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Joan E. Strassmann · Carlos R. Solís · Colin R. Hughes
Keith F. Goodnight · David C. Queller

Colony life history and demography of a swarm-founding social wasp

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Abstract Colonies of social insects are sometimes viewed as superorganisms. The birth, reproduction, and death of colonies can be studied with demographic measures analogous to those normally applied to individuals, but two additional questions arise. First, how do adaptive colony demographies arise from individual behaviors? Second, since these superorganisms are made up of genetically distinct individuals, do conflicts within the colony sometimes modify and upset optima for colonies? The interplay between individual and super-individual or colony interests appears to be particularly complex in neotropical, swarm-founding, epiponine wasps such as *Parachartergus colobopterus.* In a long-term study of this species, we censused 286 nests to study colony-level reproduction and survivorship and evaluated individual-level factors by assessing genetic relatedness and queen production. Colony survivorship followed a negative exponential curve very closely, indicating type II survivorship. This pattern is defined by constant mortality across ages and is more characteristic of birds and other vertebrates than of insects. Individual colonies are long-lived, lasting an average of 347 days, with a maximum of over 4.5 years. The low and constant levels of colony mortality arise in part from colony initiation by swarming, nesting on protected substrates, and an unusual expandable nest structure. The ability to requeen rapidly was also important; relatedness data suggest that colonies requeen on average once every 9–12 months. We studied whether colony optima with respect to the timing of reproduction could be upset by individual worker interests. In this species, colonies are normally polygynous but new queens are produced only after a colony reaches the monogynous state, a result which is in accord with the genetic interests of workers. Therefore colony worker interests might drive colonies to reproduce whenever queen number happens to cycled down to one rather than at the season that is otherwise optimal. However, we found reproduction to be heavily concentrated in the rainy season. The number of new colonies peaked in this season as did the percentages of males and queens. Relatedness among workers reached a seasonal low of 0.21–0.27, reflecting the higher numbers of laying queens. This seasonality was achieved in part by a modest degree of synchrony in the queen reduction cycle. Worker relatedness reached peaks of around 0.4 in the dry season, reflecting a decrease to a harmonic mean queen number of about 2.5. Thus, a significant number of colonies must be approaching monogyny entering the rainy season. Coupled with polygynous colonies rearing only males (split sex ratios), this makes it possible for a colony cycle driven by selfish worker interests to be consistent with concentrating colony reproduction during a favorable season.

Key words Genetic relatedness · Eusociality · Social wasps · Colony survivorship · Superorganism

Introduction

Social insects live in cooperative colonies which, like individual organisms, have life cycles involving birth, reproduction, and death. Colony life histories can therefore be studied in a manner analagous to conventional individual life histories, potentially yielding insights into the success of social species. However, the demography of colonies is not simply the sum of the demographies of their constituent individuals, and this leads to two particularly interesting questions.

First, one can ask how individuals work together in ways that lead to altered, and possibly adaptive, colony demographies. Do they obtain efficiencies of scale, or do they interact in ways that lead to novel emergent prop-

J.E. Strassmann (✉) · C.R. Solís · C.R. Hughes[1]
K.F. Goodnight · D.C. Queller
Department of Ecology and Evolutionary Biology,
Rice University, 6100 Main, Houston, TX 77005–1892, USA
Fax: (713) 285–5232

Current address:
[1]Department of Biology, University of North Dakota,
Grand Forks, ND 58202, USA
E-mail: STRASSM@RICE.EDU

erties at the colony level? For example, for organisms with extended parental care, a major advantage of living in colonies in the first place relies on a property that emerges with cohabiting adults. A solitary adult who dies loses all its dependent young, but grouped adults provide insurance against this cost when survivors complete the unfinished investments (Queller 1989, 1994a, 1995; Strassmann and Queller 1989; Gadagkar 1990; Reeve 1991). Once colonies evolve, the potential for selecting adaptive colony-level characteristics increases, and many researchers have found it profitable to treat the colony as if it were an individual organism (or superorganism), adapted in its own right (Wheeler 1911; Seeley 1989; Oster and Wilson 1977; Wilson and Sober 1989; Ratnieks and Reeve 1992).

