ORIGINAL PAPER

Two experimental tests of the relationship between group stability and aggressive conflict in *Polistes* wasps

Elizabeth A. Tibbetts · Hudson Kern Reeve

Abstract Two field experiments were used to examine how the relative benefits of cooperation influence within-group conflict in foundress associations of the paper wasp *Polistes dominulus*. *P. dominulus* foundresses can either nest alone or cooperate with other foundresses. We experimentally manipulated the relative benefits of co-foundress associations vs independent reproduction and tested the effect on aggressive within-group conflict. First, we examined aggression between alpha and beta co-foundresses before and after lower-ranking foundresses were removed. Removal of subordinates increases the relative contributions of the remaining subordinates to group reproductive output as there are fewer adults to care for the brood. Transactional models predict that group conflict over reproductive shares will increase as the relative benefits of grouping increase. As predicted, aggression between the co-foundresses significantly increased following subordinate removal. Second, we experimentally reduced ecological constraints on independent nesting by placing a previously orphaned, adoptable nest comb near the occupied nests. Providing an independent breeding opportunity is predicted to increase the benefits of independent reproduction relative to those of cooperating, thereby reducing group stability and aggression. As predicted, aggression between dominant and subordinate foundresses significantly decreased after the orphaned comb was presented. Therefore, group members sense variation in ecological constraints and relative productivity contributions and quickly modulate their behavior in response. Overall, these two experiments suggest that paper wasps behave as if within-group competition is limited by the threat of group dissolution such that stable groups where cooperation is strongly favored can withstand higher levels of conflict than unstable groups.

E. A. Tibbetts (✉)
Ecology and Evolutionary Biology, University of Michigan,
Ann Arbor, MI 48109, USA
e-mail: tibbetts@umich.edu

H. K. Reeve
Department of Neurobiology and Behavior, Cornell University,
Ithaca, NY 14853, USA
e-mail: hkr1@cornell.edu

Introduction

Even the most cooperative social groups experience conflict. The degree of conflict can vary markedly from species to species and between different groups of the same species. Consequently, there has been strong interest in identifying the factors that influence the extent of within-group conflict (Clutton-brock and Parker 1995; Ratnieks et al. 2006). Recently, quantitative models of conflict within animal social groups have arisen. These models explore how conflict is mediated and predict the factors that influence the degree of conflict within groups (Reeve and Ratnieks 1993; Johnstone 2000; Reeve and Keller 2001; Reeve and Shen 2006).

Transactional models are models of within-group conflict which predict that group stability is influenced by the relative reproductive benefits of cooperation. When cooperation provides a net reproductive benefit, reproduction within a group is expected to be divided such that each individual does better by cooperating than they would by nesting independently. As a result, groups are expected to be stable when cooperation provides a net benefit. On the other hand, if the group's reproductive output is smaller than the sum of the group members' potential individual reproductive output,

groups are predicted to become unstable and dissolve. Therefore, transactional models predict that groups will be stable whenever there is a net benefit to cooperation and larger benefits of cooperation will yield groups with greater net stability (Reeve and Ratnieks 1993).

Transactional models also predict that group stability influences within-group conflict over reproductive shares. Stable groups are expected to withstand higher levels of conflict than unstable groups. As a result, conflict over reproductive shares is predicted to increase when group living is more strongly favored and decrease when group living is less strongly favored (Reeve 2000; Reeve and Shen 2006). This occurs because there is more 'extra' reproduction to compete over when cooperation is more strongly favored. For example, imagine a two-individual group in which the dominant requires at least three units of reproduction to cooperate instead of leaving to nest independently, while the subordinate requires two units of reproduction to cooperate instead of leaving to nest independently. If cooperation is strongly favored such that the total group output is ten units, the group members can compete over the remaining five reproductive units (case 1). However, if the group is near the break-even point such that the total group output is only five units, there is no 'extra' reproduction to compete over (case 2). Consequently, conflict over reproductive shares is predicted to be lower in the group in which there is relatively smaller benefits of cooperation, as in case 2. This prediction has not been tested (Cant 2006), so we propose to experimentally test whether animals repeatedly assess the relative benefits of cooperation and modify their aggression levels in response.

