Genetic support for the evolutionary theory of reproductive transactions in social wasps

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Recent evolutionary models of reproductive partitioning within animal societies (known as 'optimal skew', 'concessions' or 'transactional' models) predict that a dominant individual will often yield some fraction of the group's reproduction to a subordinate as an incentive to stay in the group and help rear the dominant's offspring. These models quantitatively predict how the magnitude of the subordinate's 'staying incentive' will vary with the genetic relatedness between dominant and subordinate, the overall expected group output and the subordinate's expected output if it breeds solitarily. We report that these predictions accord remarkably well with the observed reproductive partitioning between conesting dominant and subordinate queens in the social paper wasp *Polistes fuscatus*. In particular, the theory correctly predicts that (i) the dominant's share of reproduction, i.e. the skew, increases as the colony cycle progresses and (ii) the skew is positively associated both with the colony's productivity and with the relatedness between dominant and subordinate. Moreover, aggression between foundresses positively correlated with the skew, as predicted by transactional but not alternative tug-of-war models of societal evolution. Thus, our results provide the strongest quantitative support yet for a unifying model of social evolution.

Keywords: reproductive skew; social wasps; cooperation; conflict

1. INTRODUCTION

Some evolutionary models of the distribution of reproduction within animal societies predict that a dominant individual will often concede reproduction to a subordinate individual to provide the latter with an incentive to stay in the group and help rear the dominant's offspring. These models are known as 'optimal skew' (Vehrencamp 1983; Reeve 1991; Reeve & Ratnieks 1993), 'concessions' (Clutton-Brock 1998) or 'transactional' (Reeve *et al.* 1998*a*) models of reproductive skew, i.e. the degree of reproductive monopolization by the dominant. The models quantitatively predict how the magnitude of the dominant's reproductive payment to the subordinate (i.e. the 'staying incentive', expressed as a fraction of the dyad's total output) will vary according to (i) the genetic relatedness between dominant and subordinate, (ii) the overall expected group output and (iii) the subordinate's expected output if it breeds solitarily (Vehrencamp 1983; Reeve & Ratnieks 1993; Johnstone *et al.* 1999).

The cooperative associations of social wasp queens are ideal systems for testing transactional theories of reproductive skew (Reeve 1991). In social wasps of the genus *Polistes* (Vespidae: Polistinae), multiple queens often cooperate in founding spring nests after overwintering (West-Eberhard 1969; Noonan 1981; Reeve 1991). A linear dominance hierarchy develops among these foundresses and the most dominant foundress (alpha) produces most but not all of the eggs. In *Polistes fuscatus* the first brood develops into early females, some of which become workers (which sometimes reproduce as replacement queens; Klahn 1981) but many or most of which leave the nest to become foundresses the following year (Reeve *et al.* 1998*b*). Later brood develop into males and late

females, the latter also becoming part of next year's pool of foundresses (West-Eberhard 1969; Noonan 1981).

A subordinate (beta) foundress is favoured to join an alpha foundress because of the lesser probability that a colony with more foundresses will fail due to chance loss of all colony adults before emergence of the first workers (Reeve 1991). This 'survivorship insurance' benefit is strongly indicated by demographic data from our study population (Reeve & Nonacs 1997) as well as by a comparative analysis (Reeve 1991).

According to reproductive transaction theory (Vehrencamp 1983; Reeve 1991; Reeve & Ratnieks 1993), a beta foundress should require a smaller staying incentive (i.e. alpha's reproductive skew should be larger) as (i) the colony's overall productivity increases, (ii) as beta's genetic relatedness to alpha increases and (iii) as beta's reproductive output if it were to solitarily found a new nest decreases. The same factors which increase the reproductive skew should also increase the frequency of aggression between an alpha foundress and a beta foundress by increasing the extent to which each can selfishly augment its reproductive share without causing dissolution of the group (Reeve 2000). We tested these predictions with a genetic (microsatellite) analysis of reproductive partitioning and a behavioural analysis of foundress aggression within 24 multiple-foundress *P. fuscatus* colonies in our study population near Ithaca, New York, USA.

