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Paternalism, reproduction and conflict in vespine wasps: a model system for testing kin selection predictions

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Abstract The Vespinae wasps (*Vespa*, *Provespa*, *Dolichovespula*, and *Vespula*) are an excellent group for testing kin selection predictions. There is considerable variation in kin structure and conflict resolution in a group of known phylogeny where all species have a similar basic biology: morphologically distinct queens and workers, and annual nests headed by a single queen. Vespine kin structure can be described by a single variable “effective paternity”, which is defined by queen mating frequency and sperm use. Low effective paternity, which causes high worker relatedness, is basal in the group (*Vespa*, *Dolichovespula*), with high paternity (ca >2) restricted to *Vespula* whose queens mate more and use sperm more equally. Paternity variation correlates well with observed patterns of reproduction and conflict. As predicted by theory, male production by workers is common in *Dolichovespula* but not in *Vespula* where worker policing occurs (*Vespula vulgaris*). The theory is also supported by intercolony variation in *Dolichovespula*, with facultative worker policing (*Dolichovespula saxonica*) and sex allocation biasing by workers (*D. arenaria*) occurring in response to paternity. In addition, queen loss in reproductive colonies of nine species is negatively correlated with paternity, in line with the prediction that matricide is only expected at low paternity. However, paternity does not explain the reproductive characteristics of *Vespa crabro*. Although paternity in *V. crabro* is only 1.1, the same as the mean in six *Dolichovespula* species, its reproductive behaviour is different from *Dolichovespula*. More like *Vespula*, *V. crabro* has worker

policing, workers that rarely have active ovaries, and little queen loss in reproductive-phase colonies.

Keywords Kin selection · Levels of selection · Reproductive conflict · Vespinae wasps · *Vespa* · *Dolichovespula* · *Vespula* · Relatedness · Paternity · Worker policing · Mutual policing · Sex allocation · Matricide · Diploid males · Intraspecific parasitism

Introduction

In non-clonal societies, there is potential for conflict over reproduction between group members (Hamilton 1964; Ratnieks and Reeve 1992; Maynard-Smith and Szathmáry 1995). A major question in the study of sociality is how and if reproductive disputes are resolved without too great disruption to the group (Keller 1999). The study of conflicts and their resolution has been central to our current understanding of kin selection theory (Hamilton 1964; Bourke and Franks 1995; Crozier and Pamilo 1996; Keller and Reeve 1999) and natural selection (Leigh 1999).

The eusocial Hymenoptera (bees, ants, wasps) are particularly interesting for the study of reproductive conflict. Their haplodiploid genetics and social structure cause diverse and unusual colony kin structures and the potential for a wide range of conflicts (Ratnieks and Reeve 1992; Bourke and Franks 1995; Crozier and Pamilo 1996). Conflicts between the queen and the workers over sex allocation (Trivers and Hare 1976) and the production of males (Starr 1984) appear to be particularly important. However, our understanding of these conflicts and the extent to which they depend on kin structure is still at an early stage. This is partly because the powerful techniques required for determining kin structure have only recently become widely available (Queller et al. 1993a).

One group that has been particularly neglected in the study of reproductive conflict is the Vespinae (hornets and yellowjackets), the sister group of the more exten-

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		Effective Paternity	# broods	% males	% workers	Ref
		paternity range	analyzed	worker	active	
				sons	ovaries	
Polistinae (outgroup)	<i>Polistes sp.</i>	< 1.05	1-2	-	-	1,2
<i>Vespa</i>	<i>crabro</i>	1.11	1-3	14	0	1
<i>Provespa</i>	<i>anomola</i>	1.00	1	1	-	5
<i>D. maculata</i> grp	<i>maculata</i>	1.00	1	10	21	6
	<i>media</i>	1.08	1-2	10	7	5
<i>D. norvegica</i> grp	<i>arenaria</i>	1.09	1-4	20	17	4
	<i>sylvestris</i>	1.15	1-2	10	10	7
	<i>norvegica</i>	1.08	1-3	10	3	10
	<i>saxonica</i>	1.35	1-3	10	35	11
<i>V. vulgaris</i> grp	<i>germanica</i>	2.35	1-7	55	-	0.6
	<i>maculifrons</i>	7.14	-	30	0	2
	<i>vulgaris</i>	1.90	1-4	17	0	0.4
<i>V. koreensis</i> grp	no data	-	-	-	-	-
<i>V. rufa</i> grp	<i>rufa</i>	-	≥2	1	-	-
<i>V. squamosa</i> grp	<i>squamosa</i>	3.33	-	17	0	-

