

Transactional Skew and Assured Fitness Return Models Fail to Predict Patterns of Cooperation in Wasps

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ABSTRACT: Cooperative breeders often exhibit reproductive skew, where dominant individuals reproduce more than subordinates. Two approaches derived from Hamilton's inclusive fitness model predict when subordinate behavior is favored over living solitarily. The assured fitness return (AFR) model predicts that subordinates help when they are highly likely to gain immediate indirect fitness. Transactional skew models predict dominants and subordinates "agree" on a level of reproductive skew that induces subordinates to join groups. We show the AFR model to be a special case of transactional skew models that assumes no direct reproduction by subordinates. We use data from 11 populations of four wasp species (*Polistes*, *Liostenogaster*) as a test of whether transactional frameworks suffice to predict when subordinate behavior should be observed in general and the specific level of skew observed in cooperative groups. The general prediction is supported; in 10 of 11 cases, transactional models correctly predict presence or absence of cooperation. In contrast, the specific prediction is not consistent with the data. Where cooperation occurs, the model accurately predicts highly biased reproductive skew between full sisters. However, the model also predicts that distantly related or unrelated females should cooperate with low skew. This prediction fails: cooperation with high skew is the observed norm. Neither the generalized transactional model nor the special-case AFR model can explain this significant feature of wasp sociobiology. Alternative, nontransactional hypotheses such as parental manipulation and kin recognition errors are discussed.

Keywords: wasps, *Polistes*, *Liostenogaster*, reproductive skew, cooperative breeding, haplodiploidy.

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Most animals live solitary lives and do not interact cooperatively with conspecifics beyond what is needed to find mates and perhaps raise offspring. Outside of the reproductive season, most interactions with conspecifics over food and territory are likely to be competitive. This follows from the Darwinian logic that resources gathered for oneself go to propagate one's own genetic interests. Altruism rewards the genetic interests of others at a cost to one's own direct reproductive success. Although they are in a definite minority, many species nevertheless exhibit spectacular levels of cooperation in group living settings. This often includes facultative or obligate suppression of reproduction. Indeed, Darwin (1859) viewed sterile helpers as perhaps the single greatest threat to his theory of natural selection.

In many species, all group members directly benefit through reduced predation risk or increased efficiency at finding food (reviewed in Nonacs 2001). Darwin's evolutionary problem arises, however, when such groups exhibit consistently unequal sharing of the group benefits (i.e., skew *sensu* Keller and Reeve [1994]). This is particularly true if this skew extends to reproduction, such that some individuals are far more successful than others. A solution to Darwin's dilemma of how reproductive inequality can evolve is kin selection (Hamilton 1964). Altruistic acts can be adaptive if directed toward individuals likely to be genetically related. This recaptures Darwin's logic of behavior favoring self-interest. Cooperative breeding can evolve as long as inclusive fitness of all group members is higher than for solitary individuals.

Recently, two general types of models have extended Hamilton's basic premise of kin selection by predicting the ranges of conditions that favor the evolution of cooperative breeding. These are transactional skew and assured fitness return models (Queller 1989; Gadagkar 1990; Nonacs 1991, 2002; Reeve and Ratnieks 1993; Reeve et al. 1998*b*; Johnstone 2000; Reeve and Emlen 2000; Reeve 2001). Transactional skew (TS) models predict cooperation as a "social contract" between a dominant and a subordinate. Subordinates benefit sufficiently to favor staying over living solitarily. Dominants retain enough reproduc-

tion to favor having the subordinate in the group over evicting it. Head start or assured fitness return (AFR) models predict that subordinate behavior can evolve when non-descendent kin have potentially higher survival than direct offspring. Both TS and AFR models incorporate genetic and ecological benefits. Subordinates are more likely to forgo reproduction when relatedness to the dominant is higher and when working together greatly increases group success.

Notwithstanding these basic shared similarities, the theoretical development and experimental testing of both models has flowed in almost completely separate tracks. Studies concerned with TS models have emphasized reproductive partitioning between individuals with similar expected future reproductive potential (e.g., wasps emerging from hibernation to cooperatively initiate nests: Field et al. 1998; Reeve et al. 2000; Liebert and Starks 2006). Initially, AFR was modeled across individuals with high asymmetries in expected future reproductive success (e.g., newly emerged wasps deciding to either disperse from their natal nest or remain as sterile helpers to the queen: Queller 1989; Gadagkar 1990; Nonacs 1991). A situational convergence is clearly evident in several recent studies that test AFR models during colony initiation (Field et al. 2000; Shreeves et al. 2003; Tibbetts and Reeve 2003). None of these studies, however, simultaneously applied their data to test TS models.

In this article, we pursue two objectives. First, we show that the AFR model is a special case of the more general TS models. Second, we use multiple independent data sets from studies of cooperative breeding in wasps to test whether observed cooperation by subordinates is consistent with a transactional framework.

Deriving a Skew Model for the Evolution of Cooperation

Variants of TS models differ in assumptions about the degree to which dominants and subordinates control each other's reproduction (Johnstone 2000; Reeve 2000; Reeve and Keller 2001). Previous treatments (e.g., Reeve and Keller 2001) have differentiated the variants as either "transactional," when the dominant or subordinate allocates skew (concession, restraint, and bidding game models), or "compromise," when the parties both have some measure of control ("tug-of-war" model). Common to all variants, however, is the basic stability condition under which it is simultaneously advantageous for an individual to be a reproductive subordinate and for a dominant to allow that subordinate into the group (Nonacs 2001). Therefore, in this article we define all the models that derive from Reeve and Ratnieks's (1993) original formulation as being in the TS framework. All such TS models

predict that stable cooperation is possible only within an allowable and defined range of reproductive skew. One end of the range is bounded by the minimum proportion of a group's total direct reproduction required by a subordinate to join a dominant (p_{\min}). When modified to apply to all group sizes (the N -person transactional model of Reeve and Emlen [2000]), the predicted minimum to be divided equally by n subordinates is

$$p_{\min} \geq \frac{n\{x_s - r[k_n - (n-1)x_s - x_d]\}}{k_n(1-r)}, \quad (1)$$

where k_n is the productivity of a group with one dominant and n subordinates. The productivity of the dominant and subordinates by themselves is x_d and x_s , respectively, and r is the genetic relatedness of the other individuals in the group (all assumed to be equally related) to the potential subordinate. The other bound is the maximum proportion of reproduction that a dominant would be willing to share (p_{\max}). Again, extending Reeve and Ratnieks's (1993) model to groups with n subordinates gives

$$p_{\max} \geq \frac{(k_n - nr x_s - x_d)}{k_n(1-r)} \quad (2)$$

to all subordinates combined. Cooperation is possible only when $p_{\max} \geq p_{\min}$. This condition can be met only if

$$k_n \geq x_d + n x_s. \quad (3)$$

This minimum stability condition is independent of genetic relatedness or whichever party controls reproduction. Productivity terms in equations (1)–(3) are the products of the number of offspring (b) and survival (s) of single individuals or groups with n subordinates, such that $x_s = b_s s_s$, $x_d = b_d s_d$, and $k_n = b_n s_n$. If dominants and subordinates do equally well by themselves ($x_d = x_s$), a group of a given size can be stable if $k_n/x_s \geq n + 1$. In other words, the ratio of the productivity of a stable group relative to single individuals has to exceed the group size. Once the stability condition is met, the difference between p_{\max} and p_{\min} is the range of reproductive skew over which a stable association is possible. The size of this range depends on genetic relatedness. Thus, equation (3) predicts qualitatively whether cooperation is possible, and equations (1) and (2) predict the range of quantitative skews that is possible for individuals of any given relatedness value.