The social flexibility of *Polistes* paper wasps makes them a good system for testing the factors that influence the degree of aggression within groups. Nests can be founded by one or many overwintered, inseminated female wasps (foundresses). Foundress groups benefit through increased productivity, reduced risk of nest usurpation, and higher individual and colony survival, but single foundress nests are common and successful (West-Eberhard 1969; Tibbetts and Reeve 2003). When multiple foundresses cooperate, they form a linear dominance hierarchy. Within the hierarchy, dominants do the least work and receive the largest share of reproduction (Reeve 1991; Queller et al. 2000; Reeve et al. 2000). Group composition is flexible and subordinate group members can leave their original group to nest alone or join another group (Nonacs and Reeve 1993, 1995). Aggression levels between co-foundresses vary considerably from nest to nest and generally increases from nest foundation until worker emergence (Gamboa and Stump 1996; Reeve and Nonacs 1997; Tibbetts and Reeve 2000; Cant et al. 2006).

Aggression has multiple functions in animal societies. According to a recent review (Cronin and Field 2007),

aggression in societies of totipotent individuals reflects three main types of conflict: (1) conflict over work (Reeve and Gamboa 1987; Clutton-Brock and Parker 1995; O'Donnell 2001; Sumana and Starks 2004; Nonacs et al. 2004), (2) conflict over reproductive shares (Reeve and Ratnieks 1993; Tibbetts and Reeve 2000), and (3) conflict over anticipated future fitness (e.g., nest inheritance; Cant and Johnstone 2000; Cant et al. 2006). In this study, we used a paired experimental design to isolate the effect within-group conflict over reproductive shares on aggression. We measured aggression before and after experimentally manipulating the relative benefits of cooperation. Transactional models predict that, as the relative benefits of cooperation increase, group stability will increase, and conflict over reproductive shares will also increase. As the relative benefits of cooperation decline, groups will become less stable and conflict over reproductive shares will decline.

We examined aggression within foundress groups of the temperate wasp *Polistes dominulus* as part of two experimental tests of the relationship between the relative benefits of cooperation and aggressive within-group conflict. First, we altered the subordinate's contribution to group productivity by removing lower-ranked subordinate foundresses from nests. The removals increased the benefits of grouping relative to the group members' potential solitary breeding success. Transactional models predict that aggressive conflict over division of the colony's future reproductive shares will increase as the relative benefits of grouping increase (Reeve and Shen 2006). Second, we tested how increasing potential for solitary breeding influenced group conflict. We presented a solitary breeding opportunity to the subordinate by placing a previously orphaned, adoptable nest comb full of pupae near the foundresses' original nest. Workers readily adopt advanced nests. They use the workers raised by the previous queen to rear their own reproductive-destined offspring (Nonacs and Reeve 1993, 1995). As solitary breeding opportunities improve, there will be a smaller net reproductive benefits for grouping, and aggressive conflict over reproduction within the colony is expected to decline (Reeve and Shen 2006).

Materials and methods

Behavioral observations were conducted on a total of 20 naturally nesting, multiple-foundress colonies of *P. dominulus* in the late spring and early summer during the founding (pre-worker) phase of the colony cycle. We found these nests on the eaves of houses and barns in rural and semi-rural areas including the Liddell Field Laboratory near Ithaca, New York. We discuss separately the general procedures and those specific to the two experimental studies, the subordinate removal study and the comb transplant study.

General procedures

Foundresses were marked individually with paint on the thorax from May 8, 1999–June 10, 1999. After marking, each colony was either videotaped or observed directly until the dominance rank of each foundress could be ascertained (prior to experimental manipulations). Dominance rank was assessed by stereotypical dominance interactions such as mounting and by relative time spent on the nest, as in many other studies (e.g., Tibbetts and Reeve 2000, 2003).

In both experiments, colonies were videotaped for 2 h on the day immediately before manipulation (control observations) and again for 2 h at the same time on the day immediately after manipulations (treatment observations). Colonies in the comb transplant study were also videotaped up to several days after manipulation (see below). In all cases, videos were recorded while wasps are most active between noon and 3 P.M. Shade air temperature was recorded during the taping sessions.

Before videotape transcription, the labels for control and treatment videotapes were masked. The videotapes were randomly chosen for transcription from the pool of all tapes for all colonies in both experiments to reduce or eliminate observer knowledge about the treatment status of an observed colony. From the videotapes, we recorded all aggressive encounters including darts, lunges, mounts, bites, and grapples (see Reeve 1991). Rate of aggression was calculated as the number of aggressive acts directed toward the alpha or beta-foundress per hour that they 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).