Fig. 1 Paternity in the Vespinae wasps, including representative data from their sister group, the Polistinae, for outgroup comparison. *Effective paternity* is the evolutionarily important value. This takes into account the relative contribution of each male to the female progeny and is proportional to worker relatedness. No study reports significant inbreeding in vespines, suggesting that paternity is indeed the key factor determining kin structure. % males worker sons and % workers active ovaries are for queenright colonies. Diploid males appear to be rare in the Vespinae, and have been reported in only one out of the ten vespine species where male production has been studied (*Vespa crabro*, 1/15 colonies had adult diploid males; Foster et al. 2000). Active ovaries contain at least one full-sized egg. The phylogeny is from Carpenter (1987). References: 1 Field et al. (1998); 2 Peters et al. (1995); 3 Foster et al. (1999); 4 Foster et al. (2000); 5 K.R. Foster (unpublished data); 6 Foster et al. (in press); 7 F.L.W. Ratnieks and J.J. Boomsma (unpublished data); 8 M.A.D. Goodisman, R.W. Matthews and R.H. Crozier (unpublished data); 9 Ross (1985); 10 Ross (1986); 11 Foster and Ratnieks (2001); 12 Thorén et al. (1995)

sively studied Polistinae (paper wasps; Turillazi and West-Eberhard 1996). The Vespinae are a relatively small group of four genera with a well-supported phylogeny (Fig. 1; Carpenter 1987): *Vespa* (23 species), *Provespa* (3 species), *Dolichovespula* (13 species) and *Vespula* (22 species). They have a similar basic biology, typically with an annual monogynous colony, enclosed paper nest, a morphologically distinct queen caste and workers that are unable to mate, facilitating across-species comparison based upon differences in kin structure (Foster et al. 1999). Here, we discuss a number of studies on vespine wasps which provide new insight into the evolution of kin structure and reproductive conflicts.

Evolution of kin structure

Kin selection theory predicts that relatedness will be extremely important in reproductive behaviour because, by favouring the rearing of close relatives, a helping individual can increase the transmission of their genes

(Hamilton 1964). Knowledge of kin structure, which determines relatedness patterns, is therefore central to the study of reproductive conflict. Vespine wasps have a relatively simple kin structure that is highly amenable to study because societies are nearly always headed by a single outbred queen. This makes queen mating frequency (specifically effective paternity) the key variable causing variation in colony kin structure. Effective paternity is the evolutionarily important measure of queen mating frequency that takes into account sperm use (Starr 1984). Observational data of queen mating frequency have proved an unreliable predictor of paternity [Boomsma and Ratnieks (1996); compare Starr (1984) and Page (1986) with Fig. 1]. However, DNA microsatellites have made accurate paternity assessment routine and a number of vespine species have now been analysed. In combination with Carpenter's (1987) phylogeny of the Vespinae, this allows inferences to be made on the evolution of kin structure (Fig. 1).

Cladistic analysis suggests that high effective paternity (>2) is a derived trait, restricted to *Vespula* (Boomsma and Ratnieks 1996; Foster et al. 1999). A partial exception is *Dolichovespula saxonica*, where initial paternity estimates were high (Thorén 1998). However, further analysis has shown that, while multiple paternity is common, it does not occur in all colonies (Foster et al., in press). High paternity also appears to be derived in the corbiculate bees (Apidae) and fungus-growing ants, where it seems to be restricted to the honeybee genus *Apis* (Estoup et al. 1994; Peters et al. 1999) and to the ant genera *Atta* (Villesen et al. 1999) and *Acromyrmex* (Bekkevold et al. 1999; Boomsma et al. 1999). The increase in effective paternity in *Vespula* seems to have occurred by two mechanisms. *Vespula* queens probably engage in more matings because more fathers are detected (Fig. 2). In addition, paternity bias seems to be lower than in *Dolichovespula* and *Vespa* (Table 1). The contribution of majority males in double-paternity families in *Vespula vulgaris* is significantly lower than in *Dolich-*