The second question arises out of the first. Colonies might show adaptive demographies, but there is the potential for disruption by behavior that is adaptive for particular individuals or classes within the colony. Within-colony conflicts have been well documented, particularly in the area of sex ratios (Trivers and Hare 1976; Boomsma and Grafen 1991; Mueller 1991; Sundstrom 1994; Queller et al. 1993a) and in competition among reproductives (wasps: West-Eberhard 1969; Strassmann 1981; Ishay et al. 1983; ants: Balas and Adams 1996; Bernasconi and Keller 1996; bees: Michener 1974). The question of conflicts between levels of selection is relevant at many levels in the hierarchy of life (Maynard Smith and Szathmáry 1995) but is perhaps most easily studied in social insects. Nevertheless, the interplay between life-history strategies and conflict has been explored in very few theoretical studies and almost no empirical ones (reviewed in Bourke and Franks 1995).

In this paper, we explore aspects of these questions in the epiponine wasp, *Parachartergus colobopterus*. At the colony level, we focus particularly on colony mortality schedules and on the timing of colony reproduction. We also explore whether the optimal timing of reproduction may be disrupted by within-colony conflicts. To understand the kind of conflicts that can arise in epiponine wasp societies an overview of the colony cycle is necessary. The epiponine wasps are a tribe of the Polistinae within the Vespidae comprised of 23 genera and about 200 species that occur in the Neotropics from southern Texas to Argentina (Richards 1978; Carpenter 1993). In this group, colonies are initiated by swarms consisting of workers and mated queens (Forsyth 1981). These females build a paper nest and the queens lay eggs in it. The first adults emerging from the nest are mainly worker females; workers continue to be produced throughout the colony cycle. As the colony grows, the number of queens declines, and no new queens are added. Fighting among queens may be the primary cause of this decline in queen number (Forsyth 1978; West-Eberhard 1978). Production of reproductive females, or new queens, occurs only when queen number falls to one or nearly one (West-Eberhard 1978; Strassmann et al. 1991; Queller et al. 1993a). By contrast, males are produced in colonies when there are many queens present (Queller et al. 1993a). Evidence for this pattern, called cyclical oligogyny, has been found in all epiponines examined in detail thus far (West-Eberhard 1978; Forsyth 1978; Strassmann et al. 1991, 1992; Gastreich et al. 1993; Hughes et al. 1993; Queller et al. 1993a, b).

This pattern of male and queen production is consistent with kin-selected worker preferences for rearing males when there are multiple queens and reproductive females when there are few queens (Queller et al. 1993a). This preference pattern arises in the Hymenoptera (ants, bees, wasps) because males hatch from unfertilized eggs and are therefore haploid. Fathers therefore contribute genetically identical sperm to their daughters. As a consequence, worker females are related to full sisters by 3/4 but to brothers by only 1/4, generating a preference for rearing sisters. Workers (who are female in Hymenoptera) on multiple-queen colonies rear mainly cousins, and are equally related to the male and female offspring ($r = 3/16$). Workers favor female production when full sisters are available (colonies with only one queen) and male production when relatedness to males and females is equal (colonies with more than one queen; Boomsma and Grafen 1991; Pamilo 1991). Queens, by contrast, have no relatedness asymmetries to female and male young. Although selection operating at the colony level and at the individual level play important roles in epiponine colony growth and reproduction, the two levels have rarely been considered in a single study. In particular, it is not known how the selfish genetic interests of the workers regarding production of sexuals meshes (or fails to mesh) with the seasonal factors affecting optimum reproduction of the colony or superorganism. The present study ties prior work on individual factors to colony level mortality and reproduction in the neotropical, swarm-founding wasp, *Parachartergus colobopterus*. We assessed birth, death and reproduction of colonies by counting new colonies and following them through time, collecting samples of workers, queens and males, and, in particular, by estimating change in genetic relatedness among colony members through time.

Methods

Study population and measures of seasonality

We collected data for this study during 16 trips to the campus of the Universidad Central de Venezuela, Maracay, Venezuela (10°15′ N 67°36′ W, altitude 445 m), beginning in August 1988 and continuing to July 1993. Nests were located on trees, barns, sheds, classrooms, and laboratories. Nearly all nest sites were within 100 m of forest that continued up the mountains to Henri Pittier National Park. Nests were mapped and photographed to facilitate identification on subsequent trips. We were careful to sample all colonies in the study area (the area sampled enlarged slightly over time as our permission for access to certain areas changed) until the final two trips when no new colonies were added to our sample. Each colony's longevity was estimated from the dates it was first and last seen active, with the addition of half of the inter-trip intervals preceeding and following this period.

