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Social and Genetic Structure of Paper Wasp Cofoundress Associations: Tests of Reproductive Skew Models

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ABSTRACT: Recent models postulate that the members of a social group assess their ecological and social environments and agree on a "social contract" of reproductive partitioning (skew). We tested social contracts theory by using DNA microsatellites to measure skew in 24 cofoundress associations of paper wasps, *Polistes bellicosus*. In contrast to theoretical predictions, there was little variation in cofoundress relatedness, and relatedness either did not predict skew or was negatively correlated with it; the dominant/subordinate size ratio, assumed to reflect relative fighting ability, did not predict skew; and high skew was associated with decreased aggression by the rank 2 subordinate toward the dominant. High skew was associated with increased group size. A difficulty with measuring skew in real systems is the frequent changes in group composition that commonly occur in social animals. In *P. bellicosus*, 61% of egg layers and an unknown number of non–egg layers were absent by the time nests were collected. The social contracts models provide an attractive general framework linking genetics, ecology, and behavior, but there have been few direct tests of their predictions. We question assumptions underlying the models and suggest directions for future research.

Keywords: reproductive skew, *Polistes*, relatedness, microsatellites.

Animals choose to live in groups for a variety of reasons (e.g., Emlen 1991; Reeve 1991; Seger 1991). A recent focus of research has been the question of how efficient group function can be maintained despite the inevitable potential conflicts between genetically nonidentical group members (e.g., Ratnieks and Reeve 1992). The most obvious potential conflict concerns partitioning of reproduction (reproductive "skew") in groups lacking morphologically differentiated castes. The first attempt to model skew (Vehrencamp 1983) was based on the assumption that the dominant individual controls partitioning. If the dominant is in control, why should we expect any partitioning at all? The answer Vehrencamp suggests is that if subordinates have a choice between staying in the group or leaving to reproduce alone, they will stay only if by staying they propagate more copies of their own genes. The question then becomes, how much direct reproduction must the dominant allow a subordinate to induce her to stay? Retaining the same basic assumptions, Reeve and Ratnieks (1993) extended Vehrencamp's work, focusing particularly on social insects. The models make several predictions (table 1). A counterintuitive prediction is that the dominant can afford to exploit the subordinate to a greater extent if the subordinate is a closer relative. The more closely related they are, the more efficiently the subordinate can propagate her own genes indirectly, by boosting the dominant's reproduction, and so the less direct reproduction she needs to be allowed. A second prediction is that as the reproductive success that a subordinate can expect from independent nesting decreases, due to increased ecological constraints, the smaller the incentive necessary for her to stay. Apart from leaving, another potential option for a subordinate is to fight the dominant in the hope of assuming dominance herself. As well as a staying incentive, the dominant may therefore have to allow the subordinate a "peace incentive" (Reeve and Ratnieks 1993). The greater the subordinate's fighting ability relative to the dominant, the greater the peace incentive must be.

There are also secondary predictions that can be derived from the models. Reeve (1991) and Reeve and Ratnieks (1993) hypothesize that as partitioning of reproduction becomes less even (high skew), subordinates have a greater incentive to "test" the dominant because there is more to gain by usurping her position, so that we should expect heightened aggression in high skew societies. Since high skew is associated with high relatedness in the models, this prediction is again somewhat

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Table 1: Predictions of the social contracts models, null predictions, and results observed in *Polistes bellicosus*

	Cofoundress relatedness vs. skew	*Ecological constraints vs. skew*	*Fighting ability (dominant/subordinate) vs. skew*	*Aggression vs. skew*	*Cofoundress relatedness*	*Group size vs. skew*
Social contracts	+	+	+	+	Variable	?+[a]
Null prediction	No	Unclear	+	−	Less variable	−
Observed	−	Not tested[b]	No	−	Less variable	+

Note: + = positive relationship; − = negative relationship; no = no relationship with skew.

[a] A tentative prediction from the social contracts models is that P_d, the proportion of offspring of a dominant-subordinate pair that are offspring of the dominant, should increase with group size (see text).

[b] But see discussion of relationship between skew and season in text.

counterintuitive: other things being equal, there should be more aggression between closer relatives. A second implication of the theory is that within-group relatedness should be highly variable. Under the theory, a subordinate's inclusive fitness is constant, however closely related she is to the dominant. If she is unrelated, she will be allowed as much direct reproduction as she would have achieved alone. If she is a close relative of the dominant, she will be allowed less direct reproduction, but the shortfall will be compensated for indirectly through her boosting the reproduction of a relative. Hence, as noted by Reeve (1991), relatedness drops out of the conditions for joining, and we predict considerable variation in within-group relatedness.

Reeve and Ratnieks's (1993) models apply to groups of size two. Predicting how group size affects skew is complex. Two tentative assumptions are that total group productivity increases with group size and that the increase in productivity with each additional subordinate is greater than the incentive the subordinate must be given, so that the dominant always creams off some extra direct reproduction. As group size increases, the dominant's share of reproduction should also increase if it is measured as a proportion of the total reproduction by any dominant-subordinate pair (table 1).

In this article, we evaluate social contracts theory by using DNA microsatellites to measure partitioning of reproduction in paper wasp cofoundress associations, *Polistes bellicosus*, during production of the first brood. The small number of cofoundresses and small physical dimensions of preworker *Polistes* nests imply that the dominant could potentially control reproduction, as assumed by social contracts models. The option of independent nesting is demonstrably open to *Polistes* foundresses, and polistine wasps are one of the taxa that Reeve and Ratnieks (1993) had in mind when developing their models.

The essence of the models is that group members assess their ecological and social environment, then agree on a "social contract" of reproductive partitioning (Reeve and Nonacs 1992). Although there is no well-specified alternative to the social contracts models, it is important to consider what we would expect if their assumptions did not hold. There are three critical assumptions: individuals must be able to assess their environments and make the correct long-term strategic decisions; social contracts must be stable; and the dominant must have complete control. In table 1, we contrast the predictions of social contracts theory with null predictions that might follow if the basic assumptions were violated. These null predictions should not necessarily be seen as a coherent model that stands or falls as a whole. Rather, they allow us to test specific assumptions of the social contracts models.

First, for the theory to apply within populations, individuals must be able to assess variables such as relatedness. This seems feasible, except that *Polistes* foundresses appear to distinguish between only natal nest mates and nonnatal nest mates (Queller et al. 1990; Reeve 1991). Rather than a smooth correlation between relatedness and skew, we might thus expect two discrete levels of skew, one associated with the average relatedness between natal nest mates and the other with the (lower) relatedness between nonnatal nest mates. The second critical assumption is that social contracts can be evolutionarily stable: dominants must not cheat on future payments, even when the subordinate has few options for retaliation. A subordinate stays because the contract gives her a certain amount of direct reproduction, including some in the future. But natural selection might favor a dominant that accepted early help, then later denied the subordinate her egg-laying rights once the season had progressed to the point when the subordinate would have little chance of reproducing if she left to nest independently. If stable contracts cannot be made, low relatedness no longer guarantees a large staying incentive, and the null prediction from kin selection theory (Hamilton 1964) is that relatedness will be high and less variable than under social contracts theory (table 1). The result may be that only natal nest mates form associations. If wasps cannot distinguish relatedness within that category, a within-population correlation between skew and relatedness is obviously no longer expected (table 1).

The third critical assumption of social contracts theory is that the dominant has complete control. If within-group competition is not completely suppressed, the null prediction is that dominants with greater relative fighting ability will be able to force a higher reproductive skew. This is the same prediction made by social contracts theory (table 1), but for a different reason. However, if aggression is a mechanism by which subordinates increase their share of the reproduction, the null prediction is that increased aggression will be associated with low skew, opposite to the prediction from social contracts theory (table 1). The final null prediction is that as group size increases, the dominant increasingly loses control and skew decreases.

The social behavior of *Polistes* has been extensively studied (reviewed by Reeve 1991). The life cycle starts in spring, when overwintered inseminated females (foundresses) begin new colonies, either alone or in groups. In multiple-foundress associations, one female is behaviorally dominant, rarely leaves the nest, and lays most of the eggs, while subordinates carry out most of the risky foraging to feed the developing brood. In northern populations, the first brood of offspring consists of nonreproductive female workers, then a brood of reproductives of both sexes is produced, with the female reproductives overwintering to become the next year's foundresses (e.g., Noonan 1981). In our Texas populations, however, more than 50% of dominants die during the long nesting season before reproductives are produced (e.g., Strassmann 1981; Queller and Strassmann 1988). Every "worker" is a potential replacement queen, which foundresses should compete to produce, so that social contracts theory should apply even to the first brood. The high frequency of males in the first brood (see the "Results" section) is a reflection of this, since these "early" males presumably inseminate replacement queens (Strassmann 1981; Reeve 1991). In some species, replacement queens are normally the oldest living workers (Strassmann and Meyer 1983; Hughes et al. 1987), suggesting that the first workers are particularly valuable.

