Reproductive skew in primitively eusocial wasps: how useful are current models?

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Summary

In this chapter, we compare the predictions of reproductive skew models with data from primitively eusocial wasps, the insect taxon in which skew has been best studied. These wasps share some key biological features with cooperatively breeding vertebrates, but represent a more experimentally tractable system. We describe a useful classification of skew models based on concepts of 'battleground' and 'resolution' models, and suggest how the basic biology of a taxon can help to identify which models and predictions in our classification are relevant. In primitively eusocial wasps, dominants have been assumed to control the allocation of reproductive shares at low cost. *A priori*, we therefore expect dominants to offer the minimum share required to retain a subordinate in the group (the staying incentive) or deter it from fighting (the peace incentive). Optimization constraints are unlikely to apply because the cost of producing eggs is relatively low and non-accelerating. Out of eight detailed genetic studies of primitively eusocial wasps, only one has found strong support for the concession model of skew. None of the other studies found clear relationships between skew and relatedness, productivity, or relative body size. Skew was typically high, often uniformly high across groups. There are several possible explanations for this apparent lack of fit between empirical studies and the concession model. First, there may be shortcomings of the data, such as small sample sizes and uncertainty concerning the chance of inheritance by subordinates. Second, strong ecological constraints and a good chance of inheritance reduce the need for staying incentives, in which case other factors such as the threat of fighting must be invoked to explain reproductive sharing. Across studies the predictions of the peace incentive model were not supported, since there was no consistent correlation between relative body size and skew. However, there is experimental evidence from one species of *Polistes* that skew is linked to the probability of escalated conflict, and that body size may not be a good predictor of fighting ability in wasps. A final possibility is that skew is determined by a simple convention, in which case we would not expect it to depend on variables such as relatedness. An important challenge for future empirical studies is to determine the direction of causality between skew and other behaviours, such as aggression and helping.

Introduction

Vehrencamp's (1983) theory of reproductive skew, elaborated by Reeve & Ratnieks (1993), assumed that a dominant individual has complete control over reproductive partitioning. The dominant may yield a reproductive 'concession' to another individual in order to induce it to remain in the group. In assuming complete dominant control, Reeve & Ratnieks (1993) had in mind co-foundress associations of *Polistes* wasps. There are usually fewer than five individuals in these associations, and the dominant can monitor the entire nest, where all reproduction must occur, in a matter of seconds. If ever there was a scenario where complete control by the dominant seemed feasible, this was it!

In this chapter, we review studies of reproductive skew in primitively eusocial insects and evaluate the implications of the empirical results for reproductive skew theory in general. We focus on primitively eusocial wasps because by far the most work has been carried out on them (but see Paxton *et al.*, 2002; Langer *et al.*, 2004 in bees). By 'primitively eusocial', we mean that as in cooperatively breeding vertebrates, there are no obvious morphological differences between helpers ('workers') and reproductives ('queens'), except sometimes in mean size. It is therefore reasonable to assume that any individual can potentially reproduce, as has been demonstrated through observation and sometimes experimental manipulation (e.g. Hughes *et al.*, 1987; Field & Foster, 1999; Strassmann *et al.*, 2004). This raises the possibility that studies of tractable insect systems may provide insight into the factors affecting the evolution of skew in vertebrate societies.

The chapter is divided into four sections. In the first section we describe a useful framework for classifying models of reproductive skew based on the concepts of 'battleground' and 'resolution' models of evolutionary conflict (Godfray, 1995; Cant, 2006). We discuss the implicit assumptions underlying the models and the relevance of these to biological systems.In section 2, we summarize of the nesting biology of primitively eusocial wasps and review empirical studies of skew that have been conducted in them. One of the main empirical findings is that skew is typically high. In the third section we discuss possible explanations for this general pattern in the light of our theoretical framework. In the fourth section, we conclude with some remarks about the similarities and differences between insect and vertebrate systems, and the future directions for studies of reproductive conflict in both taxa.

1. Types of skew model

Skew theory is an attempt to understand what is essentially an economic problem: how to share the profits of a cooperative association. The profits in question are the extra young that a group can raise compared to a solitary breeder. As with many economic problems, a good first step is to simplify the analysis by focusing on the interaction between two individuals only. A general feature of skew models is that they start by assuming an asymmetry between the players: one individual is labelled ‘dominant’ and the other ‘subordinate’. This is reasonable in a biological model because social animals usually do form hierarchies of some form for access to resources such as food or mates.

Different skew models make different assumptions about the nature of the asymmetry that distinguishes the two individuals. Transactional models assume, albeit implicitly, a sequential structure to the game. That is, one player makes a ‘first move’ which is observed by the other player before deciding on its response. The game then ends: in game theory these are known as ‘one-shot’ sequential (or ‘Stackelberg’) models (von Stackelberg 1934). The ‘concession’ and ‘peace incentive’ models (Vehrencamp, 1983; Reeve, 1991; Reeve & Ratnieks, 1993) assume that the dominant makes the first move, allocating reproductive shares to itself and the subordinate at zero cost. The subordinate then chooses whether to stay peacefully or disperse (in the concession model), or to fight for control of the nest (in the peace incentive model). In this case, the role of first mover puts the dominant in a much stronger position than the subordinate, because the first mover can propose a division that is just acceptable to the subordinate (in other types of game, there may be a second mover advantage: for example, where winning a conflict involves outbidding an opponent). By contrast, the restraint model (Johnstone & Cant 1999) allows subordinates to choose a division of reproduction first, after which dominants can respond by evicting them from the group. Dominant status in this model is therefore defined as the ability to evict one’s opponent, rather than the ability to allocate reproductive shares.

In contrast to these one-shot sequential games, the ‘tug-of-war’ model of Reeve *et al.* (1998a) assumes that no player has the advantage of a first move: both players invest simultaneously in selfish acts to increase their share of reproduction, but dominant individuals are assigned an efficiency or strength advantage in their conflict with subordinates. Finally, the ‘costly young’ model of Cant & Johnstone (1999) is an optimization rather than a game-theoretic model: dominants have full control over reproduction but can maximise inclusive fitness by sharing with a related subordinates if the costs of offspring production rise with the number produced.

The variety of model types and their assumptions about what dominance entails has hampered attempts to produce a coherent framework capable of accommodating all the various models (Johnstone, 2000; Reeve, 2000; Magrath *et al.*, 2004; Buston *et al.*, 2007). There are always models that must be left out, or treated as special cases (e.g. Cant & Johnstone, 1999). This problem can be remedied, however, by borrowing some concepts from other areas of evolutionary theory that deal with the resolution of conflict between parties with shared interests. In particular the concept of 'battleground' and 'resolution' models in parent-offspring conflict theory is equally applicable to reproductive skew theory, and can encompass models with different assumptions and informational structure (simultaneous, sequential, etc). The distinction between the two types of model is explained below.

