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The rise and fall of transactional skew theory in the model genus *Polistes*

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Transactional Skew (TS) theory predicts that cooperative breeding associations can be adaptive for all group members as long as they properly allocate reproduction within a social contract. *Polistes* wasps have been the preeminent model genus for testing TS models. Most tests have focused on either the patterns of skew or on patterns of aggression between wasps, which has been assumed to set skew. However, the totality of evidence suggests that aggression (observed as darts, lunges and bites) has no connection to establishing reproductive skew. Although some patterns of reproductive skew support TS theory, most of the reproductive data are either non-supportive or inconclusive relative to the models. Of particular significance are recent findings of high skew associations between distantly or unrelated wasps when TS theory strongly predicts skew should be low. A possible evolutionary explanation for the failure of TS models is derived through a simple model. Although the TS strategy optimizes fitness, its relative advantage over a much simpler conventional rule for group formation is never greater than 3% and often less. Therefore, even small costs in evolving the cognitive mechanisms needed to form social contracts may preclude their appearance. Although TS theory may have failed in *Polistes*, reproductive skew is now a well-described phenomenon. Finding new viable explanations for reproductive skew and extending the theory to skews in non-reproductive contexts will maintain *Polistes* in its role as a model taxonomic group in the study of the evolution of social behavior.

Introduction

Over the last decade, the genus *Polistes* has played a pivotal role in the development of models for the evolution of cooperation through shared reproduction. The basic premise, which is best known as Transactional Skew (TS) theory, is that under a wide range of ecological conditions individuals can cooperate to achieve reproductive success (Reeve 2000). All members of the group should achieve inclusive fitness equal or exceeding that which they could gain by living solitarily.

As with many models concerning the interactions of possible genetic relatives, the history of TS theory traces back to William D. Hamilton's (1964) original insights. The simplicity of Hamilton's rule is that altruistic cooperation is favored whenever the benefit gained by the recipient, weighted by the recipient's genetic relatedness to the altruist, exceeds the cost of the act to the altruist. This is, of course, immortalized as $rb > c$. Almost 20 years after Hamilton's paper, a major new advance appeared in the work of Sandra Vehrencamp. Vehrencamp persuasively argued in two synchronous publications (1983a, 1983b), that within any cooperatively-breeding group it is to the dominant's advantage to appropriate as much reproduction as it can. The dominant's level of selfishness is checked only by the threat of over exploited subordinates leaving the group. Exactly how much reproduction the dominant can take before reaching the subordinates' departure threshold is affected by genetic relatedness, group productivity, and the expected success rate of individuals on their own. This was the birth of reproductive skew theory predicting that groups would have biased reproduction (i.e., skewed) in favor of dominant members.

Despite the rigor of Vehrencamp's arguments, the application of skew theory to the evolution of cooperation languished for another decade. The next major advance took place in 1993 with the publication of two book chapters by H. Kern Reeve and Francis Ratnieks, and by Laurent Keller and Edward Vargo[1]. Reeve and Ratnieks (1993) explicitly quantified the range of skew that could be possible between two cooperating individuals. From their equations they derived a minimum ratio of group versus solitary productivity above which cooperation could be adaptive for all individuals (this is the stability condition). If group productivity exceeds this threshold, a potential range of adaptive skews can occur. One end of the range is bounded by the most extreme skew the dominant can demand before the subordinate leaves the group. The other end is bounded by the maximum amount of reproduction a subordinate can claim without being evicted[2]. This range of reproductive skew is greatly affected by relatedness. All other things being equal, the range of adaptive skews increases with genetic relatedness. However, the truly exciting insight is that if the stability condition holds, any individuals can form a stable social contract by properly adjusting the level of reproductive skew. Fitness-enhancing cooperation is not restricted to close genetic kin, or even to kin at all. Thus, transactional skew theory was born.

In parallel to the development of TS theory, Kern Reeve and I were manipulating patterns of reproduction on nests of *P. fuscatus*. As seemed entirely consistent with the existence of a social contract, removal of eggs affected the pattern of aggression between the dominants and their subordinates (Reeve & Nonacs 1992, 1993, 1997). The combination of a model that was broadly applicable across many species, new molecular and statistical techniques to quantify reproductive skew, and a model system highly amenable to experimentation triggered an explosion of work on the evolution of cooperation. The full history of the rise and the promise of TS theory is well documented elsewhere (Reeve 1998, 2001, Reeve & Keller 2001). In this paper, I instead track the apparent demise of TS theory in *Polistes*.