Methods

Fieldwork

During the first half of the 1993 spring preworker phase, we located 37 nests of *Polistes bellicosus* in their natural habitat by searching low-growing native prairie vegetation within an area of 4 ha at Brazos Bend State Park near Houston, Texas. This is the site of previous research on *P. bellicosus* (Strassmann et al. 1987, 1988). When discovered, nests contained an average of 23 brood and 80% had more than one foundress (mode = 3). We marked foundresses individually using enamel paint and censused nests during daylight, on average once per day until they were collected. During a 2-wk period (April 12–27) toward the end of the preworker phase, we videotaped behavior on each of the 24 nests that had survived predation and still had more than one foundress. We videotaped in situ continuously between approximately 1000 and 1700 hours on 1–3 d per nest (8.67 ± 0.88 h/nest). As soon as each nest had been videotaped, we collected it along with the foundresses and stored them at −80°C. On average, we collected nests 15 d after their discovery. We failed to collect only one foundress known to still be associated with a nest at the time of collection. Characteristics of the nests and foundresses used in the study are given in appendixes A and B, respectively. When collected, nests had an average of 2.8 foundresses associated with them (range 2–5) and contained 9.0 ± 0.9 eggs, 15.0 ± 1.0 larvae, and 4.1 ± 0.8 pupae (app. A).

Behavioral and Dissection Data

We scored a variety of behaviors from the videotapes, including aggressive interactions and which wasp initiated them; arrivals and departures; whether arriving wasps were carrying prey, building material, or nothing visible; percentage of time each wasp spent on the nest; and egg laying. Aggressive interactions almost all fell into one of two categories: chew, where one wasp applied its mouthparts to the body of another wasp for up to 35 s, during which time the recipient became motionless (37% of aggressive interactions), and lunge, where one wasp made a sudden rush at another wasp, which retreated (62%).

We dissected abdomens in 10% saline and scored ovarian development. All foundresses were inseminated. We used five parameters to identify the foundress that was dominant at the time of nest collection: number of mature eggs (eggs with a chorion) in the ovaries, percentage of time spent on the nest, rate of initiation of aggressive interactions per minute on the nest, number of eggs laid during videotaping, and number of offspring produced (see below). For all parameters, we scored the foundress with the highest value as the dominant. On 18 of 24 nests, all five measures gave the same result. On other nests one ($n = 5$ nests) or two ($n = 1$) measures gave a different result to the others. For analyses, the foundresses categorized as dominant (indicated in app. B) are those identified by the majority of the five measures.

We glued the right forewing of each foundress to a card and measured the maximum length of the first discoidal cell using the public domain program NIH-Image (1993) on a digitized picture of the wing that was captured through a Wild dissecting microscope, then transferred to a Macintosh computer. We size-ranked foundresses within nests, with rank 1 for the largest wasp.

Molecular Techniques

We extracted DNA from the thorax of all foundresses and from a sample of immature offspring. We dissected spermathecae out of foundress abdomens and extracted DNA from the sperm to obtain the genotype of the mate(s) of each foundress (Peters et al. 1995). We attempted to amplify five microsatellite loci from all samples: Pbe203AAG, Pbe411AAT, Pbe424AAT, Pbe440AAT, and Pbe492AAT (see Strassmann et al. 1997 for details). Each locus had between nine and 26 alleles represented in our samples, with heterozygosities of 0.66–0.93. All molecular protocols closely followed those given in an earlier study (Strassmann et al. 1996). We divided offspring into two categories for data analysis: eggs plus larval instars 1–3 ("late" offspring: mean = 8.8 ± 0.7 per nest), and larval instars 4–5 plus pupae ("early" offspring: mean = 8.3 ± 0.6). Where available, we attempted to amplify from 10 early and 10 late offspring. We amplified DNA from all foundresses twice separately at all loci as a check, since errors in foundress genotypes could result in all offspring on a nest being misassigned.

Maternity Assignment Using Sperm Data

We obtained genotypes at all five loci for all foundresses. We attempted to assign only female offspring that had genotypes available from three (1.5% of offspring), four (11%), or all five (87.5%) loci. *Polistes bellicosus* foundresses were singly mated (see the "Results" section). We assigned a female offspring to a particular foundress when the offspring genotype included both the foundress's sperm allele and one of her two maternal alleles at each locus. Apart from her true mother, the closest adult relative of a female offspring that could have been present was her aunt (mother's full sister). Given the observed population allele frequencies, we calculated that the probability of an offspring matching the sperm and maternal genotype of her aunt is 8.85×10^{-5} (less than one in 11,000). This was calculated from the equation:

$$P = 1 - \prod_{l=1}^{L} (1 - E_l), \tag{1}$$

where P is the probability of excluding a candidate mother using L independent loci, and the exclusion probability (E) for each locus is obtained by substituting $r = 0.75$, $m = 1$, and observed allele frequencies into equation (1) of Peters et al. (1995). In addition to checking each offspring against the potential mothers on its nest, we checked against foundresses on all other nests since some foundresses switch nests.

We assumed offspring were males if they were homozygous at all five loci. With the heterozygosities at our loci, the probability of a female being homozygous is only 1.07×10^{-4}. We did not attempt to assign male offspring to foundresses. Only maternal genotypes are relevant to male parentage in haplodiploids. For a male offspring, an aunt is excluded at one locus with probability

$$E = \sum_i p_i(1 - 0.75)(1 - p_i)^2, \tag{2}$$

where p_i is the population frequency of allele i. Substituting these E values into equation (1) gives $P = .39$, which is unacceptably low.

At locus Pbe492AAT, we identified a probable null allele on five spatially adjacent nests. On these nests, foundresses were all homozygous at locus Pbe492AAT. We could assign approximately half of the offspring in the normal way, but 23 others, though matching the maternal + sperm genotype of a particular foundress at the other four loci, were apparently homozygous for the allele carried by that foundress's mate at locus Pbe492AAT. We assumed in these cases that the foundress and the offspring were in fact heterozygotes for a null allele.

Division of Unassigned Female Offspring into Sib Groups

We did not obtain paternal genotypes for six of the 24 nests because of initial problems with extracting sperm DNA. Without paternal genotypes, the probability of a female offspring matching her aunt's genotype is unacceptably high (.51). In addition, some offspring did not match the maternal genotype of any collected foundress (offspring of "missing" foundresses). Although these two groups of offspring could not be assigned, we used a likelihood-based method to divide them into sib groups using the computer program Kinship 1.1.2 (Goodnight and Queller 1997). The program takes each pair of female offspring within a nest and uses population allele frequencies to calculate the probability P that their genotypes could have been produced if they were full sisters, assuming Mendelian genetics, single mating, and outbreeding (e.g., two females with genotypes AB and CD have $P = 0$). The null hypothesis is the probability that the two genotypes arise if the females are cousins (the next closest possible relationship). The output is the log-likelihood ratio for sisters/cousins. In order to obtain significance cutoffs, we used the observed population allele frequencies to generate genotypes at the five loci for 10,000 random pairs of sisters and 10,000 pairs of cousins. The results suggested that a suitable cutoff was a $\log_{10}$ ratio of 0.0, with observed ratios >0 assumed to represent full sisters. Since only 2.6% of simulated full sisters had ratios of zero or below, this should detect approximately 97% of true full sisters. Of the simulated pairs of cousins, 5.3% had ratios above 0, giving a conservative $\alpha = 0.053$. This procedure appears valid: 2.7% of offspring pairs identified as full sisters using sperm data had $\log_{10}$ ratios of 0 or below, very similar to the 2.6% in the simulations. We assumed that groups of female offspring within nests were siblings if, for each pair within the group, $\log_{10}$-likelihood ratios were above 0; the group as a whole contained no more than three alleles at each locus; and all members of the group shared at least one allele at each locus. The third criterion stems from foundresses being singly mated (see the "Results" section). In the very few cases where it was questionable whether to add an *n*th individual to a sib group of $n - 1$, we added the individual if the majority of log-likelihood ratios were greater than 0. We also examined sister/cousin log-likelihood ratios for cofoundresses within nests and conducted other likelihood ratio tests in an analogous way.

Comparison with Social Contracts Models: Predictions Tested

We tested the predictions of social contracts theory summarized in table 1, using two different measures of reproductive partitioning. First, since the theory is framed in terms of interactions between the dominant and individual subordinates, we measured partitioning between a dominant-subordinate pair using P_d = (no. offspring by dominant)/(total no. offspring by dominant and subordinate). Second, we calculated the skew index proposed by Reeve and Ratnieks (1993) and Keller and Vargo (1993):

$$S = (N_b^2 v + N_n)/(N_b + N_n),$$

where N_b and N_n are numbers of breeders and nonbreeders, respectively, and v is the observed variance in reproductive output among breeders. This provides a measure of skew for whole nests, but information on pair-wise interactions is inevitably lost. The alternative indices suggested by Pamilo and Crozier (1996) produced almost identical values. To test the effect of fighting ability, we assumed that size (wing length) reflects fighting ability (Reeve 1991). For each subordinate foundress, we calculated the size ratio (dominant − subordinate)/(mean for the pair). We looked for a relationship between this size ratio and P_d. We also looked for a relationship between the skew index and the size ratio (dominant − average for subordinates)/(mean for all foundresses on the nest).

