

Reproduction in foundress associations of the social wasp, *Polistes carolina*: conventions, competition, and skew

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Who reproduces in colonies of social insects is determined by some combination of direct competition and more peaceful convention. We studied these two alternatives in foundresses of the paper wasp, *Polistes carolina*, by examining two different contexts: what determines who becomes the dominant reproductive and what determines the amount of reproduction obtained by subordinates. The dominant queen on most nests was the foundress to arrive first, rather than the largest foundress, expected to be best at fighting. This suggests that dominance is initially determined by convention, although the persistence of some aggressive conflict throughout the foundress period suggests that this convention is not absolute. Attempts to explain the division of reproduction using several skew theories were generally unsuccessful. Skew was not correlated with relatedness, size differences, colony productivity, and challenges by the subordinate. *P. carolina* showed high constraints against solitary nesting, with a minority of females attempting to nest alone, and none succeeding. In this situation, most skew theories predict that group stability will be independent of relatedness, yet nearly all collected subordinates were full sisters to the queen. Reproductive partitioning in early *P. carolina* colonies may have more to do with enhancing worker production than with conflict over direct fitness. *Key words*: Hymenoptera, microsattellites, *Polistes*, Polistinae, queues, reproductive dominance, reproductive skew, wasps. [*Behav Ecol* 13:531–542 (2002)]

Reproductive conflicts in animal societies arise because individuals are not genetically identical, and they may have different optimal strategies for maximizing their fitness. Individuals may compete directly for personal reproductive opportunities, or they may settle reproductive conflicts by various conventional means. Conflicts involving both overt aggression and displays characterize founding associations of *Polistes* wasp females (e.g., Noonan, 1981; Pardi, 1942, 1948; Strassmann, 1981; West-Eberhard, 1969). Often, the conflict results in a dominance hierarchy in which all or a major part of reproduction is monopolized by only one individual, the queen. Subordinates specialize on foraging but may sometimes obtain a minority of reproduction.

Because each group member would transmit more genes if it reproduced directly, two questions arise. First, what determines who becomes the queen? Second, how much do subordinates reproduce and why? In each of these contexts, individuals might compete overtly for reproductive rights or arrive at a more peaceful social contract.

Consider first the decision of who will be queen. Under physical competition for queenship, larger individuals should often be able to physically dominate others. However, an extended conflict over dominance may be costly and decrease the fitness of all group members, including the winner of the conflict, especially in animals with potentially lethal weapons such as stings. In such cases, everyone might benefit from a conventional settlement, even if some benefit more than others (Maynard Smith, 1982; Maynard Smith and Parker, 1976;

Pollock, 1996). The settlement might be based on some factor, such as size, correlated with who is likely to win, but it could even be based on an arbitrary asymmetry, particularly if the participants are closely related (Hughes and Strassmann, 1988; Maynard Smith, 1982; Maynard Smith and Parker, 1976; Pollock, 1996; Queller et al., 1997). Often the owner of a territory or resource wins disputes, and such precedence conventions could be either arbitrary or correlated with expected outcomes (Maynard Smith, 1982). *Polistes* nests are usually started by single foundresses and are subsequently joined by others (Reeve, 1991), and precedence is sometimes correlated with who becomes dominant (Strassmann et al., 1987; West-Eberhard, 1969).

In *Polistes*, queenship is often not absolute in that subordinate foundresses may obtain some share of the reproduction. A rich body of theory has developed in an attempt to explain how reproduction is partitioned, so-called reproductive skew. To bring some structure to our analysis, we focus primarily on three kinds of skew theories, as delineated by Johnstone (2000). The first involves the most overt competition and continuing conflict. The model is formalized as a tug of war in which both participants make optimal investments in competition but differ in the efficiency of converting investment into reproduction (Reeve et al., 1998).

We contrast this with models of reproductive skew that include elements of peaceful settlement or social contracts. We focus on two models in particular. In one, called the concessions model, the dominant individual concedes to her subordinate the minimum reproduction required to persuade the subordinate to stay and help, which yields slightly more inclusive fitness than the subordinate could obtain on her own (Reeve, 1991; Reeve and Ratnieks, 1993; based on Vehrencamp, 1983). Tests of this model have met with variable success (e.g., Clutton-Brock, 1998; Field, 1998; Keller and Reeve, 1994; Reeve and Keller, 2001; Reeve and Nonacs, 1992; Reeve and Ratnieks, 1993; Reeve et al., 1998, 2000; Strassmann, 1993). In the other model, called the restraint model, the

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Table 1
Predictions of three models on reproduction skew, compared with observed results

	Tug of war	Dominant concessions	Subordinate restraint	Observed results
Skew under high ecological constraints	No prediction	High skew	Low skew	Intermediate skew
Change of skew with time	Increase ^a	Increase	Decrease ^a	Increase
Only related groups stable	Sometimes ^a	No	No	Yes
Correlation of relatedness and skew	None or negative	Positive	Negative	None
Correlation of size difference and skew	Positive	Positive	Positive	None
Correlation of colony productivity and skew	None	Positive	Negative	None
Correlation of subordinate aggression and skew	Negative	Positive	Positive	None

^a Predictions that may not have been formally proposed in the literature, but which seem to follow from the models. Some predictions are qualified in the text.

dominant is assumed to be unable to limit the subordinate's reproduction except by evicting her. The subordinate therefore reproduces as much as she can without passing the point at which the dominant does better by evicting her (Johnstone and Cant, 1999).

The main difference between the concessions and restraint models lies in who claims the surplus reproduction in groups; in the concessions model it is the dominant, whereas in the restraint model it is the subordinate, subject only to eviction by the dominant if she reproduces too much. For this reason, the two theories often make opposite predictions. Some key predictions of the three models are summarized in Table 1, but explanation of these predictions will be left to the "Discussion" section. There we also address some of the complications introduced by consideration of other skew models, which have been proliferating rapidly.

We studied who becomes dominant and the reproductive conflicts that follow in the social wasp, *Polistes carolina*, during the foundress period before the young nests had produced adult workers. We thus focused on early dominance among the mated foundresses who were capable of being the sole colony queen. Foundress associations in *Polistes* wasps provide a good model system because they have clear dominant-subordinate relationships, with the dominant eventually gaining most reproduction (Noonan, 1981; Pardi, 1948; Strassmann, 1981; West-Eberhard, 1969). Furthermore, foundress associations are small, which makes them easy objects for behavioral and genetic studies. Foundresses sometimes move between nests, providing opportunities to examine choices between different reproductive opportunities.

Among *Polistes*, *P. carolina* provides the advantage of nesting in cavities. By providing wooden boxes as nest sites, we could study a large fraction of the whole population in a given area. Compared with species that nest on vegetation, cavity nesting makes it easier to find colonies at their inception and easier to follow movements from one colony to another. Predation may also be lower. The long growing season of this species provides both a disadvantage and an advantage. The disadvantage is that the foundresses are producing mostly workers rather than the next years' reproductives (but see Discussion). The advantage is that any temporal patterns in skew change during our study will not be confounded with a switch between production of workers and reproductives, as might be the case in *Polistes* at the northern edge of its range (e.g., Noonan, 1981; Reeve et al., 2000).