A plethora of model variants and predictions

The original skew models of Vehrencamp (1983a, 1983b) and Reeve and Ratnieks (1993) assumed that reproductive shares were determined by the dominant. This variant of a TS model has come to be known as the "Concession" model, because the dominant concedes reproduction to entice subordinates to stay (Clutton-Brock 1998). Relaxing this assumption of total dominant control led to other variants of TS models. One model assumes that dominants control group membership but cannot enforce sterility on subordinate group members (Cant 1998,

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[1] This is not to imply that Vehrencamp's original papers disappeared into obscurity. Indeed, in the years 1984–1993, 57 papers cited one or both of her papers (citation search through ISI Web of Science®). This is an enviable citation average rate of 5.7 new papers per year! Nevertheless, after the publication of the book edited by Laurent Keller in 1993, Vehrencamp's papers were clearly discovered by a much wider audience. From 1994–2004, her two papers are cited by an average of 20.9 new papers per year, reaching a maximum citation rate of 29 times in 2000.

[2] *See* the original literature for the equations of the skew models. The most expansive model derivations are given by Johnstone (2000) and Nonacs (2002).

Johnstone & Cant 1999a). Thus, reproduction by subordinates is limited only by the threat of eviction. Absolute subordinate control over their own reproduction is now best known as a "Restraint" model, in that subordinates restrain themselves rather than being policed into not making more offspring (Reeve & Keller 2001). If neither dominant nor subordinate entirely determines reproductive shares, a "Tug-of-War" situation ensues where the final skew reflects the relative competitive abilities of the interactants (Reeve *et al.* 1998a, Johnstone 2000). Two variants of models for TS theory have also sought to incorporate population ecology into their predictions. The first is known as the "Bidding Game" where multiple neighboring groups allow potential subordinates to choose which dominant they will join (Reeve 1998). Dominants are thus forced to offer valuable subordinates better reproductive skews than they might receive from competing dominants. If, however, nest sites or territories are limited and population density is high, subordinates may have relatively few groups available for joining. Groups become "Saturated" in that productivity constraints set a maximum group size (Reeve & Emlen 2000). When a group is saturated, subordinates stop joining because they do better by joining other smaller groups or remaining solitary.

Although all five models trace their origins to Hamilton (1964) through Reeve and Ratnieks (1993) and Vehrencamp (1983a, 1983b), previous treatments have separated the Tug-of-War model out of the transactional fold and specially identified it as a "Compromise" model (Reeve 2000, Reeve & Keller 2001). I disagree with this treatment. The only unique feature of the Tug-of-War model is a prediction of consistently high aggression between dominants and subordinates. In the other models, aggression may be implied rather than continually expressed, such that it occurs only under specific circumstances (e.g. as punishment for altering agreed upon levels of skew, Reeve & Nonacs [1992]). If the definition of a 'transaction' is expanded to include both reproduction and the aggressive acts that determine reproductive share, Tug-of-War is clearly well within TS theory. Indeed, Johnstone (2000) demonstrated that a single TS model can potentially incorporate an entire continuum of outcome ranging from Concession, through Tug-of-War, to Restraint. Recently Reeve and Shen (2006) claimed to derive a new model, called the Bordered Tug-of-War, which generates a radically new prediction: that skew is set only relative to the expected success group members would have on their own. Neither relatedness, competitive ability, nor expected group productivity have any effect on skew. However, these conclusions rest on two dubious assumptions. First, that at the ESS solution all group members must have fitness within the group that is exactly identical to the fitness they would expect as solitary individuals. Second, that when an individual has equal fitness as a group member to its solitary fitness, it will always choose to be in a group. Relaxing these flawed assumptions (P. Nonacs unpubl. data) reveals that the new model is just a particularly arbitrary version of the more general Tug-of-War model (from Reeve *et al.* 1998a).

All model variants share the unique TS theory property of being dynamic across groups. Thus, social groups within the same population can have very different reproductive skews reflecting each group's specific combination of genetic relatedness and competitive ability. This dynamism in predicted skew levels is in stark contrast to a "Conventional" process of group formation (Nonacs 2001, Seppä *et al.* 2002). Conventions predict that group formation reflects a given asymmetry between group members (e.g. size, age, order of joining the group, etc.). The conventions establish a dominance hierarchy with minimal aggression and evaluation of the characters of a potential partner. This leads to a prediction of similar skews across groups and independent of whatever traits are not part of the convention.

Although the five major variants of TS models follow from the same general theory of maximizing inclusive fitness, they vary widely in their predictions and sometimes predictions also vary within a model depending on the set of assumptions (Table 1)[3]. This creates a logical dilemma: no matter what the results of an experiment or a natural observation are, they may broadly support TS theory because they are likely to be consistent in some way with at least one model variant. Therefore, it has been argued that tests of TS theory must first clearly identify the variant that is most likely to apply (Clutton-Brock 1998, Magrath & Heinsohn 2000). A seemingly perfect example of this confusion is in the observed patterns of reproductive skew on *P. bellicosus* nests. Field *et al.* (1998) interpreted them as definitively rejecting a Concession model. The results were then later reinterpreted as either support for a Tug-of-War model or the Saturated extension of the Concession model (Reeve & Keller 2001). Further complicating the testing of TS models is that relationships that include solitary individual productivity (x) are best measured at a population level. It is impossible to know what x could have been for an individual that decides to be a subordinate. Average values can be estimated for populations, but individual variation in condition may mean that each wasp perceives different expected values of x (and therefore a different relative advantage in increasing group productivity, k). Thus studies that claim to alter x and k (as in Reeve & Nonacs [1997]), have no quantitative estimate as to how much they are changed for the individuals involved. Comparing populations that vary in these two parameters can provide correlative support for TS theory, but causation through experimental manipulation cannot be addressed at this level.

