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Aggression and resource sharing among foundresses in the social wasp *Polistes dominulus*: testing transactional theories of conflict

Abstract Tug-of-war models of within-group conflict predict that the frequency of conflict will be positively related to the degree of reproductive sharing within the group; in contrast, a negative relationship supports transactional models, in which reproductive payments among group members limit the degree of within-group selfishness. We tested predictions of the tug-of-war and transactional models by examining cofoundress interactions during the founding (preworker) phase of colony development in 30 naturally nesting colonies of the paper wasp *Polistes dominulus*. We found that the mean rate of foundress aggression and the mean probability of food sharing were significantly negatively associated, which supports the prediction of the transactional, not the tug-of-war model. Further, cofoundress aggression significantly increased over the founding phase (independently of temperature), while the fraction of aggression initiated by the dominant (alpha) foundress significantly decreased over this period. We show that both of these results are predicted by the transactional model of within-group conflict. Interestingly, the alpha's rate of aggression was significantly positively temperature dependent, while the beta's was not. This indicates that the alpha's aggression level may often be near her physiological maximum, while the beta's aggression is limited by other factors, contradicting the prediction of the tug-of-war model. Moreover, the alpha's aggression was significantly positively temperature dependent only in the second half of the founding period, as predicted by the transactional model since this is when there is least reproductive sharing. Finally, our results indicate that the alpha's level of aggression depends on the resources controlled by the beta.

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Introduction

Rigorous theoretical models of conflict within animal social groups have recently sprung up from models of reproductive partitioning within those groups. Transactional models of within-group conflict emphasize that although dominant members of the society could fully dominate the subordinate members, dominants may be required to make reproductive "payments" to subordinates in return for cooperation. Reproductive payments that prevent subordinates from leaving are called staying incentives; payments that prevent subordinates from fighting to the death for complete control of colony resources are called peace incentives (Emlen 1982; Vehrencamp 1983a, 1983b; Reeve and Ratnieks 1993; Keller and Reeve 1994). The minimum required payment limits the degree of within-group conflict (Fig. 1; Reeve and Keller 1997; Reeve 2000). In particular, the difference between the maximum value of the subordinate's fraction of group reproduction that the dominant can tolerate before ejecting the subordinate (p' in Fig. 1) and the subordinate's minimum staying or peace incentive (p in Fig. 1) defines the "window of selfishness." The window of selfishness predicts the amount of within-group conflict by delimit-
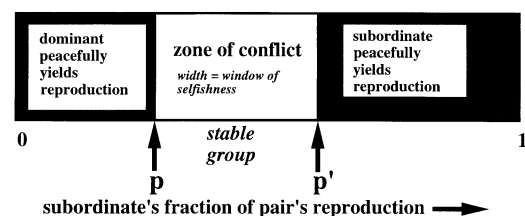

Fig. 1 The transactional model of within-group conflict where p is the subordinate's minimum staying or peace incentive and p' is the maximum value of the subordinate's reproduction that the dominant can tolerate before ejecting the subordinate

ing the maximum amount of selfish enhancement of one's reproductive share that can occur without destabilization of the group (Reeve 2000). The zones outside the window of selfishness correspond to peaceful concession of reproduction by the dominant (left-most zone in Fig. 1) and by the subordinate (right-most zone in Fig. 1).

If the subordinate's expected reproductive share is initially within the window of selfishness, the dominant will attempt to push (e.g., via aggression) the subordinate's actual share down to p but not below this threshold lest it lose the subordinate. If the subordinate's initially expected reproductive share is to the right of the upper limit of the window of selfishness, the subordinate should peacefully yield reproduction to the dominant until the subordinate's expected share falls to p' (lest the dominant eject it). At p', the dominant should again try to aggressively push the subordinate's actual share down to p, but not below. The dominant should often succeed in pushing the subordinate's reproduction to p, given its presumably greater competitive efficiency (as in social wasps: Reeve et al. 1999). Therefore, p, the subordinate's ultimate fraction of reproduction, measures the extent of actual reproductive sharing, whereas the window of selfishness (p'–p) measures the extent of aggression. Reproductive sharing and aggression are always inversely related in the transactional model of conflict when the dominant ultimately determines the subordinate's reproductive share. The window of selfishness will tend to increase (and reproductive sharing to decrease) with increasing group reproductive output, increasingly harsh ecological constraints on solitary breeding and, counterintuitively, increasing relatedness between subordinate and dominant. The subordinate's fighting ability also influences the size of the window of selfishness, though its precise effect varies according to other characteristics of the group (Reeve 2000).