Battleground models

Battleground models seek to define the zone of conflict between two parties over a limited resource. The limits of the battleground are found by solving for the best outcome of the conflict from the perspective of first one, then the other party, assuming that each party can choose any division of the resource at zero cost. If there were no overlapping interests between the two players (i.e. the game were zero-sum), the best choice of partition would be to take all of the resource and leave the opponent with none. The insight of skew models, however, is that individuals in a cooperative association have a shared interest in group productivity. The level of this shared interest varies with genetic and ecological factors and acts to constrain the zone of conflict between the players. The defining feature of transactional skew models, for example, is that they incorporate 'outside options', that is, alternative strategies to peaceful cooperation that can be triggered if the share an individual is offered is too low (see Johnstone & Cant this volume). Even though a first-mover can propose any division of reproductive shares, it must still take into account the outside options of the other player when choosing its allocation. The response of the second mover acts as a threat to constrain the maximum share of reproduction that the first mover can take. In transactional models there are two types of constraint arising from these outside options: group stability constraints set by the threat of departure or eviction; and peace constraints, set by the threat of fighting by either party if its own share of reproduction falls too low (Figs 1A & 1B).

A third set of constraints, which may overlay those of the transactional models, arise not because of outside options or threats, but because the law of diminishing returns can apply to reproduction as it does to other resources. For example, increased production of offspring will often entail accelerating costs (Cant & Johnstone 1999; Cant 2006). Under these circumstances each player has a kin-selected incentive to share reproduction with a relative, so there is nothing to gain from attempting to increase one's own share above a threshold level (Fig 1C). These 'optimization constraints' will be particularly important for vertebrates because offspring are costly to produce and there are usually relatively stringent physical or physiological constraints on the number of young that can be produced.

Resolution models

Rather than defining the zone of conflict, resolution (or 'compromise') models attempt to explore how conflict within it will be resolved. Resolution models assume that both players exert partial, costly control over the outcome, so that the result is a compromise between the best possible outcomes for dominants and subordinates. Unlike transactional models, in which one party gets to allocate shares to both individuals at zero cost, resolution models assume that 'pulling' the division of reproduction in one's favour involves direct fitness costs. They also assume that a player can choose its own level of effort in the competition, but not that of its opponent (Reeve et al. 1998; Cant 1998). The resolution will depend on the relative costs to each individual of a given level of competitive effort. The best-known resolution model is the 'tug-of-war' (Reeve et al., 1998a; Johnstone, 2000), in which dominants and subordinates can increase their own share of reproduction at a cost to group productivity. To put it another way, increased effort leads to a larger slice of a smaller 'pie'.

The tug-of-war provides a very broad framework to model the resolution of conflict over communal resources, and may be a particularly useful tool to help understand evolutionary transitions to cooperation across levels of organization (Reeve & Hölldobler 2007). However, its very abstraction and generality makes it rather difficult to test. Other models sacrifice some generality by making specific assumptions about the behavioural mechanism through which individuals attempt to control reproduction: for example, elevated offspring production (Cant, 1998); infanticide (Johnstone & Cant, 1999; Hager & Johnstone, 2004); or aggression (Reeve & Ratnieks, 1993; Cant *et al.*, 2006b). These models are useful because in addition to testing the predicted outcome of conflict, one can measure the behaviours that are assumed to reflect each party's 'effort' and compare these with the levels of effort predicted by the model.

It is important to recognize some of the limitations of resolution models as models of behavioural conflict. The tug-of-war, like many other evolutionary models (e.g. the biparental care model of Houston & Davies 1985) solves for the evolutionarily stable combination of *fixed* effort levels. That is, the best effort levels given that neither player can observe and respond to the other on a behavioural time scale (MacNamara et al. 1999; Cant & Shen 2006). In the conflict over reproduction, however, group members clearly do observe and respond to each others' attempts to claim reproduction, for example by egg-tossing or egg-destruction (Vehrencamp 1977; Mumme et al. 1983), infanticide (Young & Clutton-Brock 2006), or acts of aggression (Reeve & Nonacs 1992; Cant et al. 2006b). Because responsiveness is such a crucial determinant of the outcome of conflict, an important challenge for future theoretical work is to incorporate such responses in a biologically meaningful way. One promising approach (developed to study sexual conflict over parental care) is to solve for evolutionarily stable 'rules for responding' rather than evolutionarily stable fixed efforts (McNamara et al. 1999). A similar approach to reproductive conflict may shed light on a raft of cooperative and agonistic behaviours that seem to be involved in negotiation or bargaining over reproduction. This type of model would represent an advance because it would help to identify and understand what the process of conflict resolution looks like in nature, and whether the outcome depends on the details of the bargaining process.

Finally, there have been two notable attempts to produce a 'synthetic' model which incorporates both group stability constraints and a tug-of-war within them (Johnstone 2000; Reeve & Shen 2006). Both of these models make somewhat arbitrary assumptions about how the presence of outside options influences the resolution process. The problem is that the sequence of decisions - the initial offer, the decision of whether to pursue an outside option, and how much to invest in selfish competition - is never made explicit, which makes it difficult to assess whether the models are plausible biologically, and whether the solutions obtained are sensitive to the assumed order of play. However, a very similar problem crops up in economic bargaining theory (Muthoo 2000), and theoretical work in this field suggests a simple general principle ('the outside option principle') that may help to resolve this problem in skew theory. This issue is discussed in detail by Johnstone & Cant (this volume).

We have given an explicit account of the informational structure and underlying assumptions of different skew models - sequences of moves, responsiveness etc. - because this information can help to distinguish between the models empirically. Transactional models, for example, assume that an individual will respond behaviourally if its share of reproduction falls below the threshold set by its outside option, and that this threat constrains the degree to which it can be exploited. Threats may be hard to detect, however, until the social rules are broken. For example, Wong et al. (2007) showed that the threat of eviction constrains subordinate growth in a goby size hierarchy by introducing fish that were closer in size to a dominant than is usually observed in nature: these 'rule-breaking' fish were evicted. Similarly, to test whether threats of eviction, departure, or fighting constrain the level of skew it may be necessary to perturb the status quo by manipulating reproductive shares. A detailed understanding of model assumptions can help in both the design and interpretation of future studies.

A second reason for making model assumptions explicit is as an aid to evaluating whether data are consistent with one or another model. Information on the biology and natural history of an organism can help to rule out some models as irrelevant or based on inappropriate assumptions, and suggest reasons for the fit, or lack thereof, between data and theory. With this aim in mind we focus in the next section on empirical studies of skew in a particularly tractable taxonomic group, primitively eusocial wasps, and describe the key features of their nesting biology that can help to differentiate between the various models.