High-ranking subordinates have most to gain from a dominance reversal and are the wasps that should increase their aggressive testing of the dominant when skew is high (Reeve 1991; Reeve and Ratnieks 1993). To test this, we used two measures of aggression by the second-ranked wasp: rate of initiation of interactions by rank 2 against the dominant when they were both on the nest; and proportion of interactions between dominant and rank 2 that were initiated by the dominant, which is independent of the interaction rate. The second-ranked wasp was defined as the wasp that spent the largest proportion of time on the nest apart from the dominant. There were only two wasps on four of the nests included in this analysis. On the other 10 nests, the rank-2 wasp was on the nest for 25% ± 7% more of the time than the next ranked wasp.

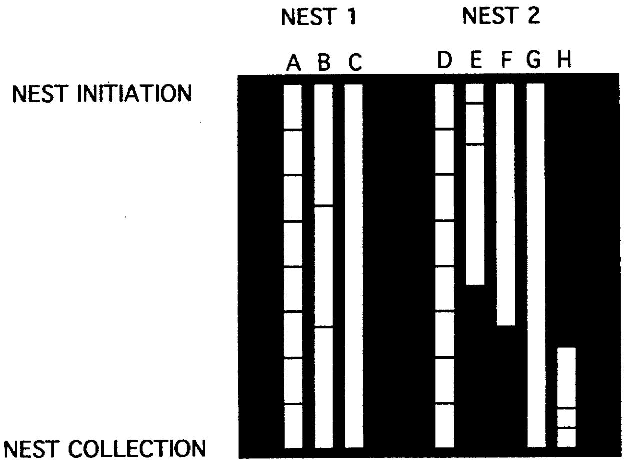

Figure 1: Hypothetical histories of two *Polistes* cofoundress associations. *A–H* are foundress identifiers, where each column represents a foundress and each horizontal line across a column represents an egg laid by that foundress. On nest 2, foundresses *E* and *F* die before nest collection, and foundress *H* joins the group partway through the preworker phase.

We used the number of foundresses collected as a measure of group size, but the total number of brood collected, which might reflect the average number of foundresses present during the preworker phase, produced the same results.

Data Sets Used

Estimating reproductive skew is complicated by repeated changes in group size and composition that result from well-known features of paper wasp biology (Reeve 1991; Nonacs and Reeve 1995). First, there is often a high rate of foundress mortality, particularly associated with foraging. Second, foundresses may join or usurp existing groups, especially after their own nests have been destroyed by predators. Figure 1 shows the histories of two hypothetical nests. On nest 1, group composition and skew remain the same throughout. On nest 2, however, foundresses *E* and *F* die before collection, and foundress *H* joins the group partway through the preworker phase. Relative egg-laying rates also change. For example, foundress *E* lays eggs only at the start of the season. There are two important consequences for our purposes. First, skew itself changes over time: even with perfect information, any skew estimate would apply to only a short segment of the history. Second, our ability to estimate skew accurately generally decreases the further back we go in the history. Our molecular data allow us to detect dead wasps that reproduced, but not dead nonreproducers. We might be unable to detect the presence of foundress *F*, we might incorrectly assume that *E* had died soon after laying its second and final egg, and we might assume that *H* had been present throughout.

In general, the younger the brood, the more likely that collected foundresses were the only ones present during brood production. Also, the smaller the period over which a sample of brood were produced, the more likely it is that the same foundresses were present throughout. We therefore estimated skew for three different data sets: (1) collected foundresses only (whether or not they had reproduced), using collected foundresses' brood of all ages; (2) reproducers (collected or not) plus nonreproducing collected foundresses, using late brood only; and (3) reproducing foundresses only, analyzed for both early and late brood. Data set 1 is most relevant for analysis of the relationship between skew and aggression or relative size because aggression and size data are available only for collected foundresses. Data set 2 gives the best analysis of recent brood. Data set 3 allows comparison of skew in early versus late brood without the potential bias of including late-season (collected) nonreproducers but not early-season nonreproducers that died before collection.

Statistics

We report regression relatedness estimated using methods developed elsewhere (Queller and Goodnight 1989) as implemented in the Macintosh computer program Relatedness 4.2b (Goodnight and Queller 1996). We weighted colonies equally. We obtained standard errors by jackknifing over colonies or over loci for colony-specific values.

We carried out other statistical analyses using the generalized linear modeling package GLIM (McCullagh and Nelder 1989; Crawley 1993), assuming normal errors (e.g., when y = skew index) or binomial errors (e.g., when $y = P_d$) as appropriate. The skew index was arcsine-transformed before analysis. Although explanatory variables are generally discussed separately below, all main effects and first-order interactions were initially fitted simultaneously in each analysis (e.g., each row of table 3). Each term was then removed from a model containing all other terms of the same order plus any significant higher-order (interaction) terms, and the change in deviance assessed using *F* ratios (normal errors) or χ^2 (binomial errors) with a $P = .05$ significance cutoff. Only significant terms were retained in the final model. The significance level reported for each of these terms refers to the change in deviance following its removal from the final model (see Crawley 1993, pp. 189, 195, for further details). We report means ± standard errors.

Table 2: Values of Keller and Vargo's (1993) index of reproductive skew in *Polistes bellicosus*

Data set (*foundresses, brood*)	*Mean*	*SE*	*Range*	*No. nests* (n)
Collected foundresses, collected foundresses	.75	.09	.003–1.0	14
Reproducers and nonreproducing collected foundresses, late	.84	.05	.45–1.0	18
Reproducers, all	.50	.06	.003–1.0	24
Reproducers, early	.49	.07	0–1.0	24
Reproducers, late	.68	.07	.01–1.0	24

Note: The index potentially ranges from 0 (no skew) to 1 (maximum skew). See the "Methods" section for description of the data sets.

Results

Maternity Assignment

We genotyped 502 offspring at three to five loci, representing 74% of brood on the 24 nests. Of these, 92 (18%) were males. Since we could not assign males, the remainder of the analysis refers only to the 410 female offspring, unless otherwise stated. We successfully amplified sperm DNA on 18 nests. Only one allele was visible at each locus for each foundress's sperm, indicating single mating. Of 311 female offspring on the nests with sperm data, none had a genotype consistent with more than one foundress-sperm combination. We found no evidence of nonrandom mating. Foundresses were unrelated to the sperm in their spermathecae ($r = -0.073 \pm 0.052$), and within nests, the mates of different foundresses were unrelated ($r = -0.012 \pm 0.042$).

General Patterns of Reproductive Dominance

Values of the skew index for various data sets are given in table 2. Most nests had several foundresses that had reproduced, but 77% ± 3.6% of all offspring came from the most productive foundress and 90% ± 4.1% of offspring of collected foundresses were produced by the

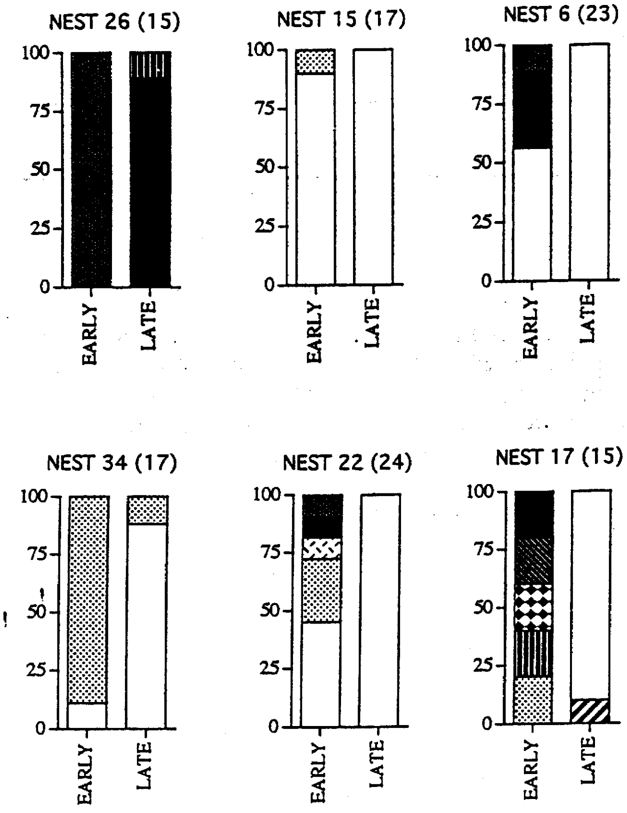

Figure 2: Partitioning of reproduction between *Polistes bellicosus* cofoundress on six nests with sperm data, early and late in the preworker phase. Early offspring were pupae and larval instars 4–5; late offspring were eggs and larval instars 1–3. The different shadings on each nest represent different foundresses. Open areas are the foundress dominant at the time of nest collection, lightly stippled areas (as on *nest 34*) are subordinate foundresses that were collected; all other shadings represent foundresses that had disappeared by the time of the collection. Numbers in parentheses after nest numbers are the number of female offspring genotyped.