The greatest amount of aggression by both parties should occur when the subordinate's expected reproductive share lies within the window of selfishness, but this does not necessarily mean that there will be no aggression outside the window. The window-of-selfishness model assumes that group members are sensitive to moment-to-moment changes within their group. Given the current rules for partitioning resources (see below), the subordinate's expected present+future share of reproduction moves back and forth the along the bar in Fig. 1. Consequently, if the subordinate's expected reproductive share by chance lies to the right of the upper limit of the window of selfishness (Fig. 1), we expect the dominant to behave aggressively to the subordinate *until* the subordinate peacefully concedes its "excess" resource. Conversely, if the subordinate's expected reproductive share by chance lies to the left of the lower limit of the window of selfishness, we might expect the subordinate to behave aggressively to the dominant until the dominant peacefully yields its excess resource. However, it is still true that the mean rate of aggression will increase as the width of the window of selfishness increases.

Two potential models of conflict could pertain to groups that partition reproduction according to the transactional model. The "window" (Reeve 2000) model described above predicts the amount of conflict that will occur over precise reproductive division within stable groups. As described above, the amount of aggression in these groups is linked to the amount of reproduction that is not required by either party and can therefore be contested. The wider the window of selfishness (Fig. 1), the more reproduction can be contested and the higher the rate of aggression. One can also envision an alternative model of conflict in which most aggression reflects threats of group dissolution. In this alternative model, most aggression occurs at or near the boundaries of the window of selfishness (p and p'), because subordinates are threatening to leave or dominants are threatening to eject subordinates. In this case, group members will be most frequently aggressive when the window of selfishness is small, because groups members will constantly be "battling on the boundaries." This "boundary" model makes exactly opposite predictions of the Reeve (2000) model. Thus, support for the window model will automatically reject the boundary model. We do not address the boundary model further below, but point out that it provides an interesting alternative that may apply to other systems.

In strong contrast to the transactional models, pure "tug-of-war" models of within-group conflict assume that reproductive sharing arises not from donation of reproductive incentives but solely from the inability of either dominant or subordinate to fully dominate its partner (Reeve et al. 1998). In tug-of-war models, both the dominant's and the subordinate's evolutionarily stable selfish efforts (i.e., investments in increasing one's reproductive share) are predicted to increase as the competitive efficiency of the subordinate increases. Further, as the subordinate becomes more efficient in competition, the equitability of resource sharing at equilibrium also increases (Reeve et al. 1998). As a consequence of the previous two predictions, the tug-of-war models predict that the mean level of conflict (selfish effort) and the degree of reproductive sharing (again measured as the subordinate's reproductive share) will be positively related. In other words, greater sharing indicates more intense competition, in sharp contrast to the prediction of transactional models. Moreover, the tug-of-war models predict that the equilibrium level of selfish effort by the subordinate will always exceed that of the dominant (Reeve et al. 1998), whereas transactional models predict that the selfish effort by the dominant can be greater than that of the subordinate (see below).

The tug-of-war and transactional models not only make opposite predictions about the relationship between aggression and the ultimate degree of reproductive sharing but also about the relationship between aggression and transfers of reproductively valuable resources between group members. Tug-of-war models predict that such transfers are fundamentally competitive. Resources are *taken* by the receiving wasp, not *given* by the re-

source holder. Therefore, there should be a positive relationship between the level of aggression on a colony and the rate at which such transfers occur. On the other hand, a negative relationship between the level of aggression on a colony and the rate of transfer supports the transactional model. Such a negative relationship suggests that most transfers are peaceful reproductive payments that represent concessions of reproduction by the dominant or subordinate within the zones flanking the window of selfishness (Fig. 1). In other words, as the widths of the concession zones increase in the transactional model, the probability that a resource controlled by one party will be peacefully donated to the other increases, and the probability of an aggressive contest over the resource decreases. The result is a negative association between the rate of aggression and the rate of resource sharing.

The above arguments assume a direct relationship between resource sharing and reproductive sharing, given that the resources positively contribute to expected reproductive output. Thus, if a packet of resource representing a total of R reproductive units is being divided up by two group members, then, in the transactional model, the dominant ensures that the subordinate receives a portion of the resource q equivalent to pR reproductive units, and the subordinate ensures that the dominant receives a portion q' qual to $(1-p')R$ reproductive units. In other words, each party attempts to retain for itself a certain fraction q or q' of each packet of resource, no matter how small each packet is (as long as the packet is divisible). Such a strategy will ensure that each party is maximizing its present+future total fraction of reproduction *without* triggering leaving or ejection by the other party. It is conceivable that each party could use an alternative rule for dividing resources, namely letting the other party have *all* packets of resource until that other party reaches its minimally required fraction of the overall present+future reproduction (p for the subordinate and $1-p'$ for the dominant). However, the latter "running-tally" rule would require the costly cognitive ability to keep an accurate running tally on the summed past amounts of resource donated to the other party, unlike the much simpler rule of the form: "take all but a fraction q (or q') of *each* packet of resource." Even if a running-tally rule is employed such that every time the subordinate succeeds in getting a little over its minimal incentive p, the dominant pushes it back down before the upper threshold p' is reached, the window-of-selfishness model still makes the correct predictions about aggression: the position of the lower threshold p still determines the fraction of all resource packets that the dominant concedes to the subordinate versus aggressively takes away from it, and the same factors that increase the window of selfishness also decrease the lower threshold p.