Nonacs (2001, 2002) also showed that, in social Hymenoptera, cooperation can be favored with lower values of p_{\min} and k_n if cooperating females gain benefits from manipulating sex ratios on their nests. In Hymenoptera, full sisters are three times more related to each other than

they are to their brothers. Thus, if a colony is composed of a singly mated female (monogynous) and her daughter workers, the workers are favored to produce a 3 : 1 female-biased investment ratio to reflect this genetic asymmetry (Trivers and Hare 1976). In contrast, if the workers come from multiple mothers (polygynous), this genetic asymmetry is reduced or absent. Boomsma and Grafen (1990) showed that if a single population has both monogynous and polygynous nests, sex investment conflict is possible. Monogynous nests should favor females, while polygynous nests should favor males. Thus, in social Hymenoptera, equations (1)–(3) absolutely hold only when investment at the population level is equal in females and males. If it is not, the equations must include both population frequencies of the sexes and their reproductive values (Nonacs 2001, 2002). Accordingly, an individual should favor being a subordinate when

$$\begin{aligned}
 & \left(\frac{k_n}{n} \left[\frac{f_s g_d \nu_F}{F} + (1 - f_s) \frac{g_s \nu_M}{M} \right] p_{\min} + \right. \\
 & (n - 1) \left(\frac{k_n}{n} \left[\frac{f g_d \nu_F}{F} + (1 - f) \frac{g_m \nu_M}{M} \right] (1 - p_{\min}) \geq \right. \\
 & \quad x_s \left[\frac{f' g_d \nu_F}{F} + (1 - f') \frac{g_s \nu_M}{M} \right] + \\
 & \quad (n - 2) x_s \left[\frac{f' g_d \nu_F}{F} + (1 - f') \frac{g_m \nu_M}{M} \right] + \\
 & \quad \left. x_d \left[\frac{f' g_d \nu_F}{F} + (1 - f') \frac{g_m \nu_M}{M} \right], \right. \quad (4)
 \end{aligned}$$

where f_s , f , and f' are the proportional investment in daughters for an individual reproducing as a subordinate, the proportional investment in daughters by all other females in the group, and the proportion of daughters produced by solitary females, respectively. Relatedness values to daughters and sons (g_d , g_s) are always 0.5 and 1, respectively (Crozier and Pamilo 1996). Relatedness values to daughters and sons of other females (g_f , g_m) are variable. Female and male reproductive values (ν_F , ν_M) are always 2 and 1, respectively (Crozier and Pamilo 1996), with F and M as the frequencies of females and males across the entire population.

From the perspective of a potential subordinate, the first term on the left-hand side of equation (4) is its direct fitness as a group member. The second term is its indirect fitness through the reproduction of the other subordinates and the dominant. The three terms on the right are the inclusive fitness of the potential subordinate if all individuals reproduce solitarily (i.e., it follows in this deri-

vation that if it is disadvantageous for one individual to be a subordinate, it will be similarly disadvantageous for all other potential subordinates). Cooperation by $n + 1$ individuals is thus favored if the sum of the terms on the left exceeds the sum of the terms on the right.

Reconciling AFR with Transactional Skew Models

The second set of models for the evolution of cooperative breeding is known as the head start or assured fitness return models (Queller 1989; Gadagkar 1990). The primary assumption with AFR is that a group with n subordinates can have both more offspring and higher survival of offspring to independence than single individuals ($b_n > b_s$, $s_n > s_s$). Nonacs (1991) modified Gadagkar's model for AFR to include the possibility that each additional joiner has a differential effect on b and s values. Thus the stability condition for joining to be favored is

$$r b_s (s_n - s_s) + r (b_n - b_s) s_n - (n - 1) r b_s s_s \geq b_s s_s. \quad (5)$$

The term on the right is the fitness of the potential joiner if it is alone. The first term on the left is the increase in the survival of the dominant's original brood by having n subordinates on the nest. The second term is the increase in the number of extra brood (due to having n subordinates) multiplied by the survival rate of the group. The third term is the direct reproduction given up by all the other subordinates. Rearranging equation (5) gives

$$r \geq \frac{b_s s_s}{b_n s_n - n b_s s_s}. \quad (6)$$

Gadagkar's AFR model explicitly includes both gains for increased offspring number and survival. However, tests of AFR have sometimes split the factors as if they were alternative models. Assured fitness has been equated with whether gains in b are maintained after the death of subordinates (Shreeves et al. 2003), and gains in s have been equated to "survivorship insurance" (Reeve and Nonacs 1997; Tibbetts and Reeve 2003). Although from an evolutionary perspective there is no reason to expect the factors to operate separately, there is a heuristic value in understanding the mechanistic differences in how cooperation can be favored.

It can be shown that the stability condition for the AFR model is a special case of TS models with $p_{\min} = 0$ (i.e., AFR as formulated in eq. [5] assumes that all the reproduction in the joined nest is by the dominant and that dominants and subordinates are equally successful on their own). Substituting $p_{\min} = 0$ and $x_d = x_s$ into equation (1) results in

$$r \geq \frac{x_s}{k_n - nx_s}. \quad (7)$$

This equation is identical to equation (6) when x_s and k_n values are replaced with their component b and s values. Therefore, given the greater generality of TS models, the analyses in this article will be only in the context of skew models. The key point we make, however, is that testing for the group stability of a TS model invariably tests for the same in an AFR model. The reverse is not true. Showing that cooperation is not favored with $p_{\min} = 0$ does not rule out the possibility that cooperation could be stable at some $p_{\min} > 0$.