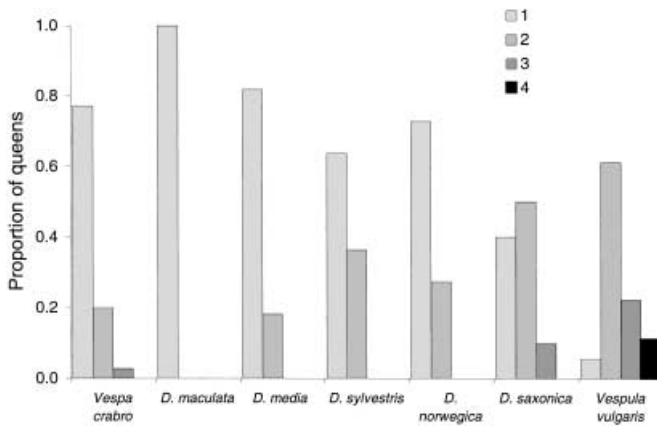


Fig. 2 The number of mates of Vespinae queens (paternity). Values are estimated from DNA microsatellite analysis of 20 workers from each of 10–17 colonies of each species. References as in Fig. 1

Table 1 Paternity bias in double-paternity nests of the Vespinae. Estimates are based on samples of 20 workers from each colony. Species are the same as in Fig. 2. The majority male contribution is significantly different to an unbiased binomial estimate (0.58) in *Vespa* ($P=0.045$) and *Dolichovespula* ($P=0.002$) but not in *Vespula* ($P=0.085$) (one-sample, one-tailed t -tests)

Genus	Number of species	Number of colonies	Majority male contribution
<i>Vespa</i>	1	7	0.74
<i>Dolichovespula</i>	5	11	0.73
<i>Vespula</i>	1	10	0.64

ovespula (one-tailed t -test, $t=1.87$, $n=21$, $P=0.04$), and although not significantly different to *Vespa* alone ($t=1.46$, $n=17$, $P=0.08$) is significantly lower than in *Dolichovespula* and *Vespa* combined ($t=1.82$, $n=28$, $P=0.04$). Why *Vespula* queens mate more and use sperm more evenly is not yet known. However, observation suggests that the opportunity for multiple mating by queens exists in all three genera, with male mating aggregations described in species from each genus (*Vespa mandarinia*, *Vespula flaviceps*: Matsuura and Yamane 1990; *Vespula rufa*, *Vespula vulgaris*, *Vespula germanica*, *D. sylvestris*: Edwards 1980 and references therein; *Vespa crabro*: K.R. Foster, personal observation). This suggests that the higher mating frequency in *Vespula* reflects a difference in queen behaviour rather than increased opportunity to mate.

Conflict over male production

As in most species of social Hymenoptera, worker vespine wasps are unable to mate but can lay haploid male-destined eggs (Wilson 1971; Bourke 1988). This leads to potential conflict between the queen and the workers and among workers over male production. Paternity is pivotal in the prediction of the outcome of this conflict (Starr

1984; Woyciechowki and Łomnicki 1987; Ratnieks 1988). Under single paternity, workers are more related to each others' offspring (nephews, $r=0.375$) than to the queen's sons (brothers, $r=0.25$). The rearing of workers' sons, therefore, is expected. This changes with effective paternity >2 because the relatedness between workers is reduced such that each worker is more related to brothers (queen's sons) than nephews (workers' sons, $r<0.25$). The collective interests of the workers is now the same as that of the queen, and workers are predicted to police each other's reproduction resulting in little male production by workers (Ratnieks 1988). In line with this prediction, worker policing occurs in the highly polyandrous honeybee *Apis mellifera* (Ratnieks and Visscher 1989) where there is a dynamic conflict between worker egg laying and policing (Visscher 1989, 1996; Ratnieks 1993).