There is one other well-known model that predicts the modulation of group aggression, the value-aggression model. This model predicts that as a group member becomes more valuable to the group, aggression toward that individual will decrease (Reeve and Nonacs 1997).

However, evidence from Savoyard and Gamboa (1999) indicates that the value-aggression model does not apply to *Polistes* wasps. They found that aggression between cofounding *Polistes* queens decreases after worker emergence. The value-aggression model predicts that aggression should increase at this time because the subordinate becomes much less valuable to the dominant after worker emergence. As the value-aggression model does not seem to predict the behavior of *Polistes* wasps, we do not test it further in this paper.

Social wasps of the genus *Polistes* are a good model for testing the above predictions of the transactional and tug-of-war models because multiple wasps cooperate in a single colony, but reproduction is partitioned unequally among them. Several over-wintered, inseminated female wasps (foundresses) often found nests together in early spring. When nests are founded by multiple foundresses, the wasps form a linear dominance hierarchy. The most dominant, or alpha foundress, lays most, but not all eggs and aggressively dominates the more subordinate foundresses. The beta, or second-ranking female, lays the second most eggs, and lower-ranked females produce fewer eggs (reviewed in Reeve 1991). Reeve et al. (1999) recently studied how reproductive sharing changed through the founding (preworker) phase in *Polistes fuscatus* and found that subordinates lay a much lower proportion of eggs late in the season than they do earlier. This and other evidence suggests that subordinates receive staying incentives from dominants primarily near colony initiation. The evidence indicates that the dominant usually does push the subordinate's reproduction to the lower threshold, p, of the window of selfishness (Reeve et al. 1999). Reeve et al. (1999) also found that foundress aggression increased as the preworker phase progressed, confirming the result of Gamboa and Stump (1996) and supporting the prediction of the transactional model for a negative correlation between foundress aggression and the subordinate's reproductive share. However, Reeve et al. (1999) did not examine the relationship between aggression and resource sharing as a test of the transactional and tug-of-war models.

We examined the relationship between aggression and resource sharing in foundress groups of the temperate wasp *P. dominulus* (recently introduced into North America) as a behavioral test of the alternative models of within-group conflict (the first such investigation of which we are aware). Resource control is closely tied to reproduction in *Polistes* wasps. In fact, unequal protein distribution among colony members may be one of the proximate mechanisms which underlies differential reproduction of these individuals (Hunt 1994). Adult wasps obtain protein in three ways: adult-adult trophallaxis, larvae-adult trophallaxis, and malaxation of prey. Prey transfer is easy to observe and quantify, while trophallaxis is very difficult to detect. Therefore, we used prey transfer and malaxation to represent protein acquisition. Such partial representation is not optimal as it could obscure the relationship between resource sharing and aggression; however, it is unlikely to create a relationship that does not exist. Control

of nest-building material is also tied to reproduction because building material can be used to build new oviposition sites. Of course, building material is often used to maintain the nest, so possession of building material is not always linked to reproduction. Nevertheless, control of resources, especially prey resources, is associated with reproduction. Therefore, resource control and sharing may be a good behavioral indicator of reproductive skew. We tested this connection by examining whether the tug-of-war or transactional model predicts the relationship between aggression and resource sharing. In addition, we explored how the rate of foundress aggression covaried with temperature, date, foundress number, and nest size. Previous studies (Gamboa and Stump 1996; Reeve et al. 1999) did not consider the effect of temperature on aggression in these poikilothermic social wasps. Although the latter studies found that the alpha's aggression increased as the founding period progressed, this increase could have resulted from an increase in ambient temperature from spring to summer, particularly if the rate of aggression by wasps is near a physiological upper limit. Thus, we examined aggression in light of temperature variation to refine tests of the tug-of-war and transactional models of within-group selfishness. We did not consider peace incentives in this study as we did not examine the relationship between fighting ability and aggression. However, since colonies were selected randomly with respect to fighting ability, this variable will not bias our results. Finally, we derived and tested a new prediction from the transactional model as applied to social wasps: the level of aggression by the alpha should exceed that of beta, but this bias should decline later in the season.