Fortunately, the testing of TS models can proceed by exploring the basic premises of the models. First, there must be a mechanism that wasps use to establish dominance and skew in a TS framework. This mechanism has been proposed as the rate and intensity of pairwise aggression. A direct connection of aggression to skew in TS theory predicts correlations through a number of measurable factors (Table 1). Further, aggression can indirectly influence some relationships and thus cause interaction effects. For example, the Tug-of-War model makes specific predictions that aggression will detract from caring for brood, and that relatives should fight less. Therefore, closer relatives should have larger nests (Langer *et al.* 2004).

Most of the remaining predictions are about the level of skew itself. Testing them requires the genetic analysis of both adults and brood. Finally, mostly in relation to the Saturated variant, there are a couple of predicted effects on group size (Reeve & Emlen 2000). Therefore to trace the demise of TS models in *Polistes*, I will first explore how the patterns of aggression fail to connect to skew. Second, I will review how TS models fail to predict reproductive skew, itself.

For the purposes of evaluating TS theory, we can mostly ignore the Saturated and Bidding Game variants. Both are special cases and it is difficult to imagine that they would have significant explanatory power if the three major variants all fail. The Bidding Game can be fundamentally rejected for most cases in *Polistes* as its strongest prediction is that there is almost no reproductive skew across individuals (Reeve 1998, 2000). Nests with no skew (when dominants and subordinates are all continually present) have yet to be described in *Polistes*. The Saturated model may be more widely applicable, but the majority of tests of TS theory have used populations with a significant number of solitarily-nesting females. So saturation at a population level is not evident.

Aggression

In the classic TV comedy, *The Honeymooners*, Ralph Kramden is the putative alpha of a cooperatively shared 'nest'. The bilious Ralph continually harasses his subordinates with a series of glares, yells, and threats of great physical violence that will deposit them on an extraterres-

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[3] Table 1 does not list all the existing derivations of TS theory. A number of authors have examined relaxing existing assumptions of TS models, or have added other factors. These include: (1) adding the possibility of inheriting dominant status (Kokko & Johnstone 1999, Ragsdale 1999), (2) costly to produce young, which limits the number of offspring dominants can produce (Cant & Johnstone 1999), (3) infanticide (Johnstone & Cant 1999b), (4) extending 2-player models to 3-player models (Johnstone *et al.* 1999), (5) dominants impose costs on subordinates that reduce their ability to succeed outside of a group (Crespi & Ragsdale 2001), (6) sex ratio conflicts between hymenopteran mothers and daughters (Nonacs 2001, 2002), and (7) changes in skew across time (Zink & Reeve 2005). Across all of these modifications of the basic TS model, cooperation is generally predicted to become more likely across wider ranges of reproductive skew. In all of these models, however, the basic qualitative predictions of how relatedness, group productivity and solitary success rates affect each other are either unchanged or not specified. Thus relative to Table 1, they make no new predictions about the relationships between variables.

Table 1. Summary of the predictions from the various Transactional Skew models and their source(s). The Saturated model is also known as the N-person model. + or – means a significant correlation is expected. 0 means no correlation is expected. A question mark indicates no prediction has been derived and a relationship is not obvious. Some models predict more than one type of relationship is possible for pairs of variables due to interactions with other variables.

	Concession		Restraint		Tug-of-War		Saturated		Bidding game	
	Predict	Source[1]	Predict	Source[1]	Predict	Source[1]	Predict	Source[1]	Predict	Source[1]
Aggression and										
overall level	Varies		Varies		Varies		Low	9	Low	4,11
r	+	1,8,10,11,12	+	11,12	–	10,11,12	0	8	0	8
	+,–,0	7								
x	–	8	–	8	0	8	0	8	?	
k	+	8	–	8	0	8	0	8	0	14
					–	13				
group size	?		?		?		–	11	0	4
skew	+	5,8,12	+	5,8,12	–	5,8,12	?		0	14
size difference	+,–	8	+,–	8	–	8	0	8	0	14
through *r* and *k*	0	13	0	13	+	13	?		0	14
Skew and										
overall level	Higher		Lower		Mid	11	Mid to High	9	Low or no skew	8,11
r	+	1,3,5,6,7, 11,12,13	–	3,5,6,7, 11,12,13	–,0	5,11,12,13	+,0	9	0	4,11
					+,–,0	6				
			+,–	2						
x	–	1,3,5,6,7, 11,12,13	+	3,5,6,7, 11,12,13	0	5,11,12,13	–	9	0	11
					+,–,0	6				
k	+	1,3,5,6,7, 11,12,13	–	3,5,6,7, 11,12,13	0	5,11,12,13	?		–	4,11
					+	2				
					+,–,0	6				
size difference	+	1,12	+	12	+	8,10,12	?		0	8
	+,–	8								
	+,0	10								
season	+	10,12	–	12	+	12	?		?	
Group size and										
r	–,0	1	?		?		+,–	9	0	14
x	?		?		?		–	9	?	