Since temperature affects rates of aggression, particularly for the alpha foundress (Tibbetts and Reeve 2000), we controlled for temperature differences between control and treatment observation days. First, we used control data to establish a regression between (transformed) aggression rate and temperature (across colonies). Treatment effects on aggression were then computed as residuals from the regression line generated by the control data, taking into account colony-specific effects on aggression in the controls. In other words, residuals were computed as log (aggression rate after treatment+1) minus the predicted log (aggression rate after treatment+1; where the predicted value was computed from the control regression line, given the treatment temperature) minus the colony's residual log-transformed control aggression rate around the control regression line. Subtracting the latter term accounts for between-colonies differences in aggression that are independent of temperature.

Two-tailed parametric statistical tests were used when normality assumptions appeared to be satisfied; otherwise, two-tailed non-parametric tests were used. In all statistical tests, colonies were treated as the independent data points. Means are reported with their standard errors, unless otherwise noted.

Subordinate removal study

Between June 2 and June 10, 1999, all foundresses other than the alpha and beta were removed from each of ten three-plus-foundress colonies the morning after each colony had been videotaped for 2 h (mean number of foundresses per nest before removal=3.5, range 3–5; mean number of foundresses removed=1.5 foundresses, range=1–3). Foundresses were gently removed by a wing with medical hemostats around 6–7 A.M. (when the nests are cool, and colony activity is low). Such removal simulates the natural disappearance of foundresses due to predation. Several prior studies have shown that the low disturbance associated with morning removal of a *Polistes* foundress by itself does not affect colony activity later the same day (Reeve and Gamboa 1987; Reeve and Nonacs 1992; also see disturbance control for "comb transplant" study below). On the afternoon after subordinate removal, the colonies were observed for another 2 h (see "General procedures"). We also recorded the air temperature during observations (mean temperature during pre-removal observations=27.3°C, range=24–31°C; mean temperature during post-removal observations=23.2°C, range=21–31°C).

Comb transplant study

Between June 11 and June 16, 1999, control observations were made on seven two-foundress colonies. All nests used in this experiment had only two foundresses. We recorded the air temperature during observations (mean temperature before nest comb addition = 27.9°C, range = 21–31°C; mean temperature during post-removal observations = 23.2°C, range = 25.5–30.5°C).

Two of the multiple-foundress colonies were used as controls in the subordinate removal study 2–3 days before control observations of the current study. Immediately after control observations, orphaned nest combs from distant (>1 km) sites were attached to the nesting substrate 15–20 cm away from five multiple-foundress colonies (one orphaned comb per colony) between 2 and 3 P.M. The mean size of the original nest was 53±16 (x±SD) cells, and the mean size of the transplant nest was 47±16 cells. All cells contained either eggs or brood. Treatment observations were made the following day. Orphaned combs were created by removing the solitary foundress from nests that contained live brood. For each of two additional treatment colonies, a solitary foundress naturally nesting within 20 cm of the multiple-foundress colony was removed from her comb to

create an adoptable comb. There was no marked difference in observed aggression levels on the naturally occurring and artificially added combs [residual (sum of aggression)= −0.20 (SE=0.06) for experimental transplant, residual (sum of aggression)=−0.46 (SE=0.40) for natural orphaning], although the sample sizes are too small for a statistical comparison.

This experiment simulates the sudden availability of an adoptable comb due to the death of a nearby solitary foundress. Orphaned combs, particularly large, mature combs, are naturally adopted by *P. dominulus* foundresses (including subordinate foundresses; Nonacs and Reeve 1993, 1995). These adoptable combs represent an independent breeding opportunity for subordinate foundresses, as the combs are full of pupae that will emerge as workers and help a new queen rear her own offspring. Indeed, daily censuses of comb transplant colonies for 1 week after transplant revealed that the beta foundress moved to the orphaned comb, at least temporarily, in six of seven cases. In these six cases, we videotaped interactions between the alpha and beta foundresses for an additional 2 h (according to the "General procedures") after such beta movements had been detected. In two of the six cases, the interactions were videotaped on the transplant comb instead of in the original comb (the prediction of reduced aggression applies even when both foundresses move to the transplant comb since, in this case, there is still a healthy, unoccupied comb nearby). Of course, aggression rates were only recorded when alpha and beta were on either the original or the transplanted comb together.