MATERIALS AND METHODS

Field observations and sampling

We studied *P. carolina* in a 10-ha section of pecan/oak riparian forest at Brazos Bend State Park, about 70 km south of Houston, Texas, USA. To attract wild *P. carolina*, which nest in hollow trees and other dark places, we nailed wooden nest boxes to trees more than a year before the study began. We checked these boxes frequently for nests. We first found wasps without nests on 23 February 1995, and the first nests were begun on 8 March, with 0–3 cells. From 21 March to 26 April, we censused intensively, at least every other day. By 28 March some nests had larvae. When we collected the nests on April 26, they all had last-instar larvae, and one (colony 39) had pupae.

We censused the colonies very early in the morning before the wasps were flying. We individually marked 87 foundresses as they joined the 30 colonies our boxes yielded. Almost half of the nests failed during our study, either because they were predated or, more often, because all their foundresses deserted the nest or disappeared. We collected the 17 surviving nests and their associated wasps on 26 April, 1995, a good stopping point for the foundress period because from this time to worker emergence few cells are added while the foundresses rear the brood they have and wait for the workers (Strassmann, unpublished data).

The average number of foundresses associated with the surviving nests was 2.8 (SD 1.8) at the time of collection, ranging from 1 to 8. We collected 46 of the 87 foundresses we had marked. Two foundresses associated with nests escaped collection (from nests 19 and 23), two foundresses collected were unmarked, and the rest of the marked foundresses had disappeared, presumably because they were predated. The average number of offspring (eggs, larvae, and pupae) collected from the 17 successful nests was 24.1 (SD 12.4), ranging from 8 to 53.

Nest fidelity of foundresses

Many foundresses moved between nests during the field period. We called the moving foundresses "movers" or "visitors," depending on whether they stayed in their new nest or not. From the field censuses, we observed 10 movers permanently moving to other nests. Nine foundresses visited other nests but returned later to their original nest. Six of the visits

were revealed by genetically detecting progeny of the foundresses in nests where they were never observed. One visitor was both censused and found to lay an egg. We observed two other visitors by censusing or from videotapes (see below). We probably failed to detect other short visits that did not result in egg laying.

Behavior

We videotaped 21 of the nests (mean 11 h per nest, total 231 h) over two periods: early from 24 March to 15 April, and late from 24 to 26 April. We used these data to augment the census data and to generate behavioral profiles and dominance hierarchies. For this study we focused on the proportion of time the subordinates spent on the nest (as opposed to time they spent off the nest foraging) and aggressive behavior. We counted as aggressive behavior any biting, chewing, lunging, stinging, or otherwise attacking other wasps. On average, the colonies filmed had about 50 aggressive acts during the early period, and another 50 during the late period. We then generated a dominance hierarchy where we minimized the number of attacks by individuals ranked lower on the hierarchy toward those that ranked higher. We recorded the proportion of total aggressive interactions that nevertheless went from subordinate toward more dominant. If the hierarchy were perfect and subordinates never challenged dominants, then this proportion would be zero. Use of this measure helps correct for any differences in general level of activity due to weather or time of day. For the same reason, we standardized the subordinate's time on the nest by dividing by the dominant's time on the nest.

Size and ovarian status

As measures of egg-laying status, we counted the numbers of mature and nearly mature eggs in each foundress's ovaries and measured the length of the longest egg or oocyte. We used head width as a size measure of the foundresses. We standardized these size measures so that they could be compared among nests by calculating a relative size score, which was the difference of the size of the foundress from the mean of her nest divided by the nest mean.

Molecular techniques

We extracted DNA from the thorax of the foundresses and from entire eggs, larvae, and pupae. We dissected the sperm from the spermathecae of the foundresses and treated it so it could be used directly in polymerase chain reaction (Strassmann et al., 1996). We genotyped these samples for seven trinucleotide microsatellite loci previously designed for *P. bellicosus* (Strassmann et al., 1997). In order of decreasing heterozygosity, the loci were Pbe424AAT, Pbe203AAG, Pbe492AAT, Pbe440AAT, Pbe102GAC, Pbe411AAT, and Pbe128TAG. We used standard methods with slight modifications for DNA extractions, amplification of microsatellites, and resolving polymerase chain reaction products (Strassmann et al., 1996). From each nest, we genotyped all adult females and the sperm in their spermathecae, 2–12 eggs (mean 8.2, total 139), and 2–28 larvae (mean 13.6, total 232; throughout, we include the few pupae on nest 39 in the larval category). This is 96% of all the offspring in the 17 nests, and adds up to 371. In addition, we genotyped 24 offspring from five nests that lost all their adults before the end of the field period. These were used only to improve estimates of the population allele frequencies used in the relatedness estimates. We genotyped all loci for larvae, but for eggs we used only the loci that were variable in the foundresses of that nest (four

to seven primers for each individual egg, usually six). The unused loci were those where all cofoundresses on that nest had an identical genotype. This kind of selection of loci probably decreased the relatedness estimate among eggs slightly.

We were also able to fill in missing genetic data on foundresses and their mating partners in two ways. First, we assigned all the offspring to their mothers (see below). Then, using the genotypes of the offspring assigned to specific foundresses, we reconstructed another 57 sperm genotypes where amplification failed (the tiny size and difficulty of collecting sperm makes failure more common than for normal genotypes). We could do this because males are haploid, so a group of full sisters will have one of their mother's two alleles, and the daughters will share an identical allele from their haploid father. We could determine the identity of the father's genotypes because females mate with only one male (see below). With these new data, we obtained 91% of the genotypes of the males. Second, in most nests some of the foundresses who had produced offspring disappeared before the collection date. Using the genotypes of their progeny, we were able to reconstruct genotypes of 11 missing foundresses and 19 missing foundress mates at one or more loci. Thus, of the individuals recognized as breeders in the population that had nests surviving to the time of collection, we lack genetic information from only 11 of 68 foundresses and three of their mates. This gives us a very complete picture of the genetic structure of this population.

Genetic relatedness

We estimated average within-colony relatednesses using Queller and Goodnight's (1989) algorithm (software Relatedness 4.2, Goodnight and Queller, 1994). Standard errors were estimated by jackknifing over colonies.

When females mate once, a question of particular interest is which progeny are full sisters. We sorted individuals into full-sister groups with the help of a likelihood method (Goodnight and Queller, 1999; see also Field et al., 1998) implemented by the computer program Kinship 1.1.2 (Goodnight and Queller, 1997, 1999). For each pair, we estimated their likelihood of being full sisters versus being maternal cousins (offspring of sister foundresses). Statistical significance of the likelihood ratios was established by simulating multilocus genotypes for 1000 random pairs of sisters and 1000 random pairs of cousins using the observed population allele frequencies (Field et al., 1998). The program groups together sets of pairs with particularly high likelihood ratios. These groupings were then inspected to make sure that each member of a group shared one allele (from the father) at every locus, and collectively possessed at most two other alleles (from the mother). Additional individuals were then added, even if they did not have significant likelihood ratios to all group members, if their genotypes fit. The nonsignificant values seemed to result from the members of the focal pair consistently having, at multiple loci, genotypes in the pattern of AB and AC. In the full-sister groups of offspring constructed in this manner, about 90% of the pairs of individuals were supported by a significant likelihood ratio. For foundresses, the likelihood calculations and groupings were done between all foundresses sampled in the population. For the offspring, the grouping was done separately for each colony.