Table 1 Sample of *Parachartergus colobopterus* colonies

A	B	C	D	E	F	G
Trip	Sample Collection and Census Date	No.total colonies sampled (No. colonies entirely collected)	No. colonies censused for mortality also present previous trip	No. colonies failed since previous trip	No. of active colonies for allozymes	No. of wasps used
V4	18 Aug. '88	24 (24)			24	375
V6	30 Dec. '88	55			54	631
V7	6 April '89	68	55	5	57	680
V8	22 June '89	70	61	8	53	575
V9	15 Aug. '89	96	62	17	68	774
V10	30 Nov. '89	109	80	19	88	959
V11	6 Mar. '90	112	90	30	81	872
V12	21 June '90	97	80	26	68	760
V13	18 Sept. '90	118	72	17	96	998
V14	10 Jan. '91	115	101	37	73	832
V15	22 May '91	94	76	25		
V16	13 June '91	92 (9)	69	1		
V17	10 July '91	118 (19)	80	10		
V18	8 Aug. '91	132 (23)	92	13		
V19	20 July '92	81	81	58		
V20	27 July '93	22	22	20		

In order to assess changes in genetic relatedness, nest initiation, and mortality over wet and dry seasons, the first ten censuses were carried out at approximately 3-month intervals (Table 1). On the first trip we collected entire colonies (Strassmann et al. 1991). On the next nine trips we collected a sample of 12 individuals from each study colony. Usually these were the first individuals that ran into a miniature zip-shut bag held over the nest entrance as we stroked the nest envelope with a finger. This technique may over – or under-sample the different classes of individuals – workers, males and queens – but is likely to do so consistently over time. Therefore we assume this technique gives accurate estimates of the relative numbers of males and queens at different times. If the nest did not have many adults, we collected fewer than 12 individuals because we did not want to hasten the colony's demise. Wasps were stored in liquid nitrogen for transit to our laboratory where the samples were held at −57 °C pending allozyme analysis. The final six trips were for censuses of nest mortality (and other projects not reported on here) and did not include allozyme work.

We obtained monthly rainfall data from the weather station in Maracay, Venezuela. To test the hypothesis that reproduction occurred in the rainy season, we looked at the relationship of rainfall with numbers of males, queens, new colonies, and relatedness. For this analysis we used rainfall for the 30 days preceding the collection date, assuming rain to have fallen evenly through the month. For evaluating the significance of correlations we did a bootstrap analysis with replacement using Resampling Statistics 4.0 (from Resampling Statistics Inc., Arlington, Va.) and ran 2000 randomizations. We did one-tailed analyses, predicting that reproduction of all sorts would be positively correlated with rainfall, and that relatedness within colonies would be negatively correlated with rainfall, as a result of many queens per colony when they are growing rapidly. The significance value, alpha, is the fraction of randomizations with correlations more extreme than the empirical value.

Laboratory analyses

We determined sex and caste by dissection (Strassmann et al. 1991). Externally, males and females look very similar. Females were categorized as queens if they had at least one mature egg in their ovaries and spermathecae containing sperm. Estimates of genetic relatedness were based on seven allozyme loci (Table 2). The low level of heterozygosity of these loci made it necessary to analyze large samples. We evaluated 7456 wasps from 662 samples collected from 286 colonies at 10 dates. Allozymes were visualized on horizontal starch gels as described in Strassmann et al. (1991).

Relatedness estimation

We used the computer program Relatedness 4.2b (Goodnight and Queller 1995; http://www.rice.edu/wasps for relatedness estimation). Standard errors were based on jackknifing over colonies (Queller and Goodnight 1989). Improved standard errors for these relatedness differences within colonies were obtained by directly jackknifing the difference (Queller 1994b). Colonies were weighted equally in all analyses.

Table 2 Enzymes scored and allele frequencies in the Maracay population of *P. colobopterus*

Enzyme	Allele frequencies		
	1	2	3
Peptidase (leucylglycylglycine) (PEPLGG)	0.816	0.183	0.001
6-Phosphogluconate dehydrogenase (PGD)	0.942	0.054	0.005
Phosphoglucose isomerase (PGI)	0.973	0.027	
Glyceraldehyde-3-phosphate dehydrogenase 1 (G3PD1)	0.995	0.005	
Glyceraldehyde-3-phosphate dehydrogenase 2 (G3PD2)	0.999	0.001	
Isocitrate dehydrogenase (IDH)	0.999	0.001	
Beta-hydroxybutyrate dehydrogenase (HBDH)	0.995	0.005	

Results

Reproduction

Our data indicate that reproduction in *P. colobopterus* occurs primarily in the rainy season from June through October (Fig. 1). The percentage of queens and numbers of new colonies were significantly higher at times of high rainfall (Table 3). Though not significant, the percentage of males in the samples was elevated at the same time. As predicted, genetic relatedness was decreased in the times of greatest rainfall (Table 3). Relatedness changed with season from a high of 0.37–0.44 (depending on year) to a low of 0.21–0.27. Overall, relatedness among nestmates collected at the same time was 0.346 ± SE 0.056 (7081 individuals on 242 nests; not including the whole-colony sample collected on trip 4). There was no inbreeding ($F = -0.004 \pm 0.079$).