To control for disturbance associated with comb attachment, on June 21–22, 1999, orphaned, adoptable combs were placed near five control multiple-foundress colonies as above, but then immediately removed. Only total foundress rates of aggression were measured in these "disturbance control" colonies, since foundresses in these colonies were not marked. "Control" and "treatment" videotape observations were made on these disturbance control colonies as described in the "General procedures".

Results

Subordinate removal study

The mean change in raw (untransformed) rate of total aggression between pre-removal and post-removal observations was positive (33.3±35.8/h), as were the mean changes in alpha's raw rate of aggression toward beta (17.6±29.0/h) and beta's raw rate of aggression toward alpha (15.7±11.2/h). However, these changes could be potentially influenced by any temperature differences between control and treatment observations (Tibbetts and

Reeve 2000), so we corrected for temperature changes before statistical analysis.
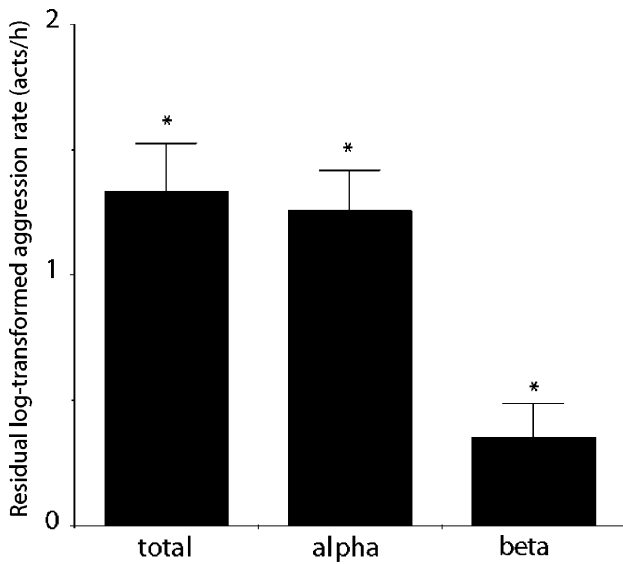
During the control observations, there was a strong, significantly positive correlation between the alpha's transformed aggression rate and temperature ($r_{10}=0.83$; $F=17.3$; $P=0.003$) and between the transformed total aggression rate and temperature ($r_{10}=0.75$; $F=10.6$; $P=0.012$), but not between beta's transformed aggression and temperature ($r_{10}=0.35$; $F=1.1$; $P=0.328$) (see also Tibbetts and Reeve 2000). Thus, we controlled for temperature differences between control and treatment observations for alpha's aggression and total aggression by expressing these transformed treatment aggression rates as residuals (observed minus expected values) from the regression of the appropriate transformed aggression rate on temperature in control observations (see "Materials and methods" for details).

The mean residual transformed total aggression rate (aggression after removals) was significantly greater than zero (1.329±0.199; $n=10$; $t=6.66$; $P<0.0001$, one-sample t test), demonstrating that temperature-adjusted total aggression rate significantly increased after subordinate removal. The mean residual transformed aggression from alpha toward beta was significantly greater than zero (1.253± 0.177; $t=7.09$; $n=10$; $P<0.0001$, one-sample t test), demonstrating that alpha significantly increased its temperature-adjusted rate of aggression toward beta when subordinates were removed. The beta's transformed rate of aggression toward alpha (which does not require temperature adjustment) also significantly increased when the subordinates were removed (mean change = 0.351±0.138; $t=-2.55$; $n= 10$; $P=0.032$, one-sample t test; Fig. 1).

The increase in alpha's and beta's level of aggression toward each other following subordinate removal is not simply the result of each focusing a fixed amount of aggression on the sole remaining co-foundress, instead of distributing it across all original co-foundresses; it is well documented that alpha and beta females focus most of their aggressive interactions on each other even when other foundresses are present (Downing and Jeanne 1985; Reeve 1991). Moreover, a multiple regression analysis revealed that alpha's transformed rate of pre-removal aggression toward beta was not significantly associated with the number of foundresses (partial regression coefficient=−0.094; $t= −0.361$; $P=0.73$, temperature controlled), and a beta's transformed rate of pre-removal aggression toward alpha was not significantly correlated with the number of foundresses (regression coefficient=−0.044; $F=0.10$; $P=0.92$).

