

Conflict over sex ratio and male production in paper wasps

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Received 15 Dec. 2005, revised version received 28 Nov. 2006, accepted 6 Dec. 2006

Tsuchida, K. & Suzuki, T. 2006: Conflict over sex ratio and male production in paper wasps. — *Ann. Zool. Fennici* 43: 468–480.

Kin selection theory has been used to generate several useful frameworks in the field of evolutionary ecology. We briefly review the research on two main theoretical predictions for sex ratio variation among colonies, and for worker policing, using a relatedness framework in paper wasps. Contrary to the studies of advanced eusocial wasps, conclusive evidence showing worker control of sex ratio has not been shown in primitively eusocial *Polistes*, which suggests that collective worker control is not active at the primitively eusocial stage when colony size is small. Worker control of colony investment might be facilitated in an advanced eusocial system when colony size is large. Therefore, a relatedness-based theoretical framework does not seem to be important in explaining the sex ratio variation among colonies of *Polistes* wasps. Worker policing, however, has been observed in monogynous and monandrous colonies of *Polistes* and *Dolichovespula*, in which relatedness benefits for workers do not exist. The observed policing behavior seems to be termed as ‘selfish policing’. Fertility signals and egg marking pheromones by queens are the likely proximate factors that determine the fate of workers’ eggs. We also discuss the influence dominance order among workers may play in regulating worker reproduction. This is a form of decentralized regulation, which may be associated with larger colony size.

Introduction

Sex determination via haplodiploidy is one of the key parameters for kin selection theory, which helps explain why we often observe eusociality among animals with haplodiploidy rather than diplo-diploidy — the exceptions being diploid termites, aphids, snap shrimp and naked mole rats. Empirical support for this theoretical framework has been proposed using many ant species. Indeed, facultative sex ratio manipulation has repeatedly been reviewed using mostly

ant studies (Nonacs 1986, Boomsma & Grafen 1990, Chapuisat & Keller 1999, Sundström & Boomsma 2001). Here, we briefly review the studies of sex ratio variation and of worker policing behavior using mainly *Polistes* wasps.

Kin selection and sex ratio theory

Altruistic, or self-sacrificing behavior of group members has been observed in many animal societies, but the most prominent and well-stud-

ied altruistic system is that of worker and/or soldier castes in social insects. Hamilton (1964a, 1964b) first proposed the famous kin selection theory under an inclusive fitness framework to explain the evolution of self-sacrificing behavior, which had been difficult to explain using the classical direct fitness framework. "Hamilton's Rule" shows that helping will be selected for if $rB - C > 0$, where B is a recipient's fitness benefit due to the donor's helping behavior, C is the donor's fitness cost due to the helping act, and r is the relatedness between the recipient and donor. Measuring relatedness is nowadays quite easy using neutral genetic markers, whereas measuring B and C is complex and laborious. Indeed, there have been only three studies in social insects that have measured these latter parameters and have supported inclusive fitness theory (Metcalfe & Whitt 1977a, 1977b, Noonan 1981, Queller & Strassmann 1988).

Although kin selection theory explains the evolution of helping behavior among kin groups, the theory counter intuitively predicts conflicts among kin caused by asymmetrical relatedness between males and females in haplodiploid species. The pioneering work of Trivers and Hare (1976) has provided a novel tool with which to test kin selection theory by measuring sex ratio instead of measuring B and C . This theory predicts that the adaptive population-wide sex ratio in monogynous and monandrous colonies is 3:1 (female:male) under worker control, and 1:1 under queen control.

However, in nature, we often see polymorphism in colony structures: orphan colonies vs. queen-right colonies and monogyny vs. polygyny. The former case is analyzed theoretically by Taylor (1981), and his predictions are that, in response to excess male production by orphan colonies, the sex ratio of queen-right colonies should be slightly female-biased under both queen and worker control (i.e., sex ratio compensation). Split sex ratio theory which is a general prediction of individual colony sex ratio variation associated with variation of genetic colony structures was proposed by Boomsma and Grafen (1991). The critical parameter for this theory is relatedness asymmetry, which is the ratio of the relatedness of workers to sisters, with that of workers to the males they rear. The

theory predicts that those colonies with a relatedness asymmetry above the average relatedness asymmetry of the whole population should invest only in females, whereas those colonies with a relatedness asymmetry below the average should invest only in males.

