



Taming of the skew: transactional models fail to predict reproductive partitioning in the paper wasp *Polistes dominulus*

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Female *Polistes* paper wasps can initiate colonies either solitarily or in cooperative groups. Reproduction is often distributed unequally in groups, even to the point of complete monopolization of breeding by the dominant group member. Transactional models of reproductive skew predict the degree of reproductive partitioning, assuming that the dominant controls group membership and will yield a proportion of reproduction to a subordinate as an incentive to stay peacefully in the group. Using a combination of demographic, genetic and morphological data from a population of *P. dominulus*, we test predictions of 'classical' two-person skew models as well as more complex 'N-person' models. This is the most comprehensive study of skew in this species to date, and the results generally do not support transactional models. We found no relationship between skew and relatedness for dyads, and complete skew was observed in unrelated groups despite the prediction for this population that such groups should not occur. In contrast to N-person model predictions, group size tended to increase with relatedness. Although we did find the predicted positive correlation between group size and skew for groups of nonrelatives, this relationship was weak. The zone of conflict between the predicted minimum and maximum staying incentives often spans the entire possible range of reproductive skew, suggesting that a 'tug-of-war' scenario may be more appropriate than a transactional framework for understanding within-colony dynamics. Overall, our results demonstrate that transactional skew models have little predictive power and are therefore unlikely to yield further insight into *Polistes* wasp societies.

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In the colony-founding phase of *Polistes* paper wasp societies, mated females called foundresses have several nesting options. Traditionally, these included the three options of building nests solitarily, joining cooperative nesting groups and usurping the dominant position on an active nest (reviewed in Reeve 1991), which were later expanded to include the option of waiting to adopt an orphaned nest (Nonacs & Reeve 1993; Starks 1998). Before emergence of the first offspring cohort, foundresses perform all colony tasks, including foraging for nest materials and hunting for prey to feed the developing brood. In cooperative nesting groups, some foundresses assume subordinate roles despite being physiologically capable of independent breeding. Solitary and cooperative colony-founding tactics are often maintained within the same *Polistes* population (reviewed in Queller 1996), creating an ideal opportunity for investigation of

ecological and genetic factors influencing cooperative behaviour.

Many studies have investigated possible advantages to cooperative colony foundation. Multiple-foundress colonies are often less likely than solitary-foundress colonies to fail before offspring emergence (reviewed in Reeve 1991; Starks 2001; Seppä et al. 2002; Tibbetts & Reeve 2003; but see Shreeves et al. 2003; Liebert et al. 2005a). Solitary foundresses are also less likely to rebuild their nests after predation (Gibo 1978; Strassmann et al. 1988; Nonacs & Reeve 1995). These advantages most likely can be attributed to the lower probability that two or more foundresses will die in a given period compared to a lone foundress, an effect sometimes called 'survivorship insurance' (Queller 1989; Gadagkar 1990). Multiple-foundress colonies also tend to be more productive than solitary-foundress colonies (e.g. West-Eberhard 1969; Gibo 1978; Nonacs & Reeve 1995; Tibbetts & Reeve 2003). However, because per capita productivity tends to decrease with additional group members (reviewed in Reeve 1991), indirect reproductive benefits via kin selection may be necessary to make cooperation an equal or

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better choice than independent reproduction. Cooperation among nonrelatives when solitary nesting appears to be an option is therefore more difficult to explain (Liebert et al. 2005a; Queller et al. 2000).

Reproductive Skew Theory

Reproductive skew models have been developed as a unifying theory to explain the partitioning of reproduction within cooperatively breeding groups (review of models in Johnstone 2000). The level of skew indicates the degree of monopolization of reproduction, with lower skew values indicating a more equitable distribution. There are two major types of skew models, known as 'transactional' and 'compromise' models. Transactional models assume that the dominant group member controls access to group membership, and the level of skew is determined by the amount of sharing required for group stability. In the 'classical' skew model (Emlen 1982; Vehrencamp 1983a, b; Reeve 1991), expanded upon by Reeve & Ratnieks (1993), skew is predicted to vary according to three parameters: x , the expected reproductive success a potential subordinate would have as a solitary breeder relative to a dominant on its own; k , the productivity of a group compared to a solitary individual; and r , the symmetrical genetic relatedness between the dominant and subordinate. The relationship between these parameters and skew differs depending on the model used.

Transactional models can be further divided into 'concessions' and 'restraint' models, which differ according to whether the dominant controls access to reproduction. The concessions model assumes that the dominant allocates the minimum possible share of reproduction (p_{\min}) required by a subordinate as incentive to stay peacefully in the group. This minimum staying incentive can be calculated for a two-person group as:

$$p_{\min} = (x - r(k - 1)) / (k(1 - r)) \quad (1)$$

In contrast, the restraint model assumes that the subordinate takes the maximum reproduction possible (p_{\max}) before being evicted by the dominant. This is shown by:

$$p_{\max} = ((k - 1) - rx) / (k(1 - r)) \quad (2)$$

The difference in the basic assumption of who has control means that predictions of the two models are exactly opposite (Table 1). Dominant *Polistes* wasps appear to physically dominate subordinates, and they also rarely leave the nest and thus can remove eggs while subordinates are foraging. Therefore, the concessions model has generally

Table 1. Basic two-person model: predicted effect of three variables on reproductive skew for different versions of the model (modified from Reeve & Keller 2001). High levels of skew indicate less equitable sharing of reproduction

Variable	Concessions	Tug-of-war	Restraint
x	Negative	None	Positive
k	Positive	None	Negative
r	Positive	None or negative	Negative

been treated as the most appropriate model for this genus (Reeve & Keller 2001).