Calculating Inclusive Fitness of Subordinate Behavior

Measures of reproductive skew within groups have to varying degrees supported TS models (Reeve 2001; Reeve and Keller 2001). None of these reproductive skew studies, however, has explicitly addressed the question of whether the subordinate has the same or greater fitness than a solitary female. It is possible to address this question in 11 populations of four species of wasps, *Polistes dominulus*, *Polistes fuscatus*, *Polistes aurifer*, and *Liostenogaster flavolineata*. Tests of skew models have also been done in *Polistes bellicosus* (Field et al. 1998) and *Polistes carolina* (Seppä et al. 2002). However, these studies did not contain specific data on survival and productivity for both solitary- and multiple-female colonies. We first test the general prediction of TS models that, in populations of wasps with significant numbers of multifemale nests, the stability condition of equation (3) will hold. This prediction is general in the sense that it directly follows from Hamilton's rule and does not predict how reproduction is apportioned or what level of skew is possible. We then test the specific predictions of transactional models that observed levels of skew between full sisters, cousins, and unrelated females fall within the boundaries of equations (1) and (2) or as these boundaries are modified by equation (4). We cannot quantitatively predict a single numerical skew value for each population because such predictions are based on knowing the relative level of control dominants and subordinates have over each other's reproduction within the group (Johnstone 2000). However, the absolute range of possible skews (p_{\min} to p_{\max}) is independent of all assumptions of reproductive control. Hence, support for the specific predictions will result if observed levels of reproductive skew fall within predicted ranges.

General Methods across All Studies

In most of the data sets considered here, there are no relatedness estimates for any pairs of cooperating wasps. This is not, however, a limitation to testing TS models. In all the species of wasps considered, one or several cooperating females initiate nests. Cooperating females are likely to be in one of three relationships. They could be full siblings ($r = 0.75$, $g_f = 0.375$, $g_m = 0.75$). They could be cousins produced by cooperating full siblings ($r = 0.1875$, $g_f = 0.09375$, $g_m = 0.1875$). Note that because wasps tend to mate with only one male, half-sibs are rare (Queller et al. 2000). Finally, the cooperators could be unrelated. Thus, in testing TS models we simply need to examine each set of relatedness values. Using values of b and s derived from the field studies (see below), we calculated from equations (1) and (2) the p_{\min} and p_{\max} for a single subordinate in a two-female nest and, if possible, for subordinates in a three-female nest. Although four or more cooperating females are found together, such nests were either rare in the studied population or the numbers of subordinates were lumped into categories. Thus, we did not have full confidence in having comparative estimates of b and s with more than two subordinates.

In this initial analysis, we assumed that populations had either 1:1 sex investment ratios or that all nest types produced the same investment ratios. Under this scenario, cooperation is adaptive if equation (3) holds. This scenario is the most restrictive for favoring cooperation. As shown by Nonacs (2002), cooperation between females can become more likely if there are sex ratio investment conflicts with workers. Unfortunately, we do not know whether any of the studied populations were female biased and whether multifemale colonies eventually produced relatively more male offspring than single-female colonies. Nevertheless, we can overcome this lack of information by testing transactional models with female-biased populations, as described in equation (4).

To do so, we assumed that for a particular level of relatedness between cooperating females (full sister, cousin, or unrelated) colonies maximize their fitness by producing broods of all males. Thus, $f_s = f = 0$, $f' = F$, and $M = 1 - F$. Subordinate reproduction, however, may occur early in the colony life cycle (Reeve et al. 1998a, 2000). If early male production is not possible, then a subordinate female's only direct reproductive option will be to produce daughters, resulting in $f_s = 1$. We paired these two endpoints of subordinate investment ratios with two levels of dominant control over their investments: complete control of sex ratio (resulting in the optimal $f = 0$ in female-biased populations) and weak control that would produce less female-biased offspring ratios than in the population as a whole ($f = 0.6$, when $f' \geq 0.6$). We

then solved for the minimum population-level female bias (F) that would produce $p_{\min} = 0.2$ for subordinate cooperation in each of the four possible combinations of subordinate and dominant male investment patterns. A p_{\min} value of 0.2 was chosen because recent field data show subordinates may get some direct reproduction in the presence of a dominant, but they rarely get more than 20% (Field et al. 1998; Queller et al. 2000; Reeve et al. 2000; Liebert and Starks 2006).

Each field study provides measures for nest survival (s) and offspring number (b) of single- and multifemale nests. We assume that dominants and subordinates would have done equally well as solitary females ($b_{d,s_d} = b_{s,s_s}$). Thus, predicting cooperation depends on the relative productivity of groups versus solitary individuals (the ratio of $b_n s_n$ to $b_s s_s$). Although we accept the field measures as accurate, there is notable variation across nests in size. Likewise, there is some variation across populations in nest survival. Therefore, we calculated the 95% confidence intervals (CIs) from the population data for b_s and then the CIs of the ratio of productivity of a pair of wasps to a single wasp (k_1/x_s). The latter CIs estimate how likely a given population is to fit a transactional model. For example, in nests with one subordinate, if the mean ratio value of k_1/x_s is <2 and the 95% CI does not include 2, then the model would strongly predict that cooperation in the population would be rare. Conversely, if the entire CI range is >2 , then cooperation is predicted to be common. Varying productivity of multifemale nests or the survival of nests would have similar effects to varying b_s . Unfortunately, for most of the populations, CIs for these values are not as reliably estimated. Therefore, these were held constant for simplicity in this analysis.

Each study differed in methodology and thus in how relative b and s values could be calculated. Eight populations of *P. dominulus* were reported across three articles and from previously unpublished census information. Additionally, reproductive success was measured in one population each of *P. fuscatus*, *P. aurifer*, and *L. flavolineata*. For each, we describe how we derive our productivity estimates.

Nonacs and Reeve (1995)

Nonacs and Reeve's (1995) study followed 195 naturally initiated nests of *P. dominulus* in the Boston area in 1991. Growth rates for single- and multifemale nests were measured across the season. Individual nests, however, were often removed for experimental purposes, so the relative success of each nest type was not measured at the end of the season or when workers started to emerge. Therefore, to compare reproductive success, we regress nest size against the last day it was measured and the number of

females on the nest (fig. 1). In a stepwise regression, both date and number of females were significant in the equation. Offspring number (table 1) is estimated for day 50 from the resulting equation: $b = -9.487 + 0.891(\text{day}) + 11.549(n + 1)$. The confidence interval for the nest size (b_s) of a single female was estimated from the regression as described by Sokal and Rohlf (1995) with day = 50 and $n = 0$. Survival was estimated from unmanipulated nests. Nonacs and Reeve (1993) reported that nest survival rates varied across the season in relation to the demands required to take care of offspring at different stages of development. A single female was estimated to have a 0.36 probability of survival until worker emergence. To get a similar estimate for multifemale nests, we assume the dominant wasp does not forage for food and therefore has a daily survival rate of 1. Subordinates do all of the dangerous foraging and have a daily survival rate equal to that of single females. If all the subordinates die, the dominant assumes their work and their survival rate. We did a Markov process to calculate the probability that at least one adult survives until worker emergence by working backward over an estimate of 39 days from laying the first egg to worker emergence (data from Nonacs and Reeve 1993). This yields $s = 0.72$ and 0.91 for nests with one or two subordinates, respectively. This method probably underestimates multifemale nest mortality in one way because dominants probably have a greater than zero probability of dying in the presence of subordinates. However, this may be balanced by overestimating dominant mortality if