Empirical support for split sex ratio theory has been presented for several ant species, in which relatedness asymmetry differs among colonies due to the queen's facultative mating frequencies (Sundström 1994, Evans 1995, Sundström *et al.* 1996). Polygyny is the prevailing system in swarm-founding wasps, and it has been thought that kin selection theory cannot readily explain its maintenance, as relatedness among workers is very low. However, under cyclical oligogyny (or seasonal monogyny; West-Eberhard 1978), in which the number of queens decreases as the season progresses, daughter queens are produced only after a bottleneck in the number of old queens. As such, these queens are highly related, often as full sisters. This elevates relatedness among the worker progeny of the new queens, and promotes cooperation.

Importantly, cyclical oligogyny is not in conflict with split sex ratio theory; workers can enjoy their optimum during the mono- or oligogyny stage, when they produce only gynes due to high relatedness asymmetry, and the polygyny stage, when they produce only males due to low relatedness asymmetry (Strassmann *et al.* 1991, 1992, 1998, Queller *et al.* 1993, Gastreich *et al.* 1993, Hastings *et al.* 1998, Henshaw *et al.* 2000, Tsuchida *et al.* 2000, Kudô *et al.* 2005). Although unexplored questions regarding cyclical monogyny remain (e.g. how to continue to supply a large worker force, irrespective of the substantial loss of productivity, via having a single-queen stage; see Henshaw *et al.* 2000, Kudô *et al.* 2005), all studies have consistently shown high queen-queen relatedness relative to low worker-worker relatedness, which supports cyclical oligogyny. Therefore, a unified worker force seems sufficient to influence the timing of reproductive production even in complicated polygynous colonies such as swarm-founding wasps.

In addition to relatedness-based sex ratio theory, there are two main explanatory frameworks of individual sex ratio variation: the

queen–worker conflict hypothesis (Herbers 1984) and the resource availability hypothesis (Nonacs 1986). Herbers (1984) explained that colony-level sex ratio approaches 1:1 as queen numbers increase, because queens, as a whole, gain increasingly more power to control colony investment (*see also* Banschbach & Herbers 1996). On the other hand, Nonacs (1986) explained that female-biased sex ratios in larger colonies are predicted due to high resource availability resulting from the collective effort of a large work force. This theory predicts male-biased sex ratios in smaller colonies because female progeny become workers, instead of gynes, with relatively low resource acquisition (*see also* Rosenheim *et al.* 1996).

The variation in resource availability also causes a split sex ratio in the presence of sex-biased local interactions (e.g., local resource competition, local mate competition, and local resource enhancement, Frank 1987, Crozier & Pamilo 1996). There exists supporting evidence for this perspective in a few ant species (Tsuji & Yamauchi 1994, Hasegawa & Yamauchi 1995). In *Formica exsecta*, split sex ratio within colonies was observed in polygynous populations; however, colonies producing only males did not have greater relatedness asymmetry from the perspective of the adult workers who rear the brood (Brown & Keller 2000). Brown *et al.* (2002) proposed the queen-replenishment hypothesis, in which colonies produce gynes only when queen number is so low that colony production of brood is reduced, or colony survival threatened. These theories are also likely candidates for explaining split sex ratio within a population.

Life history and sex ratio variation of annual *Polistes* wasps

Sex ratio studies on wasps are relatively few as compared with those on ants. There are two main reasons for this: (1) a lack of distinct morphological castes in wasps makes it hard to divide females into workers and gynes, and (2) it requires laborious effort to collect sufficient data on colony-level sex ratio of wasps in the field. There are three natural history traits that create variation in relatedness asymmetry

among colonies of *Polistes*. First, in general, an overwintered foundress constructs a nest either cooperatively or solely in spring, thus generating variation among colonies in terms of monogyny and polygyny. In monogynous colonies, workers should invest in a female-biased sex ratio due to high relatedness asymmetry, whereas in polygynous colonies workers should invest in a male-biased sex ratio due to low relatedness asymmetry. (Note that this prediction holds true only when foundresses are related, as is the case for most pleiomorphic *Polistes*.) Second, workers sometimes mate with early males and, if these mated-workers become replacement queens after an original queen's death, the relatedness asymmetry from the workers' point of view becomes absent. This is because workers then rear their sister-queen's offspring (nieces), in which the relatedness is equivalent to that of the workers to their own sons. As such, a colony headed with a replacement mated-worker (parasocial colony) should invest in a male-biased sex ratio, and one headed by an original queen (eusocial colony) should invest in a female-biased sex ratio (Muel-ler 1991). Third, un-mated worker reproduction decreases the relatedness asymmetry, and colonies with relatively more worker reproduction should invest in a male-biased sex ratio, while colonies with less worker reproduction should invest in a female-biased sex ratio.