The comparison of *Vespula* with *Dolichovespula* provides further support for these predictions (Foster et al., in press). *Dolichovespula* societies are characterised by low paternity and queen-worker conflict. Although workers only succeed in producing a minority of the males (Fig. 1), many have active ovaries with full-size eggs (Foster et al., in press) and lay eggs in the presence of the queen (*D. maculata*: Baldulf 1954; Greene 1979; *D. arenaria*: Greene et al. 1976; *D. media* and *D. saxonica*: Foster et al., in press). In contrast, high paternity in the *Vespula vulgaris* and *squamosa* groups (Fig. 1) is associated with very few ovary-activated workers (Ross 1985; Foster and Ratnieks 2001), an absence of worker laying (*Vespula pensylvanica*: Akre et al. 1976) and queen-only male production (*Vespula squamosa*, *Vespula maculifrons*: Ross 1986; *Vespula vulgaris*: Foster and Ratnieks 2001). Furthermore, work on *Vespula vulgaris* has shown that the absence of worker reproduction in *Vespula* is probably due to worker policing (Foster and Ratnieks 2001). In egg introduction experiments into two queenright discriminator colonies, all worker-laid eggs were removed by workers whilst the majority of queen-laid eggs remained (0/120 worker-laid versus 80/120 queen-laid eggs remained after 16 h).

An apparent exception to the comparison of *Dolichovespula* and *Vespula* is *D. saxonica* which like *Vespula vulgaris* has worker policing (Foster and Ratnieks 2000). Consideration of paternity within individual colonies, however, reveals that this is predicted by worker-policing theory. Single-paternity colonies have considerable worker male production, while multiple-paternity colonies have very little (Fig. 3). Observational data and ovary dissections further show that this pattern is not explained by differences in worker laying with, if anything, more worker laying in multiple-paternity colonies. In single-paternity colonies, workers laid 32/51 eggs (one colony) and 8% (5/60) of workers had full-sized eggs in their ovaries (three colonies), while in multiple-paternity colonies, 132/204 eggs were laid by workers (three colonies) and 14% (14/100) of workers had activated ovaries (five colonies). Egg removal in the multiple but not in the single-paternity colonies is therefore required to explain the absence of male production in the multiple-

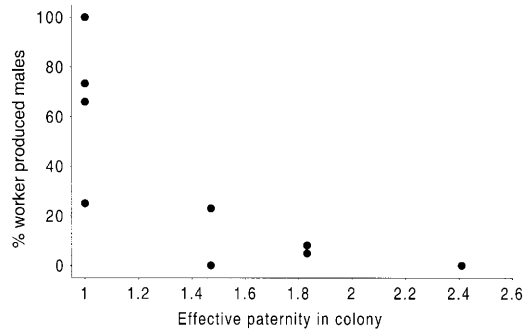


Fig. 3 Paternity against worker male production in nine colonies of *Dolichovespula saxonica*. Spearman's rank correlation, $P=0.004$ (adapted from Foster and Ratnieks 2000)

paternity colonies. *D. saxonica* workers seem to police each other facultatively, only policing if they find themselves among low-related siblings caused by multiple paternity (Foster and Ratnieks 2000). The conflict over male production has been resolved uniquely in *D. saxonica*. Paternity in the other five *Dolichovespula* species is most similar to the *D. saxonica* colonies in which the workers dominate male production. However, in the other *Dolichovespula* species, workers produce a minority of the males (Fig. 1), more in line with the queen's interest. Why this should be the case is not clear. The effectiveness of queen policing may be an important variable. Queens remove worker eggs in *D. maculata* (Balduf 1954; Greene 1979), *D. arenaria* (Greene 1979), *D. saxonica* and *D. media* (Foster et al. in press) although there is not yet evidence that they remove less in *D. saxonica*. Worker policing may also be important if it has evolved in the other *Dolichovespula* species at a lower paternity than in *D. saxonica* and *Vespula vulgaris* (cf. *Vespa crabro* below). Worker policing should now be tested for more widely in *Dolichovespula*.