[1] The predictions' sources are numbered as follows: (1) Reeve & Ratnieks 1993, (2) Cant 1998, (3) Johnstone & Cant 1999a, (4) Reeve 1998, (5) Reeve *et al.* 1998a, (6) Johnstone 2000, (7) Johnstone & Cant 2000, (8) Reeve 2000, (9) Reeve & Emlen 2000, (10) Reeve *et al.* 2000, (11) Reeve & Keller 2001, (12) Seppä *et al.* 2002, (13) Langer *et al.* 2004, (14) Extrapolated from (4,11) predictions of no aggression and no effects of *r*.

trial body. Ralph's threats are often immediately countered in kind by the beta individual (Alice, his wife). Yet Ralph never follows up his warnings with action, nor do his put-upon subordinates ever depose him out the window.

In hundreds of hours of watching *Polistes* interact, I see an analogy to the Honeymooners. Wasps continually dart, lunge and bite at each other. Their postures are threatening: bodies raised and wings flared. To an intruder (a non-nestmate wasp, ant, spider, or collecting forceps), the follow through is vicious grappling and often attempts to sting. However among nestmates, just as with Ralph and Alice, I never see the interactions escalate to injury or expulsion from the nest. The aggression always stops at the threat level, although admittedly these observations are all confined to the time period immediately before and after workers first appear on the nest. Nevertheless, this is the time period when most tests of TS predictions occur.

There is one critical difference, however. The blustering Ralph, despite his size and hostile nature, is usually frustrated in attaining his goals. In contrast the alpha wasp appears to achieve her overriding goal. If she survives, all or almost all of the reproductive offspring will be her sons and daughters (Queller *et al*. 2000, Reeve *et al*. 2000, Seppä *et al*. 2002, Liebert & Starks 2006). Logically, therefore, it appears that aggression works in *Polistes*.

Kern Reeve and I certainly strongly believed that darts and lunges must be connected to reproduction in some way. Therefore, we decided on a simple manipulation: to remove eggs that were fated to become reproductive females and males. We were initially surprised that the manipulation only increased the darting and lunging rate of the subordinate, as we assumed that the majority of eggs belonged to the dominant (Reeve & Nonacs 1992). In the 1992 paper, we projected this outcome to result from a greater proportional destruction of the subordinate's direct fitness rather than the dominant's[4]. Following up on this work, we further manipulated colonies by removing eggs and pupae destined to be workers, and wingclipping subordinates to reduce their foraging efficiency. We predicted aggression levels with a more expansive model that estimated the relative value of having cooperative group members throughout the season. Depending on the treatment, wasps increased or decreased their aggression rates as predicted by the value model (Reeve & Nonacs 1997). All these results were later reinterpreted (Reeve 2000) as also supporting TS theory because of changes to group productivity (k) and potential to nest alone (x). A subsequent discussion of the data (Reeve & Keller 2001) cites the results as entirely supportive of the Concession model. The decline in aggression with removal of worker brood is due to the dominant maintaining a staying incentive for the subordinate. The subordinate's increase of aggression in response to removal of sexual-destined eggs is mainly due to subordinates being more favored to escalate competition over an unexpected last opportunity for egg laying.

An alternate explanation was provided almost immediately by Strassmann (1993). She proposed that empty egg cells signaled a weak queen and that triggered dominance testing by the subordinate. This explanation was rejected because the patterns of aggression did not seem to follow dominance testing (Reeve & Nonacs 1993), or were not stimulated by empty cells alone (Reeve & Nonacs 1997). Moreover, the 'weak queen' hypothesis is not a true alternative to a TS skew model, because TS models assume that skew will be renegotiated if the relative competitive abilities of the interactants change.