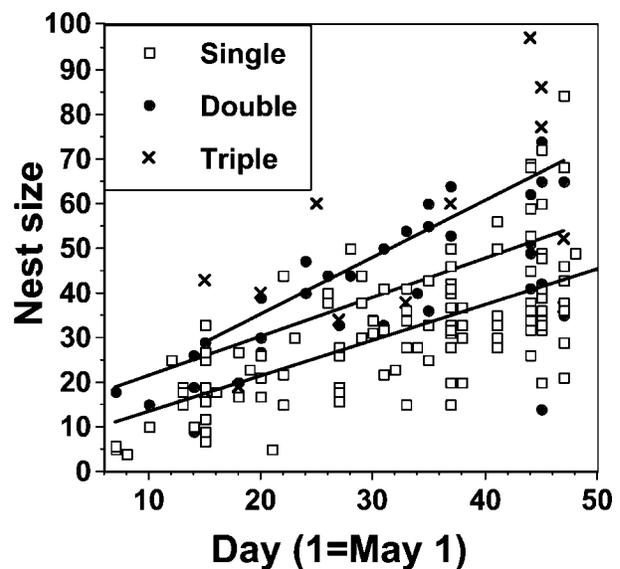


Figure 1: Last observed nest size of single-, double-, and triple-female nests in the 1991 *Polistes dominulus* population in Boston. Regression lines are shown for each group size.

Table 1: Range of reproductive skew for potentially stable associations of full sisters, cousins, or unrelated females

Study, n	b_s	s_s	b_n	s_n	k_n/x_s	$r = 0.75$		$r = 0.1875$		$r = 0$	
						p_{\min}	p_{\max}	p_{\min}	p_{\max}	p_{\min}	p_{\max}
<i>Polistes dominulus</i> (USA):											
Nonacs and Reeve 1995											
1	46.6	.36	58.2	.72	2.50	.000	1.000	.355	.645	.401	.599
2			69.7	.91	3.78	.000	1.000	.434	.783	.529	.736
Tibbetts and Reeve 2003 (Boston)											
1	35.0	.42	46.2	.71	2.23	.137	.863	.424	.576	.448	.552
2			57.2	.85	3.32	.026	.987	.558	.721	.603	.699
Tibbetts and Reeve 2003 (Ithaca)											
1	88.0	.36	124.6	.65	2.56	.000	1.000	.341	.659	.391	.609
2			161.2	.80	4.07	.000	1.000	.370	.815	.491	.754
Starks (Carlisle, 1996)											
1	41.9	.44	78.4	.92	3.91	.000	1.000	.143	.857	.256	.744
Starks (Ithaca, 1996)											
1	40.8	.35	106.1	.74	5.50	.000	1.000	.035	.965	.182	.818
Starks (Ithaca, 1997)											
1	68.8	.39	116.3	.85	3.68	.000	1.000	.166	.834	.271	.729
Starks (enclosure, 2001)											
1	35.9	.65	66.8	1.00	2.86	.000	1.000	.280	.720	.349	.651
Mean: <i>P. dominulus</i> (USA)											
1					3.32	.020	.980	.249	.751	.328	.672
<i>P. dominulus</i> (Spain):											
Shreeves et al. 2003											
1	9.04	.60	13.48	.60	1.49	1.000	.000	.749	.251	.671	.329
<i>Polistes fuscatus</i> :											
Starks (Ithaca, 1996)											
1	27.4	.45	56.0	.80	3.63	.000	1.000	.171	.829	.275	.725
<i>Polistes aurifer</i> :											
Liebert et al. 2005b											
1	10.8	.42	10.50	.50	1.16	1.000	.000	1.000	.000	.866	.134
<i>Liostenogaster flavolineata</i> :											
Field et al. 2000											
1	5.36	.45	10.72	.57	2.53	.000	1.000	.346	.654	.395	.605
2			16.08	.80	5.33	.000	1.000	.173	.913	.375	.813

Note: The range of skew is bounded by the minimum proportion of reproduction (p_{\min}) subordinates must have and the maximum proportion (p_{\max}) that a dominant is willing to give up. If more than one subordinate is present, p_{\min} and p_{\max} are assumed to be split evenly between them. Expected offspring number (b) and nest survival rates (s) are given for solitary nests and nests with one or two subordinate females (n). These values are used to calculate the expected relative productivity of single- and multifemale nests (x_s and k_n). If $k_n/x_s \geq (n + 1)$, then $p_{\max} \geq p_{\min}$, and a stable association is possible within the ranges of skew values. Study lists the cited reference source of the data, except for Starks's unpublished results, which give the year of data collection.

all subordinates are gone. Evidence suggests that their mortality rates are still somewhat lower than solitary females because they may cannibalize brood rather than forage (Tibbetts and Reeve 2003).

Tibbetts and Reeve (2003)

Tibbetts and Reeve's (2003) study followed 51 naturally initiated nests of *P. dominulus* in the Boston area in 1993 and 98 nests around Ithaca, New York, in 2000. The goal was to measure whether subordinates increased nest survival and whether their offspring contributions were maintained after their removal. In both populations, no assured

fitness was demonstrated, but there was significant positive survival insurance. Both studies included unmanipulated control nests. These nests can be used to compare fitness of subordinates with that of single females. In the Boston population, 16 single-female nests had an average of 35 ± 15 (SD) cells just before worker emergence (table 1). Their 95% CI is ± 8.0 cells. Multifemale nests were lumped in the data set and had an overall average of 54 cells. Given an average of 1.7 subordinates per multifemale nest and assuming linear increases in offspring numbers, this leads to an estimate that the addition of each subordinate adds 11.2 cells to the nest ($= [54 - 35]/1.7$). Survival rate until worker emergence for single-female nests

was observed as 0.56. This rate, however, is measured for only approximately the last two-thirds of brood development. To estimate survival rate for the entire period, we calculated from the observed data a daily survival rate of 0.978, which gives a survival rate (s_s) of 0.42 for a 39-day period from egg laying until worker emergence. Multifemale nests had a 0.90 survival rate, but no differentiation of this rate across number of subordinates was given. Relative to single females, this leads to an estimated daily nest survival rate of 0.996. Extrapolating across the entire season gives an expected survival of 0.85. Following the calculations for the Nonacs and Reeve (1995) study, we attributed two-thirds of this increase to the first subordinate ($s_1 = 0.71$) and one-third to the second subordinate ($s_2 = 0.85$).

In the Ithaca population, 16 of 44 single females survived from initiation until worker emergence ($s_s = 0.36$). Their average nest size was 88 cells (± 63 SD), which gives a 95% CI of ± 33.6 cells. In comparison, 12 of 15 ($=0.8$) multifemale nests survived with at least one female. Attributing two-thirds of this increase to the first subordinate gives $s_1 = 0.65$ and $s_2 = 0.80$. Multifemale nests produced an average of 184 cells and averaged 2.62 subordinate females per nest. Therefore, each added subordinate increased nest size by 36.6 cells ($= [184 - 88]/2.62$).