Comb transplant study

The mean change in raw (untransformed) rate of total aggression between pre-transplant and post-transplant observations was negative (−34.4±41.7/h), as were the

Fig. 1 Subordinate removal study. Each *bar* shows the temperature-corrected changes in transformed aggression rate (+SE). In every case, aggression significantly increased after subordinate removal
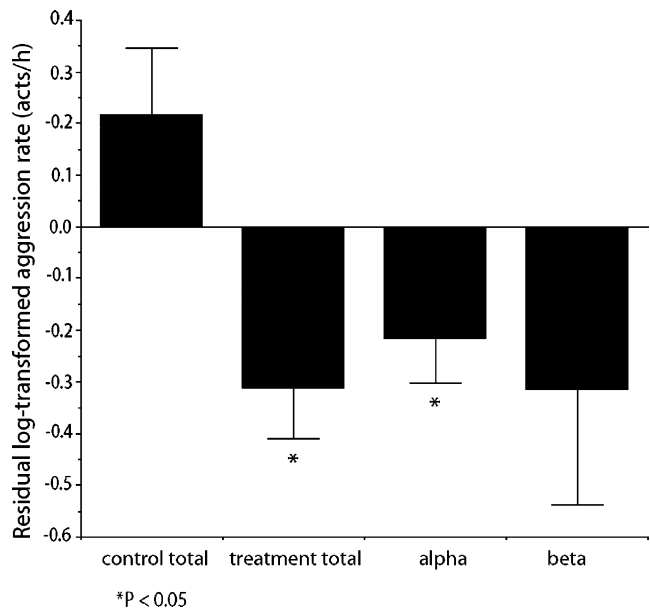
*P < 0.05

mean changes in alpha's raw rate of aggression ($-29.3\pm36.3/h$) and beta's raw rate of aggression ($-5.08/h\pm9.29/h$). However, these changes are potentially confounded by temperature differences between control and treatment observations (Tibbetts and Reeve 2000).

As before, control observations demonstrated a strong, significantly positive correlation between the alpha's transformed aggression rate and temperature ($r_7=0.94$; $f=37.0$; $P=0.002$) and between the transformed total aggression rate and temperature ($r_7=0.85$; $f=37.6$; $P=0.004$), but not between beta's transformed aggression and temperature ($r_7=0.25$; $f=0.342$; $P=0.584$). Thus, we controlled for temperature differences between control and treatment observations for alpha's aggression and total aggression by expressing these transformed treatment aggression rates as residuals (observed minus expected values) from the regression of the appropriate transformed aggression rate on temperature in the control observations (see "Materials and methods" for details).

The mean residual transformed total aggression rate (aggression after comb transplant) was significantly less than zero (-0.277 ± 0.097; $n=7$; $t=-2.55$; $P=0.043$, one-sample t test), demonstrating that temperature-adjusted total aggression rate significantly decreased after the orphaned comb was transplanted. Moreover, the mean residual transformed total aggression rate for the seven treatment colonies (mean$=-0.352\pm0.101$), with the disturbance control colonies now contributing to the pre-treatment regression of log aggression rate on temperature, was significantly less than that for the five control colonies (mean$=0.216\pm0.154$; $t=-3.55$; $n=12$; $P=0.006$, unpaired t test), eliminating disturbance due to comb transplantation as a possible cause

for the reduced aggression. The mean residual transformed aggression for alpha was significantly less than zero (mean$=-0.247\pm0.074$; $t=-3.10$; $n=7$; $P=0.015$, one-sample t test). The beta's transformed rate of aggression toward alpha did not significantly change (mean change$=-0.093\pm0.126$; $t=0.739$; $n=7$ $P=0.488$, one-sample t test).

We also examined changes in aggression rate between the pre-removal control observations and observations conducted after the beta had been seen attending the transplant comb ($N=6$ colonies). The mean residual transformed total aggression rate was significantly less than zero (-0.331 ± 0.086; $t=-3.30$; $n=6$; $P=0.012$, one-sample t test), demonstrating that temperature-adjusted total aggression rate significantly decreased after the beta had been seen on the transplant comb (Fig. 2). The mean residual transformed aggression for an alpha was also significantly less than zero (-0.228 ± 0.051; $t=-3.50$; $n=6$; $P=0.007$, one-sample t test), demonstrating that alphas significantly decreased their aggression toward the beta after she had been seen on the transplant comb (Fig. 2). Moreover, this decrease was not significantly different from the levels of aggression observed just after comb transplantation [after transplant residual (sum of aggression$\pm$SE)$=-0.314\pm0.1$; after beta was seen on transplant residual (sum of aggression$\pm$SE)$=-0.277\pm0.110$; $P=0.77$; $n=6$; $t=-0.305$, two-tailed paired comparisons t test]. A beta's transformed rate of aggression toward an alpha decreased, but not significantly (mean change$=-0.316\pm0.220$; $t=-1.40$; $n=6$; $P=0.2101$, one-sample t test).