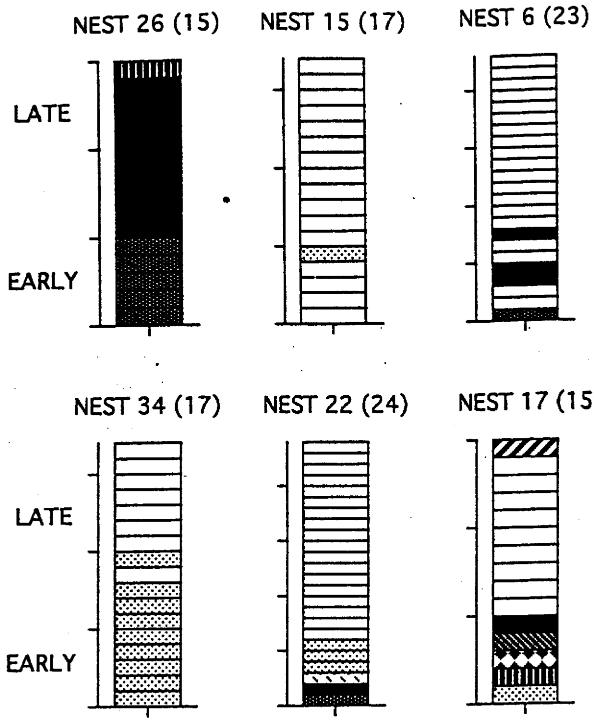

Figure 3: Sequence of oviposition by foundresses on six nests as inferred from offspring developmental stages. For each nest, the oldest offspring (pupae) are at the bottom and the youngest (eggs) at the top. Each small rectangle represents one offspring. Where several offspring are of the same age, they are ordered so as to minimize the number of transitions in egg layer. Shadings as in figure 2.

dominant ($n = 14$ nests with sperm genotypes; there were no offspring of collected foundresses on four nests). A collected subordinate had reproduced on eight of 14 nests, but we never detected reproduction by more than one collected subordinate on the same nest. On eight nests where a collected subordinate had reproduced, she had usually ($n = 7$) produced only one to three out of an average of 13.5 offspring. These molecular data correspond well with dissection and video data. On 11 of 14 nests, only the dominant had mature eggs in her ovaries, and 16 of 17 eggs laid during videotaping were laid by the dominant.

On 17 of 24 nests, one foundress had apparently been dominant throughout the preworker phase, producing the majority of both early and late offspring (fig. 2, e.g., *nests 15* and *6*), although on three nests she was missing by the time of nest collection. On three nests (e.g., *nests 26* and *34*, fig. 2), there had been a simple change in dominance, with one foundress producing most of the early offspring and a different foundress producing most of the late offspring. In one case (*nest 34*, fig. 2) we collected both foundresses, indicating that a previously dominant foundress had subsequently remained on the nest as a subordinate. On some nests, however, the situation was more complex, with up to five different foundresses reproducing within the early or late category (e.g., *nest 17*, fig. 2). There was a tendency for skew among reproducers to be higher late in the preworker phase (table 2), but the difference was not quite significant ($F = 3.56$, df = 1, 22; $.05 < P < .1$).

At a finer scale, bouts of egg laying by different foundresses were not perfectly sequential: the inferred egg-laying periods of two or more foundresses overlapped on 15 of 24 nests (e.g., fig. 3, *nests 6, 15, 34*). For example, on *nest 15* (fig. 3) foundress *Y* had produced both of the pupae and all seven eggs, but foundress *DB* had produced one of the eight larvae. Nevertheless, the data overall suggest that skew is typically high at any one time, with just the occasional egg laid by subordinates, rather than long periods during which more than one foundress routinely oviposited.

Changes in Group Composition

Our data imply frequent changes in the composition of cofoundress associations during the preworker phase. On nests with sperm data, an average of 40% ± 9.5% (range 0–100) of offspring had genotypes that were inconsistent with all of the foundresses collected. Hereafter, these are referred to as offspring of "missing" foundresses. When we used the likelihood analysis to divide these offspring into sib groups, it revealed that 1.94 ± 0.4 (range = 1–6) missing foundresses had reproduced per nest. This represents 61% of the 57 egg layers detected on these nests. On four nests, all of the offspring had been produced by one to four missing foundresses (e.g., *nest 26*, fig. 2).

Most missing foundresses had probably died before nest collection, but a few may have switched nests. An average of 0.5 ± 0.15 (range = 0–3) foundresses per nest disappeared during the 2-wk monitoring period before nest collection. Censuses carried out before these wasps disappeared indicated that at least eight of 13 were subordinates, and none was definitely a dominant. Two joined other observation nests, as did two unmarked foundresses of unknown origin. None of the unassigned brood matched the genotypes of foundresses collected on foreign nests.

Detection of Subordinate Egg Layers

Although ovarian development provided an accurate picture of partitioning of oviposition at the time of collection, it did not indicate which subordinates had oviposited in the past. Seven of the collected subordinates revealed by the molecular data to have oviposited had only 0.14 ± 0.14 mature eggs and a longest oocyte length of 1.63 ± 0.42 mm, compared with 1.73 ± 0.21 mature eggs ($t = 6.34$, df = 19, $P < .0001$) and a longest oocyte of 2.86 ± 0.13 mm ($t = 2.78$, df = 7, $P < .03$) for dominants. Even though they must once have had mature eggs, these seven subordinates had similar oocyte development to subordinates for which no reproduction was detected (mean = 0.20 ± 0.13 mature eggs, $t = 0.3$, df = 16, $P > .5$; mean longest oocyte = 1.72 ± 0.20 mm, $t = 0.2$, df = 8, $P > .5$).

Cofoundress Relatedness

Estimates of cofoundress relatedness did not support two of the predictions of the social contracts models: there was little variation in relatedness, and there was either a negative relationship between skew and relatedness or no relationship.

The foundresses collected on each nest had genotypes consistent with them being full sisters. Only one of 73 log-likelihood ratios for cofoundresses was below 0, supporting this conclusion. Within-nest cofoundress relatedness was 0.67 ± 0.035, close to the maximum possible 0.75 for full sisters, although the 95% confidence interval (0.60–0.74) was just below 0.75. The distribution of relatedness estimates for individual nests is shown in figure 4. The 95% confidence interval for 19 of 24 individual nests enclosed 0.75, two of the exceptions being nests where both foundresses had identical genotypes. Only four of 24 intervals included zero.

The relatedness data also suggested that missing foundresses were sisters of collected foundresses and not unrelated females that had been usurped. Relatedness of offspring of missing foundresses to the collected foundresses on nests with sperm data was 0.35 ± 0.048 (n = 12 nests), not significantly different from 0.375, the value expected if missing foundresses are sisters of collected foundresses. Likelihood ratios similarly indicated that only two of 96 offspring of missing foundresses were significantly more likely to be unrelated to all of the collected foundresses on their nests than to be the nieces of collected foundresses.

If cofoundresses are all full sisters, the variation in relatedness necessary to test for an effect of relatedness on skew is absent. Observed variation would simply be sampling error around 0.75. To examine this possibility, we drew 1,000 pairs of full sisters randomly from the ob-

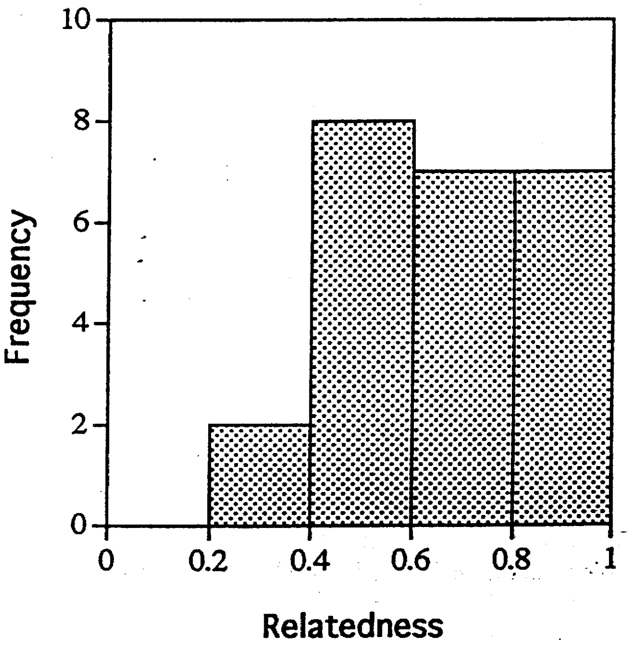

Figure 4: The distribution of cofoundress relatedness estimates for individual nests (n = 24).