In contrast to transactional models, compromise models do not address group stability. Instead, compromise models predict that the level of reproductive skew is determined by conflict between group members that each attempt to take their own optimum level of reproduction. Shared reproduction does not result from any 'social contract' among group members, but rather results because neither dominants nor subordinates can successfully monopolize reproduction. A commonly discussed compromise model is known as a 'tug-of-war' (Reeve et al. 1998a), in which group members fight for the largest share of reproduction possible balanced by the costs to productivity of fighting for additional benefits. The tug-of-war scenario can be thought of as a special case within transactional models (Johnstone 2000; Reeve 2000), where skew is determined within the 'window of selfishness' between the minimum reproduction required by the subordinate (p_{\min}) and the maximum that the dominant will allow (p_{\max}). In this case, skew is unaffected by the parameters k and x , and is either unaffected or decreases with increasing r .

Early skew models addressed the simplest scenario of solitary breeding versus cooperation between two individuals. More recently, models for multimember groups have been developed (Johnstone et al. 1999; Reeve 2000; Reeve & Emlen 2000). Predictions of these models become more complex when considering group sizes larger than two, but as Reeve & Emlen (2000) pointed out, some predictions can be contrasted directly with nonincentive-based models of group formation (e.g. Giraldeau & Caraco 1993; Higashi & Yamamura 1993; Table 2). The N -person model (Reeve & Emlen 2000) addresses group size effects on skew, in particular how skew is expected to vary according to whether groups are 'saturated' with subordinates. Reeve & Emlen define saturated groups as those that have reached their maximal stable size, which occurs when the addition of new subordinates is no longer favoured over solitary breeding, from the perspective of either the dominant or potential subordinate.

Despite the extensive theoretical development of skew theory, relatively few empirical studies have been conducted to test assumptions or predictions of the models (Johnstone 2000). *Polistes* wasps have been one of the most frequent systems used for such studies (Table 3), which is not surprising given the involvement of *Polistes* researchers in the development of transactional skew theory. Only one study to date has demonstrated clear support for multiple predictions of transactional skew models (*P. fuscatus*; Reeve et al. 2000; Table 3). Other studies that have claimed to support or refute the models have been later reinterpreted with opposite conclusions (Table 3). For example, Reeve & Nonacs (1992) interpreted their findings of increased aggression by *P. fuscatus* subordinates after experimental egg removal to be evidence for punishment of cheating, and thus evidence for the 'social contract' described by transactional skew models. However, the results were later reinterpreted by Nonacs et al. (2004) as an artefact of increased activity levels on the nest. In another case, Field et al. (1998) found no evidence for the predicted relationships between skew and

Table 2. Predicted and observed relationships between group size, relatedness and skew for incentive-based and nonincentive-based models, assuming that existing group members control group entry

Incentive-based*	Nonincentive-based†
Relationship between increasing group size and relatedness Negative/neutral Expect lower saturated group sizes with high r , but no relationship near saturation size.	Positive Group members are less likely to tolerate unrelated joiners (if joiners have 'free entry', this effect is reversed).
Relationship between group size and skew (lower value=more equitable) High r Negative (If solitary breeding success is low and groups are unsaturated.)	$r=0$ Positive (If solitary breeding success is greater than zero and groups are unsaturated.) No specific predictions made.

*Reeve (2000); Reeve & Emlen (2000).

†Giraldeau & Caraco (1993); Higashi & Yamamura (1993).

relatedness or group size in *P. bellicosus*, but Reeve (2000) suggested that these results actually did support N -person transactional models if the groups had been saturated with subordinates. Two *P. dominulus* studies have directly tested predictions of transactional skew models; one study in the introduced range found support for predictions regarding foundress aggression compared to resource sharing and seasonal timing (Tibbetts & Reeve 2000), and one study in the native range (Queller et al. 2000) did not support the models because unrelated subordinates were observed to aid dominants on nests without shared reproduction (Table 3). Reeve (2000) and Reeve & Emlen (2000) reinterpreted Queller et al.'s results as supportive of the transactional framework, however, asserting that the presence of unrelated groups is, by itself, supportive of incentive-based models.

We do not accept this assertion by Reeve & Emlen (2000). Their reasoning is that, according to the model by Higashi & Yamamura (1993), the required condition for the formation of groups of nonrelatives can never be met. This is because the fitness of a solitary group member, $w(1)$ in equation (1) of Higashi & Yamamura (1993), is equal to infinity when relatedness is zero; therefore, allowing an unrelated individual to join the group could not possibly increase the per capita fitness of existing group members and such groups should never form. However, equation (1) considers only the fitness differential of existing group members, or 'insiders'. The equation representing the 'outsider' fitness perspective sets no such limit on joining nonrelatives. Higashi & Yamamura (1993) make the point that, due to the conflict of interest created by these different perspectives, the observed group size may be a 'compromise' between the optimal insider and outsider group sizes. Thus, the formation of groups of nonrelatives is possible without a transactional framework. Given the added possibility of recognition errors in assessing relatedness (Reeve 1989; Liebert & Starks 2004), we cannot consider the existence of unrelated groups as implicit support for transactional models.