2. Testing reproductive skew theory in a model system: primitively eusocial wasps

Primitively eusocial wasps are attractive experimental systems for the study of skew with some key similarities to cooperatively breeding vertebrates. These typically include individual totipotency, small group sizes, and strong constraints on independent reproduction. Before applying our theoretical framework to studies of primitively eusocial wasps, we first outline the nesting biology of the wasps themselves.

Nesting biology of primitively eusocial wasps

The primitively eusocial wasps that have been investigated in relation to reproductive skew are in the family Vespidae, subfamilies Polistinae (paper-wasps, including *Polistes*) and Stenogastrinae (hover wasps, including *Liostenogaster* and *Parischnogaster*). Paper wasps and hover wasps probably represent two independent origins of eusociality (Hines et al., 2007). The genus *Polistes* includes more than 200 species that occur throughout most of the world (see Reeve, 1991 for a review). In seasonal habitats where *Polistes* has been best studied, the nesting cycle begins in Spring when overwintered females (foundresses) start building their characteristic paper nests attached to plants, rocks, man-made structures etc. (Fig. 2). Foundresses have already been inseminated, usually by a single male, soon after emerging from their natal nests the previous Autumn. They store the sperm in a muscular sac, the spermatheca. Sperm can then be released throughout their lives, as required to fertilize eggs that will produce female offspring. Males are haploid and arise from unfertilized eggs. In some populations, almost all nests have only a single foundress, whereas in other populations some or almost all nests have more than one foundress, with 10 or more not infrequent in some populations of *P. dominulus* (Shreeves *et al.*, 2003). On multiple foundress nests, typically one ‘dominant’ foundress lays most or all of the eggs, while the others (‘subordinates’) forage for insect prey which is pulped up and fed to larvae. Where there is only a single foundress, she must carry out all tasks alone. Each additional foundress typically enables the group to rear more offspring, although per capita productivity is usually negatively correlated with group size.

Larvae mature to adulthood in late Spring/early Summer, denoting the end of the ‘founding’ or ‘pre-emergence’ phase of the nesting cycle. Many of the first female offspring become workers on their natal nests, where they forage for larval provisions. From then onwards, the foundress typically ceases foraging and concentrates on egg-laying. The workers help the foundress to rear further offspring, some of which are reproductives of both sexes. After mating with reproductives from other nests, the male reproductives die, and the females enter diapause to become the next year’s new foundresses.

From the description so far, it may seem surprising that almost all studies to date have examined skew among offspring laid before worker emergence (e.g. Field *et al.*, 1998a; Seppä *et al.*, 2002; Liebert & Starks, 2006): many of these offspring become workers, to which skew theory may not apply. There are, however, two reasons why even the first brood of offspring may include reproductives. First, in a population of *P. fuscatus*, a proportion of the first brood apparently enter diapause to become foundresses the following year (Reeve et al., 1998b; see also Starks, 2001). This observation needs replicating in other species, but parallels findings in the primitively eusocial bee *Halictus rubicundus*, which has a similar life-cycle to temperate *Polistes*. In *H. rubicundus*, the proportion of maturing females that choose to enter diapause increases as the season progresses, until no further workers are produced (Yanega, 1989). Early *Polistes* offspring have a second chance of becoming reproductive, via foundress replacement. In many populations, foundresses often die before the end of the nesting season, at which point workers take over egg-laying (e.g. Strassmann, 1981; Queller & Strassmann, 1988). Every worker is therefore a potential replacement reproductive, which co-foundresses should compete to produce (Field *et al.*, 1998a). The significant proportion of males among the first brood in some species presumably reflects the fact that some first-brood females will reproduce (e.g. Field *et al.*, 1998a; but see Seppä *et al.*, 2002; Tsuchida *et al.*, 2004; Liebert *et al.*, 2005b).

The second group of primitively eusocial wasps in which reproductive skew has been measured are the hover wasps (Stenogastrinae: see reviews in Turillazzi, 1991; Field, 2008). There are approximately 50 described species, all restricted to the south-east Asian-Papuan tropics. Hover wasps differ notably from *Polistes* in that brood-rearing continues all year, with no Winter diapause. Nests are usually founded by a single female, occasionally joined later by one or more others. Female offspring may remain on their natal nests as helpers, or leave to pursue other strategies such as founding new nests (e.g. Samuel, 1987; Field *et al.*, 1998b). Nests are small (<100 brood-rearing cells; Fig. 3) and group size is typically 1-4 females, very rarely exceeding 10: there is not the sudden increase in group size that occurs when the first brood reaches adulthood in *Polistes*. Although reproductive skew is usually high (see below), any female can eventually inherit the egg-laying position, so that all offspring are potential reproductives.

Implications of wasp biology for reproductive conflicts

Two assumptions about wasp biology have been used to eliminate the areas of parameter space in Figs 1A-C that are likely to be irrelevant. First, optimization constraints may be relatively unimportant in wasps compared with vertebrates, so that net benefits will increase in a near-linear fashion with increasing reproductive share. This is because subordinates provide most of the costly provisioning effort, whereas the eggs laid by dominants, although not cost-free (Field et al., 2007), probably represent a smaller proportion of the total costs of reproduction than in vertebrates. In wasps, we therefore expect group stability and peace constraints (Figs 1A and 1B) to be much more important than optimization constraints.

A second assumption relates to the resolution of conflict within the battleground. Here it is usually assumed that dominants can exercise control over reproduction at little direct cost. This is because nests are small, and egg-laying is a conspicuous activity: a female inserts her abdomen into a cell and remains more-or-less motionless for one or more minutes. Furthermore, dominants rarely leave the nest, so that they are probably the only individuals that can prevent their eggs being replaced by other members of the group. It seems reasonable, therefore, to assume that a dominant can make an ‘offer’ to concede a share of reproduction to a subordinate, but not vice versa. Moreover, since dominants prevent unsanctioned reproduction by subordinates at little cost, we might expect a subordinate’s reproduction to be pushed down to the lower group stability or peace constraint boundary, so that the predictions associated with this boundary apply (Fig. 1). This has been the implict assumption behind attempts to test skew theory in primitively eusocial wasps, leading to the familiar predictions from the concessions and peace incentives models: skew should be positively correlated with genetic relatedness, group productivity and the relative fighting ability of the dominant (Reeve & Ratnieks, 1993). Below, we review the findings of the tests conducted to date.