There were other specific aspects of our results, however, that led us to replicate the egg removal experiment. One was the extremely high variance in aggression rates across pairs of wasps both before and after egg manipulation. A second was that despite many hours of observation, the subordinates were never seen to lay eggs in the emptied cells. The latter called into question the competition explanation and the former suggested that more factors were involved than just eggs being removed. Improving on our original design, we were able to measure genetic related-

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[4] This explanation was later shown to be untenable because measures of reproductive skew in *P. fuscatus* colonies at this stage indicate an almost complete skew in the dominant's favor (Reeve *et al*. 2000). Therefore, most subordinates have no direct reproduction to defend at this point.

ness and to videotape all interactions[5]. Unlike all previous experiments, a critical difference in our analysis was that we broke down aggression rates relative to the activity that engaged the wasp when aggression occurred. When analyzed this way, there was no significant effect of our manipulation on aggression (Nonacs *et al.* 2004). Instead, changes in aggression more likely followed from our experimental methods. The disturbance of removing the nest, removing (and often smashing eggs in their cells), and then reattaching the nest, makes wasps more active. They explore their handled nest more and check the newly empty cells. The more active wasps are, the more likely they are to elicit interactions. In our replication we found that every variable that correlated to activity level was also significantly correlated to aggression rate (Nonacs *et al.* 2004). By far the best predictor of whether a given wasp increased or decreased its aggression was the change in aggression of the other wasp ($R^2 = 0.807$, $n = 25$, $p < 0.0001$). Wasps responded to what others were doing and not directly in response to what had happened on the nest. Although it was not possible to completely reanalyze the data in Reeve and Nonacs (1992, 1997), those results share some uncomfortably similar patterns to the 2004 paper. Thus, I have now come to strongly believe that all the conclusions made about aggression in those earlier papers must be considered suspect.

Changes in levels of aggression have been claimed to strongly support TS models in a variety of contexts (Tibbetts & Reeve 2000, Reeve & Keller 2001). Our results, however, showed that none of these studies can be considered as conclusive support for TS theory because all the patterns could be equally well explained by concurrent changes in activity levels on nests (Nonacs *et al.* 2004). A second major blow to TS theory from our results is that aggression does not correlate with relatedness, nest productivity, or size differences. All of these are important variables in TS models (Table 1). We have since analyzed pairwise aggression rates between the queen and her workers, and between dominant and subordinate foundresses (both in the presence and absence of workers). There is no significant relationship between aggression and genetic relatedness or size for any category comparison (P. Nonacs, P. T. Starks & H. K. Reeve unpubl. data). Overall, subordinate foundresses are treated more aggressively than workers. However, this difference is apparent only before workers emerge. Once workers appear, the dominant's aggression towards all wasps is similar and independent of whether they are cofoundresses. Thus contrary to the predictions of TS models, dominants tend to treat all wasps on a nest at the same time similarly and not pairwise relative to their intrinsic characteristics. They do not differentiate based on relatedness or the potential to be a reproductive competitor.

One other recent study (Liebig *et al.* 2005) also severely challenges the connection between aggression and skew. Here, eggs were continually removed from *P. dominulus* nests. This stimulated egg production and laying in subordinates (but no increase in their aggression toward the dominant). The dominant maintained high skew in parentage, but this resulted from differential egg eating of subordinate-laid eggs by her and other wasps (i.e., queen policing). There was likewise no significant change in aggression towards adults by the dominant, even though subordinate egg-laying had obviously begun. Thus, measuring darts and lunges would have had no predictive power for estimating skew or the distribution of egg laying.

The above studies did not measure reproductive skew on the nests. Two studies in *Polistes* that did (Field *et al.* 1998, Seppä *et al.* 2002), found no relationship between aggression observed on the nest and reproductive skew. Therefore, the sum of all the evidence strongly suggests that Kramdenesque darts, lunges and bites in *Polistes* have no impact on setting reproductive skew. Instead, they may be activity regulators to get wasps moving or into productive activity (Reeve & Gamboa 1983, 1987, Sumana & Starks 2004), or as responses to changes in the activity patterns on nests (P. Nonacs, P. T. Starks & H. K. Reeve unpubl. data). It is clear, however, that to date no proximate mechanism is known for how repro-

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[5] The difference in methods is explained by the difference in being NSF-supported faculty members versus poor postdocs with no grant support.

ductive skew is set, maintained, or changed in nests across *Polistes*.

Skew

Transactional skew models are intensely competitive in nature. They predict that individuals should take as much reproduction as they can, even if less skewed distributions are possible. In some cases, cooperation could be possible with any level of skew from 100% reproduction by the dominant to 100% reproduction by the subordinate (e.g. Liebert & Starks 2006). Because exact quantitative predictions of skew levels are difficult to estimate, most studies make qualitative predictions across nests, populations and species relative to the expected effects of the variables on skew (Table 1).