Starks 1996–1997 Census Data

Data on female number, colony survival, and colony productivity of *P. dominulus* and *P. fuscatus* were collected from Great Brook Farm State Park in Carlisle, Massachusetts, in 1996. This population was censused six times between May and October, the last of which was after reproductives abandoned their natal nests. Each census was conducted before foraging activity and collected information consisting of the presence or absence of marked females and unmarked workers (workers were not individually marked). Cell number was collected during the final census. There were 34 *P. fuscatus* nests, 22 of which were single-female colonies. The likelihood that a single-female colony survived to produce workers was 45% (10 of 22), and the likelihood that a multifemale colony survived to produce workers was 80% (8 of 10). Two nests contained four females each and were excluded from the analysis. There were 50 *P. dominulus* nests, 34 of which were single-female colonies. The likelihood that a single-female colony survived to produce workers was 44% (15 of 34), and the likelihood that a two-female colony survived to produce workers was 92% (12 of 13). Three nests contained three or more females and were excluded from the analysis.

Data on female number, colony survival, and colony productivity of *P. dominulus* were collected from various

locations within Ithaca, New York, in 1996 and 1997. These nests were censused approximately every 10 days between May and October, and nest cell counts were taken after reproductives abandoned nests. Most data collection was conducted before foraging activity, and data consisted of the presence or absence of marked females and workers. In 1996 there were 79 *P. dominulus* nests, 54 of which were single-female colonies. The likelihood that a single-female colony survived to produce workers was 35% (19 of 54), and the likelihood that a two-female colony survived to produce workers was 74% (17 of 25). Two nests contained three females and were excluded from the analysis. In 1997 there were 103 *P. dominulus* nests, 62 of which were single-female colonies. The likelihood that a single-female colony survived to produce workers was 39% (24 of 62), and the likelihood that a two-female colony survived to produce workers was 85% (29 of 34). Seven nests contained three or more females and were excluded from the analysis.

Starks 2001 Enclosure Experiment

Starks's (2001) study followed 56 naturally initiated nests of *P. dominulus* in a large greenhouse in order to examine the "sit and wait" reproductive tactic (Nonacs and Reeve 1993; Starks 1998). The population contained 38 single-female nests and 18 multifemale nests. Twelve single-female nests were experimentally manipulated, and these nests are removed from analyses. Of the remaining 26 single-female nests, seven failed due to female death and two nests were successfully usurped; thus $s_s = 0.65$. Of the 18 multifemale nests, 100% survived ($s_1 = 1.0$). Of these 18 multifemale associations, 10 contained two females, four contained three females, and four others contained five or more females. Nests with more than two females were excluded from the analysis. Colony productivity was determined by counting cells after nest abandonment in the late fall.

The significant value of this experiment is that no nesting attempt was missed and nests never failed due to predation. A potential problem in field studies is that single-female nests may be less visible than multifemale nests and may fail relatively more often before being noted. Hence, the overall success rate of single-female nests may be overestimated relative to multifemale nests, leading to underestimates for the benefits of cooperation. If this is a significant biasing factor, the enclosure experiment would eliminate the bias and predict larger benefits from cooperation.

Shreeves et al. (2003)

The Shreeves et al. (2003) study removed *P. dominulus* subordinates from nests in Spain in 1999 to measure the

effects on productivity. In contrast to Tibbetts and Reeve (2003), they found no survival insurance but almost complete rearing of additional offspring. About 60% of nests survived from initiation to producing workers with no significant differences in terms of the number of females on the nests. Therefore, $s_s = s_n = 0.6$. A linear relationship was determined to be the most accurate fit to the data: preremoval brood (b) = $4.60 + 4.44(n + 1)$. The 95% CI for b_s could not be calculated from the data given in the article because single-female nests were measured at different times of the year, after which the single female was removed.

Liebert et al. (2005b)

The Liebert et al. (2005b) study followed the success of 58 nests initiated from 1999 to 2001 in a southern California population of *P. aurifer* with 86.2% solitary founding. The probability of survival to offspring emergence was 0.42 for solitary nests ($n = 50$) and 0.50 for multiple-female nests ($n = 8$). Productivity of surviving nests was measured directly by marking newly emerged offspring at censuses conducted every 2–4 days until the end of the colony cycle. Solitary- and multifemale nests produced an average of 10.82 ± 8.96 (SD) and 10.50 ± 6.56 offspring, respectively (table 1). Based on these data, the 95% CI for solitary nest productivity is ± 6.0 offspring.

Field et al. (2000)

The Field et al. (2000) study removed subordinates in a Malaysian population of *L. flavolineata* in 1998. At the time of subordinate removal, there was a linear relationship between nest size and group size: brood number (b) = $5.36(n + 1)$. We calculated a 95% CI of ± 2.5 cells for single-female nest size by estimating regression parameters (as in Sokal and Rohlf 1995) from the raw data presented in their figure 1 (p. 869). Following an unmanipulated control population, Shreeves and Field (2002) reported that single- and two-female nests had respective survival rates (s) of 0.45 and 0.57.

Results

In all seven North American populations of *Polistes dominulus*, the population of *Polistes fuscatus*, and the population of *Liostenogaster flavolineata*, group productivity exceeds the threshold for predicting cooperation between females (table 1: $k_1/x_s > 2$ and $k_2/x_s > 3$). In the one population of *P. dominulus* from Spain (Shreeves et al. 2003) and in *Polistes aurifer*, the stability threshold is not met.

Transactional models further predict the range within which skew values should be observed between individuals

of different relatedness values. Thus, in the nine populations where cooperation is predicted, a pair of full sisters could exhibit a wide range of reproductive skew, and subordinate joining never requires more than 14% of the reproduction. In contrast, cooperation between pairs of cousins requires the dominant to cede from 28% to 42% of the total offspring in five of the nine populations to attract a subordinate, and in only one of the nine populations should an unrelated subordinate be willing to cooperate with fewer than 20% of the offspring. In *P. dominulus* nests with two subordinates, the subordinates are predicted to get an even larger proportion of the reproduction. In *L. flavolineata*, two subordinates could potentially get a smaller proportion of the total reproduction.

Benefits from sex ratio conflicts can increase the potential for cooperation. These benefits are differentially gained, however, depending on the relatedness of the females and how effective they are at producing males in overall female-biased populations (table 2). We examined the effects on the three classes of potential interactants.

Full sisters. For nine of the 11 populations, high skew associations ($p_{\min} \leq 0.2$) can form without any need for added benefits from sex ratio conflicts. High skew associations can also form in the Spanish population of *P. dominulus* and in *P. aurifer* in strongly female-biased populations. Populations have to range from about 66% female (if both subordinates and dominants produce all-male offspring) to 90% female (if subordinates produce only female offspring and dominants produce a 60% female-biased sex investment ratio).