Studies of reproductive skew in primitively eusocial wasps

Microsatellite markers have been employed to test the predictions of reproductive skew models in five species of *Polistes* and three species of hover wasp (Table 1). Studies have typically tested for relationships between skew and (1) helper-dominant genetic relatedness (n=8 studies); (2) helper-dominant body size ratios, assumed to reflect differences in fighting ability (n=6); (3) group productivity (n=5) and in *Polistes,* (4) season (n=3). Only one study has found strong support for the concession model: in *P. fuscatus*, skew was positively correlated with both relatedness and productivity, though not with body size ratios (Reeve et al. 2000). None of the other studies found clear relationships between skew and relatedness, productivity or body size differences. The only consistent finding across studies is that in *Polistes*, skew is significantly (n=2 studies) or almost significantly (n=1) greater among 'late' (younger) offspring than 'early' (older) offspring in pre-emergence nests (Field *et al.*, 1998a; Reeve *et al.*, 2000; Seppä *et al.*, 2002). The same pattern was reported by Peters *et al.* (1995) in *P. annularis*. It has been argued that this pattern supports concessions theory because ecological constraints increase during the season: there is a decrease in the time available for subordinate cofoundresses to initiate new nests and produce offspring before Winter (Field *et al.*, 1998a; Reeve *et al.*, 2000; Seppä *et al.*, 2002). However, the tug-of-war model could make the same prediction if the relative fighting ability of subordinates decreases during the season because subordinates carry out more energy-expensive activities (foraging) than the dominant, and suffer repeated harassment from the dominant (Field *et al.*, 1998a; Seppä *et al.*, 2002). In addition, skew could be lower among early offspring for reasons unrelated to social contracts theory. Foundresses tend to switch nests during the first part of the pre-emergence phase, potentially leading to changes in dominance and periods of transition when dominance is in flux (Field *et al.*, 1998a).

Limitations of the data

Some features of studies to date could partially explain the lack of fit between data and models. First, sample sizes have been relatively small: 6-23 groups per study (Table 1). Statistical power to detect real relationships will therefore be low. Second, the validity of using body size ratios as a surrogate for differences in fighting ability is unproven. In a recent study of *P. dominulus*, Cant *et al.* (2006b) found that relative body size did not predict when escalated fights over dominance occurred, or the duration or outcome of such fights. Third, there was little variation in genetic relatedness in some studies (e.g. Field *et al.*, 1998a; Seppä *et al.*, 2002), although considerable variation in others (e.g. Queller *et al.*, 2000; Fanelli *et al.*, 2005; Liebert & Starks, 2006). Even in populations with significant variation, however, predicted relationships between skew and relatedness rely on foundresses being able to respond to the variation. There is little evidence for discrimination of relatedness at the individual level in social insects, except when relatedness is correlated with obvious cues such as offspring sex (Keller, 1997). In *Polistes*, for example, foundresses appear to discriminate natal nest-mates as a class, which could include cousins as well as sisters, rather than responding to relatedness *per se* (Queller *et al.*, 1990; Gamboa, 2004; but see Queller *et al.*, 2000 in *P. dominulus*). Individuals that switch nests to join non-natal nest-mates might be particularly informative, because switching would represent a cue correlated with relatedness, but such joiners have not generally been identified and may usually be rare.

A final difficulty with testing skew theory in primitively eusocial wasps follows from a major conclusion of the studies to date: skew at any one time is typically high, often uniformly high. This is especially true in the three studies of hover wasps, in which mean skew exceeded 0.85. Only 15-20% of nests exhibit any reproduction at all by subordinates (Table 1), representing only 2-4 nests in each study. With so little variation in skew, there was little opportunity to test for correlations between skew and potential explanatory variables. However, there was considerable variation in potential explanatory variables themselves, suggesting either that these variables do not determine skew in the predicted way, or that some unmeasured variable consistently takes values that lead to high skew across all groups irrespective of the values taken by measured variables (see Discussion and Sumner *et al.*, 2002; Bolton *et al.*, 2006). Mean skew is generally lower in *Polistes* (Table 1), with 50% or more nests typically exhibiting some reproduction by subordinates. However, this difference may partly be because skew was ususally measured across a wider range of offspring ages than in hover wasps (Table 1).

3. Discussion

In primitively eusocial wasps, the dominant has been assumed to have complete control over reproduction at little or no cost. Yet empirical work fails to support the predictions of the concession model, with the exception of the study by Reeve *et al.* (2000). Shortcomings of the data could partly explain this apparent failure: small sample sizes, no direct measurement of adult fighting ability, and the fact that many offspring in pre-emergence nests are destined to become non-reproductive workers. There is also a lack of variation in genetic relatedness in some studies, although wasps may lack the ability to discriminate relatedness at the individual level. An additional feature of studies to date has been that skew is typically high, often uniformly high across groups, perhaps especially in hover wasps (Table 1). We now discuss three possible reasons for this latter finding which fall within the framework of skew theory: strong ecological constraints; the possibility of subordinates inheriting the dominant position; and the costs of escalated conflict. We also discuss the possibility that conventions, rather than social contracts, are the mechanism by which skew is determined.

Ecological constraints

Like tests of other inclusive fitness models in social insects, tests of skew models have tended to focus on the predicted effects of variation in relatedness. Yet two of the three parameters in the basic concessions model are ecological: the productivity of a potential subordinate if she chooses to nest independently, and the productivity of a group if the potential subordinate joins it – both measured relative to the productivity of a lone dominant. There is little evidence of strong physiological constraints in primitively eusocial wasps: almost any individual can potentially reproduce (Reeve, 1991; Field & Foster, 1999). Ecological constraints, however, do appear to be strong across populations, providing a potential explanation for the high skews observed, and for the absence of correlations between skew and other variables. Constraints are strong because adults have short lives compared with the development periods of their offspring (Queller, 1989). Offspring are helpless larvae, requiring progressive feeding and continuous adult protection in order to survive: the death of an independent nester typically leads to the failure of all of her part-reared offspring (Queller, 1996; Field *et al.*, 2000; Shreeves *et al.*, 2003). Among 19 populations of polistines surveyed by Queller (1996), on average only 34% of independent nesters (range 0-62%) live long enough to produce any surviving offspring. In the hairy-faced hover wasp *Liostenogaster flavolineata*, less than 50% can expect to produce independent offspring (Samuel, 1987; Field *et al.*, 2000).

Subordinate helpers may live no longer than independent nesters, but their investment can be preserved after their death through various forms of insurance (Queller, 1996). For example, after a helper dies, the offspring that she contributed to are usually reared through to independence by her surviving nest-mates (Field *et al.*, 2000; Shreeves *et al.*, 2003, but see Tibbetts & Reeve, 2003). Short lifespans for independent nesters compared with the offspring development period could help to explain why most subordinates are prepared to accept little or no direct reproduction. The importance of this life-history for female reproductive decisions is implied by the positive correlation between independent nesting failure rates and the frequency of multiple foundress associations across *Polistes* populations (Reeve, 1991). Care is needed with this interpretation, however, because ecological constraints could cut both ways: if the dominant herself would have little reproductive success without helpers, she may be prepared to offer a large reproductive incentive to induce them to stay. However, this argument applies primarily to the first helper. While all helpers have the same expected payoff through independent nesting, from the dominant's viewpoint each successive helper increases the probability of group survival by a smaller amount, and might thus receive a smaller incentive. Insurance mechanisms have been little investigated in cooperatively-breeding vertebrates, but may be less important because adult lifespans are longer relative to offspring development time in vertebrates, and because vertebrate groups are unable to recycle excess offspring left after a carer dies (Queller, 1996; Shreeves *et al.*, 2003).