Sex ratios observed in Polistinae wasps are listed in Table 1, in which values are cited from Suzuki (1986) unless otherwise stated. Noonan (1978) reported that the population sex ratio of *P. fuscatus* was 1:1, thus supporting the queen control hypothesis. However, in single-foundress colonies, sex ratio was slightly female-biased as compared with that of multiple-foundress colonies. This trend does not contradict a relatedness asymmetry hypothesis. Metcalf (1980) reported that sex ratios of both *P. metricus* and *P. variatus* were 1:1, again supporting that the queen controls colony investment. Strassmann (1984) studied *P. exclamans*, and observed female-biased sex ratio in years with low overall nest success due to bird predation, this was because male production was likely to cease late in the season. She proposed the caste-plasticity hypothesis, in which females — which become workers or gynes — are produced before males (protogy-

nous production) whenever there is uncertainty in the timing of producing reproductives.

Suzuki (1986) pointed out that there are multiple associations between sex ratio and production schedules of reproductives; simultaneous production with an unbiased sex ratio, and either protandrous production or protogynous production with a female-biased sex ratio. In species with simultaneous production, observed sex ratios were 1:1. In these systems, there was no worker reproduction, which suggests that when queen control over worker reproduction is effective, the resulting sex ratio becomes even. In species with protandrous production, in which males are produced before females, female-biased sex ratios were observed. This relationship can be explained within a sexual selection framework, in which protandrous production favors a female-biased sex ratio when early reproductive females are of better quality than later reproductive females (Bulmer 1983), or through a queen-worker conflict over male production framework, in which the queen allows some portion of worker control of investment while also

forcing workers to rear its haploid eggs (Bulmer 1981). In species with protogynous production, in which females are produced before males, female-biased sex ratios were observed in years when colony cycles ended early (Strassmann 1984). Suzuki (1986) categorized 13 wasp species into the three production schedules mentioned above (Table 1), and pointed out that frameworks other than those based on relatedness are useful for describing sex ratio variation both within and across species.

Inagawa *et al.* (2003) reported sex ratio variation in *P. snelleni*. In this species, reproductives are produced protandrously and nest cells are not re-used (one cell per individual). Therefore, the production sequence for each caste is easy to follow, and one can get an accurate estimate of the sex ratio by using nests at the end of the colony cycle. The sex ratios were dependent on colony size, where a female-biased sex ratio was observed in the larger colonies. This trend might be explained by a balance of power between the queen and workers; in larger colonies, the collective worker force is strong and workers would

Table 1. Sex investment ratio and related characters in 13 species of Polistinae wasps. The investment ratios were determined by Suzuki (1986), unless otherwise stated.

Species	Sex investment ratio (male ratio)	References	Other trends in sex investment ratio
Simultaneous production			
<i>Polistes fuscatus</i>	0.50	Noonan (1978)	–
<i>P. metricus</i>	0.50	Metcalf (1980)	–
<i>P. variatus</i>	0.49	Metcalf (1980)	–
<i>P. jokahamae</i> (= <i>jadwigae</i>)	0.51	Suzuki (1986)	Female-biased sex investment in larger colonies ⁽⁴⁾
<i>P. rothneyi</i>	–	Suzuki (1986)	–
<i>Parapolybia varia</i>	0.18	Suzuki (1986)	–
Protandrous production			
<i>P. snelleni</i>	0.15	Suzuki (1986)	Female-biased sex investment in larger colonies ⁽⁵⁾
<i>P. japonicus</i>	0.18	Suzuki (1986)	–
<i>P. mandarinus</i>	0.35	Suzuki (1986)	–
<i>P. sp. cf. nimpha</i>	0.18	Yamane (1980) ⁽³⁾	–
Protogynous production			
<i>P. exclamans</i>	0.34 ⁽¹⁾	Strassmann (1984)	–
<i>P. chinensis antennalis</i>	0.39 ⁽²⁾	Suzuki (1986)	Male-biased sex investment in larger colonies ⁽⁶⁾
<i>Parapolybia indica</i>	0.03	Suzuki (1986)	–

⁽¹⁾ mean value in investment for queen-right colonies in Strassmann (1984) calculated by Suzuki (1986).