Table 3: Results of comparisons with social contracts models

		X variables					
				Size ratio			
Y variable	n[a]	r[b]	Group size	Dominant-rank 2	Dominant-subordinate	Dominant-average	P_d[c]
Skew: reproducers (early, late, or all broods)	24	NS	NS	. . .	. . .	. . .	. . .
Skew: reproducers and collected nonreproducers (late brood)	18	NS	NS	. . .	. . .	. . .	. . .
Skew: collected foundresses	14	NS	*(+)	. . .	. . .	NS	. . .
P_d: dominant/(dominant + rank 2)	14	**(−)[d]	**(+)[d]	NS	. . .	. . .	. . .
P_d: dominant/(dominant + subordinate)	29	****(−)[d]	****(+)[d]	. . .	NS	. . .	. . .
Aggression by rank-2 wasp	11	NS	NS	NS	. . .	. . .	***(−)

Note: Each row represents a separate ANCOVA with the specified *Y* and *X* variables included, except that the first row summarizes three analyses using different sets of brood. All possible first-order interactions were initially fitted except for the final row, where too many treatment combinations were missing to allow this. See the "Statistics" section in "Methods" for further details. NS = not significant. (+) = positive relationship; (−) = negative relationship.

[a] Sample size = number of nests, except for the penultimate row, where $n = 29$ dominant-subordinate pairs on 14 nests. There were 24 nests, but sperm data were unavailable from six, and four others had no reproduction by collected foundresses. We obtained video data for 11 of the remaining 14 nests.

[b] First three rows: subordinate-dominant relatedness averaged over the subordinates on each nest. Last three rows: relatedness between the appropriate pairs of wasps (e.g., dominant–rank 2 in rows 4 and 6).

[c] P_d = proportion of the offspring of a dominant-subordinate pair that were offspring of the dominant. Dominant/dominant + rank 2 considers only dominant–rank 2 pairs; dominant/dominant + subordinate considers all possible dominant-subordinate pairs.

[d] Significant interaction between group size and relatedness.

* $P < .05$.

** $P < .025$.

*** $P < .01$.

**** $P < .005$.

served allele distributions, then estimated relatedness for each pair. The variance in simulated relatednesses (0.024) was similar but significantly smaller than the observed variance for a single pair of foundresses drawn from each nest ($n = 24$ pairs, variance = 0.045, $F = 1.89$, df = 23, 999, $P < .025$). This suggests that relatedness does vary, but any test for a relationship between relatedness and skew is likely to have low power.

In fact, cofoundress relatedness did not predict the value of the skew index (table 3). But there was a negative relationship between relatedness and P_d for individual dominant-subordinate pairs, opposite to the predictions of the social contracts models (table 3, fig. 5). The slope of this relationship was significantly different for different group sizes (fig. 5).

Cofoundress Size

We found no evidence for a relationship between relative fighting ability and skew. The relative size ratios described in the "Methods" section did not predict skew or P_d, the proportion of offspring of a dominant-subordinate pair that were produced by the dominant (table 3). Dominants were the largest wasps on only 11 of 24 nests and were no different in size to subordinates (dominants mean wing length = 7.56 ± 0.075 mm, $s = 0.37$; subordinates mean = 7.46 ± 0.056, $s = 0.37$, $\chi^2 = 0.22$, df = 1, $P > .1$). Size ranks of dominants and subordinates within nests also did not differ ($\chi^2 = 1.87$, df = 1, $P > .1$).

Aggression, Group Size, and Division of Labor

Aggression by rank-2 wasps toward the dominant tended to decrease with increasing skew, opposite to the predictions of Reeve (1991) and Reeve and Ratnieks (1993). Aggressive interactions were generally mild and infrequent compared with some other *Polistes* species (see Reeve 1991). We saw no "falling fights," and there was an average of only 5.08 ± 0.89 aggressive interactions by all wasps combined per nest per hour of videotape (combining chewing and lunging). Nevertheless, there was considerable variation between nests (range = 0–13.9 aggressive interactions/h, or 0.2–6.9/wasp/h), but rank-2 wasps were not more aggressive toward dominants when skew was high (table 3). The proportion of interactions

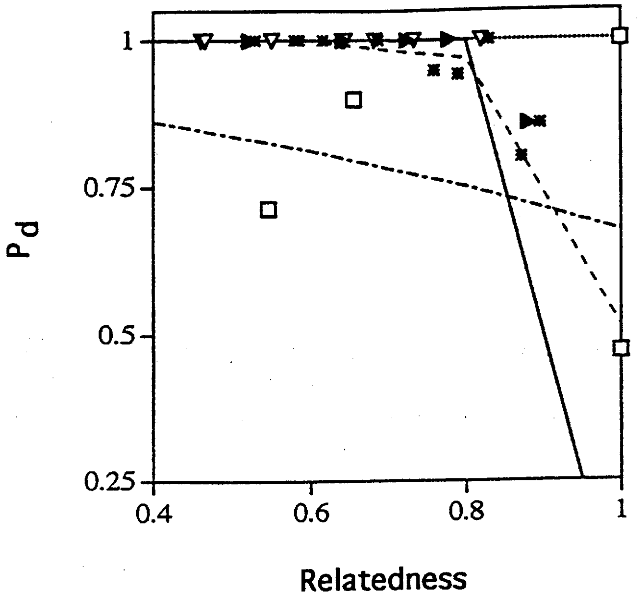

Figure 5: Relationship between genetic relatedness and P_d, the proportion of a dominant-subordinate pair's offspring that were offspring of the dominant. Points are observed values and lines are fitted values for different group sizes ($n = 29$ pairs on 14 nests). *Open squares* and *dash/dot lines* = group size 2; *asterisks* and *dashed lines* = group size 3; *dark triangles* and *solid lines* = group size 4; and *open triangles* and *dotted lines* = group size 5.

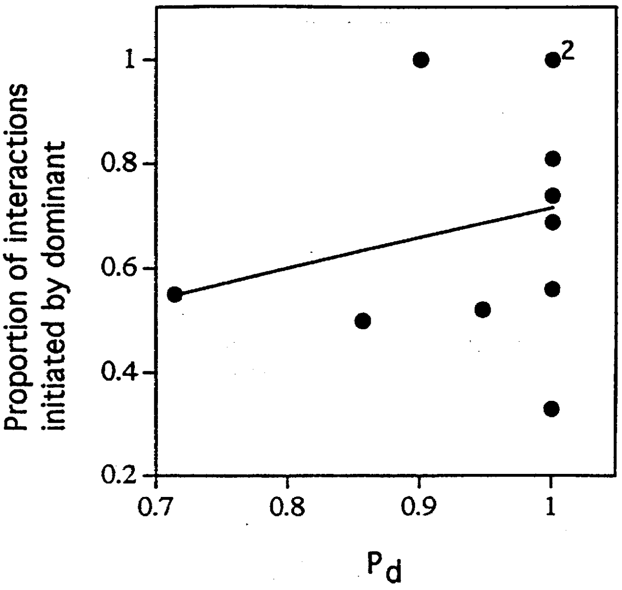

Figure 6: Relationship between the proportion (p) of interactions between dominant–rank 2 pairs that were initiated by the dominant and P_d, the proportion of the pair's offspring that were offspring of the dominant. Equation of line: $\ln[p/(1 - p)] = -1.65 + 2.58\ (P_d)$.

between the dominant and rank 2 that were initiated by the dominant actually increased with P_d ($\chi^2 = 7.46$, df = 1, $P < .01$; fig. 6). Thus, 73.3% of the total 157 interactions were initiated by the dominant on seven nests with $P_d = 1$, compared with 55.8% of 120 interactions on four nests with $P_d < 1$. Similarly, the rate of initiation of interactions by rank 2 against the dominant when they were both on the nest (range = 0–10.5/h, 4.07 ± 0.37 h available per nest) decreased with P_d ($F = 9.73$, df = 1, 9, $P < .025$), or there was no relationship if one influential point was excluded.

Skew among collected foundresses increased and became less variable with increasing group size ($F = 5.73$, df = 1, 12, $P < .05$; fig. 7), reflecting a similar increase in P_d with group size (table 3). This was quite surprising because the three nests on which more than one foundress had mature eggs in her ovaries were among the largest group sizes: both of the nests with five foundresses and one of the four nests with four foundresses. There was no effect of group size for the other data sets (table 3).

As well as being characterized by mild and infrequent interactions, some *Polistes bellicosus* nests exhibited weak behavioral division of labor: on seven of 24 nests, the dominant foundress foraged for caterpillar. These nests each had two or three foundresses and had significantly

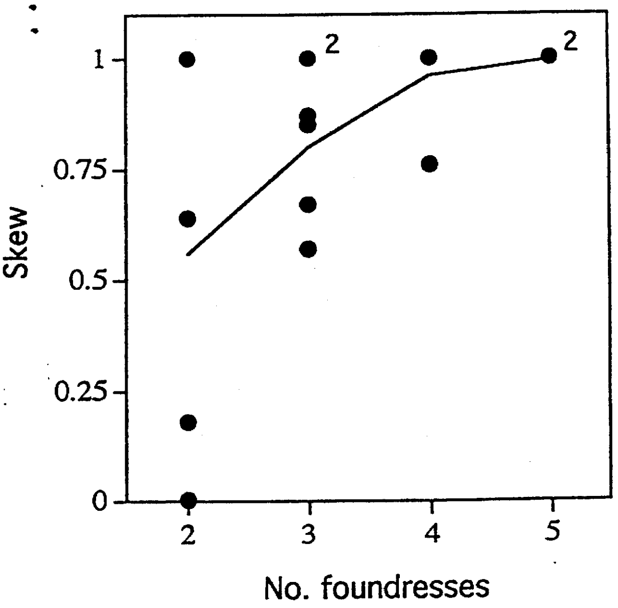

Figure 7: The relationship between group size (number of foundresses collected) and the skew index for collected foundresses. Equation of line: arcsin (skew) = 0.324 + 0.263 (group size).

