

SOME EFFECTS OF GROUP SIZE ON THE OUTPUT OF BEGINNING NESTS OF *MISCHOCYTTARUS MEXICANUS* (HYMENOPTERA: VESPIDAE)

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ABSTRACT

It is not known how pleometrosis (nest initiation in groups) and haplometrosis (nest initiation alone) are both maintained in the paper wasp *Mischocyttarus mexicanus* (Saussure). To answer this question, reliable measurements of the reproductive success of each tactic are needed. It is shown here that females that begin nests alone are more likely to raise a few daughters in rapid succession rather than many daughters at the same time. Females in small groups or alone also tend to have smaller first daughters than those females working in large groups. This difference in resource allocation between small and large groups causes measurements of per capita rates of production to correlate differently with group size depending on whether the number of cells, number of offspring, or weight of offspring added per day is measured. These data are consistent with the observation that haplometrotic females receive more predator and conspecific attacks than pleometrotic females, and thus produce their first daughters quickly to guard the nest. In addition the chronic mystery of a negative correlation between per capita productivity and group size in social insects is shown to be an expected outcome and not necessarily an indication that efficiency decreases with an increase in group size.

Key Words: *Mischocyttarus mexicanus*, paper wasps, efficiency, social behavior, Polistinae, per capita productivity

RESUMEN

No se sabe como pleometrosis (iniciación de nido en grupos) y haplometrosis (iniciación de nido solo) son mantenidos en la avispa de papel *Mischocyttarus mexicanus* (Saussure). Para contestar esta pregunta, se necesitan medidas confiables del éxito reproductivo de cada táctica. Se demuestra aquí que hembras que comienzan nidos solos son mas propensas a criar unas pocas hijas muy rápidamente en vez de muchas hijas al mismo tiempo. Hembras en grupos pequeños o solas también tienden a hacer sus primeras hijas más pequeñas que aquellas hembras trabajando en grupos grandes. Esta diferencia en asignación de recursos entre grupos pequeños y grandes causa que evaluaciones de producción promedio per capita sean correlacionadas diferentemente con el tamaño del grupo dependiendo en que el numero de células, numero de crías, o el peso de la cría sumado por día sea evaluado. Estos datos apoyan la noción que hembras haplometroticas reciben mas ataques de predadores y conespecificos que hembras pleometroticas, y por lo tanto producen su primera hija rápidamente para proteger el nido. Adicionalmente, el misterio crónico de una correlación negativa entre productividad per capita y tamaño del grupo en insectos sociales es demostrado ser un resultado esperado y no una debilitación de la hipótesis que grupos mayores son más eficientes.

When females of *Mischocyttarus mexicanus* (Saussure) (a Polistine paper wasp) begin nests, they can be found doing this alone or in groups of sisters (Litte 1977). The existence of solitary nest-founding (haplometrosis) together with group nest-founding (pleometrosis) is common in paper wasps (West-Eberhard 1967; Litte 1981; Strassmann 1983; Reeve 1991; Gadagkar 1996) and some other hymenopterans (Michener 1964; Mintzer 1979; Tschinkel and Howard 1983; Mintzer & Vinso 1985; Rissing & Pollock 1987, 1988; Stark 1992). Since haplometrotic and pleometrotic sisters can often be found working near one another, it is compelling to hypothesize that these two modes of nest initiation are the result of deci-

sions made by females: they must decide whether to join a sister, and sisters must decide whether to accept help (Strassmann 1996; Clouse 1997). How these two tactics are maintained in the population is an exciting topic for those who study the selective advantages of social and solitary behavior.

It has become increasingly clear that for many Polistines, nests require guarding to survive, and this may be a driving force behind the evolution and maintenance of pleometrosis. We know already that nests of *M. mexicanus* and other paper wasps suffer continuous intrusions by conspecifics which prey on larvae and/or usurp the current foundress, and we know that lone females suffer more from these attacks (Gamboa 1978; Makino &

Sayama 1991; Kasuya et al. 1980; Kasuya 1982; Klahn 1988; Gamboa et al. 1992; Clouse 1995; Katada & Iwahashi 1996) as well as attacks by ants, birds, and other predators and parasites (Yamana 1996). This is because lone females cannot both guard their nests and forage, so their nests are left vulnerable for part of every day. Moreover, since initial attacks on haplometrotic nests are more successful than those against pleometrotic nests, haplometrotic nests probably receive a higher rate of return attacks than pleometrotic ones. However, haplometrotic females seem to compensate by making numerous and brief foraging trips, and, at least in some populations, haplometrotic females are larger than even the highest-ranking pleometrotic females (Clouse 1997).