⁽²⁾ 0.47 in Tsuchida *et al.* (2003) for queen-right colonies.

⁽³⁾ cited from Suzuki (1986).

⁽⁴⁾ data from T. Sameshima & E. Kasuya (unpubl. data).

⁽⁵⁾ data from Inagawa *et al.* (2001).

⁽⁶⁾ data from Tsuchida *et al.* (1986). Production schedule in *P. chinensis antennalis* varied among colonies.

prefer a female-biased sex ratio. Alternatively, the relationship between colony-size and sex ratio could be explained by the resource availability hypothesis. Interestingly, mated workers were observed in queen-right colonies of *P. snelleni*, and they contributed to female production in orphan colonies (Suzuki 1985). If mated workers succeed colonies after the original queen's death, a variation in relatedness asymmetry will emerge among colonies, such that eusocial colonies (a mother–daughter relationship) will coexist with parasocial colonies (a daughter–daughter relationship; Mueller 1991, but see also Strassmann 1984). Further studies are needed to evaluate the genetic colony structures of *P. snelleni*, and to determine how frequently mated-workers become replacement queens and how many offspring a replacement queen can produce.

In *P. chinensis antennalis*, worker reproduction is frequently observed even in queen-right colonies. Interestingly, early males are sometimes produced, but they lack reproductive potential, because they are diploids (Tsuchida *et al.* 2002, 2004). In monogynous and monandrous colonies, relatedness theory predicts that workers should prefer to reproduce by themselves, because the relatedness of a worker to its sons is higher than to its nephews and brothers. Tsuchida *et al.* (2003) studied sex ratio variation in this species for 3 years and found that larger queen-right colonies invested more in males, whereas smaller queen-right colonies invested more in females. Population sex ratios were 1:1, suggesting queen control, even after allowing for male production by workers. Production schedules varied among colonies, in which larger colonies were protandrous and smaller colonies were protogynous. Queens in larger colonies can produce male haploid eggs early and force its workers to rear them, as well as giving partial allowance of reproduction to workers (as predicted by Bulmer 1981). In smaller colonies, queens may continue to lay diploid female eggs until relatively late in the season, because females become both workers and gynes (bed-hedging), resulting in delayed haploid egg production by the queen due to a lack of sufficient resources. In addition, worker reproduction was rarely observed in smaller colonies, suggesting that workers might refrain from ovipositing in order to avoid direct harsh conflict with the queen.

Worker reproduction in smaller colonies should impose larger costs than in larger colonies. In any event, these results suggest that colony size and/or worker reproduction in *P. chinensis antennalis* are important determinants for colony sex ratio irrespective of a relatedness framework.

One aspect of sex ratios that researchers have not yet taken into account is the time lag of males from emergence to mating. Mate-searching activity is most vigorous in late August and early September for *P. snelleni* and *P. mandarinus*, whereas it is late October for *P. chinensis antennalis* and *P. jukahmae* (former = *jadwigae*) (Kojima & Suzuki 1986, Suzuki 1995, see also Beani 1996). Therefore, males in the latter two species have to survive for more than a month until mating. Furthermore, when the worker force is considered, prey supply might be scarce in orphaned or smaller colonies, which would reduce the survival rate of reproductives due to lower worker numbers. The effect of food shortage could affect male quality in these colonies, in terms of their body size and longevity. Larger males have an advantage in retaining mating territories and copulating with females in several *Polistes* wasps (Post & Jeanne 1983, Beani & Turillazzi 1988, Polak 1993, 1994). The evaluation of male quality by a prospective partner should be important in understanding which type of colonies have opportunities to contribute to the future gene pool.