Support for TS theory comes from skew progressively increasing over time in *P. fuscatus* nests (Reeve *et al*. 2000). However, this change is also predicted independent of TS theory if foundresses and their workers are in sex ratio conflict (Trivers & Hare 1976, Nonacs 2001, 2002). Dominants should favor early reproduction by subordinates if the resulting genetically diverse workforce is more likely to favor late male production. Stronger support for TS theory from the *P. fuscatus* data is that distantly related subordinates produce a significantly higher fraction of the early brood than do full sisters. This result is not predicted by sex ratio conflict, and fits well into TS theory if significant numbers of the early brood reject becoming workers and pursue reproductive options. Many of the early brood females do leave the colony rapidly in *P. fuscatus*, but their success rate is not well measured (Reeve *et al*. 1998b). In other species (*P. dominulus* and *P. aurifer*), early females have low fitness (Starks 2001, Liebert *et al*. 2005). If the early female strategy indeed has a low fitness payoff across *Polistes*, then the skews in the early brood of *P. fuscatus* no longer strongly support TS theory.

A number of other studies find TS models to poorly predict skew. *P. bellicosus* shows a negative relationship between relatedness and skew which rejects a Concession model (Field *et al*. 1998). Reeve and Keller (2001) suggest, however, that *P. bellicosus* nests are saturated and thus no relationship is expected. Seppä *et al*. (2002) examined several predictions across Concession, Restraint, and Tug-of-War variants of TS models in *P. carolina* and found tepid support for Tug-of-War[6]. A better predictor of *P. carolina* social dynamics is a convention in which the first wasp to begin building the nest becomes the dominant. Finally, Liebert and Starks (2006) found no relationship between genetic relatedness and skew across pairs of *P. dominulus* foundresses.

The degree to which the above studies support or reject TS theory is arguable relative to which variant of the TS models actually applies. To circumvent this problem two recent papers have instead tested all TS models simultaneously through their shared stability condition (which is determined by the productivity of groups relative to solitary individuals). As described above, all skew model variants have a range of allowable levels of reproductive partitioning. This range will expand as genetic relatedness increases. Thus, Liebert and Starks (2006) measured the success rate of pairs and single foundresses in a population of *P. dominulus*. Full sisters are favored to cooperate with any level of skew, but TS models predict that cooperation between unrelated individuals requires low skew. Contrary to TS theory, all pairs had high skew. Nonacs *et al*. (2006) examined 10 other populations of *Polistes* and one of *Liostenogaster flavolineata*. Almost ubiquitously, pairings of wasps with low or no relatedness could not be consistent with any TS model variant. Therefore, the relative commonness of such groups (e.g. Queller *et al*. 2000, Liebert & Starks 2006) suggests either that wasps often make mistakes when applying TS theory, or that TS theory is not involved during pair formation.

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[6] A slightly disturbing trend in recent tests of TS models is that the results (to the degree that they are supportive), favor whichever model variant makes the fewest specific predictions relative to the variables measured (e.g. Reeve *et al*. 2000, Seppä *et al*. 2002, Sumner *et al*. 2002, Langer *et al*. 2004, Liebert & Starks 2006).

Why do Transactional Skew models fail?

The immense attraction of TS models is the force of their logic. Individuals should make decisions that increase their inclusive fitness, and by sharing reproduction, pairs of cooperating wasps could both have higher fitness than nesting alone. How can it be that unrelated or distantly related wasps are willing to join groups without receiving sufficient direct reproduction?

One explanation is that there is no reliable mechanism to ascertain kinship and therefore wasps cannot adjust skew as predicted by TS models. Certainly, nepotism has been predicted to be advantageous in brood rearing. Yet, despite apparently large potential fitness gains, there is no convincing evidence for wasps exhibiting genetically biased cooperation or nepotism towards brood (reviewed in Hughes *et al.* 1993, Gamboa 2004). Brood rearing, however, differs in one significant way from the formation of cooperative groups. If one group of developing offspring is favored, it is at the expense of other offspring. Within this disfavored group, there would be countervailing selection to scramble recognition signals in order to foil nepotism (Reeve 1989, Liebert & Starks 2004). Therefore, brood-rearing has strong selection both for and against improving kin identification. In contrast, if two wasps are negotiating a social contract, it is to the advantage of at least one of them (and no worse than selectively neutral in the other) to correctly identify kinship. Recent evidence has shown that sufficient variation exists in chemical signatures to identify kinship (Dani *et al.* 2003, Dapporto *et al.* 2004, Gamboa 2004, Sumana *et al.* 2004) and that wasps can recognize individuals and remember their hierarchical rank (Tibbetts 2002, Tibbetts & Dale 2004). Therefore, with motive, method, and opportunity, it is curious why cooperating wasps do not react to kinship in setting reproductive skew.

Another possibility is that TS models are inherently unstable (Kokko 2003). If the subordinate individual cannot accurately access the reproductive skew, there is no limit on the dominant's ability to cheat. Evolutionarily, this cheating destabilizes cooperation and favors individuals that reproduce solitarily rather than be exploited as subordinates. This may be a serious problem in social species where parentage is difficult to definitively ascertain, but the data in wasps suggest that they can keep track of brood parentage (Klahn & Gamboa 1983, Liebig *et al.* 2005). Therefore, cheating by a dominant can be detected, and in theory, punished. Thus, the failure of TS models in *Polistes* cannot be explained by an inherent evolutionary instability in their assumptions.