This study is the first to integrate genetic and morphological data in the testing of transactional skew model predictions for an introduced population of *P. dominulus*.

Polistes dominulus is native to Mediterranean and central Europe, but its range has expanded widely over the last few decades. After being introduced to North America in the late 1970s (Eickwort 1978; Hathaway 1981), it has spread throughout the northeastern U.S. and is rapidly becoming established in central and western states (Cervo et al. 2000). Research on the social dynamics of *P. dominulus* colonies has a long history, including the first description of the linear dominance hierarchy within foundress groups (Pardi 1948a). Studies of *P. dominulus* have continued to investigate reproduction in nest-founding groups in the native range (e.g. Queller et al. 2000; Shreeves et al. 2003), as well as in the introduced North American range (e.g. Nonacs & Reeve 1993; Starks 1998, 2001; Tibbetts & Reeve 2003). Johnson & Starks (2004) showed that population genetic diversity of introduced *P. dominulus* in the northeastern U.S. is comparable to diversity in the native range, and therefore studies of these populations are not confounded by genetic bottleneck effects often associated with introduced species.

In this paper we address four goals. First, we examine whether the degree of ovarian development accurately predicts reproductive dominance within multiple foundress *P. dominulus* colonies. Second, we use the transactional framework to calculate predicted staying incentives for two-foundress colonies of varying relatedness, and compare these to observed values of reproductive skew. Third, we examine the following assumptions of N -person transactional skew models as described by Reeve (2000) and Reeve & Emlen (2000).

(1) Productivity is a concave function of group size.

(2) Populations containing nests that vary in group size should also show variation in relatedness, skew and productivity.

Finally, where assumptions are supported, we test general predictions of incentive-based models versus compromise or nonincentive models regarding the relationships between group size, relatedness and reproductive skew. These predictions include the following.

(3) Saturated group size should be smaller when relatedness is high. Nonincentive-based models assuming 'group-controlled entry' predict the opposite.

Table 3. Review of *Polistes* studies that have tested predictions of skew models

Study	Species (location*)	Methods†	Predictions tested	Test of N-person model?	Conclusions: overall support for concessions model?
Reeve & Nonacs 1992, 1997; (but see Nonacs et al. 2004)	<i>P. fuscatus</i> (Massachusetts, U.S.A.)	B	Aggression as skew-determining mechanism; presence of 'social contract'	No	Yes; subordinates become more aggressive than dominants after egg removal
Field et al. 1998	<i>P. bellicosus</i> (Texas, U.S.A.)	B,G,D,M	Relationships between skew and seasonal timing, relatedness, aggression and group size	No	No; but interpreted by Reeve & Emlen (2000) and Reeve & Keller (2001) as 'Yes' due to the possibility of saturated groups
Tibbetts & Reeve 2000	<i>P. dominulus</i> (introduced: New York, U.S.A.)	B,D	Aggression vs seasonal timing, prey sharing and temperature	No	Yes; but reinterpreted by Nonacs et al. (2004) with alternative hypothesis of altered activity patterns
Queller et al. 2000	<i>P. dominulus</i> (central Italy)	B,D,G	Relationship between skew and relatedness	No	No; unexpected high skew in unrelated foundress groups. Reinterpreted by Reeve (2000) as 'Yes' due to unrelated groups
Reeve et al. 2000	<i>P. fuscatus</i> (New York, U.S.A.)	B,D,G,M	Relationships between skew and seasonal timing, relatedness and productivity	No	Yes; trends expected by concessions model found in all cases
Seppä et al. 2002	<i>P. carolina</i> (Texas, U.S.A.)	B,D,G,M	Relationships between skew and relatedness, ecological constraints, foundress size differences and productivity	Yes	No; none of the patterns expected under transactional models were supported except increased skew over time
Nonacs et al. 2004	<i>P. fuscatus</i> (New York, U.S.A.)	B,G,M	Reanalysed Reeve & Nonacs (1992, 1997) and used new data to test idea of aggression as skew-determining mechanism	No	No; aggression relates to activity patterns; 'aggressive' behaviours are unlikely to set skew in paper wasps as assumed in Reeve & Nonacs (1992, 1997)
Liebert et al. 2005a	<i>P. aurifer</i> (southern California, U.S.A.)	B,D,G	Relationships between skew and seasonal timing, relatedness	No	No; but no cooperative groups expected at all
Current study	<i>P. dominulus</i> (introduced: Massachusetts, U.S.A.)	D,G,M	Relationships between skew and relatedness, group size; relationship between group size and relatedness	Yes	No; although weak support for one prediction of N-person model, majority of evidence is inconsistent with transactional models

*All species are native to the region of study except where noted as introduced populations.

†Key to symbols: B = behavioural, D = demographic, G = genetic, M = morphological (size, weight measurements, reproductive tract dissections).

(4) If relatedness is zero and solitary breeding success is greater than zero, staying incentives always decrease (skew increases) with increased group size. Combined, these results will provide the most comprehensive examination to date of the relevance of transactional skew models for *P. dominulus*.