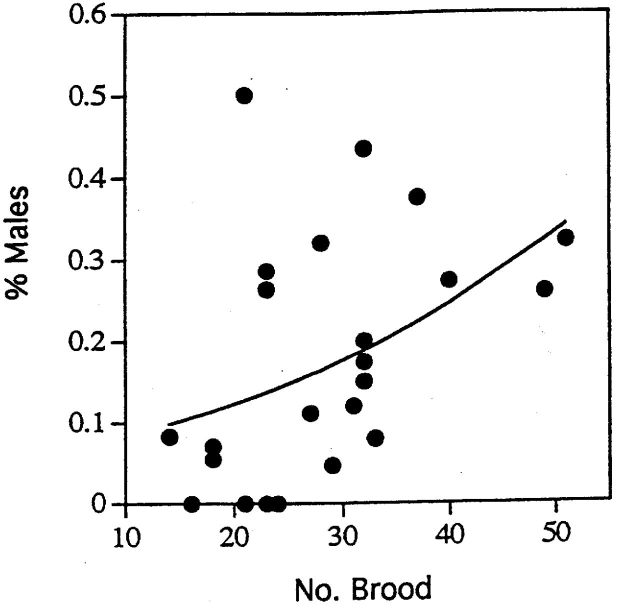

Figure 8: The relationship between the number of brood in a nest and the percentage (p) that were males. Equation of the line: $\ln[p/(1 - p)] = -2.8 + 0.042$ (brood).

fewer foundresses than nests at which the dominant was not recorded foraging ($\chi^2 = 4.52$, df = 1, $P < .05$).

Male Offspring

The above analyses refer to female offspring. Although we could not assign males, we found no evidence that dominants specialize more on one sex of offspring and subordinates more on the other. To test for this possibility, we used the fact that offspring of either sex are equally related to their mother. If a foundress produces equal proportions of the male and female offspring on a nest, the difference between their relatednesses to her ($r_{\text{fem}} - r_{\text{male}}$) should be zero. For the 20 nests that produced both male and female offspring, the average difference $r_{\text{fem}} - r_{\text{male}}$ was 0.038 ± 0.038 for dominants and -0.045 ± 0.026 for subordinates. Neither value is significantly different from 0.

Twenty out of 24 nests produced at least one male offspring and the proportion of males was almost identical among early (18.4% males, $n = 244$) and late (19.0%, $n = 258$) offspring. However, nests containing more brood produced a larger proportion of males ($\chi^2 = 13.3$, df = 1, $P < .001$; fig. 8).

Discussion

Our analyses, summarized in table 3, clearly do not support the predictions of the social contracts models (table 1). We first discuss each of our results in turn.

Genetic Relatedness

Our finding that reproduction is partitioned more evenly between dominant-subordinate pairs when they are more closely related (fig. 5) is opposite to the predictions of the social contracts models. This finding might reflect the lower costs in total fitness of ceding reproduction to a closer relative. The absence of a relationship between skew and cofoundress relatedness in our other data sets (table 3) might perhaps be a reflection of little variation in relatedness in *Polistes bellicosus,* but low variation itself creates problems for the social contracts models. These models imply that potential subordinates should not care how closely related they are to the dominant, so that cofoundress relatedness should be variable. A counter to this argument is that, given a choice, dominants themselves should prefer closely related subordinates, to whom they have to give up less direct reproduction (Keller and Reeve 1994). However, this fails to explain the existence in *P. bellicosus* of significant numbers of lone foundresses (Strassmann et al. 1987), which presumably did not have a choice of relatives yet still did not accept nonrelatives. If ecological constraints were weak, the reproductive incentive required to induce an unrelated subordinate to stay might be more than the dominant would be prepared to give up. However, if ecological constraints were weak, social contracts theory would also predict that multiple founding would be rare and that skew would be low on those nests that were multiply founded (Reeve and Ratnieks 1993), neither of which is true. Our results, and the general rarity of associations between foundresses from different natal nests in *Polistes* species (Reeve 1991), suggest that relatedness is important in joining decisions, as predicted by Hamilton's Rule (Hamilton 1964).

Relative Size

There was no relationship between skew and relative size, a result inconsistent with both social contracts theory and our null prediction based on incomplete control (table 1). It is possible that size is not a good predictor of fighting ability, since successful nest usurpers do not tend to be larger than the females they usurp in *Polistes fuscatus* (Klahn 1981). However, there is some evidence that *P. fuscatus* foundresses can assess relative body size and use it to modulate their aggressive response to reproductive "cheats" (Reeve and Nonacs 1992; but see Strassmann 1993).

Aggression and Division of Labor

Our finding that rank-2 foundresses are less aggressive toward dominants when skew is high is opposite to the predictions of Reeve (1991) and Reeve and Ratnieks (1993). There are at least two possible explanations. One is that rather than representing dominance testing, aggression is simply a mechanism by which subordinates increase their share of the reproduction, as suggested by our null prediction (table 1; see also Reeve and Nonacs 1997). A second possibility is that the prediction from social contracts theory is flawed. Reeve and Ratnieks (1993) may have exaggerated the benefits of a dominance reversal when skew is high. They state that the subordinate stands to inherit the high skew after a reversal, but if high skew is a reflection of a weak subordinate, that subordinate is unlikely to be able to impose a high skew if she becomes dominant herself. In addition, skew may be high because the subordinate has low fighting ability relative to the dominant. Increased aggression may then be futile and costly; in general, animals are expected to fight less hard if they are unlikely to win (e.g., Krebs and Davies 1993). However, skew was negatively correlated with aggression even with the dominant/subordinate size ratio included in the model, suggesting that costs of fighting do not modify the relationship. Reeve (1991) and Reeve and Ratnieks (1993) suggest that at the interspecific level, low skew is associated with mild dominance interactions in *Polistes*. *Polistes bellicosus*, with high skew yet relatively mild and infrequent interactions, again does not conform.

Reeve (1991) and Reeve and Ratnieks (1993) also hypothesize that skew could influence task specialization and suggest that there is evidence for an interspecific association between high skew and greater task specialization in *Polistes*. *Polistes bellicosus* again contradicts this. Skew is high, yet unusually for *Polistes* species, dominants foraged for caterpillar on more than one-third of nests. However, high skew can actually lead to decreased task specialization under some conditions in Reeve and Ratnieks's (1993) models.

Group Size and Ecological Constraints

The relationships we found between P_d and group size and between skew and season could be interpreted as being consistent with the social contracts models, but the models' predictions are less clear-cut. The increases in skew and P_d with group size occurred only among collected foundresses, and the prediction of social contracts models depends on how skew is controlled in groups of more than two individuals (Reeve and Ratnieks 1993). It is, however, worth noting that our data failed to support the null prediction that the dominant increasingly loses control of reproduction in larger groups. This may reflect the small range of group sizes and small size of preworker nests (maximum width 2.5 wasp body lengths). There was a hint of decreased control in three of the largest groups, in which more than one foundress carried mature eggs.

The tendency for partitioning to be less even late in the preworker phase (see also Peters et al. 1995) could be consistent with social contracts theory if it reflects increased ecological constraints on independent nesting. Late in the season there is less time left in which to build a new nest and reproduce, and subordinate reproductive potential and fighting ability may have declined due to food monopolization by dominants. However, increased skew if the subordinate's fighting ability has declined is also consistent with one of our null predictions, and it is also possible that any seasonal effect is associated with seasonal changes in group size. The positive association between ecological constraints and skew predicted by social contracts models will probably be best tested at the population level.

The Application of Social Contracts Theory to Real Data

The social contracts models provide an attractive general framework linking genetic relatedness, ecological constraints, and behavior in social groups (Bourke and Heinze 1994; Keller and Reeve 1994). To date, empirical evidence supporting the models (Bourke and Heinze 1994; Keller and Reeve 1994; Heinze 1995; Reeve and Keller 1995; Emlen 1996) is largely indirect, since accurate skew data are generally unavailable. We found that skew varied widely in *P. bellicosus* (table 2). The average proportion of offspring produced by the dominant was similar to the dwarf mongoose, in which within-species patterns are consistent with social contracts models (Creel and Waser 1991; Keane et al. 1994). In *P. bellicosus*, however, within-species patterns and between-species patterns relating to aggression and task specialization did not generally support the models. Yet *Polistes* cofoundress associations are relatively simple societies, and the crucial assumption of the models, that the dominant has absolute control, seems feasible. Although research on *Polistes* has often involved temperate species, the subtropical population we studied is if anything likely to be more typical of the genus, which has a tropical center of distribution (Reeve 1991).