Another exception to the contrast of *Dolichovespula* and *Vespula* is the *Vespula rufa* group (Fig. 1) where worker laying in queenright colonies has been reported. Akre et al. (1982) observed several worker ovipositions in both of their observation colonies of *Vespula consobrina*. In addition, worker ovary activation (1% of workers), worker laying and overt queen-worker aggressions have been reported in *Vespula acadia* (Reed and Akre 1983). This may represent a different resolution to the conflict over male production than in the *Vespula vulgaris* and *squamosa* groups. However, no worker laying was seen in three colonies of *Vespula atropilosa* (Akre et al. 1976) which is a close relative of *Vespula consobrina* and *acadia*. Conflict resolution and paternity therefore may also vary within the *Vespula rufa* group. Paternity data from this group are currently restricted to one colony of *Vespula rufa*, which had multiple paternity (Fig. 1). More study of this group is called for.

In contrast to *Vespula* and *Dolichovespula*, data from the European hornet *Vespa crabro* are not consistent with relatedness predictions. Despite low paternity, there was no genetic evidence of workers' sons in 272 males from

14 queenright colonies or evidence of worker laying in 50 h observation of four nests housed in glass-fronted boxes (Foster et al. 2000). Furthermore, ovary dissection data from *Vespa crabro* (6/500 workers from 8 colonies had full-sized eggs: Foster et al. 2000) and *Vespa analis* (1/1,062 in 16 colonies: Matsuura 1984) suggest that the level of worker ovary activation is similar to *Vespula* (Fig. 1). Foster et al. (2000) suggested that hornet queens might be exerting pheromonal control over the workers. This is supported by the occasional observation of royal courts in hornets (Nixon 1985a; Matsuura 1991), a phenomenon not seen in either *Dolichovespula* or *Vespula*. Recently, however, another explanation has emerged. Egg introduction experiments into two queenright colonies have shown that as in *Vespula vulgaris*, *Vespa crabro* workers remove worker-laid eggs but leave the majority of queen-laid eggs (1/79 worker-laid eggs but 46/72 queen-laid eggs remained after 16 h: K.R. Foster, J. Gulliver, F.L.W. Ratnieks, unpublished data). This suggests that, rather than being under queen pheromonal control, workers are prevented from reproduction by mutual policing. Interestingly, this response was found to be facultative, with workers in two queenless colonies removing significantly more queen-laid than worker-laid eggs (30/44 worker-laid eggs but 13/41 queen-laid eggs remained after 16 h). This may represent an adaptation to counter queen parasitism (K.R. Foster, J. Gulliver, F.L.W. Ratnieks, unpublished data). The discovery of worker policing in the hornet with its very low paternity is extremely interesting, because workers are killing their closer relatives (nephews) to favour more distant relatives (brothers). This apparent paradox can be explained if worker reproduction significantly reduces colony productivity (Ratnieks 1988; Ratnieks and Reeve 1992) or if worker policing lowers the cost of the conflict over sex allocation by reducing the energy lost through worker killing of males (K.R. Foster and F.L.W. Ratnieks, unpublished data; see Conclusions). However, why this should especially affect *Vespa* but not *Dolichovespula*, where workers lay eggs and succeed in producing males in many colonies (Fig. 1), remains unclear.

Matricide

Where the queen's presence reduces their reproduction, workers of annual societies may gain by killing the queen when she has produced enough workers and gynes (Ratnieks 1988; Bourke 1994) (if unmated, workers are unable to lay female eggs). There are several anecdotal reports of worker aggression towards the queen just preceding her death (Bourke 1994; Foster et al. 2000). Matsuura (1984) reported that the royal court behaviour of *Vespa crabro* involves workers biting the queen, which may kill her. Janet (1895) also described a *Vespa crabro* worker biting the queen just before the queen's death, and Ishay (1964) suggested that *Vespa orientalis* workers "licked" the queen to death. Finally, *D. maculata* workers have been reported to kill their queen by

Table 2 Queen absence in reproductive vespine wasp nests. Only reproductive nests are considered because queen death prior to reproduction would be non-adaptive to workers as there is no benefit from producing males prior to the production of gynes. A reproductive nest is defined as a one with the large cells that are used to rear the majority of sexuals, and/or sexual pupae. Data are referenced in Fig. 1 except for 39 of the *Vespula vulgaris* colonies and the *Vespula germanica* colonies (Spradberry 1971)

