

Research article

Per-capita productivity in a social wasp: no evidence for a negative effect of colony size

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Abstract. Optimal colony size in eusocial insects likely reflects a balance between ecological factors and factors intrinsic to the social group. In a seminal paper Michener (1964) showed for some species of social Hymenoptera that colony production of immature stages (productivity), when transformed to a per-female basis, was inversely related to colony size. He concluded that social patterns exist in the social insects that cause smaller groups to be more efficient than larger groups. This result has come to be known as “Michener’s paradox” because it suggests that selection on efficiency would oppose the evolution of the large and complex societies that are common in the social insects. Michener suggested that large colony size has other advantages, such as improved defense and homeostasis, that are favored by selection. For his analysis of swarm-founding wasps, Michener combined data from colonies of different species and different developmental stages in order to obtain adequate sample sizes; therefore, his study did not make a strong case that efficiency decreases with increasing colony size (across colonies) in these wasps. We tested Michener’s hypothesis on the Neotropical swarm-founding wasp *Parachartergus fraternus*, while controlling for stage of colony development. We found that small colonies were more variable in per-capita productivity relative to larger colonies, but found no evidence for a negative relationship between efficiency and size across colonies.

Keywords: *Parachartergus fraternus*, Polistinae, social wasps, per-capita productivity, colony size.

Introduction

Mature colony size in the social Hymenoptera spans a broad range, from less than a dozen individuals in colonies of halictid bees, to hundreds in the ponerine ants, thousands in the vespine wasps, tens of thousands in honey bees, hundreds of thousands in the fire ants, and millions in at least one swarm-founding epiponine wasp and some army ants (Michener, 1964; Wilson, 1971; Hölldobler and Wilson, 1990; Zucchi et al., 1995). Species with larger average colony size are characterized by a suite of covarying traits, including decentralized colony control, increased morphological skew between queens and workers, reduced reproductive conflict, smaller body size, higher worker tempo, greater worker specialization, more complex tasks, and more complex systems of communication (Oster and Wilson, 1978; Karsai and Wenzel, 1998; Bourke, 1999; Anderson and McShea, 2001; Jeanne, 2003). There may also be a wide range in colony size within species (Michener, 1964; Wilson, 1971; Hölldobler and Wilson, 1990; Tschinkel, 1998, 2006; Jeanne and Bouwma, 2002), but less is known about the effect of intraspecific variation in group size on colony traits (Tschinkel, 1991).

A seminal paper by Michener (1964) examined the relationship between intraspecific colony size variation and reproductive efficiency, using published data for a number of species of ants, bees, and wasps. Since there existed at the time few direct measures of the number of reproductives produced by colonies, for most taxa in his study Michener used data on numbers of non-reproductive young being reared by colonies. That is, he made the reasonable assumption that ability to rear workers should correlate with ability to rear reproductives. (In the

present paper we refer to these measures of immature stages and other forms of colony output as productivity [Jeanne and Nordheim, 1996] rather than reproductivity, since productivity is a more general term and thus more accurate.) Michener (1964) found that total colony productivity was positively correlated with colony size, but, when transformed to a per-female basis, productivity was inversely correlated with colony size for most species. Thus, Michener (1964) observed that the larger the colony, the less the “reproductive efficiency,” or per-capita productivity. Michener (1964) concluded that this “indicates the existence of social patterns causing higher efficiency per female the smaller the group” (Michener, 1964: 334). The pattern has been referred to as “Michener’s paradox” (Wenzel and Pickering, 1991; Jeanne and Nordheim, 1996) or “the per-capita paradox” (Karsai and Wenzel, 1998) because it suggests that selection on reproductive efficiency will oppose the evolution of large and complex societies such as those that are widespread in the social Hymenoptera. Michener (1964) suggested that large group size has other advantages, such as more efficient homeostasis and more effective defense, that counter the reduced reproductive efficiency and favor the evolution and maintenance of large colony size.

Colony size is correlated with colony age and, for colonies in seasonal climates, with season (Wilson, 1971; Oster and Wilson, 1978; Hölldobler and Wilson, 1990; Tschinkel, 2006). As colonies age they may shift allocation of resources from population growth to defense and/or homeostasis (Spradbery, 1973; Oster and Wilson, 1978; Tschinkel, 1988, 1993, 1998; London and Jeanne, 2003; Thomas, 2003; Howard and Jeanne, 2005), potentially reducing per-capita production of offspring (but see Tschinkel, 1993). Therefore, it can be difficult to disentangle effects on colony productivity due to colony size from effects due to colony ontogeny (Michener, 1964; Jeanne and Nordheim, 1996). In Michener’s (1964) study, his stated aim was to determine the effect on productivity of colony size *per se*, exclusive of effects due to ontogenetic stage. He tried to minimize the effect of ontogeny by using data on colonies collected during the same season.