2. METHODS

(a) *Colony collections*

Between 25 May and 23 June in 1993–1995, all foundresses in a total of 24 multiple-foundress colonies (mean = 2.56 foundresses per colony) were paint marked, censused every two to ten days and videotaped just before collection of all remaining colony members 19.0 ± 7.2 (mean $\pm$ standard deviation) days after worker emergence. Twelve foundress groups were also

videotaped for 2 h each for a total of 24 h from 25 May to 13 June (before early-female emergence). Aggressive acts among foundresses (darting, lunging, biting, mauling, grappling and stinging) in the latter colonies were recorded as in previous studies (Reeve & Nonacs 1992, 1997) and the number of initiated aggressive acts per hour together on the nest (x) was transformed as $\ln(1 + x)$ to satisfy the normality assumptions for parametric statistical tests.

(b) *Genetic analyses*

Screening of microsatellite primers derived from social wasps and sent to us by courtesy of J. Strassmann and D. Queller (Rice University, TX, USA) revealed eight polymorphic micro-satellite loci. The primer, mean heterozygosity and numbers of alleles at each locus are, respectively, (i) Pbe128TAG, 0.61 and six, (ii) Pbe269bAAG, 0.82 and 12, (iii) Pbe411AAT, 0.84 and nine, (iv) Pbe424AAT, 0.86 and 12, (v) Pbe440AAT, 0.91 and 21, (vi) Pbe442AAT, 0.70 and eight, (vii) Paco3155TAG, 0.65 and six and (viii) Paco3219AAG, 0.60 and four.

The methods of Strassmann *et al.* (1996) were used to obtain microsatellite genotypes at the above loci for a total of 166 early females and 32 foundresses (18 alpha foundresses and 14 beta foundresses). We also obtained the genotypes of 71 late-female larvae and 143 male larvae (third−fifth instars) from 15 of the 1995 colonies. We used the Relatedness 4.2 program (Goodknight & Queller (1994), based on the logic of Queller & Goodknight (1989)) to estimate the mean relatedness among cofoundresses.

(c) *Maternity assignment*

Of the 24 colonies collected, 25% had lost their alpha foun-dresses and 42% their beta foundresses by collection (a mean of 19 days after worker emergence). We first reconstructed the genotypes of missing foundresses which contributed to brood production. A full-sister group (i.e. female brood sharing the same father and foundress mother) was the largest group of females simultaneously satisfying two criteria for every locus: (i) all females shared at least one allele (and the same allele), because full sisters all inherit the same allele from their haploid father and (ii) the number of all alleles excluding the paternal allele was less than or equal to two, because a full-sister group could receive a maximum of two distinct alleles from their mother. The set of alleles detected in (i) reconstructed the paternal genotype and that in (ii) the maternal genotype (the reconstructions were performed with a Mathematica^{TM} computer program which is available from the authors). The accuracy of the method for reconstructing the genotypes of the missing foundresses was verified in three ways. First, we recon-structed the genotypes of the alpha and beta foundresses collected (behaviourally identified from the videotape records, as in Reeve & Nonacs (1992)). As in previous studies (West Eberhard 1969; Noonan 1981), the alpha foundresses were significantly larger than the beta foundresses (0.141 versus 0.119 g, respectively; paired *t*-test $p = 0.0006$). Of the inferred alpha (i.e., foundress genotypes accounting for the most brood overall) and beta genotypes (i.e. foundress genotypes accounting for the second largest group of brood overall) 99.7% correctly matched the actual genotypes in a locus-by-locus comparison. Second, reconstructions of the foundress genotypes from a Monte Carlo simulation which created full-sister foun-dresses from a panmictic population with the observed micro-satellite allele frequencies were 99.7% correct (20 brood in each of 50 randomly formed full-sister foundress associations). Third,
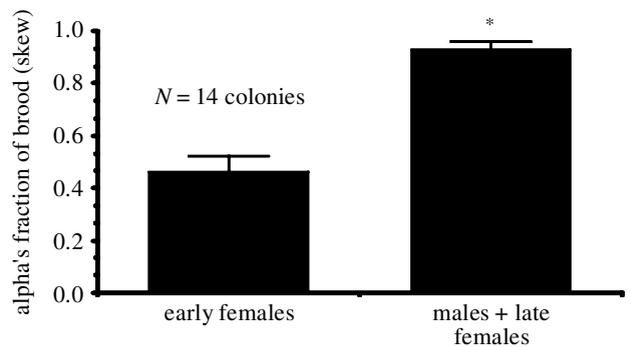