Maternity assignment

We assigned to specific mothers only the offspring for which we had genotypes for at least three loci. This meant we discarded information from 14 offspring (3.8%) with less com-

Table 2
Genetic relatedness (r) and inbreeding (F) in *P. carolina*

	No. of nests (no. of individuals)	Estimate \pm SE
r among cofoundresses	17 (57)	0.644 \pm 0.063
r among mates of cofoundresses	17 (62)	-0.002 \pm 0.007
r of foundresses to their mates	17 (56)	0.029 \pm 0.040
r of mates to foundresses	17 (56)	0.030 \pm 0.019
r among offspring	17 (367)	0.408 \pm 0.024
F (foundresses)	17 (57)	-0.142 \pm 0.030
F (foundress sister groups merged)	13 (65)	-0.104 \pm 0.032
F (offspring)	17 (367)	-0.020 \pm 0.022

plete genetic information. They were included, however, when estimating overall relatedness among offspring.

We excluded potential mothers by comparing genotypes of both the offspring individually and the offspring as full-sister groups to the genotypes of the foundresses and their mates. Using full-sister groups generally gave greater power because the group as a whole specifies the parental genotypes more completely. We did this first within individual nests and then for the entire population as a check for offspring produced by mothers collected from a different colony. Assignment is achieved by excluding all other possible candidate mothers sampled. Although the candidate mothers are often close relatives, assignment can be made reliable using genotypes of the dead fathers (Peters et al., 1995). The probability of two males sharing an identical multilocus genotype was never $>10^{-4}$ and was usually much lower. Using male genotypes to help assign maternity was helpful because the foundresses mated only once.

Reproductive skew

We estimated two of the many measures (Kokko et al., 1999) of reproductive skew. We used the Pamilo and Crozier (1996) index, S , because it is simple and has been widely used in other studies. The index is calculated as $S = (N_T - Q_E) / (N_T - 1)$, where N_T is the total number of foundresses, and Q_E is the effective number of foundresses defined as $Q_E = 1 / (\sum p_i^2)$, with p_i being the proportion of reproduction by each female. Skew potentially ranges from 0 (equal reproduction by all females) to 1 (total monopolization of reproduction by one female).

We also calculated Nonacs' (2000) skew measure, B , because it has two useful features absent from the S index. First, it corrects for different amounts of random variation in groups of different sizes. It also adjusts for the time interval over which each individual was present, so that skew is not altered simply because dead or absent individuals are no longer reproducing. The measure is

$$B = \sum_{i=1}^N \left(p_i - \frac{n_i}{N_i} \right)^2 - \frac{1}{K} \left(1 - \frac{1}{\bar{N}} \right).$$

K is the total reproduction, p_i is the proportion of reproduction obtained by the i th foundress, n_i is the number of days individual i was present, and N_i is the sum of n_i for the colony. \bar{N} is a weighted mean group size defined as $\bar{N} = N_i / n_{\max}$, where n_{\max} is the length of the observation period. This index takes the value of 0 for randomly distributed reproduction, positive values for greater than random skew, and negative values for skew more evenly distributed than random.

Full-sibling groups that could not be assigned to collected foundresses were assigned to uncollected foundresses according to their tenure, with the foundresses present longest being

assigned the largest groups of offspring. This step leads to conservative estimates of B , but has no effect on S .

We analyzed skew for two periods. Early offspring were already larvae when we collected the nests; late offspring were still eggs. We judged that the cutoff between the two was about 16 April, so early skew roughly corresponds to the time frame of early videotaping and late skew to late videotaping. We estimated both skew measures using all colony members. Because the Pamilo-Crozier measure does not adjust well for group size, we also estimated it separately for the top two individuals in each colony.

RESULTS

Breeding structure of the population

No foundress showed evidence of mating more than once. Microsatellite phenotypes of the sperm samples typically showed only a single band corresponding to the haploid sperm. Where additional alleles appeared, they were always identical to the genotype of the foundress from whose spermatheca the sperm had been dissected and were therefore assumed to be from maternal DNA. The probabilities of these genotypes being from genuine double mating rather than maternal contamination were minute (in all foundresses $<10^{-7}$) using the methods of Chapuisat (1998). One foundress was unseminated and had no sperm in her spermatheca (foundress 16 in nest 31).

Males were unrelated to their mates and also to other males mating with females from the same colony (Table 2). Only two foundresses, from colonies 100 m apart, had mated with males with an identical multilocus genotype. The probability of two random, unrelated males sharing this particular multilocus genotype is 5.0×10^{-7} , suggesting that these two foundresses probably mated with the same male.

Inbreeding coefficients showed a small but significant excess of heterozygotes in the foundresses, but not in the offspring (Table 2). We believe that excess of heterozygotes among foundresses is partly a statistical fluke (false positive), and partly an artifact that results from the data containing groups of full-sister nests. Because these are not independent samples, they distort allele frequencies in the data and cause a computational excess of heterozygotes. If full-sister nests are merged, the inbreeding coefficient approaches zero, but still remains significantly below zero (Table 2).

Among the 395 offspring analyzed, there were only two individuals, both from nest 31, who showed a single allele at all loci we studied and were therefore probably haploid males. The expected Hardy-Weinberg probabilities for these individuals to be diploid multilocus homozygotes are 1.0×10^{-2} and 2.3×10^{-7} (based on two and five loci, respectively). One of the males could have been the son of either the dominant foundress or an unmated subordinate. The other was consis-

tent with another subordinate, who was unrelated to the dominant. The near absence of early males in the offspring is consistent with the fact that adult males are generally not seen until July in this species, whereas other species in this area of Texas produce early males (Strassmann and Hughes, 1986).

Only one of the collected foundresses was inconsistent with being a full sister of her nest mates (female 17 on nest 31). However, among the 11 uncollected foundresses whose genotypes were inferred from offspring, 6 were not full sisters to the other foundresses on their nest (the average relatedness of all 11 uncollected foundresses to collected foundress nest mates was nevertheless fairly high: 0.56 ± 0.14 SE). Five of the six non-full-sister foundresses reproduced only at the very beginning of the nest-founding period and then left the nest. In one of these nests (19), none of the three reproducing foundresses were sisters. In another nest (23), two of the three reproducers were full sisters. Nest 42 was first occupied by three foundresses (a, b, c), two of whom were full sisters. Then all three disappeared, and the nest and brood were adopted by two other full-sister foundresses (39, 40), who were not full sisters of the previous occupants.

Choices made by foundresses are revealed by movers and visitors. Moving foundresses clearly preferred their relatives by always (six of six cases) joining full-sister nests. If the movers had chosen the nests they moved to randomly in the population, only one of six would have joined a related nest, a highly significant difference (chi-square with Yates correction: $\chi^2 = 24.3$, $p < .001$, 1 df). We could estimate relatedness only in two original nests, and the mover was a full sister in one, but not in the other. In contrast, of the five visitors, defined as those who did not remain on the visited nest, only two were visiting full sisters, but visitors were full sisters on their nests of origin in all cases we could determine (three of three).