For the swarm-founding wasps (Polistinae: Epiponini), Michener (1964) used data (from Richards and Richards, 1951) on colonies collected during a two-month period in Guyana. His analysis may nevertheless have been confounded by ontogeny. Because Guyana lacks a cold winter, colony development is asynchronous; that is, colonies in all stages of development can be found at any time of year (Richards and Richards, 1951; Richards, 1978). Indeed, the data set used by Michener (1964) included colonies of different developmental stages (Richards and Richards, 1951). Furthermore, his use of the number of eggs in the nest as a measure of colony productivity may have compounded the problem. This is because the egg/female ratio in a nest is likely to be higher for young (i.e. small) colonies of swarm-founding wasps

than for mature ones (Richards and Richards, 1951; Wilson, 1971).

Another shortcoming of Michener’s (1964) analysis for the swarm-founding wasps is that his plots combined data from multiple species. In order to obtain adequate sample sizes to plot, he pooled data from two species of *Polybia* in one analysis and eleven species in five genera in another (Michener, 1964, Figs 4 and 5). The plots showed a decrease in eggs per capita with increasing colony size. Recognizing that species differ widely in average mature colony size, Michener (1964) concluded that plots for the group of eleven species suggested that the evolution of species with larger colony size was accompanied by a decrease in productivity per capita. However, the relationship between per-capita productivity and colony size could be different across species from the relationship within species. Because of this caveat and the potential contribution of ontogenetic effects, Michener’s (1964) analysis for the swarm-founding wasps does not support the conclusion that within a species, during a given ontogenetic stage, large groups are less productive per capita than small ones.

In the swarm-founding wasps (Polistinae, Epiponini), founding-group size varies intraspecifically over wide ranges (Richards, 1978; Forsyth, 1981; AMB, pers. obs.; RLJ, pers. obs.) and colonies can be easily induced to re-nest, which resets the colony stage to founding (Jeanne and Nordheim, 1996; Howard and Jeanne, 2004; Bouwma et al., 2005). Thus, these wasps are ideally suited for studying the effect of group size on productivity, independently of the effect of ontogeny. Two studies on per-capita productivity in the swarm-founding wasp, *Polybia occidentalis*, have controlled for colony stage in this way (Jeanne and Nordheim, 1996; Bouwma et al., 2005) and have failed to support Michener’s pattern. Here we extend the test of Michener’s hypothesis to a second swarm-founding wasp genus, *Parachartergus*. As in the *Polybia* studies, we find no support for the Michener pattern.

Methods

We conducted field studies on *Parachartergus fraternus* at Finca Las Pumas (adjacent to the property formerly known as Centro Ecológico La Pacífica) near Cañas, Guanacaste, Costa Rica (10° 25’N, 85° 7’W) from 16 September to 10 December, 1996, and 23 May to 22 August, 1997. Cañas is located in the tropical dry forest (moist province transition) life zone (Tosi, 1969), marked by strong wet-dry seasonality, with the wet season extending from May into November. Mean annual rainfall at the site is 1430 mm (1921–99; W. Hagnauer, pers. comm.). Native vegetation is tropical dry forest, but this has been widely replaced with pasture and cropland. Colonies of *P. fraternus* commonly nest in trees in pastures and along roadsides.

In order to reset the colony cycle to the founding stage, we induced colonies to form absconding swarms by dismantling their nests. When the nest is destroyed, adult females emigrate as a swarm to a nearby site and re-nest (Jeanne, 1991). These highly aggressive wasps always mounted a spirited defense of the nest and, in addition to stinging behavior, sprayed their venom seemingly directly at the eyes of anyone in proximity of the nest, filling the air with atomized venom (Richards,

1978; but see Jeanne and Keeping, 1995). Eye goggles and dust masks, in addition to full bee suits and veils, are necessary protective gear for any work with these wasps (Schmidt, 1992). To distinguish each swarm from others in the area, we paint-marked a subset of the adults using DecoColor® Opaque Paint Markers. We monitored the swarms until they emigrated and began building their new nests. We designated the departure time of each swarm from the old site as the time of initiation of the new nest. If swarms departed the old nest site before 1200h, we counted that day as day 1 of colony development. If swarms moved after 1200h, we counted the next day as day 1.