In a penetrating review, Nonacs *et al.* (2006) went further by asking whether field estimates of survival and productivity in relation to group size are quantitatively consistent with observed levels of skew in 11 populations of primitively eusocial wasp. Although ecological data were consistent with high skew among close relatives (sisters, r=0.75 in haplodiploids), skews observed in *Polistes* were more extreme than what should be adaptive for more distant relatives such as cousins (r=0.1875). Almost all group members are sisters in some *Polistes* (e.g. Field *et al.,* 1998a; Seppä *et al.*, 2002), but cousins are frequent in other populations (e.g. Reeve *et al.*, 2000; Field *et al.*, 2006), and unrelated cofoundresses occur commonly in *P. dominulus* (Queller *et al.*, 2000; Liebert & Starks, 2006). Nonacs *et al.* (2006) concluded that social contracts models fail to predict patterns of skew in wasps, but we believe that this conclusion could need qualifying. In the next two sections, we discuss how two features of wasp biology might help to explain the high skews observed within the social contracts framework. First, however, we discuss aspects of the available data that might also explain the discrepancy.

Eight of the 11 populations analysed by Nonacs *et al.* were the same species, *P. dominulus*, the only species in which associations of unrelated cofoundresses are common (Queller *et al.*, 2000). Of the other three populations analysed, *P. aurifer* is also unusual in that multi-female groups are hardly more productive than independent nesters. Multi-female groups are indeed rare in *P. aurifer*, and it is perhaps no surprise if cooperation is not adaptive. Ecological data from the remaining two populations, *P. fuscatus* and *L. flavolineata*, were not inconsistent with observed skews. As noted above, cofoundresses in many *Polistes* species may respond to mean natal nest-mate relatedness rather than relatedness at the individual level (but see Queller *et al.*, 2000). Mean relatedness in Reeve *et al.*'s (2000) study of *P. fuscatus* was 0.57, well above the threshold required to explain even complete monopolization of reproduction by the dominant.

In *L. flavolineata*, Nonacs *et al.* estimated group survival using 40 groups that were monitored for 2 months (Shreeves & Field, 2002). Their calculations suggested that while subordinates could accept complete monopolization of reproduction by a dominant sister (r=0.75), they should require significantly lower skew if the dominant is a cousin (r=0.1875). In reality, dominants almost completely monopolize reproduction at any one time in *L. flavolineata*, yet cooperation among cousins is not infrequent (Sumner *et al.*, 2002; Field *et al.*, 2006). However, using a different dataset, consisting of survivorship data for individual females extrapolated over the 100-day offspring development period, Queller's (1996) insurance-based model predicts that complete monopolization should be acceptable above a relatedness threshold of 0.21. This is close to the value expected for cousins and well below the mean observed relatedness of approximately 0.5 that is relevant if hover wasps cannot discriminate relatedness at the individual level (see Field *et al.*, 2000, 2006). This highlights the fact that the ecological data available to Nonacs *et al.* (2006) were sometimes based on small samples and were originally collected for varying purposes, often from populations different from those where skew itself was measured. Nonacs *et al.*'s (2006) synthesis suggests that ecological constraints cannot alone explain the skews observed in some populations of *P. dominulus*, but this may not be true of primitively eusocial wasps in general

Inheritance

Strong ecological constraints may be one factor with the potential to explain the high skews seen in most primitively eusocial wasps. A second factor, which could act in concert, is inheritance. Subordinates that have a good enough chance of eventually inheriting an egg-laying position themselves may accept a high skew while they wait to inherit (Kokko & Johnstone, 1999; Ragsdale, 1999). The model of Kokko & Johnstone shows that incorporating inheritance greatly reduces the parameter space for which a subordinate requires a staying incentive to remain in the group (Fig 4). Inheritance has a similar effect in the peace incentive model: subordinates have more to lose from risky fights and so are less likely to require a share of reproduction to deter them from challenging.

Like cooperatively-breeding vertebrates, primitively eusocial wasps typically live in small groups in which subordinates have a predictable chance of inheriting dominance by outliving the individuals ranked above them. Hard data are scarce, however: studies of *Polistes* have generally not been focussed on inheritance and usually report its frequency within only one slice of the nesting cycle. For example, Cant & Field (2001) found that 4/20 dominants were replaced before offspring emergence in *P. dominulus*, and Queller *et al.* (2000) report that 10% of subordinates could expect to inherit during that time (see also Nonacs *et al.* 2006). On 30% of nests of *P. bellicosus* and *P. carolina*, offspring genotypes indicated that most of the younger offspring were not produced by the foundress that had produced most of the older offspring (Field *et al.*, 1998a; Seppä *et al.*, 2002; see also Peters *et al.*, 1995). Similarly, 25% of *P. fuscatus* colonies had lost their original dominant foundress within 19 days of worker emergence (Reeve *et al.*, 2000). These data do suggest that inheritance is common, but are too incomplete to provide robust estimates. Inheritance may be particularly important in the relatively aseasonal tropical environment of hover wasps, in which nests are perennial and waiting times are unconstrained by the arrival of Winter (Field *et al.,* 1999; Shreeves & Field, 2002).

Escalated conflict and peace constraints

In the queue to inherit an egg-laying position, it is the highest ranking subordinates that have the best chance of surviving to inherit: those at lower ranks have little chance (e.g. Field *et al.*, 1999; Cant & Field, 2001). Theoretically, this means that lower ranked individuals would require a greater staying incentive to remain in the group than higher ranked individuals. On the contrary, *P. dominulus* rank 2 subordinates exhibit much greater ovarian development than subordinates at lower rank (M. Cant & S. English, unpublished data). This suggests that low ranked foundresses favour group membership over dispersal even though they receive little direct reproduction and have little chance of inheriting (Cant & English, 2006). In these circumstances the threat of departure is an empty, non-credible threat, and cannot be used as leverage to obtain a share of reproduction.