Overall genetic relatedness among nest-mate foundresses was high, but the impact of the non-full sisters was enough to make relatedness significantly < 0.75 (Table 2). In four cases foundresses from the same full-sister group, and therefore from the same natal nest, divided themselves among multiple spring colonies.

Eleven additional uncollected foundresses in nine nests laid only one egg each, and so their genotypes could not be inferred from the genotype of their sole offspring. However, most of these foundresses were also likely to have been full sisters of the collected foundresses of their nest because the collected foundresses were related to the offspring of these foundresses ($r = .303 \pm .071$ SE) approximately as aunts would be expected to be related to nieces ($r = .375$, two-tailed $t = 1.01$, $p > .35$, 8 df).

Parentage assessment and reproductive structure of the preemergence colonies

We observed no egg eating and no egg guarding on the videotapes, so parentage patterns are probably an accurate reflection of egg laying. Overall, about 80% of the offspring were assigned to a specific living foundress collected from their own nest, or in a few cases, from other nests. We assigned the rest of the offspring to uncollected foundresses who had presumably died before the study ended.

In any given nest, one foundress usually dominated reproduction, but not completely. The dominant foundress produced 60% of the offspring, but on average 2.7 (SD 1.2) subordinates also produced some offspring, and only 20% of all foundresses associated with the nests did not produce any offspring. Dissection of the ovaries confirmed the dominance patterns emerging from parentage assessment. Usually only the final dominant foundress had well-developed ovaries with mature eggs. The differences between dominant and subor-

dinate foundresses in all ovarian measures were significant (Mann-Whitney: number of layable eggs, $p < .011$, number of nearly layable eggs, $p < .001$; length of the longest oocyte, $p < .001$). In two nests (14, 31), the dominant had the largest ovaries among the permanent residents of the nest, but these nests had also been visited by a foundress that had even larger ovaries at the time of collection. Only in one nest (8) did the final dominant not have the largest ovaries, but in that nest none of the foundresses had well-developed ovaries.

Reproductive dominance increased during the preemergence period (Figure 1). The number of foundresses reproducing at the beginning of the nesting period was significantly higher than the number of foundresses reproducing later (Mann-Whitney U, $p = .001$). This was also corroborated by relatedness. Relatedness among earlier offspring (larvae at the time of collection; $r = .371 \pm .041$ SE) was significantly lower than among later offspring (eggs at the time of collection; 0.545 ± 0.053 ; two-tailed $t = 38.6$, 16 df, $p < .001$).

Reproductive structure of the nests was not always simple (Figure 1). In 12 of 17 nests, the same foundress laid most eggs both early and late in the nest-founding period. In eight of these nests (19, 23, 26, 31, 33, 34, 35, 46), the dominant foundress increased her share of the total production, and in four other nests (8, 15, 29, 5), the share of the dominant foundress decreased. In two nests (36, 44) there were clear dominance reversals, with the previous dominant remaining on the nest after losing her dominant position. On another (42), the original foundresses, including the queen, disappeared before being replaced by another set of females who did not destroy the eggs of the first set. On another two nests (14 and 39) the dominant in the second period laid only one egg fewer than the top egg layer in the first period, so we did not consider these clear reversals. In nest 39, four foundresses shared almost 90% of the nest's total production in the beginning, each of them producing five to seven offspring. We had analyzed 37/46 offspring, giving us a nearly complete picture of reproduction. We missed one foundress each in collecting from nests 23 and 19. It appears that the female we missed on nest 19 was the queen.

Most movers (five of seven) had laid eggs in their original nests. In 3 of 10 nests, a mover was a subordinate, and in one nest dominant-subordinate relationships could not be resolved. In six nests, the mover was the only foundress present, so her departure meant the failure of her original nest. Moving foundresses did not increase their reproductive rank by moving. Most movers (five of seven) laid eggs in their new nests, but only one became the dominant foundress and then only because all females had disappeared before the mover arrived.

Who becomes the dominant?

We were able to determine absolute order of arrival for 12 colonies. In 11 of these, the first foundress to arrive became the dominant queen (though on nest 44 she was subsequently overthrown). If dominance were random with respect to order of arrival, the expectation would have been 4 of 12, which is significantly different from what we observed (G test with Williams correction, $G = 17.37$, $p < .001$). In two other nests there were two females on the nest when we first marked them, and the eventual queen was one of them. In another three nests, the first female and the queen were either dead or not collected when we collected the nest. In these cases, we could not tell for sure that the first female was the first queen, but it is likely that she was. Thus, only on nest 14 could the first foundress to arrive not have been the queen in the early period. There were only 4 of 17 cases where the first to

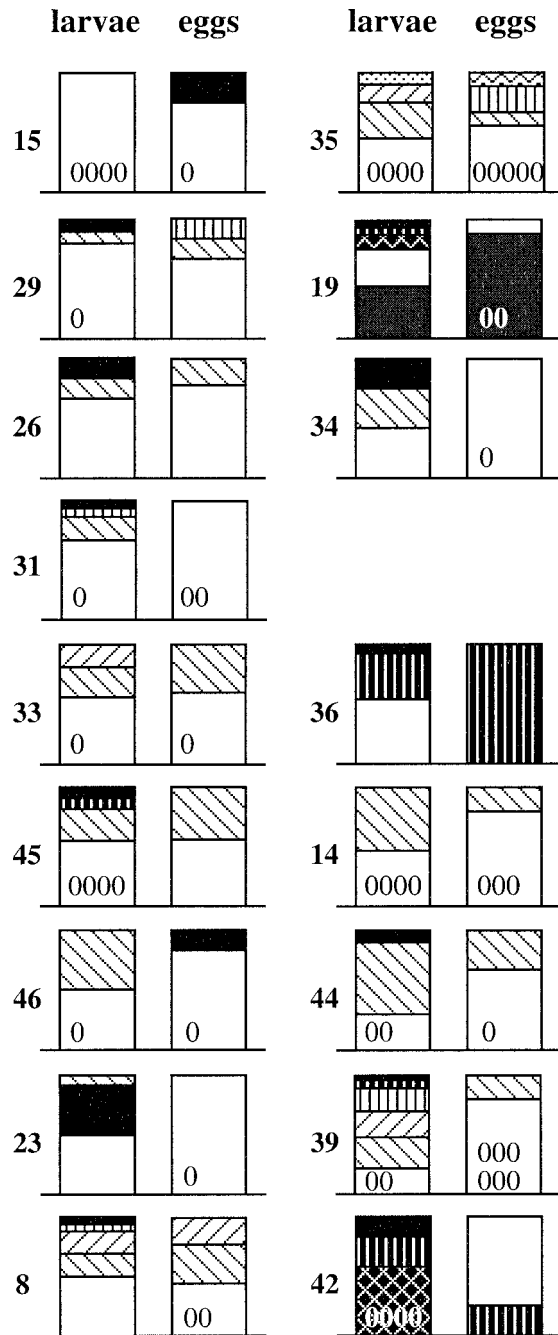


Figure 1
 Reproduction by foundresses in *P. carolina* colonies. Colony numbers are listed to the left of each graph. Within each colony, each different pattern represents a reproducing foundress, and the area covered is proportional to her contribution to the colony's reproduction. Patterns shared across colonies do not represent the same individuals. Uncollected foundresses are indicated by dark patterns, collected ones with light patterns. Each zero indicates a foundress who was present during the period but did not have any progeny in that period. From nests 19 and 23 one foundress escaped collection, presumably the one whose reproduction is indicated by the solid dark bar. Nest 42 had a complete changeover of females between early and late periods. Only nests 36 and 44 had turnover in queens during our study.

arrive could not have been the final queen at the end of our observations.