We allowed each swarm to construct a nest at the new site and rear brood undisturbed for 25 days, which we expected to be less than the egg-to-adult development time, based on data from *Polybia occidentalis* (Machado, 1977; Howard and Jeanne, 2004). After dark on the evening of the 25th day, we collected the colony with its nest. The next morning we collected any escapees and/or foragers that had spent the night away from the nest; these typically formed a cluster within a few cm of the nest site. By collecting our colonies before adult offspring emerged, we ensured that the collected adults were all members of the founding swarm and therefore could be counted as producers. We assumed throughout that all colonies experienced the same rates of attrition during the 25 days. Bouwma et al. (2003, 2005) showed that large colonies of *Polybia occidentalis* experience slightly lower rates of attrition than small colonies. If this were also true for *Parachartergus fraternus*, our use of the day 25 census as the measure of colony size could slightly underestimate the per-capita productivity of larger colonies over the 25 days, making our test for Michener's pattern a conservative one.

Upon collection we counted the brood cells in the nest. We removed all the brood (eggs, larvae, and pupae) from the nest and preserved them in Kahle's fixative. We vacuum-filtered each colony's mass of brood on pre-weighed, oven-dried filter paper over a Büchner funnel, then desiccated the brood and filter paper to uniform dryness in a vacuum oven at 60°C and weighed them to the nearest 0.1 mg. Subtracting the weight of the paper gave us the dry weight of the brood. For each colony, we counted all adults and then dissected them under a dissecting microscope while still fresh to determine caste. We defined queens as inseminated females with at least one opaque egg (egg with yolk) per ovary. We keyed specimens to species using Richards (1978) and Willink (1959). Vouchers are deposited in the University of Wisconsin–Madison Insect Research Collection.

Analysis

Our two measures of productivity were the number of brood cells built by the swarm (C = nest size) and the dry weight of brood produced (B = brood productivity) through day 25 (Jeanne and Nordheim, 1996). By measuring both nest size and brood productivity we covered the two main forms of colony output by these wasps. We assessed the effect of colony size (total adults = queens + workers; A) on each measure of productivity. For these productivity data there are two closely related approaches to regression analysis (Jeanne and Nordheim, 1996). In one approach, total colony productivity (either C or B) is fitted to a multiple-regression model with A and A^2 as the primary independent variables. A significant A^2 term would indicate that per-capita productivity is affected by colony size.

In the second approach measures of total colony productivity are divided by A , giving per-capita measures of nest size (C_{pc}) and brood productivity (B_{pc}), and regressed on colony size. This transformation allows for a more direct analysis of the relationship between per-capita productivity and colony size than the use of the total colony output; therefore, we used this approach for our regression analysis. (We provide plots of total colony productivity on colony size as in Michener [1964], but do not report regression analyses for the data in this format.)

The per-capita data were heteroscedastic for both response variables, with residual plots showing greater variance in per-capita productivity for smaller colonies. We corrected for heteroscedasticity by using weighted multiple-regression analysis, which gives observations with large variance less weight in calculating model parameters (Chatterjee et al., 2000). We used the Box-Cox procedure (Box and

Cox, 1964) to assess the degree of heteroscedasticity and to quantitatively determine the weights to use in the weighted regression. In the Box-Cox procedure, a parameter (λ) is estimated so that the response variable Y^λ has constant variance ($Y = C_{pc}$ or B_{pc}). The use of weighted least squares was preferable to the alternative of a direct transformation of Y , since such a transformation would affect both the variance and the linearity of the relationship between the response and predictor variables. Our goal was to assess the relationship between per-capita productivity and colony size in the original scale; thus, we used weighted regression.

We analyzed data from the two years in the same regression model. If not controlled for, year effects (colonies being more productive per capita on average during one year relative to another) and interactions with year (different relationships between per-capita productivity and colony size in different years) have the potential to mask the true relationship between per-capita productivity and colony size (Jeanne and Nordheim, 1996). Therefore, we used a class variable for year and tested for interactions between the year variable and all other explanatory variables (see below). If significant, the year and interaction terms would allow the model to have different intercepts and slopes for each year (Jeanne and Nordheim, 1996). (For both measures of per-capita productivity, analysis of the data from the two years combined did not produce different results for the effect of colony size than analysis of the two years separately.) To control for potential effects of season, we assigned each colony a collection-date variable, defined as the number of days elapsed between its collection date and the first colony's collection date in each year (Bouwma et al., 2005).