The observation that *M. mexicanus* nests suffer regular intrusions is consistent with the finding that adult females on a nest are significantly less related than full sisters (Strassmann et al. 1995). Strassmann et al. (1995) also asserted that *M. mexicanus* females mate only once, and Litte (1977) observed that nests had only a single egg-layer, so queen replacement—whether by daughters, co-foundresses, or outside usurpers—is the most probable explanation for low relatedness. Since hymenopteran sisters who share both parents are more related to each other than to their own offspring, low relatedness between hymenopteran females of any species disqualifies perhaps the most elegant explanation for their cooperation.

Even if pleometrotic females are raising relatively unrelated nieces, if they are producing many more of them than they would alone, low relatedness may not matter; Strassmann et al. (1995) suggest that Litte's (1977) data on nest sizes, survivorship, and production rates support this hypothesis. Indeed, many studies of social insects (including *M. mexicanus* (Litte 1977)) have focused on comparing the productivity of pleometrotic and haplometrotic nests (Table 3). Investigators divided some measure of reproductive output (cells, eggs, larvae, etc.) by the number of foundresses, obtaining a per capita productivity statistic for each female that could be compared across groups of various sizes (Gadagkar 1996). However, the results of such studies were almost always that females could expect to produce fewer offspring if they worked in larger groups (Brian 1953, 1956; Michener 1964; West-Eberhard 1967; Gibo 1974; Hermann & Dirks 1975; Gibo 1978, Noonan 1981; Strassmann 1981; Itô 1987, Klahn 1988; Queller & Strassmann 1988; Wenzel & Pickering 1991; Tschinkel 1993). Not only have these results thwarted another hypothesis for the evolution of social behavior in insects, but they have also been interpreted as running counter to the intuitive and theoretically defensible (Queller 1996) notion that the costs of working in groups are offset by gains in efficiency. Thus, per capita

productivity data in social insects have become a serious snag in our understanding of the evolution of social behavior in general.

Recognizing that there were fundamental problems with the measures of per capita productivity to date, I did this study to obtain improved measures of per capita productivity for a social insect. First, previous measures rest on the assumption that all females have the same intrinsic reproductive potential, an assumption that is probably not true and not testable (Clouse 1997); so I attempted manipulating nests such that females could not control the size of the group to which they belonged. Second, by discounting failed nests, previous studies did not count the output (albeit, zero) for many foundresses, so I kept a record of nest survivorship and presumed causes of mortality. Third, the types of output measures chosen by previous studies were subject to different biases if females altered the way they allocated resources in small versus large groups. It has been shown already that colonies of the fire ant *Solenopsis invicta* Buren produce smaller daughters when foundress associations are large (Goodisman & Ross 1996). Thus, I collected different types of output data for the same nests. And finally, previous measures often did not factor in the time required to produce the measured output, so I calculated output for all nests as a daily rate of production. In addition, the interpretation of per capita productivity in the broader study of the evolution of social behavior is revisited in the Discussion.

MATERIALS AND METHODS

Mischocyttarus mexicanus is well-suited for studying the selective advantage, and accordingly reproductive output, of pleometrosis and haplometrosis in social insects. Like other paper wasps, they make open paper nests that can be observed and easily manipulated. Being a resident of the Eastern subtropics, and having evolved from a tropical genus, *M. mexicanus* females start new nests year-round (Litte 1977, Hermann et al. 1985). In addition, all females (even the first daughters) are apparently capable of being the principal egg-layer on the nest. The females are timid relative to other Polistines (Hermann & Chao 1984), and they readily nest around buildings and on outdoor paraphernalia (wind chimes, ladders, etc.).

I conducted all work at Archbold Biological Station, Highlands County, Florida, between 10 May and 31 July, 1993. I used three different sets of nest to measure various parameters of production: Manipulated Pleometrotic and Haplometrotic, Restarted, and Unmanipulated nests. The methods are arranged by nest type, and the results are arranged by production measurement. All data are reported as (mean \pm standard error) unless otherwise noted.