In summary, conclusive evidence for worker control of sex ratio in the primitively eusocial wasp *Polistes* has not yet been shown. The ability of workers to control sex ratios seems to be constrained by the annual life cycle and by semelparity, as is the case with the bumblebee *Bombus terrestris* (Duchateau *et al.* 2004). Conversely, cyclical oligogyny, which is consistent with the collective sex ratio preferences of workers, is observed in the advanced eusocial wasps in the ropalidine and epiponine (Strassmann *et al.* 1991, 1992, Gastreich *et al.* 1993, Queller *et al.* 1993, Hastings *et al.* 1998, Henshaw *et al.* 2000, Tsuchida *et al.* 2000, Kudô *et al.* 2005). These results suggest that collective worker control is not active at the primitively eusocial stage with small colony size, and that worker control might be facilitated with advancing eusocial stages involving increasing colony size.

Conflict over male production

An important aspect of theories of social evolution is how to describe the evolution of worker sterility and helping behavior. There are three explanations for why workers do not reproduce. The first, using a relatedness framework, is worker policing theory (Starr 1984, Woyciechowski & Lomnicki 1987, Ratnieks 1988). In monogynous and monandrous colonies, relatedness of workers to their brothers, nephews and their own sons, is 0.25, 0.375 and 0.5, respectively. If a queen mates doubly, the relatedness of workers to their own sons and to brothers is unchanged, while that to nephews becomes 0.25, with the value decreasing as the mating frequency of the queen increases. Therefore, worker policing theory predicts (1) workers prefer to reproduce when the queen is singly mated, unless worker reproduction imposes some extra cost on the colony, and (2) workers mutually kill nephew-eggs when the queen mates more than twice.

The second explanation involves the sexual deception hypothesis (Nonacs & Carlin 1990). For this hypothesis, assume that a worker tries to destroy queen-laid male eggs and replace them with its own. Upon egg destruction, workers should discriminate queen-laid male eggs from queen-laid female eggs, because the former ($r = 0.25$) is less valuable to workers than are the latter ($r = 0.75$). If the queen conceals the sex of its offspring using a chemical substance, workers cannot discriminate the sex and they refrain from destroying them so as to avoid the costly destruction of female eggs.

The third explanation involves the egg viability hypothesis. Pirk *et al.* (2004) found that worker-laid male eggs of *Apis mellifera* are less viable than queen-laid male eggs. This result, however, was recently questioned by Beekman and Oldroyd (2005). These researchers found that the survival rate of queen-laid eggs was greater than that of worker-laid eggs, irrespective of egg viability. This result strongly suggests that queen-laid eggs could be chemically or physically different from worker-laid eggs (see Katzav-Gozansky *et al.* 2003).

Evidence supporting the worker policing theory has been reported in honeybees and a

wasp. Ratnieks and Visscher (1989) reported that worker-laid eggs are more swiftly removed than queen-laid eggs in highly polyandrous honeybee colonies, which is in agreement with policing theory. Other good evidence is found in the facultatively polyandrous Vespinae wasp *Dolichovespula saxonica*. In this species, the frequency of workers' sons is higher in singly-mated queen colonies than in multiply-mated queen colonies, due to worker-laid eggs commonly being removed in the latter (Foster & Ratnieks 2000). Foster and Ratnieks (2001a) examined the relationship between the queen mating frequency and workers' male production in vespine wasps, and found, as predicted, that male production by workers is uncommon in the species with high queen mating frequencies. The theory also predicts that the frequencies of workers' sons are minimal in polygynous colonies with related queens. In agreement with this prediction, queens produced all of the males in swarm-founding Epiponini wasps (Hastings *et al.* 1998, Henshaw *et al.* 2000).

Evidence against relatedness-based worker policing

In contrast to the previously described research, there have been several reports that do not support relatedness-based worker policing theory. First, worker policing has also been observed in monogynous monandrous colonies (Kikuta & Tsuji 1999, Iwanishi *et al.* 2003). In these studies, colonies were experimentally subdivided into a queen-right unit (strictly speaking, gamergate-right unit) and an orphan unit, and then reunited again. During the subdivision, a few workers became dominant and produced eggs. After the reuniting, dominant workers were aggressed and subordinate workers inhibited the dominants' reproduction. Second, worker reproduction is absent in several monogynous and monandrous species (Arévalo *et al.* 1998, Walin *et al.* 1998, Foster *et al.* 2002, Takahashi *et al.* 2002, 2004a, 2004b, Strassmann *et al.* 2003). Third, worker policing has been observed in the species with a clonal life history (Hartmann *et al.* 2003, Pirk *et al.* 2003). For example, in the Cape honeybee and the ant *Platythrea puncttata*,