Species	Effective paternity	Reproductive nests with no queen (%)	Number of colonies
<i>Vespa crabro</i>	1.11	14	14
<i>Dolichovespula maculata</i>	1.00	74	19
<i>Dolichovespula media</i>	1.08	32	19
<i>Dolichovespula sylvestris</i>	1.15	36	14
<i>Dolichovespula norvegica</i>	1.08	86	14
<i>Dolichovespula saxonica</i>	1.35	20	10
<i>Dolichovespula arenaria</i>	1.09	54	13
<i>Vespula germanica</i>	2.35	0	25
<i>Vespula vulgaris</i>	1.90	6	50

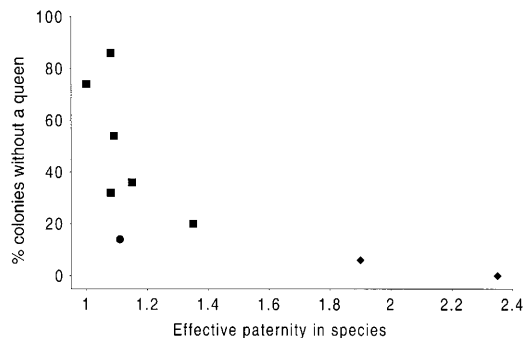


Fig 4 Effective paternity against queen loss in reproductive nests of nine vespine wasp species. Spearman's rank correlation, $P=0.005$ [genera: *Vespa* (●), *Dolichovespula* (■), *Vespula* (◆)]

stinging her (Akre et al. 1982). Despite such reports, there is no direct evidence that matricide is a general phenomenon in any one species.

Kin selection theory predicts that matricide is most likely in low-paternity species where the conflict between the queen and the workers over male production is strongest (Bourke 1994). This prediction is supported by a significant positive correlation between the percentage of queenright reproductive nests and paternity (Spearman's rank correlation, $n=9$, $r=-0.837$, $P=0.009$; Table 2, Fig. 4). Furthermore, the data suggest a link between queen loss and male production conflict. Comparable levels of queen loss were found in *Vespa* and *Vespula*, which both have effectively sterile workers (Fisher's exact test on queen loss frequency in *Vespula* versus *Vespa*, $P=0.17$), while in *Dolichovespula*, when queenright worker reproduction is common, queen loss is also more common [*Dolichovespula* has significantly more queen loss than *Vespa* ($P<0.01$) and *Vespula* ($P<0.001$); Fisher's exact test]. This link between paternity, queen-worker conflict and queen death suggests that matricide may prove to be an important aspect of the conflict over male production in the Vespinae with low paternity.

Conflict over sex allocation

Increased paternity lowers the relatedness of workers to their sisters ($0.75 > r > 0.25$) but not their brothers ($r=0.25$) and, therefore, is important in determining the optimum sex allocation ratio of workers (Trivers and Hare 1976). Furthermore, variation in paternity between colonies is expected to result in split sex ratios, with high-paternity colonies rearing more queens and low-paternity colonies more males (Boomsma and Grafen 1990, 1991; Ratnieks 1991). This pattern has been found in the ants *Formica truncorum* (Sundström 1994a, 1994b) and *F. exsecta* (Sundström et al. 1996). Facultative sex allocation biasing also occurs in response to the number of queens in colonies of the ants *Myrmica tahoensis* (Evans 1995) and *Leptothorax acervorum* (Chan and Bourke 1994) and in five epiponine wasp species (Queller et al. 1993b; Hastings et al. 1998), in line with kin selection predictions. Tests of these predictions are difficult in the vespine wasps owing to their long reproductive period, which would require continuous sampling over several weeks to get a precise estimate of the colony sex ratio. Consequently, there are few studies. However, F.L.W. Ratnieks and J.J. Boomsma (unpublished data) did find evidence of split sex ratios in *D. arenaria*. They included sexuals and sexual pupae in the analysis and were able to show that the proportional investment in gynes versus males was significantly negatively correlated with paternity. *D. arenaria* workers therefore appear to facultatively bias sex allocation in the same way that *D. saxonica* workers facultatively police. Whether both traits co-occur in either species has yet to be investigated, although F.L.W. Ratnieks and J.J. Boomsma (unpublished data) were unable to find a link between paternity and worker male production in their data. The sex ratio in five species of Japanese hornet (Matsuura 1984) varied from 0.65 to 0.42 (proportion of females) and was also variable among colonies (standard deviations 0.21–0.33), further consistent with the existence of split sex ratios. Archer's (1980, 1998) estimates of sex ratio in the British vespines suggest that near equal numbers of females and males are produced. However, vespine queens are larger than males and queen dry mass is 1.6 times male dry mass in *V. vulgaris* (Archer 1980) and *D. sylvestris* (Archer 1979). This suggests that sex allocation is significantly female biased in line with kin selection predictions. Dry mass estimates of sex allocation may be inaccurate (Boomsma 1989). However, Archer (1998) also used bomb calorimetry on *V. vulgaris*, which suggested that the relative investment in females is even greater than estimated by dry mass alone with queens having 2.2 times the calorific value of males.