Set I. Manipulated Pleometrotic and Haplometrotic Nests

The main goal of studying Set I was to measure different rates of production on nests for which I had manipulated the group size. I wanted nests that were as close to the first day of initiation as possible, and I wanted pleometrotic females to end up in small or large groups with equal probability after manipulation. Nests were found in saw palmetto (*Serenoa repens*) along roadsides and paths, and only those that had only eggs were included. Upon discovery, the initial size and shape of each nest was recorded and drawn. An attempt was made to control for group size by removing foundresses at night. I removed one female from nests that had two females, two or one female alternately from nests that had three females, and the appropriate number of females from larger nests to make nests with four or one female alternately. Females were removed by disturbing them with a pine needle until they walked onto the needle or tried to sting it, whereupon they were placed in a vial and frozen later. Many nests required more than one night to remove the required number of females, since females often dropped off their nests when disturbed. Females already found working alone and whose nests had only eggs were harassed to mimic the disturbance caused by removing foundresses. They were touched with a stick at night for several minutes, often to the point where they left the nest for the rest of the night. The number of females on each nest was recorded every night, and these data were used to calculate an average number of females working on each nest per day.

When the most mature larva spun a cocoon in which to pupate ("cell capping"), I collected the entire nest. The number of cells and offspring added since the nest was first discovered were recorded. Then the offspring were removed, dried at 60°C for five hours, and weighed to the nearest 0.01 mg. Eggs adhered too tightly to the nest paper to be removed and were included with the weight of the nest paper. The nest paper was cut back to the size upon discovery, and the paper added since discovery was dried and weighed. Four rates of daily per capita production were generated from these measurements: number of new cells, number of offspring, total weight of nest product, and weight of offspring per female per day. Only successful nests were used in final calculations, and for one nest, ambiguities over its size at collection forced me to exclude it from measures of cell and offspring addition.

Set II. Restarted Nests

As the study of Set I progressed, it became clear that most would not survive long enough to

obtain production data. The goal of studying Set II was to obtain a sample of nests for which I had determined the group size, and that had enough females to survive to first pupation. At night I cut down nests that were large enough to have produced daughters, and on the following night I searched nearby leaves for the restarted nests. For such nests, it is impossible to determine if the foundresses were haplometrotic or pleometrotic, since daughters and subordinate foundresses are indistinguishable. The group sizes were altered to form groups with either (1) four or more females or (2) less than four females. The number of females was recorded each night, and when the first cell capped on a nest, the entire nest was collected. The offspring that capped their cells (pre-pupae) were removed, dried, and weighed. When a nest had more than one offspring cap its cell, the pre-pupal weights were averaged to produce one weight for each nest. Per capita rates of production were calculated in the same way as for Set I above.

Set III. Unmanipulated Nests

The goal in studying Set III was to obtain a large sample of unmanipulated nests from which to determine how females in different sized groups allocate resources differently among their offspring. I conducted a survey of 51 pre-eclosion nests between 10 May and 15 May 1993. Each nest was censused at night and then collected, whereupon the numbers of eggs, first through fifth instar larvae, and pupae were recorded. Pre-eclosion nests were easy to recognize by the fact that they had their oldest offspring in the center cells (the first cells built), and any cells large enough to contain pupae did not show signs of previous occupation (e.g., meconium).

It was obvious from the initial survey that some foundresses had put their efforts into a few offspring rather than continually adding new ones. For example, a nest with one fifth-instar larva and two eggs had clearly concentrated resources on the one large offspring more than a nest with one third-instar larva, two first and second instars, and three or four eggs. However, it was not possible to immediately compare a nests that had a more scattered array of larval sizes. For example, the degree of concentration of nests that did not have any older larvae, just a few second- or third-instars, was not easily compared to nests that had older larvae and no eggs. Therefore I used data on the size and number of offspring to calculate a single measure of how concentrated resources were in the oldest offspring for each nest. I assigned each offspring to a size class between one and seven (egg = 1, first instar = 2, . . . fifth instar = 6, pupa = 7). I divided the size class value of the oldest offspring on each nest by the quantity of the youngest offspring. For example, if

a nest had six eggs, four second-instars, three fourth-instars, and one pupa, I divided "7" (for the pupa) by "6" (for the number of eggs). This measure I refer to as "concentration," and for this hypothetical nest, the concentration is 1.17. It is not as concentrated as another hypothetical nest that has one pupa and two eggs (concentration = 3.5), but it is more concentrated than a nest that has two fifth-instars, two fourth-instars, and six third-instars (concentration = $6 \div 6 = 1$).

