ANIMAL BEHAVIOUR, 2008, 75, 879–886
doi:10.1016/j.anbehav.2007.07.009

Subordinate wasps are more aggressive in colonies with low reproductive skew

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(Received 15 January 2007; initial acceptance 19 March 2007; final acceptance 10 July 2007; published online 18 October 2007; MS. number: 9237)

The small societies of primitively eusocial wasps have provided interesting testing grounds for reproductive skew theory because all individuals have similar reproductive potential, which is unusual in social insects but common in vertebrate societies. Aggression is a key parameter in testing the theory, but empirical studies have seldom quantified aggression together with the entire array of other relevant variables. The few studies that have done so were recently criticized for failing to control for the overall level of social activity. We analysed behaviour and reproductive partitioning patterns in the stenogastrine wasp *Parischnogaster mellyi*. We used aggression of the subordinate (β) breeder as key variable and analysed how relatedness, body size, number of breeders and productivity affect the interaction between the reproductive skew and the aggression while controlling for nest activity and actual interaction time between α and β. We showed that (1) more even reproductive partitioning (lower reproductive skew) is associated with higher levels of aggression initiated by the β subordinate independent of colony activity and (2) none of the currently available reproductive skew models is convincingly supported. Comparison of our results with earlier studies suggests that a common aggression-based mechanism for reproductive partitioning may apply across all primitively eusocial wasps despite complications arising from variable activity levels; however, currently available models may not apply.

Keywords: microsatellites; *Parischnogaster mellyi*; primitively eusocial; reproductive transactions; social behaviour; Stenogastrinae; tug of war; wasps

Elucidating why natural selection often favours individuals that give up reproduction to rear the brood of others is a fundamental problem in evolutionary biology (Leigh 1999). A series of models have produced predictions about how reproduction could be partitioned without becoming evolutionarily unstable, but their empirical support has remained controversial.

Optimal skew models (OSMs) assume that the level of reproductive partitioning is 'optimal' for all members of a society and cooperation is made possible by reproductive 'transactions'. Provided that both a dominant and a subordinate are able to monitor their share of reproduction and the dominant is in control of group composition, OSMs predict a minimum 'staying incentive' that the dominant must concede to keep the subordinate in the group and an upper limit of reproductive sharing that the subordinate can claim, above which the dominant should prefer to evict the subordinate (Johnstone 2000; Reeve 2000; Reeve & Keller 2001). Between these lower and upper limits there should be a 'window of selfishness' (WOS) where breeders are expected to compete directly over reproduction leading to a compromise situation (Reeve et al. 1998; Johnstone 2000; Reeve 2000). The reproductive transactions paradigm is usually contrasted with 'pure' compromise models, which assume that neither dominants nor subordinates have complete control over reproductive partitioning and never peacefully concede shares of reproduction. The most widely discussed compromise model is the 'tug of war' (TOWM), which assumes that the degree of reproductive skew in a society is the result of a compromise between the conflicting optima of its

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0003–3472/08/$32.00/0

members (Reeve et al. 1998; Cant 2006) and formalizes the most widespread view of the evolutionary significance of reproductive sharing (Reeve & Keller 2001). Critics of these approaches have pointed out that the level of reproductive skew may depend on additional factors and assumptions that are not explicitly addressed in most OSMs and the TOWM, such as the phase of the colony- and/or life-cycle of the individuals concerned and their (in)ability to monitor reproduction, group composition and other relevant parameters (e.g. Strassmann 1993; Beekman et al. 2003; Kokko 2003; Fanelli et al. 2005; Hart & Ratnieks 2005).

Aggression is the clearest expression of conflict; it is believed to play an important role in the partitioning of resources in animal societies and to be the key parameter for testing reproductive skew theory (Reeve 2000; Cant 2006; Cant et al. 2006). Several skew models have produced testable predictions about how aggression should be correlated with reproductive skew and associated variables. Most OSMs predict that the frequency of aggression should be positively correlated with the width of the WOS when aggression allows individuals to directly increase their share of reproduction. This implies that aggression should increase with increasing reproductive skew, relatedness, productivity and severity of ecological constraints, while it may be positively or negatively correlated with the fighting ability of subordinates (Reeve 2000). However, if aggression is a not a means to increase reproductive skew but instead allows a subordinate only to evict or subjugate the dominant, optimal skew theory predicts either a positive or a negative correlation between aggression and reproductive skew, depending on the value of the other parameters (Cant & Johnstone 2000). If the TOWM applies, then under most conditions aggression should be negatively correlated with reproductive skew and relatedness, be positively correlated with the relative fighting ability of subordinates and have no correlation with productivity and the severity of ecological constraints (Reeve 2000).