Figure 1. The observed mean skew and standard errors for early females (emerging 1 July to 1 August) versus males and late-female brood (after 1 August). Both sets of offspring came from eggs laid in the founding phase. The skew increases with time, as predicted by the survivorship insurance model. This pattern was true both for full-sister associations (skew in early brood $= 0.70 \pm 0.05$ and skew in late brood $= 0.93 \pm 0.08$) and cousin associations (skew in early brood $= 0.31 \pm 0.07$ and skew in late brood $= 0.92 \pm 0.08$). The skew in male brood (0.84 ± 0.08) was lower than the skew in late-female brood (0.96 ± 0.04) but not significantly so (matched-pairs Wilcoxon test $p = 0.17$). (One of the 15 colonies was omitted from the analyses due to the absence of early-female data). Asterisk indicates paired *t*-test $p < 0.0001$.

the total number of reconstructed missing and collected foun-dresses was always less than or equal to the maximum number of foundresses censused at the colonies.

After the genotypes of all foundresses had been determined, female offspring (early and late females) were assigned to the foundress matrilines. In the few cases in which female offspring could be assigned to more than one foundress, each foundress was credited with an even share of that offspring. The latter is a conservative procedure with respect to the predictions of incen-tive theory (Reeve & Ratnieks 1993) because it tends to reduce the skew among more-closely related foundresses, for which ambiguous maternity assignment is more likely. The skew among male offspring, which exhibited only one band at every locus, was estimated as the skew which maximized the prob-ability of obtaining the observed array of male genotypes. The skew was measured as the fraction of alpha plus beta offspring which belonged to alpha foundresses. (Analysis of gamma and delta reproductive shares requires increased sample sizes due to the infrequency of reproduction by gammas or deltas.)

(d) *Increase in skew over time*

An important prediction of transaction theory coupled to the survival insurance model of foundress cooperation is that the reproductive skew should increase over the colony cycle. This theoretical dependence of the skew on time can be derived from the survivorship insurance model which was developed to explain the demographic data from a previous study of our population (Reeve & Nonacs 1997). Let the time (days) for one complete brood cycle be T, the number of days remaining until the first workers emerge in alpha's nest be $T - t$ (t is the number of days since nest initiation) and the lifetime of a foraging foun-dress be exponentially distributed with a rate parameter m. If both foundresses in a colony die before workers emerge, the colony fails. A dominant with a subordinate has negligible mortality before worker emergence. N_1 and N_2 are the numbers of offspring produced in surviving single- and multiple-foundress
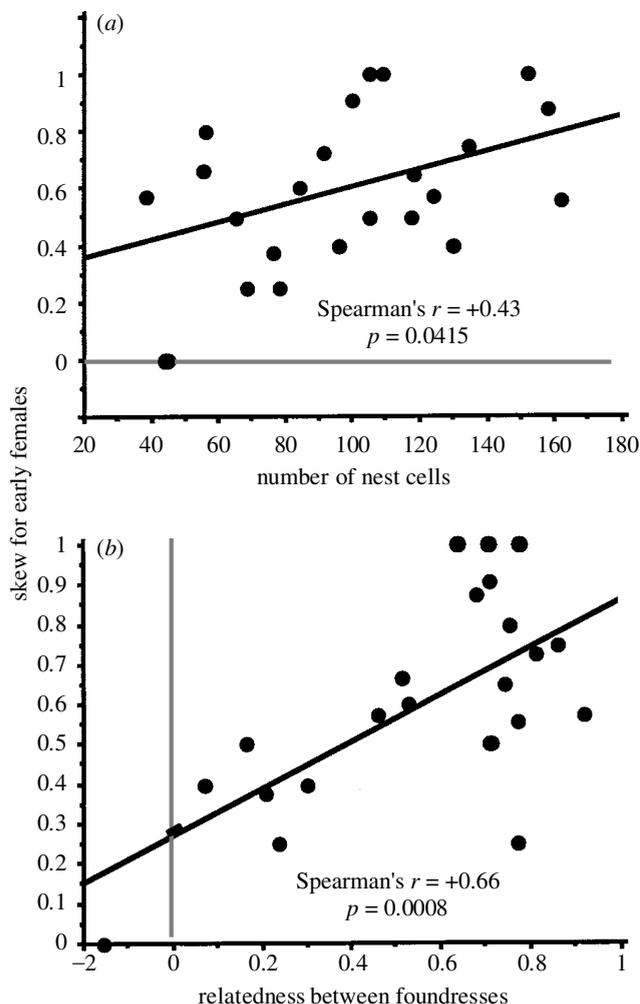
Figure 2. Reproductive skew (dominant's share of production of early females) versus (*a*) group output as measured by the number of nest cells at colony collection and (*b*) the relatedness between foundresses. The *p*-values are for two-tailed tests for the significance of the correlation coefficients. (Note that one of the 24 colonies was omitted due to lack of early-female data; two points overlap in *b*).