RESULTS

I. Per capita rates of production

Ninety-nine nests were initially included in Set I. Thirty-six percent were begun by one female, 26% were begun by two females, 21% by three females, nine percent by four females, and eight percent by five to nine females. The removal of foundresses from pleometrotic nests was not effective in assigning females to group sizes without respect to their initial group size: even after the manipulation, the average number of females on nests that originally had four or more females (mean = 3.17, SD = 0.30, N = 17) was significantly higher than the average number of females on nests that originally had three females (1.73 ± 0.58 , N = 18; Fisher's PLSD; $P < 0.01$) and those that originally had two females (1.39 ± 0.09 , N = 25; Fisher's PLSD; $P < 0.01$). In addition, 80% of nests did not survive for more than 20 days.

There were enough survived pleometrotic nests in Set I to measure productivity; however, different methods for measuring productivity on survived nests gave contradictory results. The number of cells added per female per day did not correlate with the average number of females (Spearman Rank Correlation; N = 10; $r_s = 0.33$; $P = 0.32$). However, there was a significant positive correlation between the number of offspring added per female per day and the average number of females (Spearman Rank Correlation; N = 10; $r_s = 0.71$; $P = 0.03$). There was also a significant negative correlation between the average number of females per day and both the total mg of nest product added per female per day (Spearman Rank Correlation; N = 11; $r_s = -0.70$; $P =$

0.03) and the mg of offspring added per female per day (Spearman Rank Correlation; N = 11; $r_s = -0.61$; $P = 0.05$).

I was successful in altering the group sizes in restarted nests (Set II) such that the group sizes before and after manipulation did not correlate (Spearman Rank Correlation; n = 23; $P = 0.34$). Analyzing just survived nests, there was no correlation between the average number of females on the nest per day and any of the four per capita measures of daily production.

Manipulated haplometrotic females from Set I were more productive than both manipulated pleometrotic nests in Set I and restarted nests (Set II) regardless of the production measure used (Mann-Whitney U; $P < 0.02$ for all comparisons) (Table 1).

II. The size of the largest offspring

The average weights of all pre-pupae from Sets I and II combined were positively correlated with the average number of females on their nest of origin (Spearman Rank Correlation; N = 34; $r_s = 0.63$; $P = 0.02$). The average weight (mg) of the first pre-pupa on restarted nests (Set II) tended to be positively correlated with the average number of females on the nest (Spearman Rank Correlation; N = 13; $r_s = 0.52$; $P = 0.07$).

Restarted nests (Set II) had larger pre-pupae than manipulated haplometrotic females (1.4 ± 0.06 mg, n = 13 versus 1.3 ± 0.03 , n = 12; Mann-Whitney U; $P = 0.01$), and manipulated pleometrotic females (Set I) (1.1 ± 0.09 , n = 10; $P < 0.01$). Manipulated pleometrotic (Set I) and haplometrotic pre-pupae were not significantly different in size ($P = 0.16$).

III. Concentration

Nests from Set III were more concentrated when being built by fewer females. For collected nests, concentration ratios for one-female, two-female, three-female, and four or more-female nests were significantly different (Table 2; Kruskal-Wallis; $P < 0.025$). From Set I, manipulated haplometrotic nests had higher concentration measures than manipulated pleometrotic nests (4.31

TABLE 1. AVERAGE PER CAPITA RATES OF PRODUCTION (\pm STANDARD ERROR) FOR THREE NEST TYPES: THOSE IN WHICH THE FEMALE WAS ORIGINALLY ALONE, IN WHICH FEMALES WERE ORIGINALLY IN GROUPS, AND THOSE THAT WERE RESTARTED AFTER BEING CUT DOWN.

Measurement	Manipulated Haplometrotic	N	Manipulated Pleometrotic	N	Restarted	N
# cells/female/day	0.28 ± 0.02	12	0.07 ± 0.01	10	0.15 ± 0.01	15
# offspring/female/day	0.25 ± 0.03	12	0.01 ± 0.03	10	0.13 ± 0.01	15
mg offspring/female/day	0.96 ± 0.17	12	0.57 ± 0.10	11	0.52 ± 0.06	15
total mg/female/day	1.44 ± 0.22	12	0.96 ± 0.18	11	0.84 ± 0.08	15

± 0.41 , $N = 13$, versus 2.34 ± 0.50 , $N = 12$; Mann-Whitney U; $P < 0.001$). From Set II, restarted nests with less than four females ($N = 8$, concent. = 1.69 ± 0.34) did not have significantly different concentration ratios from restarted nests with more than four females ($N = 11$, 1.35 ± 0.29 ; Mann-Whitney U; $0.25 > P > 0.15$), although the trend was similar to sets I and III.

