of the observation period. This suggests that in the treatment colonies, because construction of new cells was prevented by our manipulation, the stimulus to build became stronger with time. This could be caused by oviposition catching up to cell construction, so that brood are increasingly exposed as more eggs are laid in the still-open manipulated comb (hypothesis 3) and/or that the available cells are filling up, reducing queen-queen competition (hypothesis 4). Both could lead to increasingly strong stimuli for workers to provide more cells.

In summary, it appears that neither the housing of the adults nor the hatching of larvae is an influential proximal cue for the reduction in nest construction rate. On the other hand, there is circumstantial support for the hypotheses that workers adjust their rate of nest construction in response to the exposure of brood and/or to the demand for cells for queens to oviposit into.

A weak test between hypotheses 3 and 4 can be done by comparing polygynous and monogynous swarm-founding Hymenoptera. Hypothesis 3 predicts that both kinds of colonies should show explosive nest construction, while hypothesis 4 predicts that only polygynous species should show it. Unfortunately, quantitative accounts of initial nest-construction efforts by other swarm-founding Hymenoptera are few. Honey bees (*Apis mellifera*) are monogynous swarm founders. After a founding swarm settles into a nest site, it constructs enough comb to rear its first generation of offspring and provide storage space for honey and pollen (Pratt, 1999). In one observation colony, the fraction of empty cells in combs built by the founding swarm was 17–28 % for the first three days and thereafter dropped to around 5 % through the production of the first worker offspring (Pratt, 1999). Thus, although cell construction stays somewhat ahead of cell utilization, the first round of construction lasts for about three weeks and is followed closely by several episodic pulses whose onset coincides with periods of high nectar inflow and low available storage capacity (Seeley and Morse, 1976; Pratt, 1999), hardly a *Polybia*-like pattern. The stingless bees (Apidae, Apinae, Meliponini) are also monogynous swarm-founders. Although we are not aware of any quantitative data on rates of cell construction for any species, descriptive accounts suggest that provisioning and oviposition do not lag far behind construction of brood cells (Sakagami, 1982; Roubik, 1989; Veen and Sommeijer, 2000). Thus explosive nest construction, at least of the magnitude shown by *P. occidentalis*, appears to be absent in bees, providing tentative support for the promotion-of-reproductive-competition hypothesis. This does not, however, rule out the possibility that other factors are acting in the bees. For example, the cost of producing wax may impose a stronger constraint on rapid nest construction than on wasps, whose collected vegetable fibers are less costly.

There remains the enigma of why some swarm-founding polistines appear to lack explosive initial nest construction, instead apparently tying the rate of cell production more closely to the rate of oviposition by the queens (Jeanne and Bouwma, 2004). Whether this is due to differences in queen-queen or worker-queen relationships or to some other, yet-unidentified factor, remains to be investigated.

Acknowledgments

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