One potential problem would occur if partitioning of female offspring is different from that of males, which represented nearly 20% of the brood but could not be assigned to foundresses. However, our relatedness data suggested that dominants and subordinates produce similar offspring sex ratios, so that the patterns we report for females probably also apply to males. The only detectable pattern in male production was that larger nests produced more males, perhaps because larger nests can afford to give up more workers.

In addition to reproduction obtained while the dominant is alive, subordinates have a finite chance of eventually inheriting the dominant position themselves. The chance is probably small because subordinates have a much higher mortality rate than dominants. The early-season dominant was missing by the time of nest collection on 42% of nests (see also Peters et al. 1995), and unlike some other *Polistes* species, subordinate mortality does not suddenly increase after worker emergence in *P. bellicosus* (Hughes and Strassmann 1988). The possibility of eventually becoming the primary egg layer increases a subordinate's expected reproductive success and decreases that of the dominant. If the dominant takes this into account, it might contribute to the generally high skew we observed (table 2).

Frequent changes in group composition during the preworker phase (fig. 2; see also Reeve 1991; Nonacs and Reeve 1995; Peters et al. 1995) do create practical problems for testing social contracts models in *Polistes.* To estimate skew accurately, we need to know how many foundresses were present when the eggs were laid. On average, 40% of offspring were from missing foundresses that were probably sisters of collected foundresses. Missing foundresses that lay eggs are not problematic in one sense: with the help of likelihood analysis, we succeeded in dividing their offspring into sibships. However, we still do not know how long these wasps stayed after laying their last eggs. A bigger problem is the unknown number of missing nonreproducers. Since 60% of detected egg layers were missing and only 23% of collected wasps had reproduced, a large number of nonreproducers might also be missing, especially since they are more likely than reproducers to be involved in risky foraging. An average of 0.5 marked foundresses disappeared per nest during the 2-wk precollection monitoring. Only 0.17 wasps joined nests during this period, suggesting that another potential problem, the possibility that collected wasps were not all present throughout brood production, is less serious. In our study, variables such as fighting ability and aggression could be estimated only for collected foundresses. One approach was therefore to estimate skew among collected foundresses only, which also have the merit of being a set of wasps definitely known to have been present simultaneously. This ignores any missing wasps that were present during the production of brood by collected foundresses. On seven of 14 nests, missing foundresses had actually reproduced after the earliest reproduction by a collected foundress (e.g., *nest 6,* fig 3). Our second approach was to look at partitioning of a temporally restricted segment of the youngest brood, including missing reproducers as well as all collected wasps. This estimate of skew will be biased downward if many nonbreeders disappeared during production of this brood. Finally, we looked at partitioning between reproducers alone. This allowed us to compare partitioning of early and late brood and will reflect changes in overall skew if group size does not change too much.

Apart from the difficulties they create for quantifying skew, frequent changes in group composition introduce significant noise and may even prevent a stable skew from arising. Each foundress disappearance and joining event, perhaps sometimes involving the death or usurpation of the dominant, may entail a transition period during which foundresses assess the new conditions and during which reproduction might be less closely controlled. Foundress associations usually form when the initial foundress is joined by others (see, e.g., Strassmann et al. 1987), so that each additional foundress could represent a separate joining event.

Future Directions

In order to evaluate social contracts theory, we need better-developed models of how societies should appear if the theory's assumptions are violated: not all of the theory's predictions are unique to it (table 1; Strassmann 1993). Three of our null predictions (table 1) emphasized direct within-groups competition for oviposition, but only one was supported by the data. There are, however, many possible alternative models. Within-groups competition favors more competitive individuals, but there is a trade-off with group productivity (e.g., Frank 1995). By competing more vigorously, a subordinate can potentially increase her share of the reproduction, but the waste of time and energy involved will reduce group productivity compared with other, more harmonious groups. Conventional settlements are one way to minimize costly within-groups competition and may play a major role in partitioning of reproduction (see also Maynard Smith and Parker 1976; Pollock 1994). Size, presumed to reflect fighting ability (Reeve 1991), did not predict dominance or skew in *P. bellicosus.* Other studies suggest that dominance may be determined by apparently arbitrary cues such as order of arrival at the nest or age (Hughes and Strassmann 1987; Strassmann et al. 1987; Reeve 1991; Queller et al. 1997). Social contracts theory itself can be viewed as a mechanism ensuring harmony within groups, but unless dominants have complete control, conflict may not be completely suppressed. If between-groups selection is of paramount importance, simpler mechanisms involving conventional settlements that maximize group efficiency might explain the high skew and mild and infrequent aggressive interactions we observed in *P. bellicosus.*

The social contracts models have already been used to explain several attributes of animal societies apart from skew itself (e.g., Keller and Reeve 1994), and their increasing influence demands direct and rigorous testing. The current models do not explain the patterns of skew we observed in *P. bellicosus*, but further theoretical work incorporating group sizes larger than two and incomplete control by dominants might give different predictions. There is some evidence that might be consistent with the models in two other *Polistes* species (Reeve and Nonacs 1992; Nonacs and Reeve 1995; but see Strassmann 1993), but it is much less direct because skew itself was not measured. More empirical tests involving direct measurement of skew are urgently required. In addition, as emphasized by Emlen (1997), frequent changes in group composition are likely to be a feature of social groups and are certainly not restricted to *Polistes* (see, e.g., Bourke et al. 1997). Skew indices and tests of the theory that can accommodate or take advantage of this would obviously be helpful.

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APPENDIX A

Table A1: Characteristics of the 24 nests used in the study

Nest	Date found	Total foundresses[a]	Date collected	No. foundresses collected	Brood when collected: No. eggs	Brood when collected: No. larvae	Brood when collected: No. pupae	No. offspring scored[b]	Sperm data available?
5	March 31	7	April 17	4	14	12	3	21	Yes
6	April 1	4	April 22	3	12	16	5	25	Yes
9	April 1	4	April 22	4	15	17	0	20	No
11	April 2	3	April 19	2	4	12	0	9	Yes
14	April 6	2	April 17	2	7	11	0	13	No
15	April 2	4	April 16	3	13	17	2	20	Yes
16	April 4	2	April 19	2	2	16	3	20	Yes
17	April 4	3	April 19	2	5	14	4	21	Yes
18	April 4	4	April 19	3	8	19	5	23	Yes
19	April 4	3	April 21	2	11	10	11	23	Yes
20	April 4	3	April 30	2	6	12	3	14	Yes
21	April 6	5	April 17	5	15	28	8	28	Yes
22	April 6	3	April 23	3	7	12	8	27	Yes
23	April 6	5	April 24	4	15	19	15	26	No
24	April 12	3	April 23	3	6	17	0	22	Yes
26	April 7	3	April 28	2	11	15	11	24	Yes
27	April 10	2	April 27	2	10	8	5	19	No
29	April 13	3	April 24	3	8	19	4	25	No
34	April 10	2	April 24	2	2	13	3	18	Yes
35	April 12	3	April 24	2	5	9	0	12	Yes
36	April 13	4	April 24	3	12	15	1	25	Yes
37	April 16	5	April 23	5	16	24	0	32	Yes
40	April 16	2	April 27	2	3	10	5	14	No
41	April 18	3	April 27	3	8	14	2	19	Yes

[a] Total foundresses is the total number of foundresses associated with the nest during monitoring. All were not necessarily present at one time.

[b] Number offspring scored at three or more microsatellite loci.