METHODS

Nest Collection and Wasp Measurement

In late June 2003, we collected 30 colonies from buildings at Great Brook Farm State Park in Carlisle, Massachusetts, U.S.A. (42°31'45"N, 071°21'00"W). Twelve of these were solitary and 18 were multiple-foundress colonies, and all were near the end of the founding phase (before offspring emergence). Nests were collected in the early morning hours, when all wasps were likely to be present.

We brought the nests and adult wasps back to the International Social Insect Research Facility (I.S.I.R.F.) laboratory at Tufts University, where we mapped the contents of all nest cells before removing the brood into individually marked tubes. The adult wasps and brood were then stored in a freezer at -80°C until dissection and/or genetic analysis.

Reproductive Tract Dissections

We dissected the reproductive tracts of each collected female using methods from Chandrashekara & Gadagkar (1991). Briefly, we dissected the abdomen under a dissection microscope so that the ovarioles were clearly visible. We measured four parameters for each of the six ovarioles: (1) number of oocytes, (2) number of mature oocytes, (3) the length and (4) width of the proximal oocyte. Based on

these data, we calculated six input variables (total number of oocytes, total number of mature oocytes, length and width of the largest proximal oocyte, mean length and width of proximal oocyte), which were then used in principal component analysis (PCA). The resulting first principal component was used as an 'ovarian index' to quantify the ovarian development of each wasp. In addition, we checked the spermatheca for the presence of sperm and we noted the presence of yellow bodies as an indicator of previously laid eggs. These data allowed us to confirm that females with low ovarian development were mated, nonreproducing subordinate foundresses rather than early female offspring. Males were not present in the population at this time, so we could rule out the possibility that mated females were recently emerged early female offspring that had mated with early males. We also compared the relative ovarian development among cofoundresses to the observed skew in offspring production as determined by microsatellite genotyping. Differences between these two methods of measuring reproductive dominance may uncover situations where the hierarchy is unstable; subordinate foundresses with developed ovaries but no genetically assigned offspring in the nest may signify an attempt to compete for a greater share of the reproduction than the observed level of skew would imply.

Genetic Techniques

All genetic analysis was conducted in the I.S.I.R.F. genetics laboratory at Tufts University as described in Johnson & Starks (2004) and Liebert et al. (2004, 2005b). We extracted genomic DNA from head capsules of larval instars, stages two through five, and from one to two legs of pupae and adult wasps. We collected nests near the end of the founding or preworker phase, so the late-stage larvae and pupae would have developed primarily into worker females, and the younger larvae would potentially develop into either workers or early gynes. Skew model predictions are relevant only for offspring that have some chance of reproduction. Early female offspring of *P. dominulus* are known to include nonworking individuals and workers that can pursue direct reproduction by superseding foundresses (Gervet et al. 1986, referred to as *P. gallicus*; Mead et al. 1990; Pardi 1948b cited in Queller et al. 2000) or by leaving the nest soon after emergence and initiating a nest in the same year or the following year (Mead et al. 1995). Thus, skew model predictions should still have relevance even with workers included in the sampled brood. In addition, previous *Polistes* studies have found consistently high skew in production of late-season brood in temperate climates (Reeve et al. 2000; Queller et al. 2000), leaving the earlier-produced offspring as the only possible outlet for the testing of skew model predictions (Reeve et al. 1998b, 2000).

We extracted DNA from all 51 foundresses from 17 multiple-foundress nests, and 367 brood from these nests ($\bar{X} \pm SD : 23 \pm 8.1$ brood per nest). The sample of brood represented $87 \pm 11.5\%$ of the total numbers of larval instars two through five and pupae in the nest. After grinding frozen tissue using sterile minipestles (Strassmann

et al. 1996), we incubated the samples in 250 μ l of a 5% Chelex solution (Crozier et al. 1999, modified slightly from Walsh et al. 1991). We genotyped each sample at six to eight microsatellite loci using primers developed for this species (Henshaw 2000) and dye-labelled with IRD800. Alleles were visualized on 6.5% denaturing polyacrylamide gels using a LI-COR single channel 4200 NEN Global Edition IR² DNA Analyzer and scored with SAGA^{GT} 2.1 software.

Measuring Reproductive Skew

Measurement of reproductive skew requires accurate maternity assignment of the offspring within colonies. To accomplish this, we first manually grouped offspring into sibling groups according to the expected inheritance pattern for haplodiploids, where full sisters share only three possible alleles: one paternal allele from the haploid father and one of two maternal alleles from the diploid mother (*P. dominulus* females are known to be singly mated; Queller et al. 2000; Strassmann 2001). We then checked for alternatives to these sibling groups with the program KinGroup (Konovalov et al. 2004), which uses two separate algorithms to partition individuals into sibling groups according to the relative likelihood of a specified primary versus null hypothesis. We also used the program Relatedness 5.0.8 to calculate relatedness values among foundress and offspring groups (Goodnight & Queller 1999, based on calculations in Queller & Goodnight 1989). Nests were weighted equally to avoid bias caused by the inclusion of siblings in calculating population allele frequencies, and standard errors were calculated by jackknifing over loci.