Relative aggression by the dominant and subordinate: a new prediction from the transactional model

We first derive a prediction from the transactional model of conflict about how the relative aggression of the dominant (alpha) and subordinate (beta) should vary with the ecological factors that affect the window of selfishness. The variables entering into the basic transactional conflict model are: (1) x, the expected reproductive output of a solitary subordinate (standardized relative to an expected output of 1.0 for a solitary dominant); (2) k, the standardized total output of the dyad, and (3) r, the genetic relatedness between the alpha and beta (Reeve 2000). For the case of reproductive sharing, the minimum staying incentive p required by the subordinate is then given by (Reeve and Ratnieks 1993):

$$p = \frac{x - r(k - l)}{k(l - r)}. \tag{1}$$

The maximum fraction of the subordinate's reproduction tolerated by the dominant (lest the dominant eject the subordinate) is:

$$p' = \frac{k - l - rx}{k(l - r)}. \tag{2}$$

Thus, the width of the zone over which the beta yields reproduction to the alpha (=beta's sharing zone) is $1 - p'$, and the width of the zone over which the alpha yields reproduction to the beta (=alpha's sharing zone) is $p - 0 = p$. The larger a foundress's sharing zone, the more frequently she will yield to her cofoundress without aggression. If one foundress exceeds her allowed share of reproduction (i.e., if the subordinate's expected share of reproduction by chance comes to lie within her sharing zone), then that foundress should immediately yield reproduction to her cofoundress until each foundress has at least her minimum required reproductive share. Under these conditions, the widths of these sharing zones can be seen as inversely related to each foundress's rate of aggression toward the other foundress. The larger the sharing zone, the smaller the proportion of time that a foundress is inside the zone of conflict.

Inspection of Eq. 1 and Eq. 2 shows that the sharing zones of both the alpha and beta should decrease in width (and thus their frequency of aggression should increase) as ecological constraints on solitary breeding increase (i.e., x decreases and k increases) (Reeve 2000). Both demographic and genetic evidence indicate that the subordinate's staying incentive (Eq. 1) decreases over the founding phase due to progressively increasing constraints on solitary founding (Reeve et al. 1999). Thus, the transactional model of within-group conflict applied to social wasps predicts that foundress aggression should increase later in the founding phase.

It also follows that the beta's sharing zone is wider than the alpha's sharing zone by an amount equal to

$$1 - p' - p = \frac{1 - x}{k}. \tag{3}$$

The difference (Eq. 3) tells us that the beta's sharing zone will exceed the alpha's if there are constraints on solitary breeding ($x < 1$). This implies that the beta must share her resources and refrain from selfish aggression more frequently than will the alpha, particularly since the beta initially controls pulp and prey more frequently than does the alpha due to the subordinate's specialization in foraging (reviewed in Reeve 1991). The beta's foraging specialization means that, in *Polistes*, the subordinate's expected fraction of reproduction will usually start out on the right end of Fig. 1 and move left as the alpha and beta interact. Thus, the transactional model predicts that the beta's rate of aggression toward the alpha should be less than the alpha's toward the beta. The tug-of-war model predicts exactly the opposite (Reeve et al. 1998).

Another prediction can be extracted from Eq. 3: if we let s=the beta's absolute output for solitary breeding, g be the absolute total group output, and d=a solitary dominant's output, then Eq. 3 can be rearranged as $(d-s)/g$ since $x = s/d$ and $k = g/d$. According to the best-supported model of foundress grouping benefits in *Polistes* (the "survivorship insurance" model: Reeve 1991; Nonacs and Reeve 1995; Reeve and Nonacs 1997; Reeve et al. 1999), d and s should change slowly, but g should in-

crease rapidly as the foundress's nest grows and approaches worker emergence later in the founding period (Reeve et al. 1999). This means that the beta's sharing zone should contract faster than should the dominant's as the founding period progresses, with the result that the fraction of total aggression that is initiated by the alpha should decline with time. We tested this by examining time-dependent changes in the alpha's relative aggression, controlling for seasonal changes in temperature.

Methods

Behavioral observations were conducted on 30 naturally nesting multiple-foundress colonies of *P. dominulus*. We found these nests on the eaves of houses and barns in rural and semirural areas including the Liddell Field Station near Ithaca, New York. All foundresses from these 30 colonies were individually marked with paint on the thorax from 8–18 May 1999. After marking, each colony was videotaped once for 2 h. Videos were recorded during the founding (preworker) phase of the colony cycle, from 20 May–16 June 1999. The videos were recorded while wasps were most actively interacting and foraging, from 11 a.m.– 4 p.m. Shade air temperature was recorded during the taping sessions.