If subordinate reproduction is not explained by the threat of departure, what can account for variation in the level of subordinate reproduction in primitively eusocial wasps? One possibility that has been little studied to date is that reproductive shares reflect the threat of aggression or escalated conflict. Where fights result in the death of the loser, subordinates will remain in the group with little or no reproduction rather than risk a fight to the death with the dominant. Dominants, for their part, will allow a subordinate to claim a large share of reproduction before they are selected to fight. Wasps possess a deadly weapon in the form of a sting, so it is possible that the high skews observed in nature reflect the potentially lethal nature of fights over dominance. Where fights lead to the subordination rather than death of the loser, however, the zone of conflict is much narrower. Subordinates will require greater peace incentives and dominants will have a lower fighting threshold. For any given level of dominant control, we would expect reproduction to be shared more evenly where fights are less risky (Fig 1B).

Is there any evidence that dominants offer peace incentives to subordinates to avoid escalated fights? A recent study of *P. dominulus* lends support to the central assumption of the peace incentive model that increased reproductive suppression should be associated with an elevated risk of escalated conflict. Cant *et al.*(2006b) induced conflict over dominance rank by temporarily removing dominant co-foundresses to allow the second ranking female to inherit the nest. Once the replacement dominant was established, they replaced the original dominant and recorded the resulting interaction between the two wasps. Rank 2 subordinates with lower levels of ovarian development, and those that stood to inherit larger, more productive groups, were more likely to engage in escalated fights with the returning dominant (Fig 5). Relative body size, by contrast, had no effect on the probability of an escalated conflict. These results suggest that reproductive suppression will lead to an increased threat of escalated conflict, and hence that dominants can deter challenges by offering subordinates a share of reproduction. Interestingly, all of the escalated conflicts observed by Cant *et al.* (2006b) led to the subordination of the loser: foundresses apparently stopped short of employing stings in fights over dominance. This may be because most of the foundresses involved were full sisters, and so had a strong kin selected incentive not to kill their opponents..

Cant *et al.* (2006b) found that subordinate ovarian development increased with group size (and, hence, productivity), consistent with the idea that dominants adjust the level of suppression according to the threat of escalated fighting. However, this is also the pattern expected if dominants lose reproductive control in larger groups (Clutton-Brock, 1998; Field *et al.*, 1998a). To test definitively whether dominants respond to the threat of escalated conflict by adjusting skew would require an experimental manipulation. For example, one could try to manipulate subordinate reproductive status to look for an effect on the probability of escalated conflict, or manipulate subordinate fighting ability to look for an effect on skew.

Aggression: negotiation or protest?

Many models of aggression assume that fights over dominance are all-or-nothing affairs leading to a specific outcome (Parker 1974; Reeve & Ratnieks 1993; Cant & Johnstone 2000; Cant et al. 2006a, b). Much of the aggression observed in cooperative animal societies, however, is of a milder, non-lethal form. These low level acts of aggression may reflect a process of negotiation or bargaining within the battleground of reproductive conflict (see

Johnstone & Cant, this volume). For example, aggressive displays may signal each party's strength and motivation to enter into an escalated conflict over reproduction, allowing a resolution in terms of reproductive shares to be reached without escalation. An alternative to the hypothesis that skew is determined by the threat of aggression, however, is that the distribution of reproduction is determined in some way first, and levels of aggression reflect a subordinate's response to this level of skew (e.g. Reeve & Ratnieks, 1993). The first hypothesis assumes that the level of aggression acts to determine skew (as part of a 'negotiation'), whereas the second assumes that skew determines the level of aggression (which takes the form of a 'protest'). The issue of the direction of causality between skew and other behaviours such as helping and aggression is rarely discussed, but is extremely important for attempts to understand individual variation in helping behaviour and aggression (Cant *et al.*, 2006a), colony-level attributes such as stable group size and productivity (Cant & English, 2006), and interspecific differences in social behaviour. To date, a few studies have simply tested for a correlation between skew and aggression. There is some evidence that subordinates are less aggressive when skew is high (Field *et al.*, 1998a; Seppä *et al.*, 2002), although results could be confounded by effects of activity level on aggression (Nonacs *et al.*, 2004). Determining the direction of causality will often require more innovative experimental approaches to manipulate one factor (e.g. skew) and look for an effect on another factor (e.g. helping, aggression, or group size). Disturbing the status quo would also help to reveal whether behaviour is shaped by threats, in the way that transactional models assume (Wong et al. 2007). The information gained from such tests would greatly advance our understanding of reproductive skew and social evolution in general.

Conventions

A final explanation for the lack of fit between models and data in primitively eusocial wasps, lying outside of the skew framework presented here, is that group-members obey a simple convention, such as that the current dominant is the only egg-layer (Field *et al.*, 1998a; Nonacs, 2001; Seppä *et al.*, 2002). There is some evidence that the identity of the dominant is determined conventionally in both *Polistes* cofoundress associations and in hover wasps (Seppä *et al.*, 2002; Bridge & Field, 2007). Dominants are usually no larger on average than subordinates, and the dominant is frequently not the largest wasp on individual nests (Table 1). In the hairy-faced hover wasp, dominance is determined largely by relative age, which may represent an arbitrary convention (Bridge & Field, 2007).

Could skew itself be determined conventionally? A convention by which only the dominant reproduces would avoid competition over reproduction and the resulting costs to the group, as well as the sensory costs required for individuals to keep track of skew. Conventions might be particularly likely in situations where potential subordinates require little or no incentives to remain peacefully in the group, such as where subordinates are closely related to dominants and have little chance of successful reproduction alone, and where fights are costly (Nonacs, 2001; Seppä *et al.*, 2002). Apart from the low relatedness among *P. dominulus* co-foundresses, these conditions may apply to the populations listed in Table 1. If skew is determined conventionally, we do not expect it to be correlated with variables such as relatedness (Nonacs, 2001). Variation in skew might instead reflect dominant turnover and periods when dominance is unresolved after nest-switching, foundress death etc. Arguing against skew conventions, however, are the patterns consistent with the concessions model reported by Reeve *et al.* (2000) in *P. fuscatus*, and perhaps also the frequent aggressive interactions observed in *Polistes* cofoundress associations, if these reflect negotiation over reproduction. Furthermore, although conventional mechanisms would explain the lack of fit between data and models that assume social contracts mechanisms, they do not resolve the question of why subordinates sometimes appear to accept a higher skew than is adaptive.

4. Concluding remarks: reproductive skew in insects and vertebrates

Primitively eusocial insects such as paper wasps and hover wasps share a number of features with vertebrate systems, in which experimental manipulations are difficult and data are harder to collect. Perhaps most importantly, all group members retain the ability to reproduce, groups are usually small so that group membership typically offers substantial future fitness benefits, and there are usually stringent constraints on independent reproduction. The latter two features reduce the likelihood that group stability constraints define the lower bound of the battleground over reproduction, since both inheritance and tight ecological constraints tend to reduce the required staying incentive to zero. In primitively eusocial wasps, therefore, as in vertebrates, subordinates will often favour joining a social queue, even as a non-breeder, rather than attempting to breed independently.