To quantify the division of reproduction within two-foundress groups, we calculated the proportion of offspring produced by each foundress and noted where reproduction was monopolized versus shared between foundresses. As an overall measure of reproductive skew for colonies with two or more foundresses, we used the *B* (binomial) skew index, which indicates whether the variance in reproduction within a group differs significantly from the variance expected if all group members have equal probability of reproducing (Nonacs 2003a). The index can range from -1 to 2 , with zero representing a random distribution and higher values indicating a more skewed distribution than expected. *B* index values and significance tests were calculated using Skew Calculator 2003 (Nonacs 2003b; <http://www.obee.ucla.edu/Faculty/Nonacs/>).

All the remaining statistical analysis was performed with the program DataDesk, v.6 (Data Descriptions, Inc., <http://www.datadesk.com>). Where sample sizes were small and/or data could not be transformed to meet assumptions of normality, we used nonparametric Spearman rank correlations to examine the relationships among variables. Exact *P* values were calculated for rank correlations using the program R, v.2.0.1 (R Development Core team, <http://www.r-project.org/>). All tests are two tailed and means are reported with standard errors unless stated otherwise.

RESULTS

Measuring Skew: Ovarian Development versus Offspring Production

On most nests, the differences in ovarian development among cofoundresses closely followed the division of offspring production as determined by microsatellite genotyping. A simple linear regression of ovarian index versus the proportion of colony offspring produced by a given foundress was highly significant ($r^2 = 0.57$, $F_{1,41} = 54.8$, $P \leq 0.0001$). However, exceptions did occur where more than one foundress had developed ovaries, but offspring genotypes matched only one foundress. Genotype data also revealed 'missing' foundresses that contributed to reproduction on four of 18 nests (i.e. no collected foundress had a genotype that was consistent with having produced these offspring). We therefore used the genotype data for further analysis of reproductive skew and consulted the ovarian development data as supplementary information.

Calculation of Staying Incentives for Dyads

Using the transactional framework provided by Reeve & Ratnieks (1993) and Reeve (2000), we calculated predicted minimum and maximum staying incentives (p_{\min} and p_{\max}) using equations (1) and (2), respectively. The values of x , k and r used were as follows. First, we assumed that $x = 1$, which is likely to be true for the early part of the season when starting a new nest is still possible and thus the success of a subordinate that chose to breed independently would not differ from a lone dominant. We then determined the value of k as the productivity of a dyad relative to a solitary foundress, weighted by the nest survival probability of each group size. Productivity was measured both as the average number of nest cells and the average number of pupae per nest. Finally, we used three different values for r , representing the three main relationship categories that *Polistes* wasps are likely to encounter: full sisters ($r = 0.75$), cousins ($r = 0.19$) and nonrelatives ($r = 0$). We considered groups to be 'dyads' if two foundresses were present at the time of collection. Because offspring genotypes indicated that missing foundresses contributed to offspring production on three of the 10 nests that fit this definition, we also repeated the analyses excluding these three nests. None of the results were affected, and therefore we present data for all 10 nests.

In our population, the productivity for dyads in terms of the number of nest cells was 51.5 compared to 33.1 for solitary foundresses (in terms of pupae, the difference was 7.3 for dyads versus 2.8 for solitary foundresses). Survival probabilities were calculated as the average survival to offspring emergence of solitary and two-foundress nests across six previous data sets from introduced *P. dominulus* populations: Nonacs & Reeve 1995; P. T. Starks, unpublished data from 1996, 1997; Tibbetts & Reeve 2003, two populations. These values were 76.5% for dyads and 38.7% for solitary foundresses. Using the number of nest cells for productivity, we have $k = (51.5 \times 0.765) / (33.1 \times 0.387)$, or $k = 3.07$, so $p_{\min} = 0.326$ for nonrelatives,

0.245 for cousins and 0.000 for full sisters (incentives are bounded by 0 and 1). Thus, at constant x , sisters are predicted to cooperate even under complete skew, but cousins and unrelated subordinates are not expected to cooperate without some direct reproduction. These results are essentially the same if the number of pupae is used to calculate k , except the minimum staying incentives required by cousins and nonrelatives are slightly lower: $p_{\min} = 0.190$ for nonrelatives, 0.048 for cousins and 0.000 for full sisters.

Using the same values for r , x and k , the maximum incentive that the dominant foundress should allow is given by equation (2). The values of p_{\max} using the number of nest cells as the measure of productivity are 0.674 for nonrelatives, 0.755 for cousins and 1.0 for full sisters. For pupae, $p_{\max} = 0.810$ for nonrelatives, 0.952 for cousins and 1.0 for sisters. The window of conflict between the minimum and maximum staying incentives thus covers the entire range of skew for sisters. For cousins, the window is slightly narrower and does not include complete skew. Nonrelatives have the narrowest window, with the smallest staying incentive acceptable to the subordinate equaling 19% of the offspring.

How do the predicted values compare to our observed results? We found no relationship between reproductive skew and cofoundress relatedness on 10 two-foundress nests (Fig. 1). Skew was generally very high, with one foundress monopolizing reproduction on seven of 10 nests. The foundress groups on these seven nests spanned a wide range of relatedness values, including both nonrelatives and putative sister groups (Fig. 1).