I propose a different explanation for why TS mechanisms seem absent in *Polistes* wasps: they simply do not increase fitness very much relative to simpler rules of association. Consider the following example. A potential subordinate wasp approaches a dominant on her nest. If the subordinate is a 'Conventional' wasp, she will join the dominant if she decides the dominant is a full sister ($r = 0.75$). She will nest alone if she decides the dominant is unrelated ($r = 0$). If she joins the dominant, she will allow the dominant to lay all the eggs (= total skew). The subordinate can make two types of mistakes (Table 2, and *see* Liebert & Starks 2004). First, she can mistake a sister for an unrelated individual (a rejection error, occurring at a per encounter rate of $1 - \alpha_1$), or mistake an unrelated for a sister (an acceptance error, occurring at a rate of $1 - \alpha_2$). We can then calculate the inclusive fitness payoffs for each of the four possible outcomes. If the subordinate mistakenly rejects joining a sister, her inclusive fitness is $1 + r$. This value results from

Table 2. The expected rates at which subordinates pair with sisters and unrelated individuals and their inclusive fitness consequences. The payoffs are given for individuals that use a convention (C) or form a social contract based on the Transactional Skew Concession model (T). *See* text for definitions of variables.

	Actual identity	
Perceived identity	Sister	Unrelated
Sister		
Rate	$s\alpha_1$	$(1 - s)(1 - \alpha_2)$
Payoff (both C and T)	kr	0
Unrelated		
Rate	$s(1 - \alpha_1)$	$(1 - s)\alpha_2$
Payoff (C)	$1 + r$	1
Payoff (T)	$k[r + (1 - r)p_{\min}]$	$kp_{\min}$

setting the success rate of a single wasp equal to unity ($x = 1$) and assuming that the dominant and subordinate do equally well as solitary individuals (the model is thus as the original formula in Reeve and Ratnieks [1993]). Nesting with a sister nets an inclusive fitness of the group productivity (k), weighted by the genetic relatedness of the dominant. If the subordinate mistakenly joins and helps an unrelated dominant, her fitness is zero. Finally, if she correctly recognizes the dominant as unrelated, she nests alone (fitness: $x = 1$). Sisters are encountered in the population at a rate of s, and unrelated individuals are encountered at $1 - s$.

Now consider if the subordinate is a 'Transactional' wasp. Unlike the C-wasp, if the T-wasp identifies the dominant as unrelated, she will negotiate a minimum staying incentive of direct reproduction. Like the C-wasp, however, she also makes recognition errors, which lead to the same four possible outcomes (Table 2). The payoffs for correctly identifying a sister and incorrectly identifying an unrelated as a sister are identical to the C-wasp. The T-wasp cedes all reproduction to her 'sister'. If the T-wasp identifies the dominant as unrelated she gets the same amount of direct reproduction, regardless of whether the identification was correct or not. The analysis presented here is only for a subordinate. If the subordinate follows a convention, there is no selection pressure for the dominant to behave transactionally. The dominant is indifferent to whether her subordinate is related or unrelated, if the subordinate always gives up all direct reproduction. Transactional behavior will not evolve for dominants unless it is first favored in subordinates.

Table 3. The payoff of a conventional strategy versus a transactional strategy (given as percent fitness relative to the T strategy). Encounter rate is the probability that the dominant is a full sister. All three productivity values (*k*) for two-female nests can favor cooperation between full sisters with complete skew.

	Encounter rate (*s*)		
k	0.5	0.8	0.9
2.33	99.51	99.36	99.33
3.32	98.58	98.20	98.10
5.00	97.61	97.19	97.09

To evaluate the fitness of a T-wasp relative to a C-wasp I chose three values of k: 2.33, 3.32 and 5. The lowest value is the minimum value such that a subordinate is willing to work for a full sister, without any direct reproduction of her own (derived from Reeve & Ratnieks [1993], Nonacs [2002]). The middle value is the mean estimate of k across seven populations of *P. dominulus* (Nonacs *et al.* 2006). The highest k value is at the upper range of the seven populations. The minimum proportion of reproduction that an unrelated subordinate must obtain to favor cooperation is $p_{\min} = 0.429$, 0.301 and 0.200 with the 3 respective k values (calculations as in Nonacs *et al.* [2006]). With all three values of k, the dominant's fitness is higher with a reproducing subordinate than if she is alone. A dominant is not making a 'mistake' if she concedes reproduction. Thus, dominants will be favored to offer the above staying incentives to either sister or unrelated subordinates if the subordinates cannot be induced to join without it.