workers are capable of producing female offspring by thelytokous parthenogenesis. Despite the absence of relatedness benefit, workers' eggs were removed, presumably because worker reproduction is costly at the colony level (Ratnieks 1988). Fourth, in contrast to *D. saxonica*, facultative worker policing was not confirmed in *Bombus hypnorum*, in which — as with *D. saxonica* — mating frequencies of queens varied among colonies (Paxton *et al.* 2001). Fifth, by using wider taxonomic groups than those of Foster and Ratnieks (2001a), Hammond and Keller (2004) showed that male parentage does not vary with relatedness, and concluded that there is greater harmony and more complex regulation of reproduction in social insects than expected from simple theoretical expectations based on the relatedness alone.

Recently, worker policing in monogynous and monandrous wasps has become even more evident. Wenseleers *et al.* (2005b) reported that worker-laid eggs were policed by the queen in mostly monandrous colonies of *Vespa rufa*. Similarly, Wenseleers *et al.* (2005a) reported that worker-laid eggs were policed by both the queen and workers in monogynous and monandrous colonies of *D. sylvestris*. In addition, queen-laid eggs survived better than worker-laid eggs, suggesting that the queen-laid eggs are chemically marked and are preferentially treated. In *P. chinensis antennalis*, most queen-laid eggs hatch successfully, while only a small proportion of worker-laid eggs do. As in *D. sylvestris*, worker-laid eggs were policed both by the queen and by workers (Saigo & Tsuchida 2004). The queen oviposited both female and male eggs, and therefore workers seemed not to discriminate the sex of queen-laid eggs.

It is noteworthy that, in general, workers cannot discriminate the sex of queen-laid eggs in social insects. A plausible proximate mechanism of the high survivorship of queen-laid eggs is that they are chemically marked to conceal sex (Nonacs & Carlin 1990). The chemicals could also signal queen fertility (honest signal; Keller & Nonacs 1993). As with many ants (e.g. Peeters *et al.* 1999, Endler *et al.* 2004), cuticular hydrocarbons and/or substances in the Dufour's gland could play the role of a fertility signal in *Polistes* wasps (see Sledge *et al.* 2001, 2004, Dapporto *et*

al. 2004, 2005). For example, in *P. fuscatus*, subordinate foundress eggs that were experimentally rubbed with Dufour's extract were destroyed by the dominant foundress, whereas eggs rubbed with a secretion from the dominant were not destroyed by the subordinate (Downing 1991).

Other than relatedness, there are two factors that explain worker policing in monogynous and monandrous insect societies: (1) colony efficiency (Ratnieks 1988) and (2) efficient sex ratio manipulation in favor of a worker optimum (Foster & Ratnieks 2001b). Tsuchida *et al.* (2003) found that the frequency of worker oviposition positively correlated with colony size. This correlation could be interpreted to mean that worker reproduction in smaller colonies is costly to the whole colony, whereas that in larger colonies is not as costly. As such, in large colonies, some reproduction by workers is allowed by the queen. As mentioned above, workers in *Polistes* wasps do not seem to effectively manipulate the sex ratio for their optimum value, and therefore the mechanism of Foster and Ratnieks (2001b) does not appear to play an important role in primitively eusocial wasps.

It is noteworthy that in the three species (*D. sylvestris*, *P. chinensis antennalis* and *P. dominulus*), in which worker reproduction, and worker and queen policing have been observed, workers appear to compete with each other. In *D. sylvestris*, physical aggression to prevent egg-laying was directed at workers trying to oviposit. In *P. chinensis antennalis*, however, direct physical aggression was not observed — workers tend to remain near the cell where they have just oviposited. However, worker-laid eggs, as a rule, were policed by the queen and other reproducing workers. In other words, policing workers are also the reproducing workers. In social insects, worker policing is defined as the inhibition of direct reproduction by other workers (Monnin & Ratnieks 2001). The phenomena described above for annual Vespinae fit this definition. However, this is not the same as what Ratnieks (1988) originally called worker policing, i.e. mutual inhibition of worker reproduction in which workers who do not attempt to directly reproduce can hinder the direct reproduction of other workers. In other words, the worker policing in Ratnieks (1988) was a weakly spiteful behavior (as

the actor cannot increase direct fitness), whereas those observed in *D. sylvestris* and *P. chinensis antennalis* are selfish. Evidence strongly suggests that worker-worker competition for oviposition is another aspect of worker policing.