Testing Assumptions of Incentive-based N-person Models

Assumption 1: productivity is a concave function of group size

Observed foundress group sizes ranged from one to six, averaging 2.89 ± 0.301 foundresses per nest. If we include

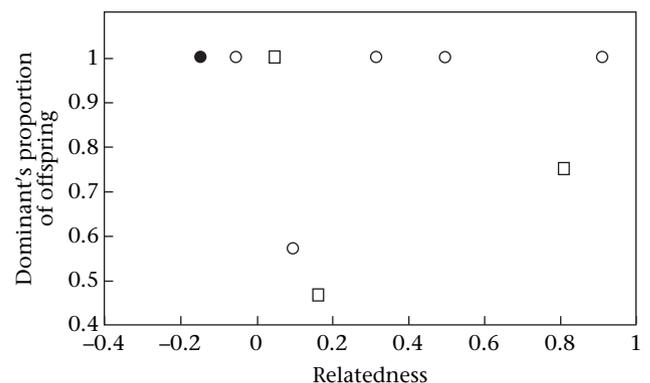


Figure 1. Relationship between cofoundress relatedness and the proportion of offspring produced by the dominant breeder. ○: nests in which offspring genetic data indicated no missing foundresses; ●: two overlapping data points; □: nests in which offspring genetic data indicated missing foundresses, which explains why one of these data points shows the dominant proportion of offspring as less than 50%.

missing foundresses identified by the genetic data, the mean group size was only slightly higher (3.17 ± 0.305). Unlike the concave function assumed by [Reeve & Emlen \(2000\)](#), overall group productivity (number of nest cells) increased linearly with foundress group size (Spearman rank correlation: $r_s = 0.836$, $N = 30$, $P < 0.000001$; [Fig. 2a](#)). This relationship remains significant if the number of pupae is used as the measure of productivity instead of the number of nest cells. However, per capita productivity decreased significantly with foundress group size ($r_s = -0.558$, $N = 30$, $P = 0.002$; [Fig. 2b](#)). These relationships are unaffected if missing foundresses are included in the group size. Hence, a second foundress augmented nest size by less than the productivity of a solitary foundress, and the contributions of additional foundresses were even smaller. The linearity of the productivity function appears to violate the assumption of the N -person transactional skew model. However, it is possible that the data are incomplete and the groups that we measured were unsaturated with subordinates ([Reeve & Emlen 2000](#)).

Assumption 2: populations containing nests that vary in group size should also vary in relatedness, skew and productivity

The 18 multiple-foundress nests varied considerably in relatedness and level of reproductive skew. Average relatedness among cofoundresses ranged from -0.148 to 0.912 ($\bar{X} \pm SD : 0.354 \pm 0.337$). We incorporated missing foundresses in these calculations wherever it was possible

to reconstruct their genotypes at three or more loci. We were able to successfully assign maternity of the genotyped offspring on 17 of 18 nests. (The 18th nest contained six putative sister foundresses whose genotypes were too similar to accurately determine maternity.) Offspring production was monopolized by one foundress on 10 of 17 nests, and some degree of sharing occurred on the remaining seven nests. Missing foundresses contributed offspring to three of these nests with shared reproduction. Calculation of the B index (including both collected and missing foundresses) showed significant positive reproductive skew on all but two nests, with values ranging from -0.0136 to 0.6761 . This means that 15 of 17 nests showed greater variance in reproduction than expected by chance if all group members had equal probability of breeding.

These results lend further support to our suggestion that groups in this population may be unsaturated according to [Reeve & Emlen \(2000\)](#). In their model, the existence of symmetrically related groups with complete skew is an indicator that groups are not saturated with subordinates. Our data contain many nests with complete skew between two or three group members. The variation in group size, relatedness and reproductive skew in this population enabled us to further examine predictions for unsaturated groups for incentive-based versus nonincentive-based models.

Testing Incentive-based Skew Model Predictions for Unsaturated Groups

Group size, relatedness and reproductive skew

Incentive-based models predict a negative relationship between saturated group size and relatedness, which occurs because closer relatives are less likely to accept a closely related joiner as group sizes increase. Non-incentive-based models assuming 'group-controlled entry' ([Giraldeau & Caraco 1993](#); [Higashi & Yamamura 1993](#)) predict the opposite; because existing group members are more likely to accept relatives as joiners, larger groups tend to be more closely related. Our data show a positive correlation between group size and relatedness, although this tendency was not statistically significant (Spearman rank correlation: $r_s = 0.424$, $N = 18$, $P = 0.080$). Reanalysis using group sizes that incorporated missing foundresses gave a similar result ($r_s = 0.412$, $N = 18$, $P = 0.090$).

For unsaturated groups, the model of [Reeve & Emlen \(2000\)](#) predicts that skew should increase with group size for nonrelatives, as long as the expected success of a solitary breeder is greater than zero. No relationship is expected for closely related groups. In our study population, skew was unrelated to group size for close relatives ($r > 0.4$; Spearman rank correlation: $r_s = -0.112$, $N = 7$, $P = 0.840$). When missing foundresses were included in the group size, this correlation became more negative but remained nonsignificant ($r_s = -0.472$, $N = 7$, $P = 0.302$). In contrast, skew in groups with low relatedness ($r < 0.4$) did increase significantly with group size ($r_s = 0.710$, $N = 10$, $P = 0.026$; [Fig. 3](#)). This relationship is driven strongly by one point, however, and therefore