In a weighted multiple regression weighted by A^2 (weighting with this term minimized heteroscedasticity; see below) (Chatterjee et al., 2000) using a backwards elimination procedure, we fitted brood cells per capita (C_{pc}) on colony size at day 25 (A), the proportion of queens in the colony (Q), collection date (D), a class variable for year (V), and interaction terms for each of the explanatory variables by year ($N = 16$ for 1996, $N = 19$ for 1997). In a separate weighted multiple regression, also weighted by A^2 , we fitted brood weight per capita (B_{pc}) on the aforementioned independent variables ($N = 15$ for 1996, $N = 18$ for 1997). We used PROC GLM for multiple regression and PROC TRANSREG for Box-Cox analyses in SAS version 8.2.

Results

The mean adult population of the collected colonies on day 25 was 266 ± 176 (SD), of which a proportion were queens (0.081 ± 0.057 SD; Table 1), and none were males. None of the colonies had brood older than early-stage pupae (head capsule not sclerotized; Howard and Jeanne, 2004); therefore, it was clear that no adult offspring had yet eclosed and all adults in each sample could be considered to be producers, distinct from the results of their efforts (nest and brood).

Regression weights

Using the Box-Cox method, we found that $\log(Y)$ and \sqrt{Y} were the optimal transformations that resulted in homoscedastic residuals for per-capita cell number and per-capita brood productivity in multiple regression models, respectively. For per-capita cell numbers, the Box-Cox confidence interval for λ included both $\log(Y)$ and \sqrt{Y} , while the confidence interval for brood productivity was narrower, including only \sqrt{Y} . In the interest of parsimony, we chose \sqrt{Y} as the best (overall) trans-

Table 1. Size and output of *Paracharturgus fraternus* swarms at the end of 25 days of growth. # = no brood produced.

Colony	Collection date	Total adults	Prop. queens	Brood cells per capita	Brood wt. (g) per capita
96216	10/26/1996	107	0.056	1.626	0.0009
96215	10/30/1996	42	0.095	4.262	0.0155
96235	10/31/1996	149	0.040	2.443	0.0022
96244	11/5/1996	429	0.049	2.956	0.0126
96254	11/17/1996	408	0.105	2.988	0.0158
96181	11/19/1996	201	0.105	1.124	0.0028
96182	11/20/1996	184	0.082	1.766	0.0090
96249	11/20/1996	545	0.024	2.688	0.0121
96256	11/25/1996	388	0.039	2.900	0.0090
96260	11/29/1996	27	0.148	5.333	0.0071
96262	11/30/1996	115	0.217	1.183	#
96265	11/30/1996	366	0.066	2.281	0.0037
96264	12/1/1996	266	0.008	3.120	0.0211
96267	12/1/1996	124	0.121	1.549	0.0014
96188	12/1/1996	268	0.093	1.966	0.0072
96247	12/6/1996	27	0.148	2.741	0.0021
97057	7/1/1997	711	0.117	4.065	0.0390
97050	7/1/1997	205	0.010	3.849	0.0422
97078	7/6/1997	735	0.057	2.562	0.0234
97089	7/9/1997	247	0.041	3.838	0.0333
97132	7/19/1997	230	0.135	2.261	0.0150
97096	7/21/1997	433	0.076	2.150	0.0143
97130	7/22/1997	165	0.006	1.624	0.0138
97131	7/23/1997	194	0.005	2.175	0.0191
97103	7/27/1997	267	0.165	2.891	0.0256
97104	7/27/1997	238	0.004	1.290	0.0037
97123	7/31/1997	342	0.099	2.810	0.0203
97125	8/3/1997	74	0.014	1.811	0.0111
97128	8/6/1997	356	0.020	2.947	0.0220
97134	8/8/1997	269	0.156	1.810	#
97138	8/9/1997	498	0.121	3.357	0.0151
97141	8/12/1997	323	0.142	3.793	0.0206
97127	8/12/1997	224	0.165	2.013	0.0114
97140	8/12/1997	131	0.084	3.962	0.0266
97142	8/13/1997	29	0.035	1.655	0.0010
		266.2 ± 176.4 SD	0.081 ± 0.057 SD	2.623 ± 0.990 SD	0.0146 ± 0.0107 SD

formation. The use of A^2 as the weights in weighted regression corresponds to a \sqrt{Y} transformation.

Nest size

The mean of brood cells constructed per capita was 2.62 ± 0.99 (SD) cells/adult. Plots clearly indicated that total brood cells (C) increased with colony size (Fig. 1A). Weighted multiple regression of brood cells per capita (C_{pc}) on colony size (A), proportion of queens (Q),

collection date (D), and year (V), plus interaction terms, did not yield a significant model (Fig. 1B, Table 2; $F = 2.02$, $P = .09$); therefore, these variables were not significant predictors of brood cells per capita. Plots of the residuals from the full multiple regression model (unweighted) on colony size (Fig. 1C) showed that small colonies were more variable than large colonies in their production of brood cells per capita, which corresponds to the Box-Cox results.