Body size did not predict dominance. The ultimate dominants were the largest foundresses only in 4 of 13 nests. If dominance were random with respect to size, the expectation would have been 5 of 13, not different from the observed (G test with Williams correction $G = 0.32$, $p > .57$). In two of the cases where it was not the first foundress who became queen, it was the largest.

Ecological constraints

There appeared to be high ecological constraints against independent nesting in this species. Few foundresses chose to nest alone. Only 6 out of 30 nests (20%) never had a second female present. The fraction of foundresses nesting alone was much lower, <7%, because multiple-female nests contribute more to this total. If we add three nests that had a second female on only one census day, the number of solitary nests rises to nine (10% of foundresses). None of these colonies survived to the collection date, although in six of them the female moved to another colony (see below).

In spite of this universal failure, some gains from starting a nest alone could be realized if solitary foundresses were subsequently joined. However, most joining occurred within 3 weeks of the time the first nest was initiated (93% of all joining and 96% of joining of solitary females). Therefore, even taking into account the possibility of getting joined, ecological constraints were high during the remaining 4 weeks of the study.

The failure of all solitary colonies suggests that at least part of the population was not saturated with helpers. Subordinate foundresses clearly helped. Among colonies that survived to collection, the average number of foundresses significantly increased productivity (Spearman rank correlation between Nonacs' [2000] time-averaged measure of foundress number, \bar{N} , and cell number at collection; $r = 0.71$, $p < .0001$). A linear regression explained most of the variation (cells = $-0.80 + 8.94\bar{N}$, $p < .0001$, $R^2 = .79$). The best-fit quadratic regression did not improve the fit ($R^2 = .82$). It revealed no signs of diminishing returns; instead, cell number tended to accelerate with \bar{N} (cells = $13.01 - 0.43\bar{N} + 1.34\bar{N}^2$; effect of \bar{N} not significant; effect of \bar{N}^2 $p < .005$).

Reproductive skew

The skew indices were highly variable across nests. The Pamilo-Crozier index S averaged 0.65 ± 0.15 (SD; range 0.36–0.87). Nonacs' index B averaged 0.085 ± 0.086 (SD; range -0.021 – 0.282). The skew indices were higher among later offspring than among the first offspring (Figure 2; except that S for all foundresses was not quite significantly different).

Predicted correlates with skew are shown in Figure 3. The top row uses the S estimate of skew and only the two top-ranked wasps; the second row uses the S measure with all wasps, and the third row uses the B estimate of skew with all wasps. Because there are two time periods, there are six correlations estimated for each predicted correlate of skew.

We found no significant relationship between colony productivity (cells/foundress) and skew (Figure 3; Spearman rank correlations, all $p > .23$). Three correlations were positive and three negative.

We found no significant correlation between relatedness and skew (Figure 3; Spearman rank correlations, all $p > .15$). The trend was negative in five of the six correlations. However, because most nest mates were full sisters, most of the variation in relatedness estimates was probably sampling vari-

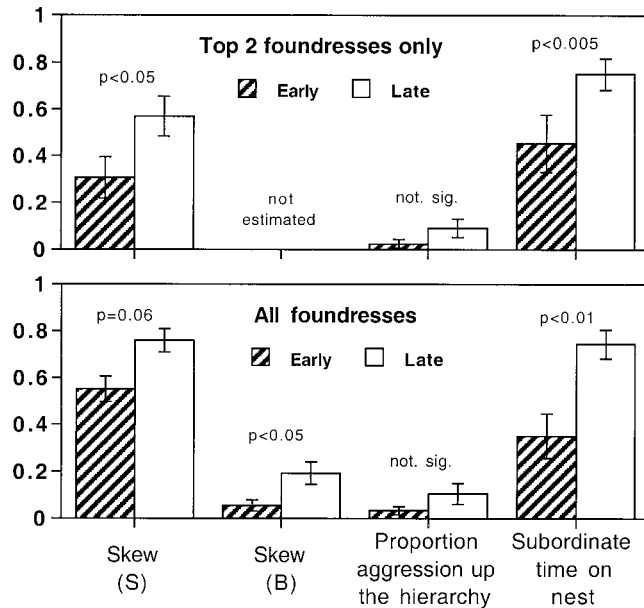


Figure 2
Skew and behavior in early and late periods, for the top two foundresses in the dominance hierarchy (top) and for all foundresses (bottom). Proportion aggression up the hierarchy is the proportion of all aggression directed against a female ranked higher. Subordinate's time on the nest is the time she was on the nest (rather than off the nest foraging), divided by the time the dominant was observed on the nest. Two-tailed p values are for Wilcoxon signed-ranks tests for skew and Mann-Whitney U tests for the behavioral variables (where pairing by colony would lose data because different colony were videotaped early and late).

ance, so there is little statistical power to detect any relationship.

We found no significant relationship between skew and relative size differences (Figure 3; Spearman rank correlations). The trend was negative in four of the six correlations, which would mean skew is higher where the queen's relative size is smaller. The only correlation that approached significance ($p < .07$ uncorrected for multiple comparisons) was a negative one between S and the relative size of all females on early nests.

We examined two possible measures of subordinate testing of dominants: aggression of subordinates on dominants and the time subordinates spent on the nest (Figure 3). There was no strongly consistent pattern with skew. The fraction of aggression that went up the hierarchy was evenly divided between negative and positive rank correlations with skew. However, when only the top two foundresses were considered, the correlations were strongly negative (early $r = -.60$, $p = .12$; late $r = -.53$, $p = .04$; the last value does not remain significant when corrected for multiple comparisons). The correlations of skew with subordinate time on the nest (as a fraction of dominant time) were negative in four of six cases (two $> .5$ and one $< -.5$), but significant in none. It may be that small sample size (not all colonies were filmed) made it difficult to detect correlations.

Our choice of nonparametric analyses (to guard against possible violations of assumptions of parametric analyses) could result in some loss of power. However, parallel regression analyses did not reveal any additional patterns. To account for possible intercorrelations among explanatory variables, we also performed some multiple regressions. For late skew, multiple regressions of skew on the five independent variables in Figure 3 (productivity, relatedness, size, aggres-

sion, and time on the nest) yielded no significant effects in explaining either B or S (with either all foundresses or just the top two). The smaller number of behavior data points prevented us from doing this complete analysis for early skew, but analyses with only productivity, relatedness, and size yielded only one significant effect. The size difference of early foundresses tended to decrease S when all foundresses were included (but did not decrease either B or S for only the top two foundresses). This effect ($p = .03$) would not remain significant when corrected for multiple tests and is in any event in the opposite direction to that predicted by the theories (relatively larger dominants, lower skew).