Cousins. For three populations of *P. dominulus* and the *P. fuscatus* population, high skew associations ($p_{\min} \leq 0.2$) can form without any need for added benefits from sex ratio conflicts. For the remaining populations, high skew associations almost always require $>60\%$ female bias across the whole population. Furthermore, in these seven populations, if subordinates produce female rather than male offspring and dominants only weakly control sex ratios, then no stable cooperation would be predicted.

Unrelated females. Only in Starks's 1996 Ithaca population of *P. dominulus* can high skew associations ($p_{\min} \leq 0.2$) form without any need for added benefits from sex ratio conflicts. For the remaining populations, high skew associations require 61%–88% levels of female bias and male production by the unrelated females. Unrelated females should never cooperate if their direct reproduction will be only daughters in a female-biased population.

The robustness of the previous results also depends on the variability associated with measures of nest productivity. The 95% confidence intervals for solitary nest size (b_s) and ratio of productivity of two-female nests versus solitary nests are shown for each population in figure 2. Plotted relative to these 95% CIs is the stability criterion

Table 2: Proportional investment in females at a population level required for subordinates to cooperate with full sisters, cousins, or unrelated females

Study	All males ^a						All females ^a					
	All males ^b			60% females ^b			All males ^b			60% females ^b		
	.75 ^c	.1875 ^c	0 ^c	.75 ^c	.1875 ^c	0 ^c	.75 ^c	.1875 ^c	0 ^c	.75 ^c	.1875 ^c	0 ^c
Nonacs and Reeve 1995	.50	.63	.75	.50	.68	.75	.50	.78	NC	.50	NC	NC
Tibbetts and Reeve 2003 (Boston)	.50	.67	.78	.50	.72	.78	.50	.82	NC	.50	NC	NC
Tibbetts and Reeve 2003 (Ithaca)	.50	.60	.74	.50	.67	.74	.50	.70	NC	.50	NC	NC
Starks (Carlisle, 1996)	.50	.50	.61	.50	.50	.61	.50	.50	NC	.50	.50	NC
Starks (Ithaca, 1996)	.50	.50	.50	.50	.50	.50	.50	.50	.50	.50	.50	.50
Starks (Ithaca, 1997)	.50	.50	.62	.50	.50	.62	.50	.50	NC	.50	.50	NC
Starks (enclosure, 2001)	.50	.58	.71	.50	.62	.71	.50	.73	NC	.50	NC	NC
Mean: <i>Polistes dominulus</i> (USA)	.50	.57	.68	.50	.60	.68	.50	.6550
Shreeves et al. 2003	.66	.78	.85	.77	.83	.85	.71	.84	NC	.86	NC	NC
Starks (Carlisle, 1996)	.50	.50	.63	.50	.50	.63	.50	.50	NC	.50	.50	NC
Liebert et al. 2005b	.74	.83	.88	.83	.87	.88	.78	.84	NC	.90	NC	NC
Field et al. 2000	.50	.63	.75	.50	.68	.75	.50	.78	NC	.50	NC	NC

Note: Subordinates are assumed to gain direct reproduction ($p_{\min} = 0.2$). A value of 0.50 means cooperation occurs without a sex ratio bias; NC = no cooperation is possible with any level of female bias. Data are referenced by study as in table 1.

^a Subordinate reproduction.

^b Dominant reproduction.

^c Value of r .

line for a two-female nest (from eq. [3], this is $k_1/x_s = 2$, with reproduction equally shared). Also plotted in a left-to-right progression of lines are the minimum k_1/x_s values that would allow stable high skew associations ($p_{\min} \leq 0.2$) of full sisters, cousins, and unrelated females, respectively. The mean values of b_s varied greatly across the studies (fig. 2), probably in part due to differing methods of measuring nest size or success. The magnitude of b_s did not significantly correlate to k_1/x_s , which strongly suggests that there is not a systematic bias in estimating the productivity of single-female nests relative to the productivity of multifemale nests across the various studies.

The mean and 95% CI of *P. aurifer* is entirely below the absolute stability criterion value of 2 (fig. 2). In four populations, the CIs exclude the possibility of adaptive high skew associations of cousins and unrelated females but do not exclude the possibility that full sisters should also not form such associations. In the remaining five populations, it is always possible for stable high skew associations to form between full sisters. Among these five, four also have the possibility of stable high skew associations between cousins. In only one population does the 95% CI include the possibility of stable high skew associations between unrelated females.

Discussion

Evolution of Cooperation in a Transactional Skew Framework

Transactional models of cooperation make both primary, general predictions about whether cooperation is evolu-

tionarily possible and secondary, specific predictions about how group reproduction is quantitatively divided. A general prediction is that groups are sufficiently productive to favor group living over solitary living. We found that nine separate populations of three species (*Polistes dominulus*, *Polistes fuscatus*, and *Liostenogaster flavolineata*) meet this minimum criterion (table 1). In an additional study on *P. dominulus*, Liebert and Starks (2006) also found that cooperation exceeded the minimum criterion ($k_1/x_s = 3.07$ in their study). In all three species, cooperation in colony initiation is indeed common (Nonacs and Reeve 1995; Reeve and Nonacs 1997; Field et al. 2000). One species, *Polistes aurifer*, does not meet the minimum criterion. This population, however, rarely exhibits cooperation between females in nest initiation (Liebert et al. 2005b) and thus is consistent with the TS model. Only the Spanish population of *P. dominulus* appears to fail the general prediction: the population exhibits a high level of female cooperation (Shreeves et al. 2003), but the TS model predicts solitary behavior. The estimates for solitary success for this population, however, are based on relatively few nests that were destroyed as part of an experimental manipulation early in the year. Thus, the success of single-female nests cannot be considered highly reliable in this particular study. More seriously, the support for the general prediction is tempered by the fact that 95% CIs on the estimates of brood production in single-female nests in four populations cannot exclude values less than the minimum criterion for cooperation (fig. 2). Thus, it