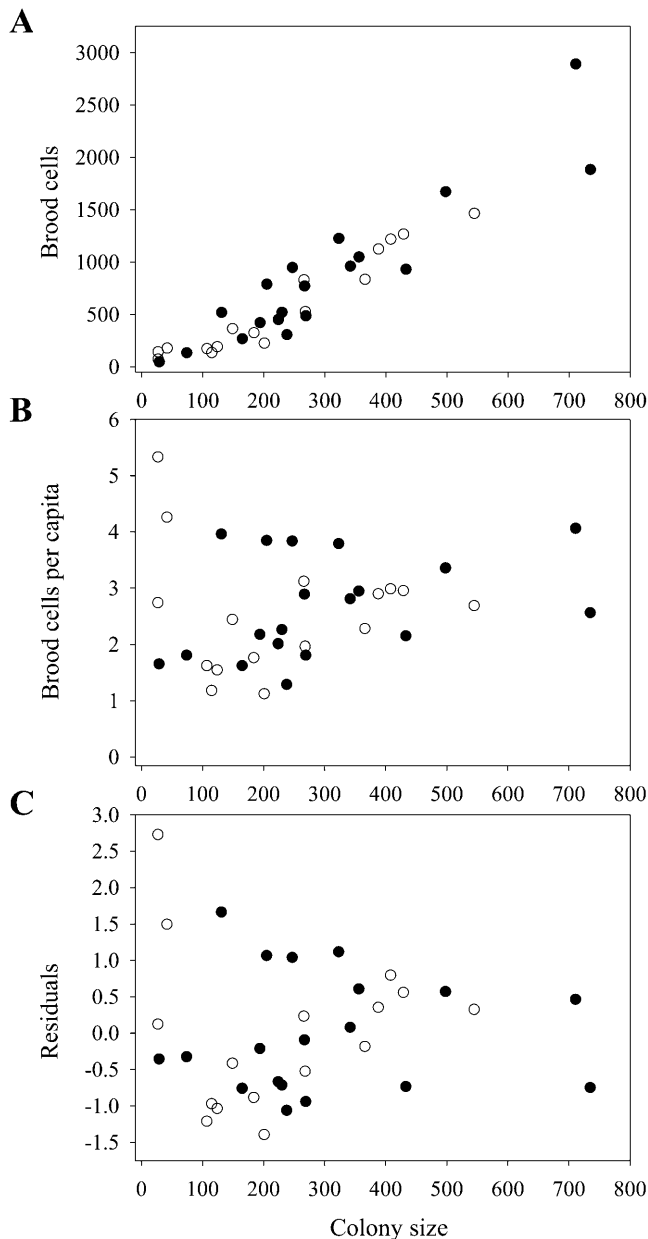


Figure 1. **A)** Brood-cell numbers in nests (C) constructed by colonies during their first 25 days of growth plotted on colony size (adults). No statistical analyses are reported for total brood cell numbers. **B)** Brood cell number/adults (C_{pc}) in nests constructed by colonies plotted on colony size. **C)** Residuals from regression model (unweighted) of C_{pc} on colony size, collection date, year, and interaction terms plotted on colony size. Open circles: 1996, closed circles: 1997.

Brood weight

The mean per-capita production of brood was $0.0146 \pm .0107$ (SD) g per adult (Table 1). Per-capita brood weight was significantly correlated with per-capita brood cell number, although it was only a moderately strong relationship (Pearson correlation $r = 0.62$, $P < 0.001$). Colony #96262 (1996, 115 adults) produced a nest with

Table 2. Weighted multiple regression of brood cells per capita (weighted by A-squared) on colony size (A), proportion of queens (Q), collection date (D), year (V) plus interaction terms. No terms were significant predictors of brood cells per capita. DF = degrees of freedom, Type III SS = type three sum of squares, F = F statistic.

$N = 35$, $F = 2.02$, $P = 0.0896$

Source	DF	Type III SS	F	P
A	1	37132	0.82	0.3735
Q	1	14457	0.32	0.5770
D	1	46318	1.02	0.3212
V	1	306	0.01	0.9351
A x V	1	11361	0.25	0.6208
Q x V	1	114667	2.53	0.1234
D x V	1	1378	0.03	0.8629

133 empty brood cells plus three cells containing eggs; colony #97134 (1997, 269 adults) had 485 empty brood cells plus two with eggs. Because these colonies were clearly deviant, failing to rear any brood over 25 days, we excluded them from models for brood weight. Since they did build nests, we opted to leave them in the analysis for brood cells. Most importantly, the inclusion or exclusion of these two colonies had no qualitative effect on the conclusion of either model.