Conflict between founding queens

Several interspecific social parasites threaten vespine wasp colonies. *Vespula austriaca*, *D. arctica*, *D. adulterina* and *D. omissa* are all obligate social parasites that

have no worker caste, and queens of *Vespula squamosa*, *Vespula pensylvanica* and *Vespa dybowskii* can facultatively parasitise nests of other species in addition to starting their own colony (reviewed by Matsuura and Yamane 1990, and Greene 1991). Evidence is also increasing for the importance of *intraspecific* competition between founding wasp queens. Innumerable reports have been made of queen take-overs within species of *Vespa*, *Dolichovespula* and *Vespula* (reviewed by Matsuura and Yamane 1990; Greene 1991; Matsuura 1991). However, such usurpation has been associated with colony failure (Nixon 1985b, 1986), raising the question as to whether usurpation is often a successful strategy (Greene 1991). Recent genetic data suggest that it is. Two worker matrilineal nests with one queen were found in 2/33 *Vespa crabro* (Foster et al. 1999, 2000) 1/10 *D. sylvestris*, 1/10 *D. norvegica*, 1/10 *D. media* (Foster et al., in press) and 1/17 *Vespula vulgaris* nests (Foster and Ratnieks 2001). With workers taking from 3–5 weeks to develop from egg to adult (Edwards 1980; Matsuura 1984), this suggests that the new queens have been successful in establishing themselves following usurpation. The frequency of successful usurpation seems low but such genetic data are likely to significantly underestimate usurpation frequency because the worker offspring of a first queen will die mid season (adult workers live for around 1 month). This means that the founding queen of usurped nests will be undetectable in the latter part of the season when samples for analysing colony reproduction are taken. It is possible, therefore, that a high proportion of successful vespine queens do not found their own nest.

Conclusions

The vespine wasps provide strong support for kin selection predictions. There is comparative evidence at the genus, species and colony level indicating the importance of kin structure in the resolution of reproductive conflict (Table 3). As expected, however, kinship and re-

latedness do not explain all of the patterns found. The data suggest that the relative *power* of conflicting parties (the queen versus the workers) and the *cost* of conflict expression are also important (Ratnieks and Reeve 1992). For example, relatedness predicts the queen-worker conflict found in *Dolichovespula*, but why the queens retain the majority of the power over male production remains unexplained. In addition, worker policing was found at a lower paternity than predicted in *Vespula vulgaris*, *D. saxonica* and, most notably, *Vespa crabro*. Worker policing may be favoured at paternity below 2 if worker reproduction reduces colony productivity (Ratnieks 1988), which could occur if reproducing workers work less or interfere with the queen's reproduction. Alternatively, selection for worker policing at paternity below two may result from an interaction between the conflicts over male production and sex allocation (K.R. Foster and F.L.W. Ratnieks, unpublished data). In ants, workers perform sex allocation biasing by killing male *larvae* (e.g. Sundström et al. 1996), presumably because they cannot determine the sex of the queen's eggs (Nonacs 1993). This favours worker policing of eggs because policing reduces the cost of killing male larvae by removing some of the males at very low cost at the egg stage. At a general level, the widespread occurrence of worker policing in the Vespinae indicates a central role for worker policing in their social evolution. This supports the hypothesis that mutual policing is a key mechanism of conflict suppression in biological systems (Frank 1995; Maynard-Smith and Szathmáry 1995; Keller 1999; Foster and Ratnieks 2001).