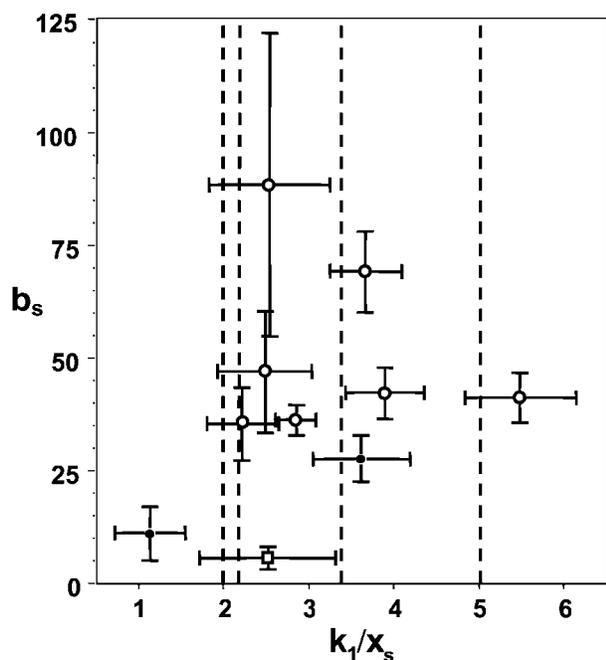


Figure 2: Observed offspring production of single females (b_s) relative to predicting cooperation. The error bars for the Y-axis are 95% confidence intervals (CIs) for offspring production. These CIs are used to generate the corresponding 95% CIs for k_1/x_s on the X-axis. Open circles = *Polistes dominulus* data sets; solid circles = other *Polistes* species; open squares = *Liostenogaster flavolineata*. The vertical line at $k_1/x_s = 2$ is the minimum for any cooperation to be stable. Proceeding left to right, the other vertical lines give the k_1/x_s values required for cooperation with $p_{\min} = 0.2$ between full sisters, cousins, and unrelated females, respectively.

is possible that as many as five of the 11 populations presented here may reject this general prediction.

The previous predictions are general because they are not exclusive to transactional models. Given that cooperation creates enough benefit for stable group formation, TS models make further unique predictions about the resulting sociobiology of the groups. Preeminent among these is that observed levels of reproductive skew should occur within the range of values given by equations (1) and (2). This is a robust prediction across all TS models that is unaffected by which individuals determine reproductive skew. Therefore, there are no ambiguities as to whether a particular result supports or rejects a TS model (e.g., Field et al. 1998; Johnstone 2000; Reeve 2000; Nonacs 2001; Reeve and Keller 2001).

Patterns of cooperation and reproductive skew are well described in *Polistes* and *Liostenogaster*. Cooperating groups are usually composed of full sisters, but cousins and unrelated females are not uncommon. Reproductive skew tends to be high with all patterns of relatedness: the

dominant gets about 80% or more of the offspring if she survives (Field et al. 1998; Queller et al. 2000; Reeve et al. 2000; Liebert and Starks 2006). Thus, if TS models fail to predict high skew associations across all levels of relatedness, then these models must be rejected.

As far as full sisters are concerned, this specific prediction is supported. Taking into account the confidence intervals on brood production, full sisters are predicted to cooperate with very high reproductive skews in up to nine of the 11 populations (fig. 2). The specific prediction, however, fails when considering cooperation between cousins or unrelated females. In only four populations do confidence intervals for the ratio of group to solitary productivity allow for high skew associations between cousins, and in two of these populations, the 95% CIs include the possibility that cousins should not cooperate. Finally, in only one population would a TS model predict that unrelated females could possibly cooperate with high reproductive skews. Thus, cousins and unrelated females seem unlikely to be maximizing their fitness by joining groups through a transactional mechanism. Recently, Liebert and Starks (2006) compared once more in the Boston area the reproductive success of single- and multifemale *P. dominulus* nests. Reproductive skew was not significantly affected by relatedness between dominants and subordinates, and it was far higher in low-relatedness nests than predicted by TS models.

Can the TS model be recouped through factors not considered in the N -person model of Reeve and Emlen (2000)? First, Nonacs (2002) showed that if sex ratio conflicts are present, cooperation is enhanced by gaining control of male production. Our analysis here shows that high skew associations between even unrelated females are possible if subordinates get to produce male offspring and the whole population is female biased. Unfortunately, what is known about these species does not suggest that such conditions are present. Subordinates tend to disappear by the middle of the colony cycle, and they rarely reproduce after workers are on the nest (Reeve 1991). Thus, the majority of their direct reproduction must occur within the first cohorts of offspring raised while they are on the nest. In these early cohorts (for *Polistes*), males are relatively rare, and thus direct reproduction by subordinates may be limited to daughters that avoid becoming workers and instead pursue other reproductive options (Reeve et al. 1998a; Starks 2001). Populations of species with both single- and multifemale colonies tend to have roughly equal investment in females and males (Nonacs 2002). Multifemale colonies produce more males than single-female colonies, but they also produce significant numbers of females (Noonan 1981; Nonacs 2002). Therefore, in a typical multifemale colony, a subordinate may get a small proportion of the direct reproduction, mostly as daughters, and lim-

ited inclusive fitness benefits from dominants being able to somewhat overproduce male offspring. In summary, sex ratio conflicts are unlikely to increase incentives for cooperation enough to explain the behavior of nonsister females.

Transactional models may predict erroneously low levels of skew for cooperation if the productivity of solitary females was consistently overestimated in many of the populations. Apart from the Spanish population of *P. dominulus* this, however, is unlikely for several reasons. Overcounts of brood numbers (i.e., b_s) must be on the order of 50%–100% for CIs in figure 2 to include the minimum levels of productivity that would allow high skew associations. Alternatively, nest survival (s_s) could have been overestimated because single-female nests may be less noticeable and more likely to fail before being recorded. This may be a possibility in the tropical species *L. flavolineata*, where new nests are started year round. The *Polistes* species, however, are all temperate and nests are initiated in a relatively brief period of time (Reeve 1991). The studies reported here generally followed all nests from very early in the period of initiation through the season. It is, therefore, unlikely that there was an unobserved period of time where solitary females suffered extreme mortality. Finally, the one study that most closely controlled and observed nest survival (enclosure study with *P. dominulus*; Starks 2001) had a relatively modest productivity advantage for multifemale nests that was well within the range observed for the species (table 1; fig 2). This suggests that if there is a bias, single-female productivity is underestimated in the field. Therefore, our models are more likely to err in overestimating the likelihood of cooperation with high skew.

One other consideration in the transactional framework is that the expected p_{\min} for a subordinate can rise dramatically if she becomes dominant after the death of the initial dominant (as in Queller et al. 2000). Thus, reproductive success for subordinates would be low in nests where they remain subordinates but high where they rise to dominance. The joining decision itself would be based on the expected mean p_{\min} because subordinates would not be able to predict dominant turnover. Queller et al. (2000) observed 110 *P. dominulus* subordinates on 28 nests. On 11 nests, the dominant disappeared and was succeeded by a former subordinate. Thus, an unrelated subordinate has a 10% chance of rising to dominant status (= 11/110). If one assumes total reproductive skew in favor of whichever wasp eventually becomes the dominant, this equates to an expected mean $p_{\min} = 0.1$ for unrelated subordinates (i.e., one out of 10 subordinates becomes dominant and gains 100% of the reproduction). This is still far below the majority of p_{\min} values predicted by the TS models (table 1). Other studies found similarly low

probabilities for subordinates to attain dominant status. Noonan (1981) estimates that only 3% of subordinates in *P. fuscatus* become dominants. Hughes and Strassmann (1988) found that only 0%–11% of subordinates eventually became dominants in *Polistes exclamans* and *Polistes annularis*.