As was the case for brood cell numbers, total brood weight (B) clearly increased with colony size (Fig. 2A). Weighted multiple regression of brood weight per capita (B_{pc}) on colony size (A), proportion of queens (Q), collection date (D), year (V), plus interaction terms, yielded a significant model (Fig. 3, Table 3B; adjusted $r^2 = 0.59$, $F = 25.61$, $P < 0.0001$); however, colony size was not a significant explanatory variable (Type III test, $P = 0.81$; Table 3A; Fig. 2B). The collection-date variable was significant, indicating that colonies collected later in the sampling period were on average less productive than colonies collected earlier. The significant year variable indicated that the average colony in 1997 was more productive than in 1996. The interaction of collection date by year (D x V) was marginally significant ($P = .0641$), thus in a visual inspection of plots of B_{pc} on D (Fig. 3) it appears that the effect of collection date was stronger in 1997 than 1996. However, since we used $\alpha = .05$ for these analyses we forced the regression lines to have the same slope. (Collection date is not a significant predictor of brood weight per capita for 1996 [Type III test, $P = 0.89$] if these data are analyzed separately from 1997.) Plots of the residuals from the full multiple-regression model (unweighted, and including non-significant terms) on colony size (Fig. 2C) showed that, as for cells per capita, small colonies were more variable in their per-capita production of brood than were larger colonies, which is also reflected in the Box-Cox results.

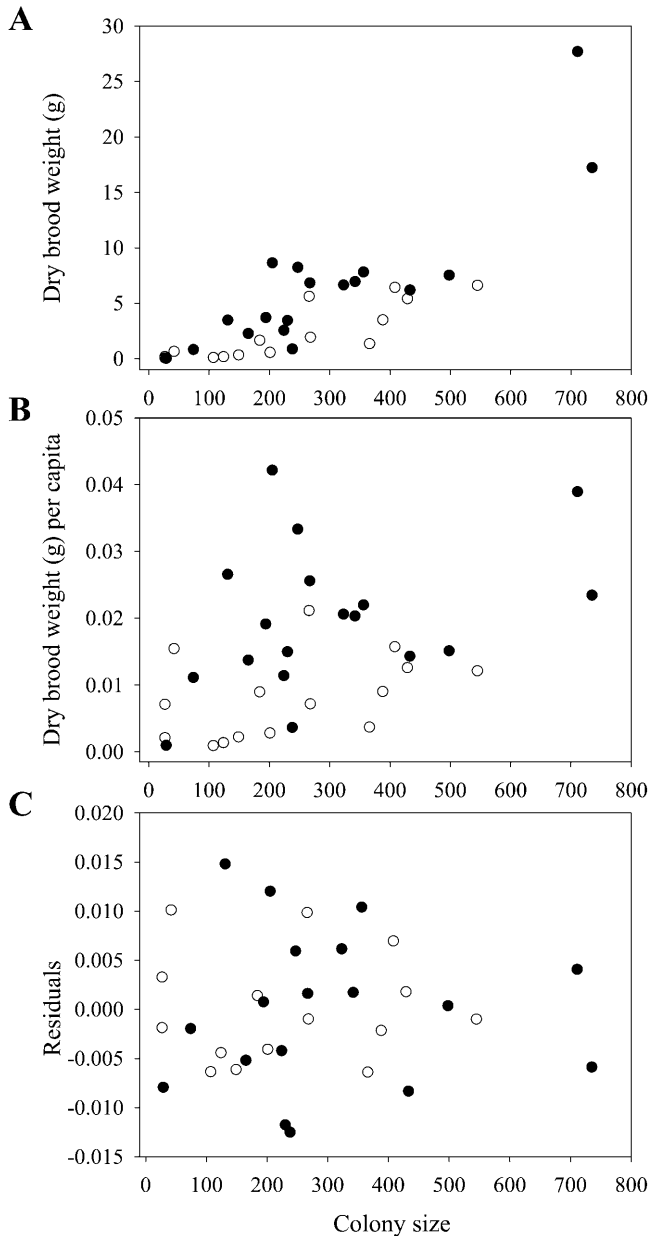


Figure 2. **A)** Dry weight of brood (g) (**B)** reared by colonies during their first 25 days of growth plotted on colony size (adults). No statistical analyses are reported for total brood weight. **B)** Dry weight of brood (g)/adults (B_{pc}) reared by colonies plotted on colony size. **C)** Residuals from regression model (unweighted) of B_{pc} on colony size, collection date, year, and interaction terms plotted on colony size. Open circles: 1996, closed circles: 1997.