*P < 0.05

Fig. 2 Comb transplant study. Each *bar* represents the temperature-corrected changes in transformed aggression rate (+SE). There was no significant change in total aggression rate after the control treatment, but total colony aggression and alpha aggression rate significantly declined after nest comb addition. Beta aggression also declined, but not significantly

Discussion

Two field experiments were used to test how group stability influences aggressive within-group conflict. We found that paper wasps quickly altered their level of aggressive competition in response to changes in subordinate contributions to group productivity and ecological constraints. Overall, individuals behave as if group conflict is limited by the threat of group dissolution.

In the first experiment, we examined how removing low-ranked subordinates influenced aggression. Subordinate removal increases the relative contributions of the remaining foundresses to group reproductive output as there are many needy brood with fewer adults to provide care. As a result, subordinate removal increases the benefits of grouping relative to the potential benefit of independent reproduction. Consequently, groups are expected to stabilize, allowing more conflict over reproductive shares within the colony (Reeve and Shen 2006) and increased aggression levels. As predicted, the temperature-corrected mean rates of alpha and beta aggression significantly and markedly increased in colonies after lower-ranking subordinates were removed.

The increase in aggression between alpha and beta after removal of other group members does not result from each focusing a fixed amount of aggression on each other rather than distributing it among all colony members. Alpha and beta females are known to focus their aggressive interactions on each other, even when other foundresses are present (Downing and Jeanne 1985; Reeve 1991). Furthermore, alpha and beta's aggression toward each other does not depend on the number of other foundresses present (see "Results"). Removal of low-ranking subordinates may have altered the other activity patterns of the alpha and the beta by increasing time spent in brood care. However, increased brood care is usually associated with lower aggression levels in *Polistes* colonies (Nonacs et al. 2004). Therefore, the increased aggression observed during experiment one indicates increased conflict over reproductive shares following subordinate removal.

In the second experiment, we examined how the expected success of a solitarily breeding subordinate influenced aggression levels. Adding a breeding opportunity for the subordinate increased the potential benefits of leaving the group, thereby decreasing the subordinate's relative benefits of cooperation. As a result, there will be less 'extra' reproduction to compete over, so transactional models predict that the dominant's aggression toward the subordinate will decline (Reeve and Shen 2006). We tested the latter prediction by measuring aggression between alpha and beta foundresses before and after a previously orphaned, adoptable nest comb, representing a solitary

breeding opportunity for the subordinate (Nonacs and Reeve 1993, 1995), was placed near the foundresses' nest. As predicted, alpha's temperature-corrected rate of aggression significantly decreased when the orphaned comb was present. Beta's aggression rate also declined, but not significantly. The differential response of alpha and beta to nest comb addition suggests that the cooperation provides different benefits to the co-foundresses. The non-significant change in beta's aggression suggests that the beta may be near the break-even point, receiving similar payoffs for cooperating and dispersing. In contrast, the consistent drop in alpha's aggression suggests that alphas had a stronger interest in maintaining group stability, perhaps because they received larger benefits through cooperation than subordinates. Therefore, experimental manipulation of group stability may provide insight into which individual controls group membership and receives the biggest benefits through cooperation.

Skew models have been the source of much debate (Johnstone 2000; Cant 2006; Liebert and Starks 2006; Nonacs et al. 2006), and there are still major gaps in empirical research on the topic. In this paper, we used field experiments to assess the premise of transactional skew models, by testing whether group conflict is influenced by the relative benefits of cooperation. We found that the relative benefits of cooperation influence aggression such that stable groups have higher levels of within-group aggression than unstable groups, as predicted by transactional models (Reeve and Shen 2006). Paper wasps sense variation in ecological constraints and subordinate productivity contributions and quickly modulate their social interactions in response. Further tests to assess the impact of group stability in other taxa are important.

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