DISCUSSION

Studies of reproduction in *Polistes* have been complicated because of changes in membership of the colonies; many foundresses either die or switch nests (Field et al., 1998; Peters et al., 1995; Reeve, 1991). However, our intensive census and microsatellite data allowed us to determine the number, and in most cases also the identity, of all the foundresses associated with the nest, and Nonacs' (2000) skew measure corrects for time spent in the association. Because we also genotyped most offspring in the nests, we have an unusually complete picture of reproduction in early *P. carolina* colonies.

Who becomes queen?

Queenship in *P. carolina* appears to be determined primarily by precedence. The first foundress to arrive usually becomes the dominant reproductive, and joiners become subordinates. Large foundresses did not become dominant more often than expected by chance.

The lack of a role for size suggests that queenship may be determined more by convention than by force. Of course, the earliest female could also be the fittest, but there are some indications that who is first could be largely stochastic. Dominance and ovarian development in *Polistes* are both associated with high juvenile hormone synthesis (*P. annularis*: Barth et al., 1975; *P. dominulus*: Röseler et al., 1980, 1985; Turillazzi et al., 1982), with the hormone levels coming first (Röseler et al., 1984, 1986). Juvenile hormone is produced by the corpora allata, which are best developed in the first female to emerge from hibernation. One randomizing feature is that there is a cycle of corpora allata size during the winter (Strambi, 1969) so that a wasp's chance of being queen depends in part on the chance that she is in the right part of the cycle when weather conditions become suitable. A second such feature depends on microclimate. Females experimentally exposed to 1 h of warmth and light per day for 10 days before the end of hibernation had more developed corpora allata, more developed ovaries, and were 86% more likely to become dominant than were females not so treated (Röseler et al., 1985). In nature, less protected hibernation sites would expose a wasp to early spring warmth and increase her chance of becoming dominant, but could also increase her chance of starving during the winter or of being predated.

Conventional settlements should be easiest to reach when there is high relatedness. Joiners were almost invariably full sisters to the resident foundresses, so they could expect indirect fitness benefits even if they had no chance to be queen. Movers also joined only relatives (in contrast to temporary visitors). Unrelated joiners should be much less likely to join knowing they will not be dominant, unless inheritance is likely or they obtain larger reproductive concessions.

Our finding that order of arrival was more important than size is surprising given the general importance of size in the animal kingdom. Size is often an important predictor of re-

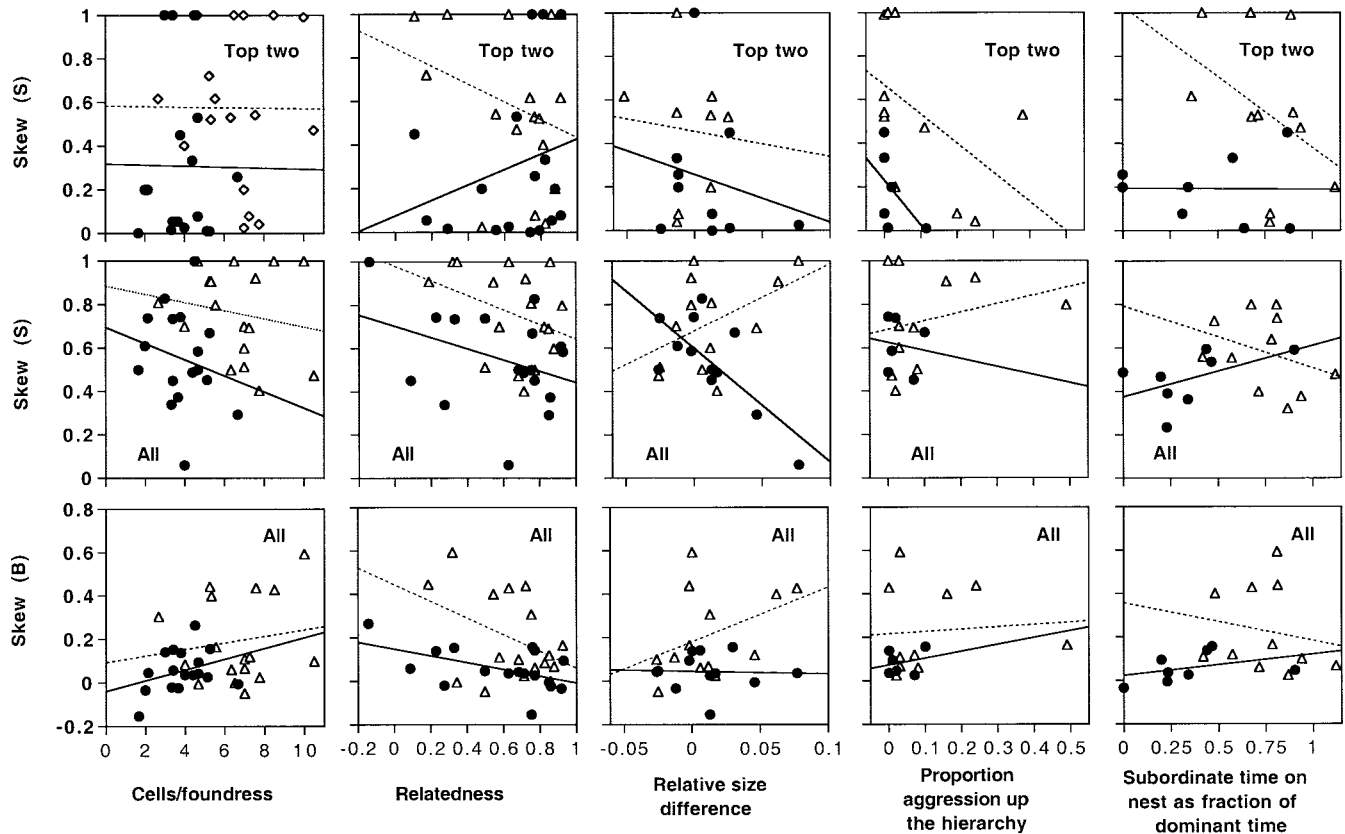


Figure 3

Skew and variables predicted to influence it. A solid dot is for the early observation period and a triangle is for later one. Although nonparametric correlation tests were used, regression lines (solid for early, dashed for late) are shown to help show trends. Relative size difference is the dominant foundress's head width minus the subordinates' head width, divided by the colony mean.

productive dominance in *Polistes* (review in Reeve, 1991), although there are exceptions (Strassmann et al., 1987; West-Eberhard, 1969). Perhaps conventional settlement applies in species where the costs of the conflict are unusually large, though we have no independent evidence of this. Even with high costs, size might be a reasonable cue to use if it is correlated with fighting ability. However, size fails in one respect as a good conventional cue: queenship will be unstable as long as larger joiners are possible. In contrast, the first wasp remains first until she dies. With precedence as a cue, there is no need to revisit the question of dominance as joiners arrive.