IV. Time to cell capping

Restarted nests (the only nests I followed since initiation), took longer to raise a daughter to prepupal stage if there were less than four females on average working on the nest (25.33 ± 1.24 days versus 22 ± 0.45 days; Mann-Whitney U; $P < 0.01$).

DISCUSSION

The mortality rates of new nests make it clear why measuring the final production of reproductive offspring has not yet been done: the mortality rate for new nests is so high (80% failed within 20 days), one would have to follow several hundred nests to have a few left for analysis in the final stages. Moreover, it indicates that when addressing the question of what a female can expect to produce, the chance of nest failure (producing nothing) must be factored into the calculation.

Among nests that did survive, two processes heavily influence measurements of production during the pre-eclosion stage in *M. mexicanus*. First, small nests seem to rush the production of their first adult daughter. This is supported here by the fact that (1) in Set I the per capita rate of adding new offspring is larger in bigger groups, but these bigger groups have a smaller per capita rate of adding biomass, (2) the "concentration" ratio was higher for nests attended by one female than by several, and (3) smaller restarted groups lagged behind large ones in the time to cell capping by only two to three days. Each of these results is what we would expect if females in small groups, especially haplometrotic females, primarily fed their oldest daughter and laid few additional eggs. The fact that the first daughter on smaller nests tended to be smaller than those from larger associations is also consistent with the idea that small nests rush their first daughter to eclosion; perhaps the first daughter herself decides to pupate early, since her own life is at stake the longer the nest lacks extra guards.

The second factor biasing productivity measures is that surviving haplometrotic females have much higher daily rates of production than pleometrotic females, regardless of what type of output one measures. It can be legitimately argued that not having lost sisters or their original nest, the lone females in this study were not nearly as traumatized as the other females in this study (and thus were more productive). But I disturbed lone females to the point that I thought they might abandon their nests, and they naturally have great demands placed on them daily by the need to procure prey, water, paper, and nectar alone. Nonetheless, even while concentrating efforts on the oldest offspring to a greater extent than any other nests, they added more cells per female per day and more biomass per day than any other group. Although the daily per capita rate of cell addition declines as group size decreases in pleometrotic nests (Set I), it rises sharply again for lone females, and thus lone females stand apart from the overall production trends. Lone female production is so much larger than group production in this study, production analyses that assume that the only behavioral difference between haplometrotic and pleometrotic females is their choice in the number of nesting associates should not be accepted.

Since per capita productivity has been used to compare the reproductive output of pleometrotic and haplometrotic females, and productivity has been the axis of discussions about synergy in insect societies, per capita productivity has been equated with "efficiency." Thus, for much of the past forty-five years, productivity measures in social insects have led to discussions of the larger question of why social behavior is apparently inefficient. However, per capita productivity merely measures the marginal productivity of each additional worker, and diminishing marginal returns from adding sisters, or any other factor of production, is quite expected (Krebs & Davies 1987). This is because as one adds additional units of a production input, while holding others constant, the additional units become increasingly redundant. (Interestingly, a few human examples exist of *increasing* marginal returns during the initial stages of production, and some wasp data reflect this phenomenon when foundress group size increases from one to two females (West-Eberhard 1967, Metcalf & Whitt 1977, Litte 1981, Noonan 1981, Strassmann 1981).)

TABLE 2. AVERAGE CONCENTRATION VALUES FOR COLLECTED NESTS. "CONCENTRATION" WAS CALCULATED BY DIVIDING THE STAGE OF THE OLDEST OFFSPRING (EGG = 1, FIRST INSTAR = 2, . . . FIFTH INSTAR = 6, PUPA = 7) BY THE NUMBER OF THE YOUNGEST OFFSPRING.