Discussion

Per-capita productivity measured as brood cells constructed by *P. fraternus* swarms over their first 25 days of development was not significantly influenced by colony size, the proportion of queens in the colony, the collection date, or year. Likewise, per-capita productivity measured as dry weight of brood reared by swarms was not significantly affected by colony size. Therefore, these

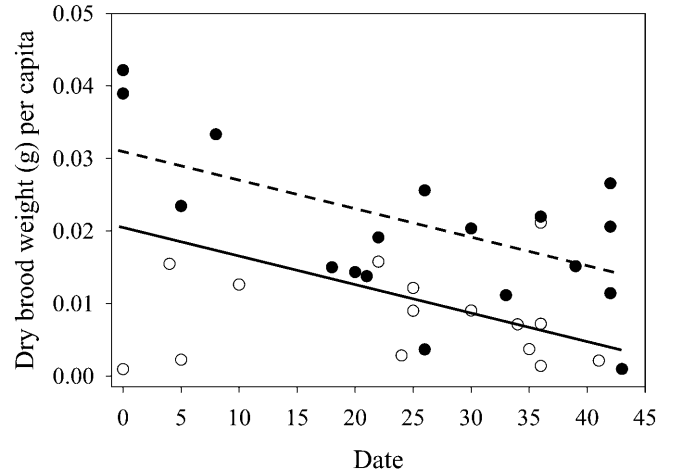


Figure 3. Dry weight of brood (g)/adults (B_{pc}) reared by colonies during their first 25 days of growth as a function of collection date (D). The model included different intercepts but the same slope for each year. Open circles and solid line: 1996, closed circles and dashed line: 1997. Colonies #96262 and #97134 did not rear any brood and are excluded from the model.

Table 3. Multiple regression (weighted by A-squared) of brood weight per capita on colony size(A), proportion of queens(Q), collection date(D), year(V), plus interaction terms. **A)** Full regression model including non-significant terms. **B)** Final multiple regression model selected by backwards elimination. DF = degrees of freedom, Type III SS = type three sum of squares, F = F statistic.

A) $N = 33, F = 9.35, P < 0.0001$				
Source	DF	Type III SS	F	P
A	1	0.2570	0.06	0.8082
Q	1	2.5193	0.59	0.4496
D	1	25.0233	5.86	0.0231
V	1	11.1654	2.62	0.1184
A x V	1	3.4254	0.80	0.3789
Q x V	1	6.7508	1.58	0.2202
D x V	1	16.0267	3.75	0.0641
B) $N = 33, \text{adjusted } r^2 = 0.59, F = 25.61, P = <0.0001$				
Source	DF	Type III SS	F	P
D	1	98.5635	20.73	<0.0001
V	1	79.5861	16.74	0.0003
Parameter	Estimate	Standard Error	t value	P
Intercept	0.03094	0.00205	15.12	<0.0001
D	-0.00039	0.00009	-4.55	<0.0001
V (1996)	-0.01047	0.00256	-4.09	0.0003
V (1997)	0	.	.	.

results do not follow Michener’s pattern of decreasing per-capita productivity with increasing size across colonies (Michener, 1964).

Per-capita production of brood was significantly greater in 1997 than in 1996, and colonies were the most productive early in the sampling period in 1997. The year

effect may be attributable to differences in rainfall between seasons. We collected the 1996 data late in the wet season, September–December, which is the rainiest part of the wet season, whereas we collected the 1997 data during the early wet season, June–August, which are drier months (W. Hagnauer, pers. comm.). In 1996 there were three week-long periods of heavy rains during daylight hours, and this may have reduced foraging opportunities for the wasps, which remain inside the nest during rain showers (AMB, pers. obs.). The negative effect of collection date on per-capita productivity observed during the early wet season in 1997 is similar to what was observed for *Polybia occidentalis* colonies during the same time of year at the same site (1998, 1999, and 2000) (Bouwma et al., 2005). The lower per-capita productivity measured later in sampling periods for both species could have been due to seasonal changes in prey abundance.