Primitively eusocial wasps are good invertebrate model systems for testing reproductive skew predictions because they potentially match the assumptions of complete control over reproduction and group composition (Reeve & Keller 2001). Genetic colony structure and patterns of aggression have therefore been intensively investigated in several species (Reeve & Nonacs 1992; Field et al. 1998; Queller et al. 2000; Reeve et al. 2000; Tibbetts & Reeve 2000; Seppä et al. 2002; Sumner et al. 2002; Nonacs et al. 2004; Fanelli et al. 2005; Liebert et al. 2005; Liebert & Starks 2006). Most of these studies provided no conclusive support for any of the current models of reproductive skew and cross-species comparison suggests that none of the key model parameters (i.e. relatedness, size difference between individuals, colony size, and productivity) is a universal predictor of reproductive skew in wasps. However, the only two studies that simultaneously analysed aggression and reproductive skew showed that they were negatively correlated; that is, the proportion of aggression by the β female was negatively correlated with reproductive skew in *Polistes carolina* (Seppä et al. 2002) and smaller colonies had both lower skew and higher levels of aggression from the subordinate towards the dominant in *Polistes bellicosus* (Field et al. 1998).

The fundamental importance of aggression for reproductive skew has recently been challenged by the suggestion that behavioural studies measuring aggression may have been flawed. In *Polistes fuscatus*, Nonacs et al. (2004) found that the proportion of aggression initiated by a subordinate was not significantly correlated with relatedness, size difference, colony size or productivity (in contrast to predictions made by OSMs) and that wasps were more likely to meet aggression when they were moving and active on the nest. Since the frequency of aggressive interactions between dominant and subordinates is strongly affected by the time they spend together on the nest and by the overall level of activity in the colony, Nonacs et al. (2004) hypothesized that the negative correlation between reproductive skew and aggression observed previously (in particular in *P. bellicosus*) could also have been due to the per capita work load and number of landings being higher in the smaller, low-skew colonies. Unfortunately, this hypothesis could not be tested in *P. fuscatus*, because genetic analyses were available for only very few colonies, which did not vary in reproductive skew (Nonacs et al. 2004).

The aim of the present study was to provide a comprehensive analysis of aggression and reproductive skew in the primitively eusocial stenogastrine wasp *Parischnogaster mellyi* while controlling for relevant covariables and possible biases due to differences in activity and incomplete data. We analysed 15 field colonies for which all marked and video-recorded females were recovered upon nest collection and for which we had information on virtually all relevant variables. To our knowledge no previous study on reproductive partitioning in wasps has been as complete.

METHODS

Natural History

The Stenogastrinae or hover wasps are a subfamily of primitively eusocial Vespidae living in Southeast Asia (reviews in Turillazzi 1991, 1996). In *P. mellyi* all adult females are potential reproductives, and often multiple females in a colony have developed ovaries and are inseminated (Hansell 1983; Fanelli et al. 2005). Nestmate females form well-defined hierarchies with division of labour, but alternative behavioural strategies are available to subordinates, which frequently move to vacant nests or join nests of unrelated colonies to become dominants or helpers (Hansell 1983; Yamane et al. 1983). Genetic analyses of natural colonies have shown that (1) within-colony relatedness is highly variable but quite low on average (ca. 0.33 ± 0.05), (2) the α female monopolizes reproduction in most colonies, although subordinates occasionally lay eggs that are raised to maturity, and (3) queen turnover occurs, so that a subordinate sometimes supersedes the α female (Fanelli et al. 2005).

Sampling

All colonies used in the experiment were collected in February 2003 around barracks near the field station of the