We later scored behavioral interactions between the alpha and the beta from these videos. The alpha and beta were identified behaviorally by stereotypical dominance interactions such as mounting and by relative time spent on the nest, as in many other studies (e.g., Reeve and Nonacs 1997). The number of foundresses on these colonies ranged from 2 to 10 (mean=3.2, SD=1.9), but we focused on the interactions between the alpha and beta foundresses since they are probably responsible for most, if not all, colony reproduction (e.g., Reeve et al. 1999). We recorded all aggressive encounters including darts, lunges, mounts, bites, and grapples. We also recorded items that wasps returned with (wood pulp, prey, or nothing visible in mandibles) and what proportion of the foraged items initially possessed by the alpha (or beta) foundress was shared with the beta (or alpha) foundress before disappearing. All prey were malaxated and then fed to larvae. All wood pulp was incorporated into the nest. The fraction of resource shared was estimated visually as the fraction (by apparent volume) of initially controlled resource that was transferred to the other foundress (alpha or beta) before the resource disappeared. For each colony, we averaged the fraction of prey shared over all recorded cases of prey possession by the alpha or the beta. During our observation period, in some colonies the alpha and beta foundresses did not exhibit control of both the pulp and prey resource categories.

To examine resource sharing and aggression, we recorded aggression in five mutually exclusive and exhaustive contexts categorized according to which wasp controlled the resources and which resources were controlled. Our context categories were: alpha has more pulp than beta, beta has more pulp than alpha, alpha has more prey than beta, beta has more prey than alpha, and neither has a visible resource (prey or pulp). Recording in a category ceased whenever the alpha or beta left the nest or received a resource from a third foundress. We began recording in a particular category every time the alpha or beta returned to the nest or received a resource from a third foundress. We then recorded all ensuing aggressive acts as belonging to one of these categories based on what the alpha or beta returned with (or received from a third foundress) and on how that item was shared. In some colonies not all five contexts were represented, which accounts for the reduced and variable sample sizes for the statistical analyses of the rates of aggression across these contexts.

Rate of aggression was calculated as the number of aggressive acts per hour that the alpha and beta were together on the nest. This rate was transformed as $\log_{10}(1+x)$, where x is the rate of aggression, to homogenize error variances about the regression line for regressions involving aggression rate as the dependent variable. Two-tailed parametric statistical tests were used when nor-

mality assumptions appeared satisfied; otherwise, two-tailed nonparametric tests were used. In all statistical tests, colonies were treated as the independent data points. Means are reported ±SE, unless otherwise noted.

Results

Relationship between prey sharing and foundress aggression

We never observed the sharing of pulp between alpha and beta foundresses. The alpha's mean fraction of prey sharing was 0.10±0.07 and the beta's was 0.32±0.11, suggesting that betas were more likely than alphas to transfer prey.

The mean fraction of prey shared (averaged over the alpha and beta) was negatively correlated with the residuals (obtained by regression on temperature) of the total transformed rate of aggression between the alpha and beta ($r^2=0.59$, $P=0.003$, $n=12$). However, the residual plot (i.e., residuals versus fitted values) from the linear regression of prey sharing on temperature-adjusted aggression indicated that the relationship would be more accurately modeled with a second-order polynomial regression, which was indeed the case ($r^2=0.728$, $P<0.001$; Fig. 2). Thus, colonies that shared more prey had significantly lower rates of aggression when the effect of temperature on aggression was controlled.

Our sample was too small for a rigorous test of how sharing varied with nest location. However, colonies located on the same building showed very different rates of prey sharing (e.g., 0–0.48), indicating that prey availability was not the primary factor which influenced the proportion of prey shared. To further control for variation in the amount of prey available to a colony in relation to the needs of its brood, we included the number of cells in the nest (a measure of colony size and total brood need), and the number of foundresses (a measure of the size of the total foraging force) as predictor variables in the above multiple regression. The overall regression was still significant ($n=12$, $r^2=0.64$, $P=0.035$), and mean prey sharing was the only component which was significantly correlated with temperature-corrected
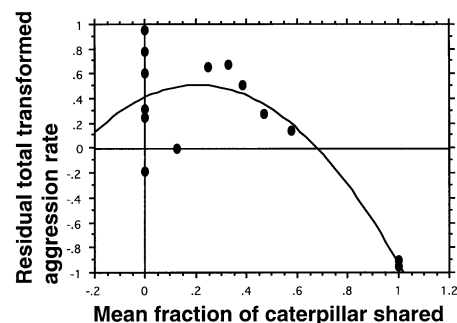

Fig. 2 Mean fraction of prey shared versus residuals from the log-transformed total rate of aggression versus temperature correlation ($r^2=0.78$, $P<0.001$)

transformed aggression rate (mean prey sharing $\beta=-1.082$, $P=0.013$; cells in comb $\beta=0.005$, $P=0.394$; number of foundresses $\beta=-0.007$, $P=0.94$).