Recently, Liebig *et al.* (2005) reported that in *P. dominulus* the frequency of worker reproduction increased when some larvae were artificially removed. Interestingly, selfish policing was also observed, and the authors inferred that workers laid eggs when they perceived a decline in queen power as represented by an increase in empty cells. In summary, in addition to colony size, mutual conflict among workers for reproduction and direct assessment of queen fertility may play important roles in determining the magnitude of worker reproduction in annual wasps. More experimental studies are needed to evaluate the proximate factors governing worker reproduction in wasps.

Dominance hierarchy as decentralized regulation of colony activity

Originally, worker policing meant the regulation of worker reproduction by workers, which is a form of decentralized regulation. Policing behavior and dominance hierarchies share the same functional characteristic, that is, the inhibition of reproduction by behavioral interaction (Monnin & Ratnieks 2001), again as a form of decentralized regulation. In dominance hierarchies, dominant individuals suppress the reproduction of lower ranked individuals. The top of the hierarchy is occupied by the queen; below the queen, several workers usually form a linear hierarchy. The ranking among workers is important in determining the replacement queen, should the original queen die. Interestingly, several authors have pointed out the existence of age-dependency in the dominance rank and, in general, younger workers become dominant in perennial ponerine ants (Tsuji & Tsuji 2005). In annual wasps, with a few exceptions, younger workers are dominant in tropical areas, whereas older workers are dominant in temperate areas.

Recently, Tsuji and Tsuji (2005) used an inclusive fitness model to analyze why such

differences might emerge and found that the length of an individual life as compared with the colony life is important for determining such seasonal differences; older individuals can dominate younger ones when the colony life is shorter than the potential individual life. Age-dependent dominance hierarchies of Vespidae, as shown in Table 2, reveal two intriguing trends. First, younger dominants are observed in both tropical and temperate areas. Second, younger dominants are associated with swarm founding.

Interestingly, older workers are dominant in *Polistes* wasps, with the exception of tropical *P. erythrocephalus*. Conversely, both types are observed in *Ropalidia*. The *Ropalidia* species shown in Table 2 all belong to the subgenus *Icariola*, which independently found colonies (Itô 1993). Species of another subgenus of *Ropalidia*, *Icarielia*, are swarm founding and have a perennial life cycle. Therefore, both age-dependent dominance types coexist in *Icariola*. These data suggest that the younger dominant type could be associated with a large colony size and a perennial life cycle.

Figure 1a shows the system of older worker dominance. According to a worker's emergence order, its physiological level increases and reaches a plateau at a certain age. The height of each plateau is age-dependent. In other words, workers form a queue according to their age, and older workers suppress the physiological level of workers below them in rank. Figure 1b shows the system of younger worker dominance. The physiological level of each worker changes in a convex fashion, and that of younger workers exceeds that of older workers after a certain time. In old worker dominance, younger workers subsequently emerge, and the age structure among workers becomes a pyramid, with the older workers on the top. In this case, all treachery by subordinate workers is suppressed by aggressive acts of a queen (centralized regulation) and/or dominant workers, but this suppression becomes less efficient as colony size increases. Alternatively, in younger worker dominance, every moment the number of younger workers exceeds that of older workers. In this case, the age structure is an inverse pyramid, where younger workers are on the top, and where worker reproduction is suppressed by a younger cohort of

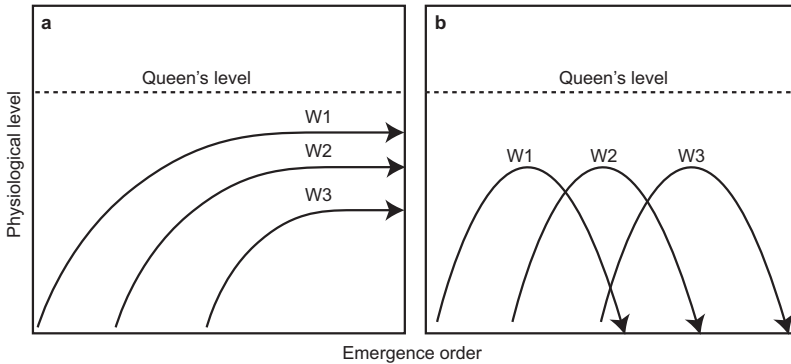


Fig. 1. Hypothetical schematic of a worker's physiological activity level in both (a) a primitively eusocial and (b) an advanced eusocial systems.

workers, which is the most abundant cohort at that time (decentralized regulation).