Table 3 Correlation of rainfall in the previous 30 days with percent of queens and males in the samples, numbers of new colonies, and relatedness

Variable	Correlation
% Of queens	0.58**
% Of males	0.47*
No. of new colonies	0.64**
Relatedness	−0.77***

$*P < 0.10$, $**P < 0.05$, $***P < 0.01$; significance levels are bootstrap values from 2000 randomizations

To obtain an estimate of the frequency of re-queening episodes on established nests, we compared relatedness among female colonymates on trip x to relatedness of these same individuals to nestmates collected on future trips roughly 3, 6, 9, and 12 months later. These values are shown in Fig. 2. Whenever a colony requeens, relatedness should fall by about a half (see discussion). Relatedness dropped from 0.35 for contemporaneous colony mates to 0.18 for colony mates separated by 9–12 months in time. This drop of about a factor of two is consistent with one re-queening event per colony per 9–12 months.

Entire colonies were collected only in August 1988. At that time relatedness among nestmates was intermediate and the percentage of queens was comparatively high, but these whole colony samples are not necessarily comparable to the samples that comprise the rest of the study. Four colonies had only one queen; six colonies had 2–19 queens; six colonies had 20–49 queens; the remaining five colonies had 50–69 queens (Strassmann et al. 1991). Larger colonies were more likely to have more queens ($r = 0.71$, $P < 0.01$, Strassmann et al. 1991). These results should be compared to those of later trips with caution because of the different sampling methods used. However, from the August 1988 study, we can conclude that colonies are not at exactly the same stage at the same time, despite the overall synchrony in reproduction.

Mortality and longevity of nests

Individual colonies were surprisingly long-lived (Fig. 3). Average colony longevity was 347 days (SD = 276,

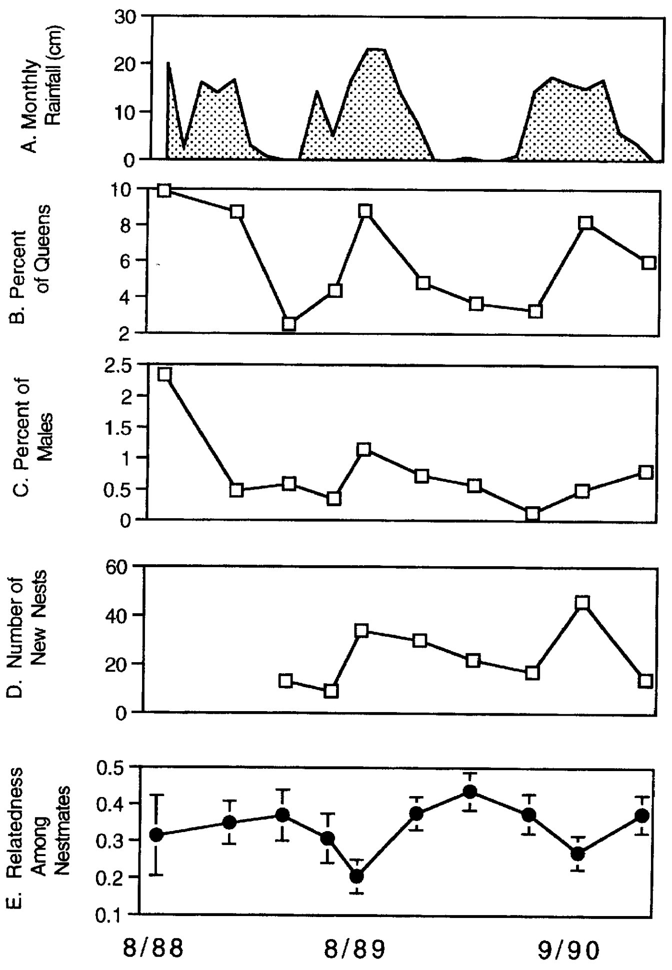

Fig. 1 Rainfall, production of queens, males and new colonies and genetic relatedness among colonymates from August 1988 to January 1991. Monthly data are given for rainfall. Sample sizes and dates of each census are in Table 1. *Bars* indicate standard errors for relatedness estimates