Foundress aggression versus date and temperature

We performed multiple regressions on the alpha's and beta's transformed rates of aggression versus date (number of days since 30 April), foundress number, size of the nest in cells, and air temperature. Thus, each partial regression coefficient reported below describes the effect of the given predictor variable after the remaining predictor variables have been statistically controlled. Since each colony was observed by only one of the authors, we examined potential observer biases by also including observer identity as a two-valued random variable (0 or 1); in no analysis was a significant observer bias detected.

Both the alpha and the beta significantly increased the number of aggressive interactions they initiated per unit time as the colony cycle progressed, as indicated by significantly positive partial regression coefficients for transformed aggression rate versus date ($n=30$; alpha: $\beta=+0.047$, $P=0.0008$; beta: $\beta=+0.050$, $P=0.0037$). The alpha's rate of aggression increased significantly as the air temperature increased ($\beta=+0.049$, $P=0.001$), but the beta's rate of aggression was not temperature dependent ($\beta=+0.0054$, $P=0.742$). The number of cells in the comb (alpha: $\beta=+0.003$, $P=0.409$; beta: $\beta=+0.008$, $P=0.100$) and the number of foundresses on the nest (alpha: $\beta=+0.022$, $P=0.677$; beta: $\beta=-0.002$, $P=0.980$) were not significant predictors of foundress aggression rates.

The temperature dependence of the alpha's rate of aggression was not uniform over the founding period. We divided the founding period into two periods, "early" and "late," according to the median observation date. The alpha's transformed aggression rate in early colonies was not significantly related to temperature [$\beta=+0.008$ (date controlled), $P=0.87$, $n=14$]. However, the alpha's transformed aggression rate in late colonies was significantly positively related to temperature [$\beta=+0.083$ (date controlled), $P=0.004$, $n=12$]. The beta's transformed aggression rate was not sensitive to temperature in either the early or the late period ($P=0.38$ and $P=0.64$, respectively).

Foundress aggression as a function of resource control

The alpha's aggression toward the beta changed, depending on whether the beta had pulp, prey, or no resource [one-way ANOVA comparing prey (beta > alpha), pulp (beta>alpha), no resource: $F_{2,45}=6.90$, $P=0.002$; Table 1]. In particular, the alpha was significantly more aggressive when the beta had more prey than when beta had more pulp (unpaired t-test, $P=0.002$, $n=26$; Table 1). Moreover, the alpha was significantly less aggressive to the beta when the latter had more pulp than when both lacked a resource (paired t-test, $P=0.04$, $n=9$; Table 1).

Table 1 Rates of aggression by the alpha and beta toward each other in different contexts of resource control. α refers to alpha and β refers to beta. Means and SEs are only for colonies with paired data for alpha and beta aggression rates. Shown are raw aggressive acts per hour on the nest together; P-values are for comparisons of log-transformed aggression rates with paired t-tests

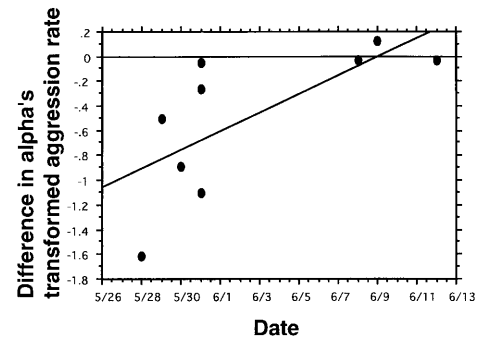| Aggression context	Alpha's aggression rate	Beta's aggression rate	Number of colonies	P-value
Overall	63±15	32±13	30	0.0003
No resource	88±23	36±15	22	0.0023
Pulp ($\alpha>\beta$)	52±13	50±14	13	0.3824
Pulp ($\beta>\alpha$)	71±34	9±4	13	0.0841
Prey ($\beta>\alpha$)	174±54	22±34	13	0.0016

Fig. 3 The alpha's aggression when the beta had more pulp minus her aggression when neither had a resource versus date ($r^2=0.49$, $P<0.04$)

When the beta had unshared prey, the alpha's aggression was positively temperature but not date dependent (multiple regression $r^2=0.593$, $n=11$; temperature: $\beta=+0.056$, $P=0.0138$; date: $\beta=+0.026$, $P=0.1843$). On the other hand, when the beta had pulp, the alpha's aggression was positively date, but not temperature, dependent (multiple regression $r^2=0.487$, $n=12$; temperature: $\beta=-0.034$, $P=0.2858$; date; $\beta=+0.160$, $P=0.0008$). Moreover, the difference in the alpha's aggression rate when the beta had more pulp versus when neither had any resource was significantly positively date dependent ($r^2=+0.49$, $P=0.04$; Fig. 3), moving from negative values early in the season to positive values late in the founding period.