Figure 3. Foundress aggression (log-transformed aggressive acts per hour in nest together) for < 30 days ($n = 4$) versus $\geqslant 30$ days ($n = 8$) after nest initiation (before worker emergence) for 12 of the study colonies (bars are standard errors). Both beta and alpha foundresses were significantly more aggressive later in the nest-founding phase when the skew is higher (two-tailed unpaired *t*-tests). $^{*}p = 0.008$, $^{**}p = 0.007$.

3. RESULTS AND DISCUSSION

As predicted by transactional theory and the survivorship insurance model (see §2(d)), the reproductive skew increased over time: the mean reproductive skew in the production of early females was significantly less than that for males and late females (figure 1). On average, betas produced nearly half of the early females, but alphas produced nearly all of the males and late females. The change in skew between early and late brood was not significantly associated with the presence or absence of the subordinate at the time of colony collection (Mann–Whitney test $p = 0.32$). We found no significant effects of year on any of the above relationships.

The alpha and beta cofoundresses had variable relatednesses in our study population. The mean ($\pm$s.e.) relatedness among cofoundresses was 0.57 ± 0.06. Our computer program, which was designed to detect full-sister groups among a set of genotypes (see §2), inferred that 75% of alpha and beta cofoundresses were full sisters. Indeed, the mean relatedness for these foundresses was 0.71 ± 0.03, which is close to the expected value of 0.75. The remaining foundress associations exhibited a mean relatedness of 0.14 ± 0.07 (range $= -0.157$ (a single negative value) to 0.302), which suggests that these foundresses were first cousins (expected relatedness 0.1875). Indeed, bootstrap analysis of the relatednesses of these putative cousins revealed that their mean relatedness was significantly greater than zero ($p = 0.022$; 10 000 iterations) despite the fact that they could not have been full sisters (as revealed by our computer program). Thus, cousin associations were not associations of single foundresses and unrelated usurpers. (Moreover, four of the six cousin associations were already formed at initial colony detection early in the founding phase and the remaining two were formed by later joining of behavioural subordinates by the mid-founding phase; in contrast, nearly 90% of usurpations occur late in the founding phase and involve escalated fighting and early brood destruction (Klahn 1981), none of which were observed in any of our colonies.)

Since reproductive sharing occurs primarily in the production of early females, which are reproductively

nests, respectively. The expected output of a newly founded single-foundress colony is $a(t) = e^{-mT}(\mathcal{N}_1)$ multiplied by some devaluation factor $(1 - f[t])$ which incorporates the seasonal termination of the colony cycle. The expected output of a lone alpha foundress is $b(t) = e^{-m(T-t)}(\mathcal{N}_1)$ and that of a two-foundress colony is $c(t) = e^{-m(T-t)}(\mathcal{N}_2 + m^{(T-t)}\mathcal{N}_1)$. In the skew model, the relative solitary-founding success is $x(t) = a(t)/b(t) = (1 - f[t])e^{-mt}$, which decreases over time, and the relative group output is $k(t) = c(t)/b(t) = h + m(T - t)$, where $h = \mathcal{N}_2/\mathcal{N}_1$. The theoretical staying incentive p_s (beta's fraction of the present plus expected future group reproduction) is $\{x(t) - r[k(t) - 1]\}/k(t)(1 - r)$ (Reeve & Ratnieks 1993). Importantly, $\partial p_s/\partial t < 0$ (since $f(t) < 1$ and $\partial f(t)/\partial t > 0$), i.e. beta's fraction of the present plus future group reproduction should decline with time if beta is receiving a staying incentive from alpha. This entails that the skew should increase as the colony cycle progresses (see the electronic appendix on The Royal Society Web site). Intuitively, this effect is predicted because the survival of a new colony initiated by beta relative to the survival of alpha's established colony declines over time and, thus, the beta foundress requires a smaller staying incentive as time passes.
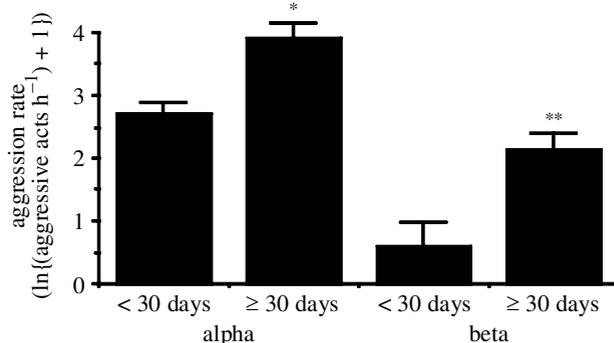
Table 1. *Contrasting predictions of the transactional and tug-of-war models of skew and aggression*