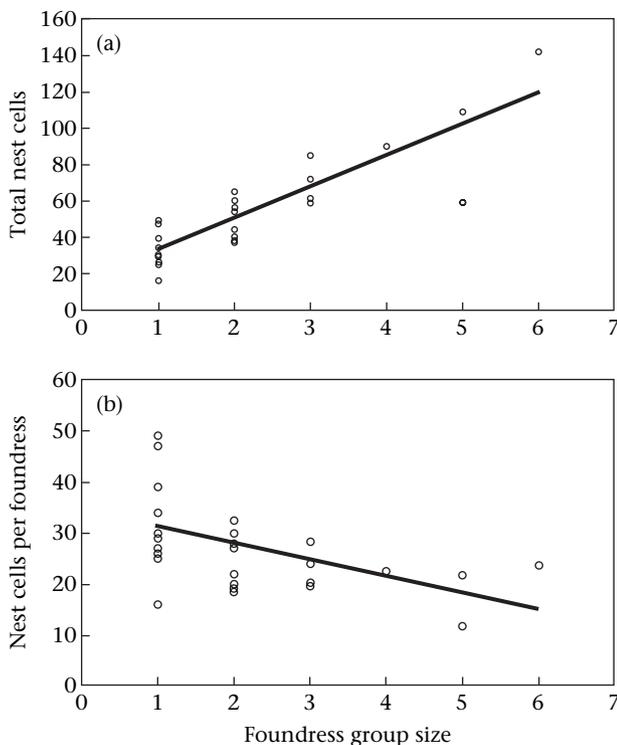


Figure 2. Colony productivity, measured by nest size, as a function of foundress group size: (a) overall productivity and (b) per capita productivity.

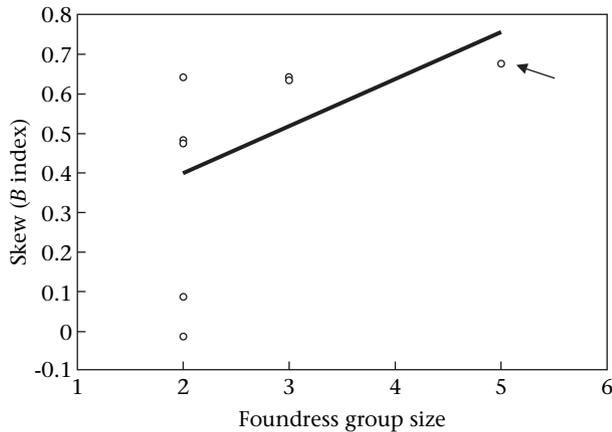


Figure 3. Skew, measured with the B index, as a function of foundress group size for groups of low relatedness ($r < 0.4$). The arrow indicates the one nest that had a disproportionately large influence on the positive correlation.

should be interpreted cautiously (Fig. 3). Reanalysis excluding this point resulted in a nonsignificant relationship ($r_s = 0.572$, $N = 9$, $P = 0.108$). The positive correlation for low relatedness groups was also weakened when missing foundresses were included in the group size ($r_s = 0.533$, $N = 10$, $P = 0.113$).

DISCUSSION

Most of our results do not support transactional skew models. For the simplest scenario of two group members, the concessions model predicts a positive relationship between skew and relatedness, whereas the restraint model predicts a negative relationship. We found no relationship between these two variables for 10 two-foundress nests, seven of which had complete skew. The minimum staying incentives predicted by transactional models for dyads are consistent with the observed skew for sister groups, because sisters are predicted to cooperate even with no staying incentives. However, complete skew is not expected for cousins or nonrelatives under a transactional framework, given the value of k in this population. The finding of full skew in groups of low relatedness is in direct opposition to predictions of transactional skew models, and thus the lack of support for predictions of transactional skew models is unlikely to be a problem of low power.

We did find population variation in skew, productivity and relatedness expected by the N -person transactional model, but the observed linear relationship between group size and productivity may violate the N -person model's assumption of a concave function. Alternatively, if groups in the study population were unsaturated, we may not have enough data at higher group sizes to observe the decelerating part of the curve. This possibility is strengthened by the finding that small group sizes showed complete skew. Assuming that groups were indeed unsaturated, the only result of this study that provides support for transactional models is the positive relationship between skew and group size for nonrelatives, as

predicted by the N -person model for unsaturated groups. However, as previously mentioned, the significance of this correlation was highly dependent on one nest. We also observed a weakly positive trend between group size and relatedness, which is opposite to the predictions of the incentive-based model and consistent with the compromise model. Overall, the results of this study do not support the transactional framework.

Compromise Models and the Window of Conflict

For many nest-founding groups in this population, the 'window of selfishness' between p_{\min} and p_{\max} spans the entire possible range of reproductive skew. Under these conditions, it would not be surprising that the dominant does not always maintain complete control of reproduction. This idea is further supported by the lack of relationship between skew and relatedness in two-foundress groups, the apparent instability of group composition as demonstrated by missing foundresses, and the finding that variation in ovarian development within foundress groups does not always mirror the observed reproductive skew. Given that previous *Polistes* studies have also found genetic and behavioural evidence of frequent changes to foundress group composition (Field et al. 1998; Seppä et al. 2002; Liebert et al. 2005a), the inconsistency in the results of studies testing skew model predictions is unsurprising (Table 3).