The beta's aggression toward the alpha did not change significantly according to whether the alpha had prey, pulp, or neither [one-way ANOVA comparing prey (alpha>beta), pulp (alpha > beta), no resource: $F_{2,46}=0.727$, $P=0.4890$; Table 1].

Relative rates of foundress aggression versus date

The alpha's transformed rate of aggression was significantly greater than beta's transformed rate of aggression overall, when neither foundress had resource, and when the beta had more prey than the alpha (Table 1). The pro-

portion of all aggressive acts between the alpha and beta that were initiated by the alpha was significantly negatively related to date, with temperature controlled (partial $\beta=-0.015$, $P=0.018$, 25 colonies with at least some aggression by the alpha or beta).

Discussion

Our results demonstrate that aggression and resource (prey) sharing are significantly inversely related; colonies with high rates of aggression had low rates of resource sharing and vice versa. The negative relationship between aggression and resource sharing supports the transactional, and not the tug-of-war, model (Table 2). The tug-of-war model predicts a positive relationship between resource sharing and aggression because transfers of resource between individuals result purely from competition (i.e., the resource is forcibly taken by the receiver). Of course, only a fraction of a colony's aggression is related to resource transfer. However, the tug-of-war model predicts that the greater the mean level of competitive aggression on a colony, the greater the mean rate at which transfers should occur in that colony. On the other hand, the observed negative relationship is expected when most transfers represent peaceful concessions of reproduction outside the window of selfishness, as in the transactional model of within-group conflict (Fig. 1). The sharing zones outside the window of selfishness represent required payments that are given without aggression. As the sharing zones get larger, more resources are shared rather than contested and, further, the window of selfishness gets smaller, resulting in a lower mean rate of aggression. Therefore, the transactional model predicts that colonies with higher mean levels of resource sharing should have lower mean rates of aggression.

The aggression of the alpha and beta toward each other increased significantly during the founding phase, independently of temperature. Thus, aggression was lowest (and resource sharing highest) early in the founding phase, which is precisely when the beta's fraction of reproduction is highest in the *Polistes* species for which early and late reproductive skews have been estimated

(*P. annularis*: Peters et al. 1995; *P. bellicosus*: Field et al. 1998; *P. fuscatus*: Reeve et al. 1999). The transactional model predicts that reproductive sharing should be higher near the beginning of the founding phase, as the relative payoff for independent founding versus staying with the dominant is greatest at this time (Reeve 1991; Reeve et al. 1999). Thus, according to the transactional model, the subordinate should demand and receive the greatest staying incentive early in the founding phase and the window of selfishness should be particularly narrow, leading to relatively low levels of aggression. Later in the founding phase, ecological constraints on solitary breeding should increase. This will reduce the subordinate's staying incentive and widen the window of selfishness, resulting in higher levels of aggression. Our behavioral data clearly support the prediction of the transactional model for a negative relationship between degree of reproductive sharing (measured as the beta's staying incentive) and the overall level of aggression, given the skew data from other *Polistes*. The tug-of-war model predicts that aggression should be highest early in the founding phase because the overall level of aggression is predicted to be positively related to the degree of reproductive sharing at equilibrium (Reeve et al. 1998); thus, once again, the tug-of-war model makes predictions that are not supported by our results.

Studies of other species have also indicated general increases in foundress aggression through the founding period. Reeve et al. (1999) found that both the alpha and beta increased their rates of aggression over time in *P. fuscatus*, but they did not take into account the effect of seasonal temperature increases. Gamboa and Stump (1996) examined temporal changes in foundress aggression in the same species and determined that the alpha, but not the beta, significantly increased her aggression from the early to the late founding period. Gamboa and Stump (1996) controlled for the interaction rate by measuring aggression as a proportion of total interactions. However, this index may not completely correct for temperature if peaceful interactions (e.g., antennation) are less limited by colder temperatures than are energetic, aggressive interactions such as aggressive mounting. Gamboa and Stump's measure of aggression is a mea-

Table 2 Predictions of tug-of-war and transactional models in comparison to observed relationships

Relationship	Tug-of-war model prediction	Transactional model prediction	Observed
Correlation between prey sharing and aggression	+	$-$[a]	$-$ see Fig. 1
Change in aggression with time	0	+	+ Alpha: $\beta=0.047$, $P=0.0008$ Beta: $\beta=0.050$, $P=0.0037$
Alpha minus beta's aggression	$-$	+	+ see Table 1
Change in alpha's proportionate aggression with time	+	$-$	$-$ Partial $\beta=-0.015$, $P=0.018$
Temperature dependence of aggression (alpha vs beta)	Alpha=beta	Alpha > beta	Alpha > beta Alpha: $\beta=0.049$, $P=0.001$ Beta: $\beta=0.0054$, $P=0.742$

[a] A negative association between sharing and aggression is predicted, provided that most transfers are peaceful concessions (see Fig. 1)

sure of the mean aggressiveness (aggressive intensity) of a single interaction, whereas Reeve et al. (1999) measured the rate of aggressive acts regardless of mean intensity. This may explain why the two studies obtained different results regarding changes in the beta's level of aggression over the founding period.