Despite the similar biology and small size of the group, the vespine wasps show significant diversity in both kinship and conflict resolution. While high paternity appears restricted to *Vespula*, the conflict over male production has had similarly peaceful resolutions in *Vespula* and *Vespa*. *Dolichovespula* is different, with significant worker reproduction and queen-worker conflict in queenright colonies. *D. saxonica* is different again in its mix of single and double-paternity colonies (Fig. 3) and facultative worker policing. In comparison to gener-

Table 3 Summary of data on kin selection predictions in the vespine wasps

Conflict	Prediction	Consistent	Inconsistent
Male production	Worker policing should occur in species where effective paternity >2	Low paternity and male production by workers in <i>Dolichovespula</i> High paternity and worker policing in <i>Vespa</i>	Low paternity and worker policing in <i>Vespa crabro</i>
	Facultative worker policing in species with variable paternity	Facultative worker policing in <i>Dolichovespula saxonica</i>	
	Matricide most favoured at low paternity	Correlation of queen loss and paternity across nine species	
Sex allocation	Female bias	Female bias in seven British vespine species	
	Facultative sex allocation biasing in species with variable paternity	Facultative sex allocation biasing in <i>Dolichovespula arenaria</i>	

al biology, therefore, paternity and conflict resolution appear to be highly labile traits in the Vespinae. This is well illustrated by the comparison of *D. norwegica* and *D. saxonica*. These species are close relatives and can be difficult to distinguish morphologically (Else 1994) but have very different patterns of paternity and male production (Fig. 1).

One important character in which the vespine wasps do display variation is colony size. Colony size is interesting because it can be viewed as both a cause and effect of reproductive conflict (Bourke 1999). For example, all *Vespula* species in which paternity and male production have been studied are large-colony species whose colonies commonly have several thousands of workers at the reproductive stage (*V. vulgaris* and *squamosa* species groups). In comparison, in *Dolichovespula*, colonies, tens to hundreds are the norm (Matsuura and Yamane 1990; *D. arenaria* is an exception reaching 1,000 workers: F.L.W. Ratnieks and J.J. Boomsma, unpublished data). Thus, by removing costly conflict, the evolution of efficient worker policing in *Vespula* has possibly caused the increase in colony size. However, the benefits of worker policing may also increase in large colonies and favour its subsequent evolution. Distinguishing between these hypotheses is extremely difficult and coevolution between the two is likely (Bourke 1999). However, the discovery of worker policing in *Vespa*, where colony size is generally also larger than in *Dolichovespula* (Matsuura and Yamane 1990) further suggests an association.

There are many avenues for future work into reproductive conflict in the vespine wasps. There are three major groups where data on paternity and reproduction are needed: *Vespa*, *Provespa* and the *Vespula rufa* group. *Provespa* species are enigmatic nocturnal wasps with cryptic nests, few of which have ever been found (Matsuura and Yamane 1990). They appear to have royal courts around their single queen, as occurs in *Vespa*. In contrast to all other vespines, the suggestion has been made that they are swarm founding, due to the extremely low numbers of queen cells found in mature nests (7–29 out of 913–2,276 cells in six nests of *Provespa anomala*: Matsuura and Yamane 1990). The *Vespula rufa* group have small colonies comparable to those of *Dolichovespula* and significant amounts of worker laying in some species (see above). In the groups where paternity is known, further tests for worker policing behaviour are desirable. In addition, accurate colony-level data on sex allocation and paternity have only been collected in one species (*D. arenaria*: F.L.W. Ratnieks and J.J. Boomsma, unpublished data). Finally, it will be interesting to study paternity in the workerless social parasites, such as *Vespula austriaca*. With no workers, paternity can have no repercussions on worker behaviour, making it interesting to compare paternity in the parasite with its non-parasitic relatives.

Although their covered nests and hostile temperament have made them inherently secretive, study of the vespine wasps has proved highly fruitful. Within their soci-

eties, we have found novel and varied resolutions to reproductive conflict that provide new insights into kin selection theory.

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