Younger worker dominance is a possible candidate of decentralized regulation of worker reproduction, and it might be a prerequisite to attain huge colony size. Under the situation where larger colony size is selected for, the younger worker dominance could facilitate the decentralized regulation of worker reproduction and may successfully attain a larger colony size to an extent that older worker dominance could not. As colony size increases, queen control may shift from physical control to pheromonal control (e.g. Brian 1980).

Similarly, it has been argued that one way in which a lineage changes from primitive to advanced eusociality is to acquire pheromonal

queen control (e.g. Wilson 1971). However, as pointed out by Keller and Nonacs (1993), pheromonal queen control over worker reproduction is evolutionary unstable, because a queen is likely to be reproductively suppressed by its own pheromones, and workers may become tolerant of the pheromone. Queens should continuously produce novel compounds, or increase the concentration of the compounds, to suppress workers and win this arms race.

Dominance hierarchies play a role in regulating the number of hopeful reproductives (Molet *et al.* 2005), as well as does worker policing (Liebig *et al.* 1999). Interestingly, *R. marginata* queens are not aggressive, and the dominant-subordinate interactions may serve as decentralized regulation of workers' foraging (Premnath *et*

Table 2. The potential replacement queen in workers, and related characters in 14 species.

Species	Potential queen in workers	Colony founding (I: independent, S: swarm)	Climate	References
<i>Polistes exclamans</i>	Old	I	Sub-tropical	Strassmann & Meyer (1983)
<i>P. instabilis</i>	Old	I	Temperate to tropical	Hughes & Strassmann (1988)
<i>P. erythrocephalus</i>	Young	I	Tropical	West-Eberhard (1969)
<i>P. chinensis antennalis</i>	Old	I	Temperate	Miyano (1986)
<i>Mischocyttarus drewseni</i>	Young	I	Tropical	Jeanne (1972)
<i>Ropalidia marginata</i>	Intermediate	I	Tropical	Chandrashekhara & Gadagkar (1992)
<i>R. cyathiformis</i>	Young	I	Tropical	Gadagkar (1987)
<i>R. variegata jacobsoni</i>	Young	I	Tropical	Yamane (1986)
<i>R. fasciata</i>	Old	I	Sub-tropical	Iwahashi (1989)
<i>R. plebeiana</i>	Intermediate	I	Temperate	K. Tsuchida (unpubl. data)
<i>Parapolybia indica</i>	Young	I	Temperate	Suzuki (2003)
<i>Metapolybia aztecoides</i>	Young	S	Tropical	West-Eberhard (1978)
<i>Synoeca surinama</i>	Young	S	Tropical	West-Eberhard (1981)
<i>Polybia occidentalis</i>	Young	S	Tropical	O'Donnell (2001)

al. 1995, Kardile & Gadagkar 2002, Sumana & Gadagkar 2003). Dominance hierarchies among workers could be interpreted as decentralized regulation of worker reproduction, and hierarchies under young worker dominance should be an important trait in considering social evolution, particularly, for the evolution to the advanced eusociality.

Recently, Giray *et al.* (2005) found that juvenile hormone (JH) titers correlated with both ovarian development of queens and task differentiation in workers of *P. canadensis*. This supports the split-function hypothesis, in which the function of JH has diverged into either reproductive or behavioral maturation as caste differences have evolved (West-Eberhard 1996). An evaluation of age-dependent worker activity, by both behavioral studies — through dominance acts — and physiological studies — through JH and some neurotransmitters like brain biogenic amines (e.g., Wagener-Hulme *et al.* 1999, Bloch *et al.* 2000, Sasaki & Nagao 2001) — should shed light on our deeper understanding of the regulation of reproduction and division of labor within colonies of social insects.

Acknowledgements

We thank E. Kasuya, J. Kojima, B. Kranz and K. Tsuji for reading and improving our manuscript. E. Kasuya kindly allowed us to use some of his original data. This study was supported in part by grants-in-aid from the Japan Ministry of Education, Science and Culture (812304048 and 00252122).

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