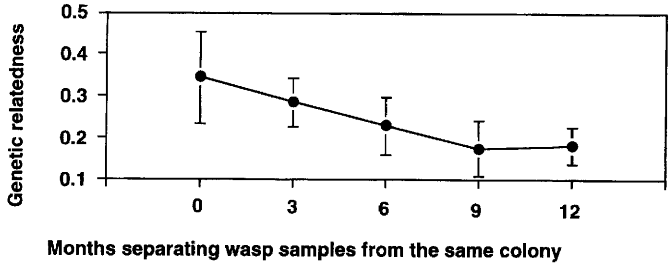

Fig. 2 Change in within-colony relatedness among females separated by time. *Bars* indicate standard errors for relatedness estimates. Sample sizes are 7081 females in 242 colonies for same time, 6110 females in 152 colonies for relatedness between females on the same nest separated in time by three months, 4538 females in 97 colonies for relatedness between females on the same nest separated in time by 6 months, 3145 females in 67 colonies for relatedness between females on the same nest separated in time by 9 months, and 1866 females in 41 colonies for relatedness between females separated in time by 12 months

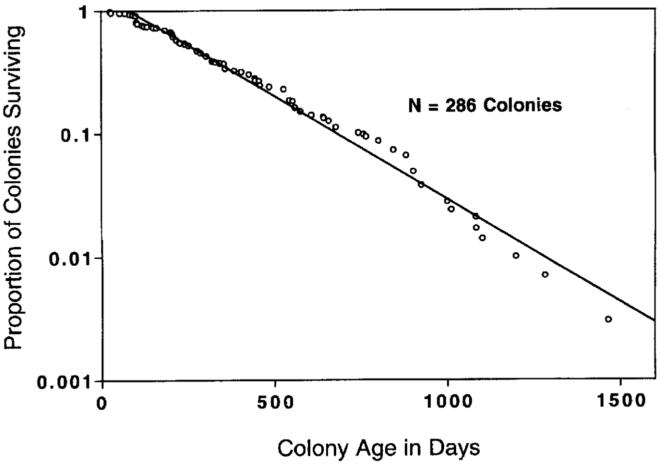

Fig. 3 Survivorship curve for 286 colonies of *Parachartergus colobopterus*. Sample sizes are given in Table 1

$n = 286$). The oldest was over 4.5 years old when it was destroyed by maintenance workers during our final trip. In general, however, such destruction by humans appeared to be rare since these wasps were widely known to be docile.

Colony survivorship can be fitted by a type II survivorship curve of constant mortality over time. Mortality was not clearly associated with season, though two of the three years showed a peak in mortality in the rainy season. Nor was mortality clearly related to stage in the queen number cycle. Relatedness among females on the final census date before colony death was 0.388 while relatedness among females on other dates for those same colonies was 0.345. The standard error of the difference between these values is 0.043, so the difference is not significant.

Discussion

Colony mortality and collective behavior

To the best of our knowledge, our data provide the first colony mortality curve for epiponine wasps. The type II curve, with constant mortality rates, is unusual for social insects. The two extremes of the curve provide good examples of how colony demography emerges as more than the sum of the individual parts.

The high survivorship at the early end of the curve is unusual in that social insect colonies are typically small and vulnerable (Oster and Wilson 1978). Our survivorship curve for *P. colobopterus* colonies indicates no such period of high vulnerability. While our estimate of early mortality does not take account of colonies that may have been founded and died during intertrip intervals, it nevertheless seems safe to conclude that early mortality is not as extreme as in many social insects. The most likely reason is that colonies are founded by swarms and therefore never pass through a stage in which survival of the colony is dependent on the survival of very few individuals. This advantage is also evident in non-swarming polistines with multiple foundresses. Colonies with single foundresses almost always fail at a higher rate than those with multiple foundresses (Queller 1995). However, in these non-swarming wasps, multiple founding depends on a few relatives encountering one another very near the parental nest site, whereas the trail-following behaviors of epiponines (Jeanne 1981) have allowed them to begin new colonies at much greater distances and with many more individuals.