	trans-actional model	tug-of-war model	observed
relationship between skew and alpha–beta size difference	none or +	+	none
relationship between skew and aggression	+	−	+
relationship between relatedness and group productivity	none	+	none

Table 2. *Effects of egg removal on foundress aggression (Reeve & Nonacs 1992, 1997) in relation to the reproductive skew*

(Removal of early-female eggs causes a significant decline in alpha's rate of aggression, in significant contrast to removal of male and late-female eggs (two-tailed Mann–Whitney test $p = 0.036$ for comparison of the two time-periods). Beta's rate of aggression does not change when early-female eggs are removed but increases signficantly when male and late-female eggs are removed (Mann–Whitney test $p = 0.027$ for comparison of two time-periods).)

treatment	alpha's mean fraction (skew) at time of egg removal	effect of egg removal on alpha's aggression	effect of egg removal on beta's aggression
early-female egg removal	0.52 ± 0.07	$-61 \pm 15\%$ ($p < 0.02$)	$-6 \pm 11\%$ ($p = 0.62$)
male and late-female egg removal	0.93 ± 0.03	$+109 \pm 65\%$ ($p = 0.12$)	$+205 \pm 88\%$ ($p = 0.04$)

valuable to foundresses (Reeve *et al.* 1998*b*), we examined how the mean reproductive skew varied with the relatedness between foundresses and with colony productivity, as measured by the cell number at colony collection. Exactly as predicted by incentive theory, the skew increased significantly as both the colony productivity and cofoundress relatedness increased (figure 2). The corresponding partial correlation coefficients are also significantly greater than zero (partial regression coefficient β for the skew with the number of cells, relatedness and foundress number controlled $= +0.51$ and $p = 0.019$ and partial regression coefficient β for the skew with the relatedness, cell number and foundress number controlled $= +0.67$ and $p = 0.001$). The skew for full-sister associations was significantly greater than that for putative cousin associations (0.70 ± 0.05 versus 0.31 ± 0.07; Mann–Whitney test $p = 0.001$), even when the two cousin associations with late-joining subordinates were excluded (0.70 ± 0.05 versus 0.42 ± 0.07; Mann–Whitney test $p = 0.008$). Full sisters also had a significantly higher skew (0.73 ± 0.07, $n = 11$) than did cousins (0.19 ± 0.11, $n = 3$; two-tailed Mann–Whitney test $p = 0.004$) in two-foundress associations ($n = 14$). The skew did not differ significantly according to whether beta or alpha foundresses were present at collection (Mann–Whitney test $p = 0.12$ and $p = 0.97$, respectively,). We found no significant effects of year on any of these relationships. The skew was not significantly associated with the size difference between the alpha and beta foundresses when controlling for relatedness and cell number (coefficient $= -0.36$ and $p = 0.92$).