The typical situation for foundress groups facing inconsistent dominant control could be described as a 'pure' tug-of-war model, or as a transactional model within which an 'incomplete control zone' or a 'window of conflict' between p_{\min} and p_{\max} is embedded (Johnstone 2000; Reeve 2000). A recent manipulative study of allodapine bees also found results consistent with tug-of-war as opposed to incentive-based models (Langer et al. 2004). However, because the tug-of-war model predicts no relationship between skew and r , x or k (Table 1), it is easier to refute incentive-based model predictions than to provide positive 'support' for the tug-of-war model (Seppä et al. 2002). Further attempts to distinguish among these models therefore seem unlikely to provide much insight. Rather, the most promising area of future research into within-colony dynamics may involve the proximate mechanisms mediating conflict and cooperation within foundress groups. Several papers have re-examined aspects of 'aggression' in *Polistes* societies (temperature thresholds: Tibbetts & Reeve 2000; artefacts of activity rate in measuring rates of aggression: Nonacs et al. 2004; potential activity-regulating function of 'darts': Sumana & Starks 2004). The integration of such studies with work on visual recognition (Tibbetts 2002, 2004; Tibbetts & Dale 2004), chemical signatures of behavioural and reproductive dominance (Sledge et al. 2001; Dappporto et al. 2004b) and subfertility of some foundresses (Liebert et al. 2004, 2005b) may provide more insight into the variation in cooperative behaviour of this model genus than will continued attempts to test predictions of transactional skew models within populations.

Natural Variation and the Future of Skew Models

The finding of unrelated dyads with complete skew is inconsistent with transactional models, given the value of k for this population. Similar results showing unexpected cooperation between nonrelatives have been found in other populations of *Polistes* (Queller et al. 2000; Liebert et al. 2005a). Queller et al. (2000) suggested that unrelated subordinates might gain by eventual inheritance of the dominant position, yet this was shown to be an inadequate benefit to explain such cooperation in other populations (Liebert et al. 2005b). Thus, it remains unclear why unrelated subordinates cooperate under such conditions.

Nonacs et al. (in press) suggest the possibility that foundresses may make recognition errors during colony founding, resulting in suboptimal cooperation among nonrelatives. Such errors would be expected if foundresses use a context-dependent acceptance threshold model of recognition (Reeve 1989; Liebert & Starks 2004). Indeed, Starks et al. (1998) found evidence that this model does work in *P. dominulus*. Foundresses may use locational cues such as the natal nest site, using a relatively tolerant acceptance threshold in the vicinity of the natal nest. This rule would generally function well because wasps tend to be philopatric, returning to the natal nest site after overwintering (Klahn 1979; Strassmann 1983; Starks 2003), but when nests are densely clustered or more than one foundress contributes to offspring production, less related wasps will call the same site 'home'. Foundresses could also assess the degree of relatedness directly, using the chemical signature produced by cuticular hydrocarbons known to be involved in *Polistes* nestmate recognition (reviewed by Gamboa 1996, 2004). The particular compounds involved in recognition (Dani et al. 2001; Lorenzi et al. 2004) and the role of these chemicals in recognition have been studied intensively in *P. dominulus* and have been found to be informative enough to distinguish among related versus unrelated nestmates (Dani et al. 2004). If foundresses assess relatedness based on similarity between their own chemical signature and that of a potential cofounder, errors could also occur if cuticular hydrocarbons become homogenized in mixed overwintering groups (Dapporto et al. 2004a) and if the original nest were destroyed over the winter and therefore became unavailable as a source for reacquiring the original signature (Sumana et al. 2005).

The likelihood of such recognition errors could be incorporated into new skew models that might more accurately predict variation in reproductive skew. But what would be the value of such models? The original purpose of skew models as a unifying theory for predicting observed differences in the division of reproduction would seemingly be lost in the attempt to fit observed patterns. Without specific, falsifiable predictions, such models would not be particularly valuable.

An alternative to the testing of skew models at the colony level is to examine larger-scale patterns. If populations generally experience the same ecological conditions, it may make more sense to test these models at

higher levels of organization where ecological conditions differ. Reeve & Emlen (2000) point out that the relationship between reproductive skew and relatedness is expected to be weaker than that of skew and ecological constraints. Future testing of these models might therefore be more fruitful as population- or species-level comparisons. However, the trouble with this suggestion lies in the exact problem demonstrated by this study: the immense variation within *Polistes* populations. An 'average' value for skew or group size for this study population would not be informative for comparison with other populations because of the wide range of observed values.

Including the present study, 10 publications have tested at least one prediction of reproductive skew models in *Polistes* wasps (Table 3). Only one of these (Reeve et al. 2000) has strongly supported transactional models. Other studies whose authors interpreted their results as failing to support transactional models were later reinterpreted with the opposite conclusion, in one case because of the existence of unrelated groups per se, and in another case because the saturation of colony groups was not considered. Here we have shown that the former argument does not hold, and we have directly addressed predictions of N -person models in addition to the simpler predictions for dyads. Our results show a lack of support for even these simple predictions and confirm the results of earlier studies that found subordinates submitting to unrelated dominants on nests without shared reproduction (Queller et al. 2000, Liebert et al. 2005a). Even if the data are consistent with one complex prediction from the N -person model, such results mean little without support for the most basic predictions about group formation. Given the general lack of support, we conclude that transactional skew models are unlikely to provide further insight into the social behaviour of *Polistes* wasps.

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