An age-based convention also applies in a different context in some *Polistes* (Hughes and Strassmann, 1988). When the dominant foundress dies, her successor is an old subordinate or, if there are no foundresses present, the oldest worker (Hughes and Strassmann, 1988; Hughes et al., 1987; Pardi, 1948; Strassmann and Meyer, 1983). This convention holds in *P. annularis* even though workers ought to prefer other successors based on relatedness (Queller et al., 1997).

The primary piece of evidence that seems to argue against order of arrival as an arbitrary convention is the evident continued competition among foundresses, long after the issue should have been settled. Linear dominance hierarchies maintained by aggression are one of the earliest and most consistent behavioral findings in *Polistes* (Pardi, 1942; Reeve, 1991). It may be that the convention is not arbitrary and that arriving first is an indicator of general fitness or fighting ability. Alternatively, an arbitrary convention could serve the function of preventing damaging contests among near equals, but aggressive probing would allow subordinates to detect a serious weakness that would allow them to take over (Strassmann,

1993). In our study there were several cases of the original queen being overthrown, yet remaining as a subordinate on the nest, cases that could be explained by this hypothesis. The hierarchy might also function to allow smooth transitions if the queen should die, which is consistent with the observation that it only exists among the top few females, the only ones with any probability of succession. Alternatively, aggressive acts could be involved in regulation of work (Reeve and Gamboa, 1983). However, aggression is not the only indication of continued competition. Subordinates also reproduce to some degree, and we now turn to this topic.

Division of reproduction

Predictions and results on reproductive skew are summarized in Table 1. The observed results do not match any of the models very well.

The first set of predictions in Table 1 concern skew under high ecological constraints. *P. carolina* appears to experience quite high ecological constraints. First, single-foundress colonies are rare (20–30%). Placed in the context of 19 other studies (16 species) of independent founding polistines compiled by Queller (1996), 30% is the third lowest level of single founding. Furthermore, all single-foundress colonies fail, a level observed in only one of the other 19 studies. During the first 3 weeks of the season, some solitary foundresses get joined, so that gains from deciding to start a nest alone were somewhat higher than would be suggested by the universal failure of unjoined foundresses. However, during the next 4 weeks there was little prospect of getting joined. Thus, all of

the late offspring, and a good fraction of the early offspring, came from eggs laid during a time of high constraints.

The concessions skew theory predicts that high ecological constraints will lead to less reproduction by subordinates (high skew) because the dominant needs to concede less to make joining pay to a subordinate with few other options (Reeve, 1991). The restraint theory predicts more reproduction by subordinates in this situation because in this model the subordinate claims the excess reproduction in groups, leaving the dominant the minimum possible (we assume that more subordinate reproduction generally means lower skew, though this can occasionally be incorrect; if a subordinate is able to claim more than half the reproduction, an increase in its reproduction raises skew). Additional subordinate fitness gained through sometimes inheriting the colony (Kokko and Johnstone, 1999; Ragsdale, 1999) should make these predictions even more extreme. Although precise quantitative predictions cannot be made for *P. carolina*, its high ecological constraints would seem to predict either nearly complete skew (concessions) or low skew (restraint), at least for the offspring produced in the last 4 weeks of the study (all late offspring and many early offspring). In fact, skew appears intermediate and comparable to other species studied (Field et al., 1998; Peters et al., 1995; Queller et al., 2000; Reeve et al., 2000). It is at least clear that skew is far from maximal, so the concessions prediction does not appear to be supported. The tug-of-war model does not consider ecological constraints, so it makes no prediction on this score.

Ecological constraints are expected to increase throughout the foundress stage of the season (Reeve et al., 2000). Reasons include the depletion of individual reserves, a possible decrease in nesting cavities, the reduced odds of getting joined, and the increased value of established nests nearing the worker stage relative to a newly established solitary nest. Therefore, the concessions theory predicts increasing skew (Reeve et al., 2000), whereas the restraint theory would seem to predict decreasing skew. In this case, the data firmly support the concessions prediction, and this pattern is the most consistent feature of skew studies in *Polistes* (Field et al., 1998; Peters et al., 1995; Queller et al., 2000; Reeve et al., 2000). The current tug-of-war model does not formally predict this outcome, but it would seem to be predicted by a natural extension that considers the possibility that the dominant gains strength with time as the result of winning contests, while subordinates decline in strength either through losing contests or because of their greater role in foraging.

Subordinate resistance to the dominant may also increase in the later period, although only time on the nest, and not direct aggression, increased significantly (Figure 2). Given that skew increases, this trend also seems consistent with the concession theory.

Concessions theory predicts that dominants should claim a larger share (higher skew) on more productive nests because they can meet the subordinate's minimum requirements with a smaller share (Reeve, 1991; Reeve and Ratnieks, 1993). Restraints theory predicts the opposite, because it is the subordinate who can claim the excess (Reeve, 1991; Reeve and Ratnieks, 1993). Neither model was correct, as there was no correlation observed. The tug-of-war theory makes no prediction.

Concessions theory predicts skew will be positively correlated with cofoundress relatedness because a dominant needs to concede less to a related subordinate who is getting indirect fitness gains (Reeve, 1991; Reeve and Ratnieks, 1993). Again, restraint theory predicts the opposite—a negative correlation (Johnstone and Cant, 1999)—because the subordinate can be less restrained when the dominant gets indirect benefits from subordinate reproduction. The bidding game variant of the concessions model (Reeve, 1998), in which dominants bid for

the services of helpers, predicts no correlation, and the tug-of-war model predicts either no correlation or a negative one (Reeve et al., 1998). In *P. carolina*, relatedness and skew tended to be negatively correlated, but never significantly so. No significant correlation with relatedness was found in either *P. bellicosus* (Field et al., 1998) or *P. dominulus* (Queller et al., 2000), while a positive correlation was reported for *P. fuscatus* (Reeve et al., 2000). Unfortunately, this test lacks power in *P. carolina* because there is so little variation in relatedness. *P. carolina* cofoundresses were full sisters in all but one nest at the time of collection, although a few less related individuals were inferred among the noncollected foundresses.

This lack of variation in relatedness creates a more serious problem for both the concessions and restraint models. The simplest models of each predict that the subordinate's condition for joining is independent of relatedness (Johnstone, 2000; Reeve, 1991), as does the bidding game variant (Reeve, 1998). When peace incentives are included in the concessions model, relatedness may even act to destabilize associations (Reeve and Ratnieks, 1993). In *P. carolina*, it is evidently low relatedness that destabilizes associations; nearly all the foundresses that were not full sisters to their nest mates either disappeared or were visitors who were in the unrelated colony very briefly. *P. bellicosus* (Field et al., 1998) and *P. annularis* (Peters et al., 1995) showed a similar pattern of most cofoundresses being full sisters. *P. fuscatus* associations include some less related pairs, but these are thought to be cousins (Reeve et al., 2000) so they, too, may be following a rule involving joining with natal nest mates, but not nonrelatives. Only *P. dominulus* appears to associate with nonrelatives to any significant degree (Queller et al., 2000).