Number of Foundresses	1 N = 28	2 N = 8	3 N = 7	>3 N = 8
Concentration	2.09 \pm 0.35	1.03 \pm 0.24	0.70 \pm 0.14	0.35 \pm 0.16

TABLE 3. PREVIOUS MEASUREMENTS OF PER CAPITA PRODUCTIVITY. THE FACTORS COUNTED TO OBTAIN EACH MEASUREMENT ("MEAS.") ARE AS FOLLOWS: F = NUMBER OF CELLS FULL OF POLLEN AND EGGS OR SMALL LARVAE, E = NUMBER OF EGGS, L = NUMBER OF LARVAE, CC = NUMBER OF CAPPED CELLS, C = NUMBER OF CELLS, O = NUMBER OF OFFSPRING, R = NUMBER OF REPRODUCTIVE OFFSPRING, P = NUMBER OF PUPAE AT FIRST ECLOSION, B = BIOMASS OF OFFSPRING, J = ENERGY EQUIVALENT OF OFFSPRING IN JOULES, I = INCLUSIVE FITNESS BASED ON ESTIMATES OF RELATEDNESS. THE CORRELATION BETWEEN PER CAPITA PRODUCTIVITY AND GROUPS SIZE ("CORR.") COULD BE POSITIVE (+), NEGATIVE (-), OR NOT SIGNIFICANT (N.S.). DATA FROM MICHENER (1964) WERE NOT ANALYZED STATISTICALLY.

Family	Species	meas.	corr.
Halictidae	<i>Pseudagapostemon divaricatus</i> ¹	F	-
	<i>Augochloropsis sparsilis</i> ¹	F	-
	<i>Lasioglossum imitatum</i> ¹	F	-
	<i>Lasioglossum rhytidophorum</i> ¹	F	-
Apidae	<i>Apis mellifera</i> ¹	CC	-
	<i>Bombus americanum</i> ¹	O	+
Formicidae	<i>Mymica rubra</i> ²	B, L, P	-
	<i>Myrmica rubra macrogyna</i>	L	-
	<i>Solenopsis invicta</i> ³	O, R, B, J	-
Vespidae	<i>Polybia bistriata</i> & <i>P. bicyttarella</i>	E	-
	49 nests from 11 Polybinae species ¹	E	-
	<i>Polistes fuscatus</i> ⁴	C	-
	<i>P. fuscatus</i> ⁵	C, O	n.s.
	<i>P. fuscatus</i> ⁶	O	-
	<i>P. fuscatus</i> ⁷	R	n.s.
	<i>P. annularis</i> ⁸	C	-
	<i>P. annularis</i> ⁹	I	-
	<i>P. annularis</i> ¹⁰	R	-
	<i>P. metricus</i> ¹¹	E	n.s.
	<i>P. metricus</i> ¹²	R	+
	<i>P. metricus</i> ¹³	R	n.s.
	<i>P. chinensis antennalis</i> ¹⁴	E, C	-
	<i>Mischocyttarus mexicanus</i> ¹⁵	C	-
	<i>M. labiatus</i> ¹⁶	C, P	-
<i>Ropalidia fasciata</i> ¹⁷	C	-	
<i>R. marginata</i> ¹⁸	O	-	

¹Michener (1964)²Brian (1953, 1956)³Tshinkel (1993)⁴West-Eberhard (1993)⁵Gibo (1974)⁶Gibo (1978)⁷Noonan (1981)⁸Hermann and Dirks (1975)⁹Strassmann (1981)¹⁰Queller and Strassmann (1988)¹¹Bohm (1977)¹²Metcalf and Whitt (1977)¹³Gamboia (1978)¹⁴Hoshikawa (1979)¹⁵Litte (1977)¹⁶Litte (1981)¹⁷Itô (1987)¹⁸Shakarad and Gadagkar (1993)

True efficiency measurements in social insects await refinement of a system by which total energy input can be accurately measured (such as in Suzuki 1981), because "efficiency" is a ratio of output to input (Brian 1953; Jeanne 1986). Using output measures which encompass total output and are thus free from the resource-allocation bi-

ases shown here should provide novel and interesting efficiency data.

Moreover, if productivity, survivorship, and relatedness can be combined to calculate reliable expectations of reproductive success for haplometrotic and pleometrotic foundresses, it could open new doors of research into the maintenance of so-

cial and solitary behavior. One possibility is that these tactics are evolutionarily stable strategies in which mothers deliberately make some large reproductive daughters who can keep the hectic pace of working alone and some small daughters who can work more slowly in groups. The overall payoff could be the same for both types of females if the large females suffer more from attacks and lose more nests, but if they survive, their nests produce more reproductive offspring in the end than pleometrotic ones. Another possibility is that one or the other strategy is more successful but can be adopted only under certain circumstances. Haplometrosis—naturally desirable since the female gets to lay all the eggs—may require a minimal body size and fat store to defend the nest and make numerous foraging trips; pleometrosis—also desirable since foundresses get to produce on a relatively well-guarded nest—may require having and finding certain types of sisters to minimize fighting between foundresses.

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