The increasing skew as the founding phase progressed was accompanied by increasing aggression in both alpha and beta foundresses (figure 3), as indicated by a prior longitudinal study (Gamboa & Stump 1996). Partial regression analyses including the date (in days after 1 May), alpha's size (grams wet weight), beta's size (grams wet weight) and total cell number at collection revealed that alpha's aggression significantly increased with the date ($\beta = +0.19$ and $p = 0.0019$) and total cell number ($\beta = 0.018$ and $p = 0.021$) and significantly decreased with alpha's size ($\beta = -42$ and $p = 0.0079$). Beta's aggression significantly increased with the date ($\beta = +0.25$ and $p = 0.0082$) and increased with the total cell number, although not quite significantly ($\beta = 0.022$ and $p = 0.083$). We found no significant effects of year on any of these relationships. The increase in skew over

time is unlikely to have resulted from weakening of the beta foundresses since the difference in the aggression rate between the alpha and beta foundresses did not change significantly over the founding phase (simple linear regression $p > 0.23$).

The aggression between the alpha and beta foundresses was higher in later nests and also in more productive nests (figure 3), the latter also having a higher reproductive skew (figure 2). Thus, our results indicate that higher aggression is associated with a higher skew, as predicted by transactional models (Reeve 2000). The opposite relationship is predicted by tug-of-war models in which reproductive sharing arises solely from the inability of competitively matched foundresses to monopolize colony reproduction profitably. A negative association between the skew and aggression in tug-of-war models arises because increasing subordinate competitive efficiency both decreases the skew and raises the evolutionarily stable levels of aggression for alpha and beta foundresses (Reeve *et al.* 1998*a*). The tug-of-war model also predicts a positive relationship between the relatedness and group productivity, but we found no significant association (multiple regression analysis of the cell number on relatedness with foundress size difference controlled $\beta = -15.8$ and $p = 0.677$). In summary, our aggression and genetic data together support the transactional and not tug-of-war models of intragroup conflict (table 1).

The increase in skew over time sheds new light on the significance of foundress responses to experimental egg removal (Reeve & Nonacs 1992, 1997; table 1). Removal of late female- and male-destined eggs late in the founding phase increases alpha's aggression towards beta and, in particular, beta's aggression towards alpha, but removal of early female-destined eggs early in the founding phase causes a significant decrease in alpha's aggression and no change in beta's aggression (table 2). The large drop in alpha's aggression when early-female eggs are removed (i.e. when a substantial fraction of the removed eggs are beta's) strongly supports the transactional interpretation that alpha is unwilling to engage in aggressive egg-laying competition when the beta foundress is at risk of losing

her minimal staying incentive. In further support of this interpretation, suppression of alpha's aggression is associated with a lack of increase in beta's aggression. Importantly, the transaction hypothesis also provides a striking explanation for the long-standing, puzzling finding that 'in early foundress associations, queens frequently exhibit behavior characteristic of subordinates in mature hierarchies' (Gamboa & Dropkin 1979, p. 919). Our skew data indicate that paradoxical dominance reversal occurs at precisely the time when the alpha foundress is peacefully conceding a staying incentive to the beta foundress.

In contrast, late in the founding phase, when beta's staying incentive is low (*ca.* 7% of the eggs according to our skew data), alpha and beta openly engage in aggressive competition to replace the removed eggs in newly emptied cells (table 2). In addition, beta may aggressively retaliate against a now more-aggressive alpha for the perceived destruction of her small staying incentive, explaining why beta's total aggression increased more in response to egg removal than did alpha's total aggression (Reeve & Nonacs 1992).

Interestingly, another social wasp, *Polistes bellicosus*, exhibits uniformly high skews regardless of relatedness and this higher skew is not accompanied by higher aggression (Field *et al.* 1998). This pattern of results is compatible with *n*-person transactional models of skew and aggression provided that most of their study colonies (unlike our colonies) were saturated with foundresses, i.e. additional foundresses were not favoured to join (Reeve 1999). Indeed, foundress associations were larger in *P. bellicosus* (79% of colonies initially had more than two foundresses; Field *et al.* 1998) than in our *P. fuscatus* population (only 40% of colonies initially had more than two foundresses). The *n*-person model also predicts that aggression should be low in saturated colonies (Reeve 1999), which may explain why Field *et al.* (1998) found very low overall levels of aggression except in their smallest colonies.

In summary, our results offer the strongest quantitative support yet reported for a general theory of social evolution. Importantly, the transactional model supported emphasizes that the exchange of reproductive incentives for beneficial cooperation is as fundamental to social organization as is conflict over reproductive rights within the society (Reeve & Nonacs 1992; Reeve *et al.* 1997).

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