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Dynamics of social queues

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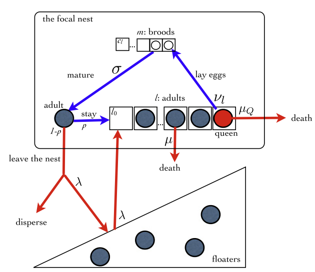
HIGHLIGHTS

- We analyze queues formed by social wasps to inherit the dominant position in the nest.
- We use a transient quasi-birth-and-death (QBD) process.
- We show that the extended nest life time due to division of labor between queen and helpers has a big impact for the nest productivity.

GRAPHICAL ABSTRACT



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ABSTRACT

Queues formed by social wasps to inherit the dominant position in the nest are analyzed by using a transient quasi-birth-and-death (QBD) process. We show that the extended nest lifespan due to division of labor between queen and helpers has a big impact on nest productivity.

1. Introduction

A wide variety of animals are known to form simple hierarchical groups called social queues, where individuals inherit resources or social status in a predictable order. Queues are often age-based, so that a new individual joins the end of the queue on reaching adulthood, and must wait for older individuals to die in order to reach the front of the queue. While waiting, an individual may work for her group, in the process often risking her own survival and hence her chance of inheritance. Eventually, she may survive to reach the head of the queue and becomes the dominant of the group.

Queueing has been particularly well-studied in hover wasps (Hymenoptera: Stenogastrinae) (Field, 2008). In hover wasp social groups, only one female lays eggs, and there is a strict, age-based queue to inherit the reproductive position. While the dominant individual (queen) concentrates on breeding, subordinate helpers risk death by foraging outside the nest, but have a slim chance of eventually inheriting dominance. Some explanations for this altruistic behavior and for the stability of social queues have been proposed and analyzed (Field et al., 2006; Kokko and Johnstone, 1999). Since both the productivity of the nest and the chance to inherit the dominant position depend critically on group size, queueing dynamics are crucial for understanding social queues,

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but detailed analysis is lacking. Here, using hover wasps as an example, we demonstrate that some basic queueing theory and non-homogeneous birth and death processes are useful for analyzing queueing dynamics and the population demographics of social queues. Our work leads to better understanding of how environmental conditions and strategic decision-making by individuals interact to produce the observed group dynamics; and in turn, how group dynamics affect individual decision-making.

2. Existing models of social queues

Various hypotheses have been proposed for the somewhat paradoxical evolution of helping behaviour, where an individual at least temporarily forfeits its own chance to reproduce and instead helps to rear another individual's offspring. A general explanation is that helpers are nearly always rearing the offspring of a relative, so that copies of the helper's genes are propagated through helping (Hamilton, 1964). But since the relative's offspring rarely carry as large a proportion of the helper's genes as would the helper's own offspring, natural selection should favour helping only if helpers compensate by being more productive than they would be nesting alone (Queller, 1996).

There are different ways in which this could happen, some of which rely on the relatively short lifespans of adult wasps compared with the long development time of their progressively fed immature offspring (Field, 2005). The extended parental care (EPC) implicit in progressive feeding means that a mother often dies before her offspring matures (Queller, 1994). For a potential helper, staying in the natal nest and rearing half-matured broods of a relative's offspring may be more productive than starting a new nest and rearing her own brood, because broods that are already part-matured are more likely to reach adulthood before the group as a whole fails (HS: Headstart hypothsis Queller, 1989). A subtlely different idea is that if a helper dies young, any dependent offspring that she has only part-reared can be brought to adulthood by the other individuals still remaining in the group, whereas for a female nesting independently, an early death means total brood failure (AFR: assured fitness return, Gadagkar, 1990; Nonacs et al., 2006). Another explanation is that if a helper has a chance to eventually inherit dominant status, it may be worth waiting without immediate fitness return if the expected reproductive success as dominant is large enough to outweigh the chance of death while waiting in the queue (DFR: delayed fitness return, Kokko and Johnstone, 1999; Kokko et al., 2001; Shreeves and Field, 2002). Further discussions of validity of these explanations can be found in Nonacs et al. (2006), Shen et al. (2011), Shen and Kern Reeve (2010), Field (2008) and Queller (1996, 1994).