In this scenario, there is strong selection for the C-wasp to improve her detection abilities (increase α_1 and α_2). Interesting for a T-wasp if both α's improve simultaneously (i.e., wasps get better at both recognizing kin and unrelateds), the effects approximately cancel. The benefits for correctly identifying an unrelated dominant are offset by a reduction of 'good' mistakes that force a sister to yield reproduction as if she were an unrelated dominant. Therefore, for the purposes of simplifying the analysis, I always set $\alpha_1 = \alpha_2 = 0.95$, defining identification mistakes to be rare.

Total inclusive fitness for the C and T strategies were calculated by summing the payoffs of the four outcomes, weighted by the probability of their occurrence. Two factors were varied: the productivity of the group, as given by the three values above; and the probability of encountering a sister ($0.5 \leq s \leq 0.9$). The T-wasp always had higher fitness than the C-wasp (Table 3). Increasing the productivity of the group and increasing the likelihood of encountering sisters increased the relative advantage of the T strategy. However, the most significant result is that the relative advantage for a wasp following a Transactional strategy was never greater than 3% over a wasp following a Conventional strategy.

The relatedness difference was maximized in this example (i.e., individuals have *r* values of either 0.75 or 0). Whenever the relatedness difference is reduced (e.g. a comparison of joining a sister or a cousin), the fitness difference between T-wasps and C-wasps are further reduced. Likewise, assuming the convention allows the subordinate wasp a low level of reproduction in the presence of a sister, improves the relative fitness of the C-wasp.

Therefore, the TS model does define the optimal strategy, but its fitness advantage is minimal over using a simpler conventional strategy. In postulating an optimal outcome, the fitness surface over which selection can act is quite important (Gladstein *et al*. 1991). When competing mechanisms result in approximately equal fitnesses, it may be the simpler one that evolves rather than the slightly more optimal solution. Given the significant neurological and behavioral mechanisms wasps would need to properly enact and keep track of reproductive transactions, perhaps it is not curious after all that wasps do not form social contracts. The benefits they would gain do not appear large enough to withstand an evolutionary cost for creating the mechanism.

The future of skew theory

Like a certain noble reptile of film[7], can Transactional Skew theory rise again in *Polistes*? There are several avenues. The one result in *Polistes* that is difficult to explain in contexts other than TS theory is the difference in reproductive skew between sister and cousin groups in *P. fuscatus* (Reeve *et al*. 2000). This difference was only in early season nests. Later in the year, both nest types had almost complete skew in the dominant's favor. The difference in the early season has fitness consequences (and therefore relevance to TS models) only if a significant fraction of those early females pursue reproductive options rather than becoming sterile workers. Some evidence suggests that they do (Reeve *et al*. 1998b), but both of these studies need to be replicated across populations and species. Further, a strong prediction of TS theory is that offspring of the subordinate are especially likely to abandon working and succeed as early reproductive females (Nonacs 2002). This has not been tested.

If skew is to vary across cooperating groups of wasps, there must be a behavioral mechanism that establishes the levels. Aggression, as previously described, does not appear to connect to skew. Nevertheless, skew may be set at the very earliest stages of group formation. No study, to my knowledge, has been able to isolate how pairs of wasps first begin to cooperate, and whether the behaviors occurring then, correlate to skew levels. If aggression does connect to skew, unilaterally changing the aggressiveness of only the dominant should result in predictable changes of reproductive skew. One recent study (Cant *et al*. 2006) managed to manipulate aggression by removing the most dominant wasp on a nest for several days. Upon reintroduction the original dominant often engaged in highly escalated fights with the new dominant that had emerged during its absence. The level of escalation was positively increased by nest size and negatively by ovarian development. The willingness of the subordinate to risk a deadly fight was therefore consistent with expected larger payoffs from winning a fight. Hence truly serious aggression appears tightly linked to the expectation of increasing direct fitness.

Polistes wasps more than any other taxonomic group have been viewed as the ideal organisms for testing TS models. Thus, the demise of TS theory in this group does not bode well for TS models when applied to species with more complicated life histories. I will, nevertheless, leave the evaluation of TS theory in non-polistines for someone else to summarize. I will instead conclude on a positive note. If TS theory is wobbling, the idea of reproductive skew is gaining strength. Reproduction is strongly skewed in *Polistes* and probably in most cooperatively-breeding organisms. Thus skew theory, per se, is alive, well and expanding. We must look with fresh eyes at new potential explanations for the causes and maintenance of reproductive skew (*see* Cant 2006). We must go beyond reproduction and measure skew in all

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[7] "*We're finally safe*!" — dialog at the end of the first Godzilla movie. (Godzilla has to date reappeared in 27 sequels.)

aspects of group behavior, from foraging to territory defense. The basic premise of TS theory that animals are dynamic actors making social decisions to increase fitness should not be lost. I believe the evolution of skew theory beyond a transactional framework will continue to have tremendous impacts for understanding all aspects of the behavioral ecology of animals.

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