At the other extreme of the survivorship curve, we also see little evidence for colony senescence, which would be manifested by increased mortality rates at advanced colony age. Again, this result should be treated with some caution. The last few survivorship points are slightly below the best-fit line, but these are based on small sample sizes. The ability to survive at advanced age fits with several aspects of the biology of epiponines in general and of *P. colobopterus* in particular. First, in epiponines, new queens are produced in large numbers by colonies that have reached the stage of having only a single queen (West-Eberhard 1978; Strassmann et al. 1991). The ability to re-queen quickly and easily frees the late-stage colony from dependence on the survival of a single individual, just as swarming does for early-stage colonies. In social insects lacking this capacity for rapid replacement, the colony usually dies after death of the queen, sometimes after a spurt of male production by uninseminated workers (van Honk et al. 1981; Matsuura 1991).

Nest architecture may also contribute to lack of colony sensecence in this species. The structure is unusually variable in this species (Schremmer 1978). In our population most nests have a series of horizontal combs that are each attached independently to a vertical substrate, the whole being covered by single envelope with an entrance at the bottom. New combs are added to the bottom while old combs rendered useless by the accumulation of meconium and perhaps parasites are left abandoned at the top. In this way, colonies can persist over a period of several years by slowly marching down a wall or tree trunk. This sort of nest structure is unusual in social wasps. Nest structures vary considerably among social wasps, but many have a single attachment point to a branch or other substrate, with the entire nest hanging from that point (Wilson 1971; Jeanne 1975; Richards 1978; Wenzel 1991). Such a structure is advantageous for keeping ants away from the brood since only a single point is defended, but it means that old combs cannot be excluded. Very large colonies may become too heavy to be supported. The result would be closely analogous to the pleiotropic effects hypothesized to cause individual senescence (Williams 1957), but at the colony level. A nest with a single attachment point may be selected because of its benefits at early ages, in spite of costs at later ages, because fewer colonies experience the late costs.

Do social constraints affect timing of reproduction?

Climate, in particular rainfall, is highly seasonal in Maracay. While *P. colobopterus* maintains active colonies rearing brood throughout the entire year, one might expect reproduction to be concentrated in the most favorable season. In fact, reproduction, measured by the numbers of queens, males, and new colonies, is concentrated in the rainy season. How is this seasonal cycle achieved in the face of the social cycle apparently driven by worker preferences? On each colony, queen numbers gradually decline, with new queens being produced only after the number of old queens reaches one.

One possibility is that the queen reduction cycle is tightly coupled with the seasonal one, so that most colonies reach the single queen stage at just the right time. However, queen number cycles are very imperfectly synchronized among colonies, as evidenced by the large variation in queen number among colonies collected at one time (in August; Strassmann et al. 1991). This variation is not unique to *P. colobopterus* (Queller et al. 1993b; reviewed in Hughes et al. 1993; Jeanne 1991). For *P. colobopterus*, it is also evidently not unique to August. Many colonies must still have multiple queens even as the rainy season begins; otherwise the mean relatedness would approach 0.75 instead of remaining at 0.45 or lower. This relatedness argument is based on the fact that queens are singly-mated (Goodnight et al. 1996).

Still, a certain amount of queen number synchrony is achieved. The population enters the rainy season with worker relatedness near 0.4. This corresponds to an effective harmonic queen number of $q = 2.5$ (based on the formula, $r_{worker} = 1/q \times 3/4 + (q-1)/q \times r_{queen}/4$, with $r_{queen} = 0.667$; Strassmann et al. 1991). Since this is a harmonic mean, the maximum percentage of single-queen colonies is 40%, a maximum that applies only in the extreme circumstance of the remaining 60% being very highly polygynous. In reality, because some of the polygynous colonies will have only a few queens, the fraction of monogynous colonies must be lower. But this suggests that a reasonable fraction of colonies are either monogynous or have few enough queens that they would subsequently reach monogyny during the rainy season.

Not all reproductive colonies need to reduce to a single queen. Colonies that fail to reach monogyny presumably specialize on males. A combination of very modest synchrony with colony specialization (split sex ratios) probably accounts for the rainy season peak of reproduction.

The modest degree of synchrony observed could be attained even if queen reduction is independent of season. Colonies reaching the single-queen stage need not reproduce immediately. Those achieving this stage in the favorable rainy season would tend to requeen, while those becoming monogynous during the dry season may try to hold out, resulting in some accumulation of single-queen colonies at the start of the rainy season.