If the threat of departure is rarely credible (because subordinates prefer staying to dispersal), the outcome of reproductive conflict is unlikely to be sensitive to variation in the level of this non-credible threat. This may account for the finding that experimental manipulation of ecological constraints has little or no effect on patterns of skew in allodapine bees or cichlid fish (Heg *et al.*, 2006; Langer *et al.*, 2004). This result may also reflect a lack of information on the part of dominants, or subordinates, about the likely success of nesting attempts outside the group. In cooperative mammals both dominants and subordinates will find it difficult to obtain information on the range of breeding opportunities outside the group, since territories are often contiguous and vigorously defended. Birds, by virtue of flight, will usually be in a better position to detect when vacancies arise outside their group, so that the resolution of reproductive conflict may be more sensitive to variation in outside options. Wasps can potentially obtain even better information: not only can they fly, but groups do not defend feeding territories. However, although this may apply to subordinates, dominant wasps rarely leave the nest, so that they may have no information about a subordinate's options outside the group. A subordinate's threat to disperse is credible only if the dominant can also detect the level of ecological constraint. A possible consequence of staying on the nest is that a dominant can commit to strategies that are insensitive to short-term changes in these constraints.

While wasps may resemble vertebrates in some respects, there are also key differences in basic biology which will have important effects on the way in which conflict over reproduction is resolved. Perhaps the most important of these differences is the cost of producing young. In social insects, eggs are probably relatively cheap to produce (but see Field et al., 2007), and any over-production of offspring can be recyled through oophagy (Mead *et al.*, 1994; Shreeves *et al.*, 2003). In birds and mammals, by contrast, the production of offspring represents a significant energy expenditure on the part of the parent, before any rearing costs are taken into account (Creel & Creel, 1991; Monaghan & Nager, 1997). Fish may represent an intermediate case (Heg *et al.*, 2006). In birds and mammals, the marginal fitness benefits of offspring production will decline as more offspring are produced (this is the basis of Lack's (1947) clutch size argument). In these circumstances, additional offspring are expensive for a dominant but cheap for a subordinate: when the two are related, dominants have a kin-selected incentive to share reproduction. We have already described how the possibility of inheritance removes the need for staying incentives. In birds and mammals, diminishing returns on increasing offspring production mean that the lower bound of the battleground over reproduction will often be defined by optimization constraints, or 'beneficial shares' (Cant & Johnstone 1999; Fig 1C). Beneficial sharing is the simplest mechanism to account for reproductive skew because it is does not require any social contract or negotiation (Cant 2006). For this reason, in birds and mammals beneficial sharing should be the first explanation for reproductive sharing to be ruled out.

Other key factors, such as the degree of reproductive control, will vary widely in both insect and vertebrate systems, and will depend strongly on the particular social biology of the species in question. For example, dominant paper wasps have been thought to exercise full control at no cost. However, the ability to suppress subordinates may be limited by the threat of a risky, escalated conflict, even though actual fights are rarely observed (Cant *et al.* 2006b). In birds and mammals, dominants often exercise control by killing the offspring of subordinates, but the efficacy of this threat will depend on their ability to distinguish a subordinate's young from their own young and avoid retaliatory attacks from the victim. The ability to discriminate parentage will also vary widely between insect systems. Even subtle forms of reproductive control, such as the use of inhibitory pheremones, must ultimately be backed up by force in order to be evolutionarily stable (Keller & Nonacs, 1993). The resolution of reproductive conflict by the use or threat of force will depend on the weaponry of the animals, the outcome of fights over dominance (e.g. whether the loser is killed, evicted, or subjugated), and the information each party has about the state and motivation of the other. The overlap between vertebrate and insect systems in many of these key features means that, despite radical differences in biology, tractable model insect systems can continue to play an important role in understanding the evolution of reproductive skew in other taxa.

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Table 1. Results from studies that have used microsatellites to investigate reproductive skew in primitively eusocial wasps. Gaps are where data were absent from the original source.

Species and data source	Dominants larger than subordinates?	Mean skew	% nests with skew<1 (total sample size)	Offspring genotyped[4]	Mean co-foundress relatedness
Polistes					
P. bellicosus Field *et al.* (1998a)[1]	No	0.84[S1]	50% (14)	younger brood[3]	0.67
P. fuscatus Reeve *et al.* (2000)	Yes	0.47[P]	87% (23)	older female brood[3]	0.57
P. carolina Seppä *et al.* (2002)	No	0.65[S2]	(17)	all brood[3]	0.64
P. aurifer Liebert *et al.* (2005a)		0.56[S1]	50% (6)	all brood	0.13
P. dominulus (USA) Liebert & Starks (2006)[2]		0.88[P]	41% (17)	older brood[3]	0.25 (0.21-0.43)
Hover wasps					

L. flavolineata Sumner *et al.* (2002)	No	0.95[S1]	15% (13)	eggs and small larvae	0.52
P. mellyi Fanelli *et al.* (2005)	No	0.87[S2]	21% (19)	eggs	0.33
P. alternata Bolton *et al.* (2006)	No	0.92[S1]	22% (9)	eggs and small larvae	0.46

[S1] corrected S index of Keller & Krieger (1997),

[S2] S index of Pamilo & Crozier (1996).

[P] proportion of offspring produced by the most productive foundress.

All three skew indexes can range in value from zero (equal reproduction by all females) to 1.0 (reproduction monopolized by a single female).

[1] Some data recalculated from Appendix B of Field *et al.* (1998a)

[2] Means for skew and relatedness in *P. dominulus* are from the 10 two-female nests in Liebert & Starks's (2006) study, calculated from their Fig. 1. Data for 7 nests with >2 foundresses were not given. The bracketed range 0.21-0.43 is the range in mean co-foundress relatedness among two years in a separate Italian population of *P. dominulus* (Queller *et al.*, 2000).

[3] All offspring genotyped were laid before worker emergence

[4] A smaller age-range of offspring genotyped provides a better estimate of skew at a particular time, whereas a wider range is a better reflection of lifetime skew.

Figure Legends

Fig 1. Defining the battleground of reproductive skew theory. Three types of constraint may limit the degree to which one party can suppress the other. .A. Group stability constraints are set by the outside options available to the subordinate. Where dominants can choose any partition (at no cost), they will push the subordinate's share *p* down to the staying incentive. Where subordinates can choose the partition, they will claim up to the dominant's eviction threshold. B. Peace constraints are set by the threat of the subordinate or dominant to fight if its share is reduced below a threshold. The solid line and dotted line constraints illustrate the bounds of the battleground when the outcome of fights is the subordination of the loser (Role Reversal, RR) or the death of the loser (Fatal Fight, FF), respectively. C. Optimization constraints arise where an increasing reproductive share brings diminishing net fitness returns. In these circumstances an individual with choice over the partition can maximise its inclusive fitness by allocating a share to the other.