These existing models aim to understand social queues from the evolutionary perspective of rational individual decision making, using rather simple mathematical models. Here, we analyze social queue from a different perspective, that of nest or population productivity and survival. As well as the above explanations for helping, we test the effect of a fifth general characteristic of sociality in insects: division of labour (DOL). In a social nest, the dominant can concentrate on laying eggs, not risking her life by foraging away from the nest, while her helpers forage. Because of this division of labour, the queen has a considerable longer lifespan than her helpers. We investigate whether this will also increase the lifespan of the nest and the total number of reproductives dispersing from it. Note that DOL is different from EPC, because, with DOL, the queen does not necessarily expect the helpers to rear her offspring after her death.

We model the details of nest productivity in the following section by using a transient quasi-birth-and-death process, and compare nest productivity under the various models discussed above.

3. Quasi-birth-and-death process for nest history of social queues

We use a transient quasi-birth-and-death (QBD) process to model not only by the number of adults but also the number of immature offspring (brood) on a nest. Fig. 1 shows an example of these dynamics in a real hover wasp nest. QBD processes are intensively studied in the queueing literatures, especially in modelling complex communication systems (see Latouche and Ramaswami, 1999 for its good introduction). By using QBD processes, we can keep track of the complex dynamics of populations such as social queue. In QBD process, each event occurs at an exponentially discrete time with its specific rate governed by the generator of the QBD process.

Considering a focal nest, we analyze its history and the productivity until the last individual dies and the nest is terminated (Fig. 2). We measure the nest productivity by the number of individuals that disperse from the nest and potentially initiate new

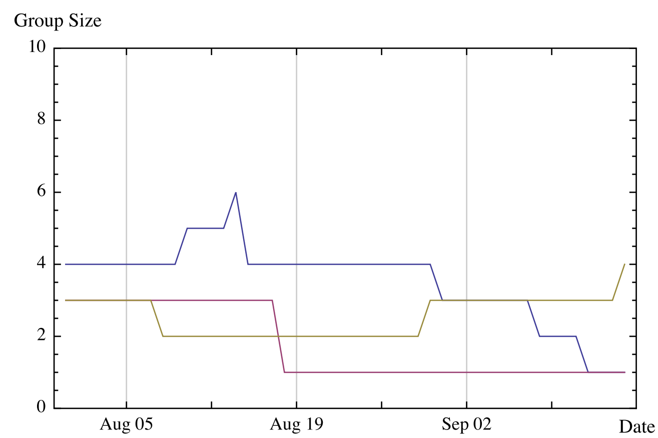

Fig. 1. Observed dynamics of a social queue of hovar wasp over a 6 week period in 2001; Lines are representing the number of adults (the blue, the top line at Aug 19), larvae (the yellow, the middle line at Aug 19), and pupae (the red, the bottom line at Aug 19). Dynamics are reanalysed from the data collected by Field et al. (2006).

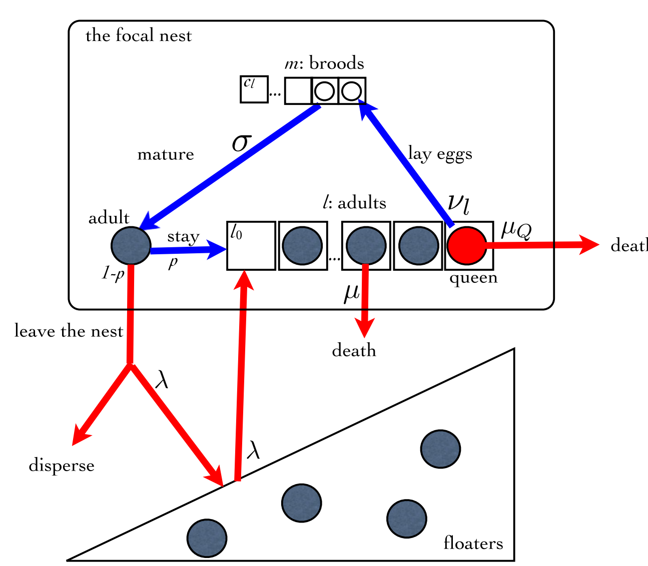

Fig. 2. Model of the social queue.