Colonies that reach the single-queen stage during the dry season would need to requeen if the aging queen becomes too weak to sustain sufficient egg production. Some degree of requeening during the less favorable dry season may represent an unavoidable cost of the colony cycle. There is no direct evidence of such requeening since we cannot distinguish new queens from old. However, there is indirect evidence because males are produced year-round, and males should be reared only if there are virgin queens in the population.

Exactly how swarming fits in with the queen number cycle remains unclear. The peak of new colony production coincides roughly with the peak in queen numbers (and the resulting trough in relatedness). This might simply be a coincidence of both occurring at the best time for reproduction. Alternatively there might be some direct relationship. One possibility is that swarming tends to follow queen production and is in part a manifestation of social competition among queens (West-Eberhard 1973). Another is that higher queen percentages are a consequence of swarming. If swarms include just one or a few queens from the parent colony (J. E. Strassmann unpublished work), they may re-queen shortly after initiating a new nest.

We conclude that the timing of reproduction in not severely constrained by the queen number cycle and the worker preference for queen production at the low extreme of that cycle. Thus, reproduction in epiponines can depend both on climate and on the pace at which queen numbers decline. Climate determines the overall timing of the reproductive peak. However, within that time window, the pattern of sexual production is determined by between-colony variation in queen number. This allows colonies to be initiated when opportunities for growth are greatest while retaining a pattern of reproduction consistent with the genetic interests of workers. Such an uncoupling may be partly responsible for the ecological success of the epiponine wasps in the neotropics.

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References

Balas MT, Adams ES (1996) The dissolution of cooperative groups: mechanisms of queen mortality in incipient fire ant colonies. Behav Ecol Sociobiol 38:391–399

Bernasconi G, Keller L (1996) Reproductive conflicts in cooperative associations of fire ant queens (*Solenopsis invicta*). Proc R Soc Lond 263:509–513

Boomsma JJ, Grafen A (1991) Colony-level sex ratio selection in the eusocial Hymenoptera. Evol Biol 3:383–407

Bourke AFG, Franks NR (1995) Social evolution in ants. Princeton University Press, Princeton

Carpenter J (1993) Biogeographic patterns in the Vespidae (Hymenoptera): two views of Africa and South America. In: Gold blatt P (ed) Biological relationships between Africa and South America. Yale University Press, New Haven pp 139–155

Forsyth AB (1978) Studies on the behavioral ecology of polygynous social wasps. PhD dissertation, Harvard University, Cambridge, Massachusetts

Forsyth AB (1981) Swarming activity of polybiine social wasps (Hymenoptera: Vespidae: Polybiini). Biotropica 13:93–99

Gadagkar R (1990) Evolution of eusociality: the advantage of assured fitness returns. Philos Trans R Soc Lond B 329:17–25

Gastreich KR, Strassmann JE, Queller DC (1993) Determinants of high genetic relatedness in the swarm-founding wasp, *Protopolybia exigua*. Ethol Ecol Evol 5:529–539

Goodnight KF, Queller DC (1995) Relatedness 4.2b. Goodnight Software, Houston TX

Goodnight KF, Strassmann JE, Klingler CJ, Queller DC (1996) Single mating and its implications for kinship structure in a multiple-queen wasp, *Parachartergus colobopterus*. Ethol Ecol Evol 8:191–198

Honk CGJ van, Roseler PF, Velthuis HHW, Hoogeveen JC(1981) Factors influencing the egg laying of workers in a captive *Bombus terrestris* colony. Behav Ecol Sociobiol 9:9–14

Hughes CR, Queller DC, Strassmann JE, Solís CR, Negrón-Sotomayor JA, Gastreich KR (1993) The maintenance of high genetic relatedness in multi-queen colonies of social wasps. In: Keller L (ed) Queen number and sociality in insects. Oxford University Press, Oxford, pp 153–170

Ishay JS, Dotan ZA, Pinchasov A (1983) Combativeness among oriental hornet queens. Insectes Soc 30:57–69

Jeanne RL (1975) The adaptiveness of social wasp nest architecture. Q Rev Biol 50:267–287

Jeanne RL (1981) Chemical communication during swarm emigration in the social wasp *Polybia sericea* (Olivier). Anim Behav 29:102–113

Jeanne RL (1991) The swarm-founding Vespidae. In: Ross K, Matthews R (eds) The social biology of wasps. Cornell University Press, ithaca, pp 191–231

Matsuura M (1991) *Vespa* and *Provespa*. In: Ross KG, Matthews RW (eds) The social biology of wasps. Cornell University Press, Ithaca, pp 232–262