Fig. 2. Pre-emergence nest of *Polistes dominulus* attached to a cactus in southern Spain. The six foundresses are individually marked on the thorax with paint spots, and white silk caps are visible closing the cells that contain pupae. Photo: J. Field

Fig. 3. Nest of the Hairy-Faced Hover Wasp *Liostenogaster flavolineata* attached to the underside of a bridge in Malaysia. The nest is made of mud, and the wasps are individully marked on the thorax with paint spots. Photo: A. Cronin

Fig 4. The influence of inheritance on the stability of two-player associations (redrawn from Kokko & Johnstone, 1999). The graph shows regions for which two-player associations are stable or unstable as a function of dispersal fitness *x* and survival rate *s* in Kokko & Johnstone's model. The example shown assumes that dominant and subordinate have equal survivorship and are related by coefficient 0.5. The diagonal contours indicate the region where the dominant must offer a staying incentive to maintain group stability. Contours show staying incentives which increase in magnitude from left to right in steps of 0.05. For comparison, the grey shaded area to the left indicates the sub-region for which groups can be stable if there is no possibility of inheritance by the subordinate (as assumed in the original concession model). Inheritance greatly increases the region of parameter space for which stable groups can form, and greatly reduces the need for staying incentives for them to do so.

Fig 5. Results of Cant *et al.*'s (2006b) study showing that reproductive suppression is associated with an increase in the probability of escalated conflict in *Polises dominulus.* Fights over dominant status were induced experimentally by removing the dominant for 3-8 days to allow the rank 2 subordinate to inherit, after which the original dominant was re-introduced. Closed circles are those rank 2 females that entered into an escalated contest with the returning dominant; open circles are those rank 2 females that immediately submitted. The solid line shows the regression for all rank 2 femelas. Both group size and the level of subordinate ovarian development has significant effects on the probability of an escalated contest. Also plotted as a dotted line is the non-significant regression of ovarian development in rank 1 individuals versus group size.

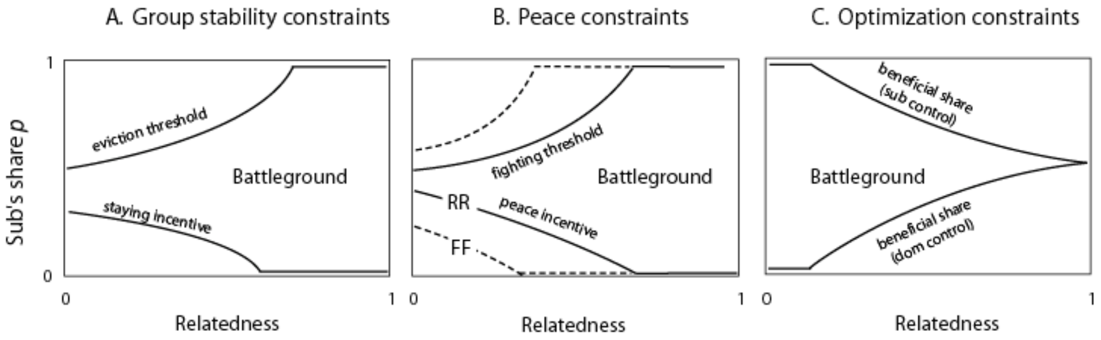
A. Group stability constraints
B. Peace constraints
C. Optimization constraints
Sub's share p
1
0
eviction threshold
staying incentive
Battleground
Relatedness
0
1
fighting threshold
peace incentive
RR
FF
Battleground
Relatedness
0
1
beneficial share (sub control)
beneficial share (dom control)
Battleground
Relatedness
0
1

Fig. 1

Fig. 2

Fig. 3

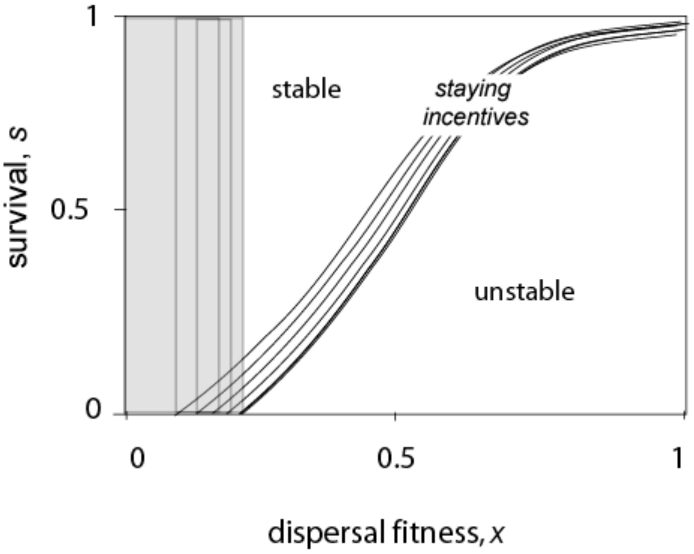
1
0.5
0
survival, s
stable
staying
incentives
unstable
0
0.5
1
dispersal fitness, x

Fig 4.

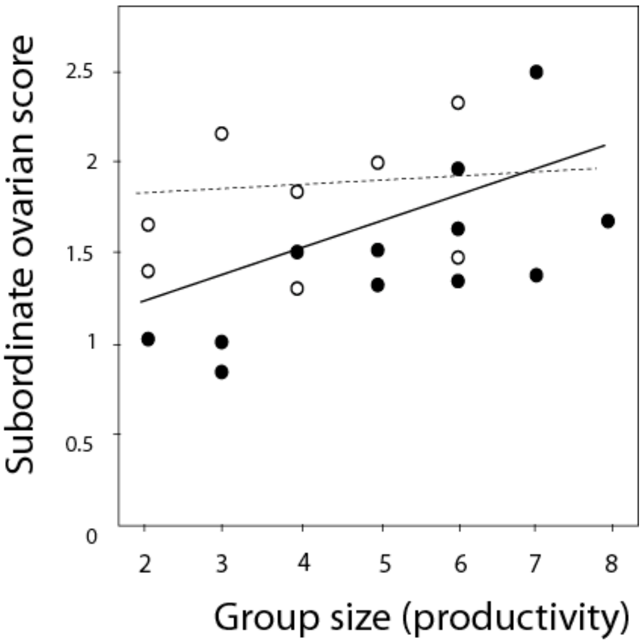
Subordinate ovarian score
0
0.5
1
1.5
2
2.5
2
3
4
5
6
7
8
Group size (productivity)

Fig 5.