The existing evidence in *Polistes* suggests that queuing in a dominance hierarchy (Kokko and Johnstone 1999; Ragsdale 1999) does not pay off often enough by itself to predict cooperation of distantly related individuals. The benefits of queuing, however, should be examined in more species and at the level of the nest (as contrasted to measuring population averages). For example, the potential of ascension to dominance may favor cooperation if unrelated individuals increase their likelihood of becoming dominant above random chance. If order of joining determines hierarchy, unrelates should be more likely to join at times when they are likely to gain a high rank. In comparison with related subordinates, unrelated individuals should be more aggressive in keeping out later joiners to reduce competition. Finally, as queue length grows, unrelates should be more prone to leaving the group in search of other reproductive opportunities. Therefore, as group size increases, the proportion of unrelated individuals in the group should decrease. To date, these predictions have not been tested, and all of them assume unrelated individuals recognize their genetic status.

Because assured fitness return models are subsumed within the transactional framework, the failure of the latter also equates with failure of the former in explaining the evolutionary maintenance of cooperation. AFR models predicted that ecological constraints on solitary reproduction in species with extended parental investment were far stronger selecting agents for cooperation than was heightened genetic relatedness (Queller 1989, 1994; Gadagkar 1990). However, the data here suggest only haplodiploid full sisters potentially gain enough in increased group productivity to cooperate without their own direct reproduction. Thus, the degree to which AFR models are consistent with the evolution of cooperation in wasps of the same generation (semisociality; Lin and Michener 1972) seems to strongly depend on haplodiploidy. However, the current data do not test the subsocial (multigenerational groups) evolutionary route to cooperation. Parents often have established resources such as nests that offspring would have to create de novo after dispersing. Thus, $x_d \gg x_s$ can be very likely, which in turn would make cooperation between more distantly related individuals possible (e.g., nieces helping aunts). Assured fitness models were originally derived in the context of predicting whether offspring should remain as helpers on their natal nests (Queller 1989; Gadagkar 1990). In such cases, adaptive cooperation

with $p_{\min} \approx 0$ across a wide range of relatedness values remains to be tested.

Cooperation in Nontransactional Frameworks

Semisocial groups would be favored if some females cannot reproduce ($x_s \approx 0$ due to impotence), which would allow them to increase fitness only by helping kin. It is important to note that the stability condition in equation (3) applies to both potentially cooperating females and their mother (or whatever kin raises them). Thus, the deliberate creation of sterile "helper" offspring can be adaptive from the parents' perspective. For example, the data from Nonacs and Reeve (1995) suggest that the relative productivity of a two-female nest is 2.5 times that of a single female (table 1). Therefore from a mother's perspective, two nests of cooperating daughters result in fitness equal to five solitary nests. At an individual offspring level, a sterile daughter that has a 0.67 probability of helping her sister raise 1.5 times more offspring has equal value to a fertile daughter that nests alone.

Evolutionarily, daughters should resist being manipulated into sterilized helper roles because their fitness would be higher when retaining reproductive potential (Keller and Nonacs 1993). Further, it is not clear how parents can successfully manipulate otherwise robust offspring into helper roles. Making smaller females does not guarantee subordinate females. As an example, the size variation across solitary *P. dominulus* females spans the variation observed in multifemale groups. There is, however, no advantage in being a larger solitary female in terms of nest construction rate or survival (Nonacs and Reeve 1995). Rather than size, Gadagkar (1991) argued that many *Ropalidia marginata* females have delayed reproductive maturation. Later experiments failed to demonstrate such widespread reduced fertility in subordinates (Shakarad and Gadagkar 1997). Further, Field and Foster (1999) found no evidence for subfertility in *L. flavolineata*. Another possibility is that "delaying" females may be reproductively capable but following an alternative reproductive tactic of waiting to usurp established nests (Nonacs and Reeve 1993; Starks 1998, 2001). To date, there is little direct support for phenotypically manipulated disadvantages creating subordinate behavior.

Recently, however, Liebert et al. (2005a) found that genetically disadvantaged females may be more common than previously thought. The authors reported the occurrence of triploid females in three different species of *Polistes* wasps. In one population of *P. dominulus*, 11.1% of 18 multifemale nests had triploid females. Triploids are sterile and thus could potentially form a class of females that gain inclusive fitness only through helping. However, triploids would have to first recognize their own sterility. Sec-

ond, the most likely origin of triploid females is from a mating with a diploid male (Liebert et al. 2004, 2005a). Thus, all full sisters would also be triploid, and indirect fitness could be gained only through locating and joining cousins or half sisters. Perhaps demonstrating the practical difficulty of executing such optimal joining decisions, Liebert et al. (2005a) found triploid females only in nesting associations with unrelated dominants.

An alternative explanation for suboptimal joining behavior is that wasps may simply make recognition errors in identifying sisters. Some such errors are expected with an acceptance threshold type of mechanism (Reeve 1989; Liebert and Starks 2004), in which an evaluator wasp accepts or rejects another based on how well the evaluated wasp's cues match the evaluator's internal kin template. Evidence suggests that wasps identify former nestmates via chemical signatures consisting of cuticular hydrocarbons (reviewed in Gamboa 2004) and that this process can be facilitated via philopatry after overwintering (Rau 1929; West-Eberhard 1969; Klahn 1979; Wenzel 1989, 1996; Starks 2003; Sumana et al. 2005). Even perfectly accurate recognition of former nestmates may sometimes result in cooperation with less related or unrelated females because there is no evidence for intracolony kin discrimination in paper wasps (Queller et al. 1990; Strassmann 1996; Gamboa 2004). Acceptance errors may also be expected because of mixing or loss of cuticular hydrocarbon signatures during winter diapause (Dapporto et al. 2004). All this raises the possibility that the proximate mechanisms wasps use to make joining decisions may preclude the fine discrimination abilities assumed by skew models. A more complete model for understanding joining decisions in wasp societies may require integration of existing inclusive fitness models with the limits of recognition mechanisms actually used by the wasps.

Conclusion

Cooperative groups of female wasps are generally productive enough that subordinate behavior could be explained by kin selection. Theoretically, this cooperation could result either as a social contract between reproductively capable individuals or as parental manipulation that creates fertile and less fertile castes of females. Neither of these explanations, however, is convincingly supported. The transactional skew models strongly predict that distantly related or unrelated females should cooperate only with low levels of skew. This is not observed in natural populations of paper wasps. The high skews that are observed can be consistent with parental manipulation models, but there is no evident mechanism for how parents could create physically robust but sterile offspring that reliably find and cooperate with kin. We have no adequate

adaptive explanation for why some female wasps appear to willingly accept reproductive subordination. We cannot rule out that cooperation with a distantly related or unrelated female is simply a mistake in recognition. Until we have a viable explanation, the evolution of cooperative breeding in *Polistes* wasps and its derivation into higher levels of eusociality will remain an unsolved puzzle.

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