APPENDIX B

Table B1: Characteristics of the foundresses collected on each nest and details of reproduction by "missing" foundresses

Nest and wasp[a]	*Wing length (mm)*	*"Early" share of reproduction (% offspring)*[b]	*"Late" share of reproduction (% offspring)*[b]	*No. layable eggs*	*Eggs laid on videos*	*% time on nest*	*Rank 2–dominant aggression*[c]	*Arrivals with prey per hour of video*	*Relatedness to dominant*
5							.50, .27		
102	7.75	. . .	55	3	1	100		0	. . .
101	7.70	11	. . .	1	0	72		.19	.88
100	7.88	. . .	. . .	0	0	66		0	.64
103	7.73	. . .	. . .	1	0	61		.19	.52
A	. . .	89	45						
6							.69, .87		
87	7.10	56	100	2	0	97		0	. . .
88	7.16	. . .	. . .	0	0	73		.18	.83
89	6.89	. . .	. . .	0	0	54		.35	.83
B	. . .	33	. . .	. . .	. . .	. . .		. . .	. . .
C	. . .	11	. . .	. . .	. . .	. . .		. . .	. . .
9							1.0, .0		
114	7.50	. . .	. . .	2	3	94		0	. . .
116	7.30	. . .	. . .	0	0	56		.33	.83
115	7.53	. . .	. . .	0	0	45		.25	.58
117	7.74	. . .	. . .	0	0	49		.25	.58
Z1	. . .	86	56	. . .	. . .	. . .		. . .	. . .
Z2	. . .	. . .	22	. . .	. . .	. . .		. . .	. . .
Z3	. . .	. . .	11	. . .	. . .	. . .		. . .	. . .
Z4	. . .	14	. . .	. . .	. . .	. . .		. . .	. . .
Z5	. . .	. . .	11	. . .	. . .	. . .		. . .	. . .
11							.0, 3.49		
425	7.11	. . .	. . .	1	2	100		0	. . .
424	7.41	. . .	. . .	0	0	11		0	.60
D	. . .	75	60	. . .	. . .	. . .		. . .	. . .
E	. . .	25	. . .	. . .	. . .	. . .		. . .	. . .
F	. . .	. . .	20	. . .	. . .	. . .		. . .	. . .
G	. . .	. . .	20	. . .	. . .	. . .		. . .	. . .
14							N, .0		
164	7.55	. . .	. . .	2	1	81		0	. . .
165	7.51	. . .	. . .	0	0	61		.23	.46
Z6	. . .	100	88	. . .	. . .	. . .		. . .	. . .
Z7	. . .	. . .	12	. . .	. . .	. . .		. . .	. . .
15							1.0, .0		
208	7.54	90	100	3	2	94		0	. . .
209	7.54	. . .	. . .	0	0	70		.81	.58
207	7.78	10	. . .	0	0	48		0	.79
16							.64, 1.58		
185	6.58	. . .	. . .	1	1	91		.22	. . .
184	7.03	. . .	. . .	0	0	59		.5	.91
H	. . .	83	100	. . .	. . .	. . .		. . .	. . .
I	. . .	17	. . .	. . .	. . .	. . .		. . .	. . .
17							1.0, .0		
426	7.77	. . .	90	1	1	87		.27	. . .
427	6.91	20	. . .	0	0	15		0	.66
J	. . .	20	. . .	. . .	. . .	. . .		. . .	. . .
K	. . .	20	. . .	. . .	. . .	. . .		. . .	. . .
L	. . .	20	. . .	. . .	. . .	. . .		. . .	. . .
M	. . .	20	. . .	. . .	. . .	. . .		. . .	. . .
N	. . .	. . .	10	. . .	. . .	. . .		. . .	. . .

Table B1 (*Continued*)

Nest and wasp[a]	*Wing length (mm)*	*"Early" share of reproduction (% offspring)*[b]	*"Late" share of reproduction (% offspring)*[b]	*No. layable eggs*	*Eggs laid on videos*	*% time on nest*	*Rank 2–dominant aggression*[c]	*Arrivals with prey per hour of video*	*Relatedness to dominant*
18							.74, 3.73		
400	7.34	...	67	?	2	84		0	...
401	6.90	...	...	?	0	58		.18	.62
399	6.48	14	8.3	?	0	19		1.35	.87
P	...	...	8.3	...	...	...		...	...
Q	...	...	8.3	...	...	...		...	...
R	...	43	...	...	...	...		...	...
S	...	43	8.3	...	...	...		...	...
19							...		
428	7.46	62.5	100	1	0	98		0	...
429	7.21	...	...	0	0	83		.06	1.0
T	...	25	...	...	...	...		...	...
U	...	12.5	...	...	...	...		...	...
20							.55, 10.50		
431	7.60	50	100	2	0	71		.15	...
430	7.30	50	...	0	0	88		.15	.55
21							1.0, .0		
136	7.33	100	89	2	2	88		0	...
135	7.29	...	...	0	0	98		0	.82
134	7.62	...	...	1	1	98		0	.64
137	7.44	...	...	0	0	55		0	.55
138	7.70	...	...	1	0	76		.19	.46
V	...	...	11	...	...	...		...	...
22							...		
433	7.69	45	100	2	1	98		.17	...
432	7.85	27.3	...	0	0	65		0	.90
153	7.57	...	...	0	0	34		0	.59
W	...	9.3	...	...	...	...		...	...
X	...	9.3	...	...	...	...		...	...
Y	...	9.3	...	...	...	...		...	...
23							.63, 1.87		
150	6.92	...	...	3	3	95		0	...
149	7.16	...	...	0	0	93		.06	.62
151	6.95	...	...	0	0	47		.30	.62
152	7.06	...	...	0	0	82		0	.75
Z8	...	93	83.3	...	...	...		...	...
A1	...	7	...	...	...	...		...	...
B1	...	...	16.7	...	...	...		...	...
24							.56, 1.90		
378	8.05	88	93	1	1	88		.16	...
434	7.47	...	...	0	0	78		.49	.69
435	8.05	...	...	0	0	44		0	.53
C1	...	12	7	...	...	...		...	...
26							.75, .36		
379	7.78	...	...	2	2	100		0	...
380	7.64	...	...	0	0	42		0	.28
D1	...	...	89	...	...	...		...	...
E1	...	100	...	...	...	...		...	...
F1	...	...	11	...	...	...		...	...

Table B1 (*Continued*)

Nest and wasp[a]	*Wing length (mm)*	*"Early" share of reproduction (% offspring)*[b]	*"Late" share of reproduction (% offspring)*[b]	*No. layable eggs*	*Eggs laid on videos*	*% time on nest*	*Rank 2–dominant aggression*[c]	*Arrivals with prey per hour of video*	*Relatedness to dominant*
27							.83, .87		
233	7.50	. . .	. . .	1	0	90		.35	. . .
234	7.23	. . .	. . .	0	0	51		0	.57
Z9	. . .	71	57	. . .	. . .	. . .		. . .	. . .
Z10	. . .	. . .	43	. . .	. . .	. . .		. . .	. . .
Z11	. . .	14.5	. . .	. . .	. . .	. . .		. . .	. . .
Z12	. . .	14.5	. . .	. . .	. . .	. . .		. . .	. . .
29							.91, .23		
258	7.55	. . .	. . .	1	1	84		0	. . .
259	7.44	. . .	. . .	0	0	83		.35	.82
260	7.01	. . .	. . .	0	0	72		0	.82
Z13	. . .	83	100	. . .	. . .	. . .		. . .	. . .
G1	. . .	8.5	. . .	. . .	. . .	. . .		. . .	. . .
H1	. . .	8.5	. . .	. . .	. . .	. . .		. . .	. . .
34							. . .		
382	7.66	11	88	1	1	99		0	. . .
381	7.38	89	12	0	0	71		.54	1.0
35							.92, .45		
383	7.79	. . .	. . .	1	0	89		.18	. . .
384	7.57	. . .	. . .	0	0	88		0	.46
I1	. . .	100	100	. . .	. . .	. . .		. . .	. . .
36							.81, 1.30		
436	8.06	75	100	3	2	87		0	. . .
437	8.06	. . .	. . .	0	0	55		.32	.78
438	8.24	. . .	. . .	0	0	29		0	.72
J1	. . .	25	. . .	. . .	. . .	. . .		. . .	. . .
37							.33, .44		
440	8.20	. . .	20	1	2	85		0	. . .
443	7.37	. . .	. . .	0	0	86		.47	.64
439	7.78	. . .	. . .	3	0	32		0	.68
441	7.98	. . .	. . .	0	0	1		0	.73
442	7.11	. . .	. . .	0	0	42		.16	.47
K1	. . .	22	67	. . .	. . .	. . .		. . .	. . .
L1	. . .	56	. . .	. . .	. . .	. . .		. . .	. . .
M1	. . .	11	6.5	. . .	. . .	. . .		. . .	. . .
N1	. . .	. . .	6.5	. . .	. . .	. . .		. . .	. . .
O1	. . .	11	. . .	. . .	. . .	. . .		. . .	. . .
40							.73, 3.47		
285	7.76	. . .	. . .	3	1	99		0	. . .
286	7.83	. . .	. . .	0	0	60		0	.84
Z14	. . .	100	100	. . .	. . .	. . .		. . .	. . .
41							.52, 2.47		
444	7.83	89	100	2	1	87		0	. . .
445	7.48	11	. . .	0	0	82		0	.76
446	7.86	. . .	. . .	0	0	32		.37	.52

Note: For each nest, the wasps listed first and second were the dominant and rank 2, respectively, when the nests were collected. Ellipses indicate no data available.

[a] Numbers represent foundresses that were collected. Letters A–Y and A1–O1 represent "missing" foundresses (see text) and Z1–Z14 represent foundresses that may or may not have been collected (on nests with no sperm data).

[b] "Early" offspring were pupae or larval instars 4–5 when collected; "late" offspring were eggs or larval instars 1–3.

[c] For each rank-2 wasp, the first figure gives the proportion of interactions between it and the dominant that were initiated by the dominant, and the second gives the rate of initiation of interactions by rank 2 against the dominant per hour when they were both on the nest. "N" indicates that there were no interactions.

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