It is not clear why colonies #96262 and #97134 failed to produce any brood over 25 days. Interestingly, #96262 had the highest proportion of queens (0.22) of any colony in 1996, and colony #97134 had the third highest (0.16) in 1997. One possibility is that these colonies lacked functional queens at the beginning of the study, and the absence of functional queens induced some workers to develop ovaries to the point of recognition as queens by the time of the census. However, we found all of the individuals with developed ovaries in these two colonies to be inseminated, and therefore they should have been able to produce female offspring.

Both measures of per-capita productivity were more variable in small than in large colonies. In a primarily theoretical study, Wenzel and Pickering (1991) predicted such a distribution (funnel shape) for mean per-capita food intake plotted on colony size, citing the Central Limit Theorem (CLT). They argued that, assuming foraging success for individual colony members is independent and sampled from a normal distribution of daily forager food intake, small groups of foragers (small samples) should experience greater variability in daily mean foraging success than large groups of foragers (large samples). The negative relationship between the variability of means and sample size cited by Wenzel and Pickering (1991) is more correctly viewed as a property of standard error, which is a more basic concept than the CLT (Sokal and Rohlf, 1995). Nevertheless, Wenzel and Pickering's (1991) point about the effect of sample size is valid. If we assume that levels of variability in colony output (productivity) are correlated with levels of variability in colony input of resources (mean foraging success), it is plausible that the higher variability in per-capita productivity we observed in the small colonies in our study was due, at least in part, to greater variability in mean foraging success in the small colonies. (An alternative explanation, that higher variability observed for small colonies was due to lower precision in measuring the per-capita productivity of such colonies, is highly unlikely since we have no reason to believe that our measurements of either cell number, brood weight, or

colony size were not comparably precise for large and small colonies.)

In a critique of Jeanne and Nordheim's (1996) study of productivity in *P. occidentalis*, Karsai and Wenzel (1998) claimed, incorrectly, that because plots of per-capita brood cells (and per-capita nest material weight) on colony size showed greater variability for small than for large colonies (per-capita dry brood weight did not show this pattern), the results agreed with Michener's (1964) pattern, citing Wenzel and Pickering (1991). Only if small colonies had higher mean per-capita productivity than large colonies would the result have agreed with Michener (1964) and this was not the case for Jeanne and Nordheim's (1996) data. Similarly, in the present study, while both brood cells per capita and brood weight per capita showed patterns of higher variability for small colonies, small colonies were no more (or less) productive per capita on average than large colonies. Thus, while our results for per-capita colony output appear similar to theoretical distributions of mean per-capita colony input predicted by patterns of standard error across colony size (Wenzel and Pickering, 1991), they clearly reject Michener's reduced per-capita productivity pattern for these wasps.

In addition to the results of the present study, four studies on the swarm-founding wasp *Polybia occidentalis* that controlled for colony ontogeny also point to no negative effect of colony size on efficiency. Two of the studies (Jeanne and Nordheim, 1996; Bouwma et al., 2005) directly measured productivity (cell number and brood weight) over the first 25 days of colony development and followed an identical protocol to the study reported here. Jeanne and Nordheim (1996) concluded that colony size had a positive effect on per-capita productivity, although this conclusion largely rested on data from two very large colonies. If these colonies are removed, the resulting analysis shows no significant effect of colony size on per-capita productivity, consistent with the results of the current study. Bouwma et al. (2005), with a much larger data set, report a negative effect of gregarine parasite infection on per-capita productivity, but no significant effect of colony size.

In another study, Howard and Jeanne (2004) measured brood developmental time, also during the founding period, and showed that larger colonies reared brood to maturity more quickly than did smaller colonies. This result is consistent with the hypothesis that larger colonies achieve a more constant resource input relative to small colonies (Wenzel and Pickering, 1991). A fourth study (Jeanne, 1986) measured efficiency of nest repair by founding-stage *P. occidentalis* colonies and found that large colonies accomplished a fixed amount of nest repair in fewer worker-minutes than did small colonies. These empirical results are supported by theory, which predicts that larger work groups in wasps with series-parallel task partitioning, such as in *P. occidentalis* (Jeanne, 1996) and *Parachartergus fraternus* (AMB, pers. obs.), would be more efficient in the exchange of nest construction

materials and information than small work groups (Anderson and Ratnieks, 1999; Jeanne, 1999).

In light of these studies, it appears entirely plausible that Michener's (1964) results for swarm-founding wasps were due to his combining data from colonies (1) of different wasp species, and (2) from different developmental stages, and (3) the use of eggs per capita, which may be a stage-dependent measure of productivity. Clearly, during the first 25 days of colony development in *P. fraternus* and *Polybia occidentalis*, there is no evidence for a pattern of lower efficiency in larger colonies.

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