Interestingly, we found that the alpha's aggression was strongly influenced by temperature, but only in the later founding period. If a cold-blooded creature is near its physiologically constrained activity limit, its activity level will be strongly influenced by temperature (Romoser and Stoffolano 1998). Thus, the temperature dependence of the alpha's aggression level may indicate that the alpha is near a physiological ceiling precisely when the transactional model predicts that she should be maximally aggressive. The beta's aggression rate, on the other hand, was unaffected by temperature throughout the founding phase, which indicates that the beta's aggression is usually limited by something other than energetics. This finding counters the tug-of-war model, which predicts that the beta should exhibit more selfish effort than the alpha. The two common types of selfish effort exhibited by *Polistes* are aggression and differential oophagy. Subordinates exhibit lower rates of differential oophagy than dominants (Gervet 1964). Therefore, the tug-of-war model predicts that the subordinate should be more aggressive than the dominant, as aggression is the other outlet for selfish effort. Although our findings counter the tug-of-war model, they support our newly derived prediction from the transactional model (see above) that the beta should be more restrained than the alpha in her aggression, and more likely to share resources: the beta's sharing zone (Fig. 1) is wider than the alpha's, and her high foraging rate means that she initially controls resources more frequently than does the alpha. If the beta is too aggressive and selfish, she risks ejection by the alpha, so she should frequently cede resources and reproduction to the alpha.

Thus, this prediction of the transactional model offers a likely explanation for why the alpha's overall level of aggression exceeded the beta's (Table 1), again contradicting the tug-of-war model prediction (Reeve et al. 1998). We also showed (above) that the transactional model predicts that the proportion of aggressive interactions between the alpha and beta that are initiated by the alpha should decline as the window of selfishness increases, i.e., as the aggression levels increase later in the founding period. This is indeed what we found (see Results), and this finding refutes the prediction of the tug-of-war models (Table 2), because the solutions for the evolutionarily stable efforts in the tug-of-war model (Reeve et al. 1998) imply that the ratio of the alpha's to the beta's selfish effort should increase with increasing overall aggression.

Our evidence indicates that the alpha modulated her aggression toward the beta according to the latter's control of resources. In particular, the alpha exhibited greatly heightened aggression toward the beta when the beta controlled more prey than the alpha and significantly less aggression when the beta controlled more wood pulp than the alpha (see Results; Table 1). These results suggest that the beta's control of prey may be a greater selfish threat to the alpha than the beta's control of pulp. This is plausible, since the beta may obtain nutrients critical for reproduction from imbibing the hemolymph of malaxated prey before feeding the prey to the larvae (Hunt 1984, 1994). On the other hand, the beta usually used pulp to enlarge nest cells (personal observation), an activity that may benefit the alpha. However, the beta's control of pulp may entail some risk to the alpha as the beta occasionally used the pulp to construct new, empty brood cells (personal observation) into which the beta is especially likely to lay an egg.

An alpha's rate of aggression toward a beta with prey remained high throughout the founding phase, exhibited no date dependence, and was strongly influenced by temperature. A transactional interpretation of this result might be that sole possession of prey always causes the beta to have more than her minimal staying incentive, so the alpha always challenges the beta's sole possession of prey. In contrast, an alpha's aggression toward a beta with pulp increased over the founding phase and was not temperature dependent. Moreover, the temperature-controlled difference in the alpha's aggression rate when the beta had more pulp versus when neither had any resource was significantly positively date dependent, moving from negative values early in the season to positive values late in the founding period (Fig. 3). The latter patterns suggest that, early in the founding period, an alpha actually suppresses her aggression toward a beta with pulp. Perhaps allowing the beta to use pulp to construct new cells (into which the beta may lay an egg) constitutes part of the beta's staying incentive. Later in the season, as the beta's staying incentive decreases and the window of selfishness widens, the alpha may be less willing to concede pulp to the beta.

In summary, our behavioral observations decisively support the transactional and not the tug-of-war model of within-group conflict (Table 2). The predictions of the two models are so diverse and sharply opposed that we predict much progress will soon be made in assessing the applicability of each model to social evolution in a wide variety of taxa. Our results support the possibility that reproductive transactions, and the limits to selfishness that their existence implies, may be central features of social organization.

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