More complex versions of the skew models do not always predict variable relatedness. The restraint model can be saved by including sufficiently high costs of eviction (Johnstone and Cant, 1999), for which we have no evidence. The concessions model can be saved if the dominant chooses joiners; she should prefer a related subordinate to an unrelated one because she then has to concede less (Keller and Reeve, 1994; Reeve and Ratnieks, 1993). However, this choice should only come into play when colonies are saturated (the same result emerges from an N -player concessions game if colonies are saturated; Reeve and Emlen, 2000), and saturation seems unlikely. One indication that saturation is unlikely is that all colonies do indeed accept many more helpers, in the form of workers, though this argument is not conclusive because the saturation threshold is predicted to be higher for workers (Reeve and Emlen, 2000). Single-foundress colonies are clearly not saturated because their failure to attract joiners results in colony failure. It seems likely that the lack of saturation goes beyond solitary foundresses, given that average foundress number explained most of the variation in productivity (cell number), and there was no hint of diminishing returns.

A tug-of-war model might be consistent with uniformly high relatedness, although group stability is not formally a part of the current model. Our reasoning is that nonrelatives expend more on competition (Reeve et al., 1998), leaving a narrower range of circumstances where cofounding is worth the effort.

We also found no correlation between skew and the size difference between the dominant and her subordinates (Figure 3). All three skew theories predict a positive correlation, as long as fighting is relevant and size is correlated with fighting abilities (Johnstone and Cant, 1999; Reeve and Ratnieks, 1993; Reeve et al., 1998; we interpret greater size difference as a lower cost of eviction in the restraint theory). Size is often, but not always, an important correlate of dominance in *Polistes* (reviewed in Reeve, 1991). The lack of a size effect on skew in *P. carolina* is puzzling, but it is consistent with the fact

that size does not determine who is dominant in the first place.

The original concessions theory predicted that aggressive testing of the dominant by the subordinate will be positively correlated with skew, on the rationale that a subordinate who detects and overthrows a weak dominant will inherit the level of skew (Keller and Reeve, 1994; Reeve and Ratnieks, 1993; but see Cant and Johnstone, 2000). This logic would appear to also apply to the restraint theory. Reeve (2000) has made another related argument for a positive correlation. There is predicted conflict over a greater range of conditions (the window of selfishness) when ecological constraints and relatedness are high—both conditions that lead to high skew in the concessions model. (Because these conditions lead to lower skew in the restraint model, an extension of this logic to the restraint model might give the opposite prediction.) The tug-of-war model predicts that greater subordinate aggression will lead to lower skew. Here, fighting is assumed to be the means by which subordinates obtain their reproduction: those who do not fight will not reproduce. In *P. carolina*, there was no correlation between subordinate aggression and skew, providing no support for any of the models. Nor was there any correlation with another index of subordinate dissatisfaction, the fraction of time the subordinate stays on the nest instead of foraging.

A more detailed model of skew and aggression (Cant and Johnstone, 2000) suggests that the predictions are more complicated than claimed by the models above. Positive, negative, or zero correlations can be predicted, depending on both the consequences of fighting and on the which factors have the greatest effect on skew. We do not know enough about these two factors to adequately test this model.

Clearly, skew theories do not currently do a very good job of explaining our *P. carolina* data. The tug-of-war theory seems to do best (Table 1), but perhaps only because it makes the fewest clear predictions. The lack of a fit could be due to limitations of our study system, limitations of the theories, or both. One limitation of the study is the sample size of 17 collected colonies; perhaps this makes it difficult to detect patterns that are present. However, we had no difficulty in detecting certain clear patterns: cofoundresses are nearly always full sisters, skew increases with time, and productivity increases with foundress number. If we missed other patterns, it was likely because they were weak.

A more serious limitation is that, in conducting tests of skew theory, we have assumed that the offspring being contested sometimes reproduce. Otherwise, subordinate reproduction at this stage of the season would consist entirely of dead-end workers that are not relevant to direct fitness. The extent to which workers reproduce in *P. carolina* is unknown. The near absence of early males seems to indicate that workers rarely become inseminated queens in this species, as they do in other Texas species of *Polistes* (Strassmann and Hughes, 1986). However, uninseminated workers would likely produce males whenever all the foundresses die, and possibly even with foundresses present (though workers do not reproduce in queen-right colonies of two other *Polistes* species in the area; Arévalo et al., 1998).

If workers never reproduce, then the poor performance of skew theories is understandable. Assuming for the sake of argument that this is so, another problem arises. The general patterns observed in *P. carolina* are often similar to those in other species where the offspring clearly do have reproductive importance, either as next year's reproductives (Reeve et al., 2000) or as takeover queens (in species with numerous early males; Field et al., 1998; Peters et al., 1995). Foundresses join with close relatives, compete aggressively for dominance, and losers serve primarily as helpers. Subordinates obtain some

reproduction, which decreases with time as a strong dominant emerges. If these patterns are to be explained by skew theory in some species, then why does *P. carolina* behave in such similar fashion if reproduction is irrelevant?

One limitation of the skew theories we have tested is that they have generally been developed for associations of two individuals. Applying their predictions to larger associations may not always be valid (Johnstone et al., 1999; Reeve and Emlen, 2000). Another possible flaw of the transactional theories lies in their assumptions regarding the exchange of reproduction for help or for peace. For example, in the concessions theory, a decision to join and help is made on the basis of payoffs expected in the future, which are vulnerable to cheating. Such exchanges seem to require the same sort of counting, trusting, and retaliating that is central to reciprocal altruism theory, and this theory has also found rather little support except in primates (Clements and Stephens, 1995; Dugatkin, 1997).

Taken together, our results seem to support a somewhat puzzling combination. The convention based on order of arrival is more important than direct competition in establishing who will be the queen. The first-arriving queen increases her dominance in egg laying as time progresses, and by the time new queens are produced, she (or a replacement) is probably the only one laying eggs (because the foundresses were full sisters, the fall nests producing them presumably had only one egg layer, unless they have unprecedented levels of within-colony discrimination; Breed et al., 1994; Queller et al., 1990). However, if the foundresses have agreed from the first day of nest founding on a queen, it seems surprising that there is any aggression among the foundresses or any egg laying by subordinates. Possible alternative functions of aggression were noted above, but the issue of reproduction remains. Again, one possibility is that the order-of-arrival rule is not arbitrary and that order of arrival indicates competitive ability or resource-holding potential. Another possible explanation is that establishing a large worker force is more important than percentage of this brood. Under this interpretation, egg laying by subordinates allows a jump start on the season, when the dominant may have a limited capacity to lay eggs and the subordinates are not yet occupied feeding offspring. This hypothesis would explain why subordinate reproduction declines later as eggs hatch.

The absence of egg eating on the videotapes supports the possibility that aggression is not primarily over reproductive share. Similarly, when a nest was abandoned by one group of foundresses and taken over by another, the second group did not eat the eggs laid by the first group. This worker augmentation hypothesis seems particularly likely for *P. carolina*, but it could be a factor even in other species where the workers have more chance at reproduction. In addition to testing increasingly complex models of reproductive competition, future studies of reproductive skew in *Polistes* foundresses should also consider that early offspring production is not strongly ruled by reproductive competition.

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