Maynard Smith J, Szathmáry E (1995) The major transitions in evolution. WH Freeman, Oxford

Michener CD (1974) The social behavior of the bees: a comparative study. Harvard University Press, Cambridge, Massachusetts

Mueller UG (1991) Haplodiploidy and the evolution of facultative sex ratios in a primitively eusocial bee. Science 254:442–254

Pamilo P (1991) Evolution of colony characteristics in social insects. I. Sex allocation. Am Nat 137:83–107

Oster GF, Wilson EO (1978) Caste and ecology in the social insects. Princeton University Press, Princeton

Queller DC (1989) The evolution of eusociality: reproductive head starts of workers. Proc Natl Acad Sci USA 86:3224–3226

Queller DC (1994a) Extended parental care and the origin of eusociality. Proc R Soc Lond B 256:105–111

Queller DC (1994b) A method for detecting kin discrimination within natural colonies of social insects. Anim Behav 47:569–576

Queller DC (1995) The origin and maintenance of eusociality: the advantage of extended parental care. In: Turillazzi S, West-Eberhard MJ (eds) Natural history and evolution of paper wasps. Oxford University Press, Oxford, pp 218–234

Queller DC, Goodnight KF (1989) Estimating relatedness using genetic markers. Evolution 43:258–275

Queller DC, Strassmann JE, Solís CR, Hughes CR, DeLoach DM (1993a) A selfish strategy of social insect workers that promotes social cohesion. Nature 365:639–641

Queller DC, Negrón-Sotomayor J, Strassmann JE, Hughes CR (1993b) Queen number and genetic relatedness in a neotropical wasp, *Polybia occidentalis*. Behav Ecol 4:7–13

Ratnieks FLW, Reeve HK (1992) Conflict in single-queen hymenopteran societies: the structure of conflict and processes that reduce conflict in advanced eusocial species. J Theor Biol 158: 33–65

Reeve HK (1991) *Polistes*. In: Ross KG, Matthews RW (eds) The social biology of wasps. Cornell University Press, Ithaca, pp 99–148

Richards OW (1978) The social wasps of the Americas excluding the Vespinae. British Museum (Natural History), London

Schremmer F (1978) Zum Einfluss verschiedener Nestunterlagen-Neigungen auf Nestform und Wabengrösse bei zwei neotropischen Arten sozialer Faltenwespen der Gattung *Parachartergus* (Hymenoptera: Vespidae). Entomol Germ 4:356–367

Seeley TD (1989) The honey bee colony as a superorganism. Am Sci 77:546–553

Strassmann JE (1981) Wasp reproduction and kin selection: reproductive competition and dominance hierarchies among *Polistes annularis* foundresses. Fla Entomol 64:74–88

Strassmann JE, Queller DC (1989) Ecological determinants of social evolution. In: Breed MD, Page RE (eds) The genetics of social evolution. Westview, Boulder, pp 81–101

Strassmann JE, Queller DC, Solís CR, Hughes CR (1991) Relatedness and queen number in the neotropical wasp, *Parachartergus colobopterus*. Anim Behav 42:461–470

Strassmann JE, Gastreich KR, Queller DC, Hughes CR (1992) Demographic and genetic evidence for cyclical changes in queen number in a neo-tropical wasp, *Polybia emaciata*. Am Nat 140: 363–372

Sundström L (1994) Sex ratio bias, relatedness asymmetry and queen mating frequency in ants. Nature 367:266–268

Trivers RL, Hare H (1976) Haplodiploidy and the evolution of the social insects. Science 191:249–263

Wenzel JW (1991) Evolution of nest architecture. In: Ross KG, Matthews RW (eds) The social biology of wasps. Cornell University Press, Ithaca, pp 480–519

West-Eberhard MJ (1969) Social biology of *Polistine* wasps. Mis Publ Mus Zool Univ Mich 140:1–101

West-Eberhard MJ (1973) Monogyny in "polygynous" social wasps. In: Proc. 7th Int. Cong. I.U.S.S.I. London pp 396–403

West-Eberhard MJ (1978) Temporary queens in *Metapolybia* wasps: Nonreproductive helpers without altrusim? Science 200: 441–443

Wheeler WM (1911) The ant colony as organism. J Morphol 22: 307–325

Williams GC (1957) Pleiotropy, natural selection, and the evolution of senescence. Evolution 11:398–411

Wilson DS, Sober E (1989) Reviving the superorganism. J Theor Biol 136:337–356

Wilson EO (1971) The insect societies. Harvard University Press, Boston

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