

Dynamics of social queues

Article (Published Version)

Toyoizumi, Hiroshi and Field, Jeremy (2014) Dynamics of social queues. *Journal of Theoretical Biology*, 346. pp. 16-22. ISSN 0022-5193

This version is available from Sussex Research Online: <http://sro.sussex.ac.uk/53274/>

This document is made available in accordance with publisher policies and may differ from the published version or from the version of record. If you wish to cite this item you are advised to consult the publisher's version. Please see the URL above for details on accessing the published version.

Copyright and reuse:

Sussex Research Online is a digital repository of the research output of the University.

Copyright and all moral rights to the version of the paper presented here belong to the individual author(s) and/or other copyright owners. To the extent reasonable and practicable, the material made available in SRO has been checked for eligibility before being made available.

Copies of full text items generally can be reproduced, displayed or performed and given to third parties in any format or medium for personal research or study, educational, or not-for-profit purposes without prior permission or charge, provided that the authors, title and full bibliographic details are credited, a hyperlink and/or URL is given for the original metadata page and the content is not changed in any way.



ELSEVIER

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

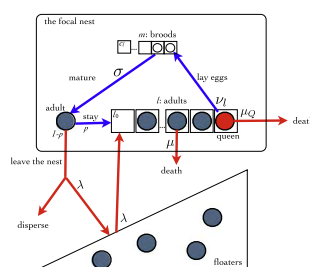
Dynamics of social queues

Hiroshi Toyoizumi ^{a,*}, Jeremy Field ^b^a Graduate School of Accounting, and Department of Applied Mathematics, Waseda University, Nishi-waseda 1-6-1, Shinjuku, Tokyo 169-8050, Japan^b School of Life Sciences, John Maynard Smith Building, University of Sussex, Brighton BN1 9QG, UK

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



ARTICLE INFO

Article history:

Received 2 June 2013

Received in revised form

15 December 2013

Accepted 16 December 2013

Available online 27 December 2013

Keywords:

Social queue

Quasi-birth-and-death process

Division of labor

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.

© 2013 The Authors. Published by Elsevier Ltd. Open access under [CC BY-NC-ND license](https://creativecommons.org/licenses/by-nc-nd/4.0/).

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,

* Corresponding author. Tel.: +81 3 3202 2293; fax: +81 3 5286 1987.

E-mail addresses: toyoizumi@waseda.jp (H. Toyoizumi), j.field@sussex.ac.uk (J. Field).

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 hypothesis Queller, 1989). A subtly 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 reproducers 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

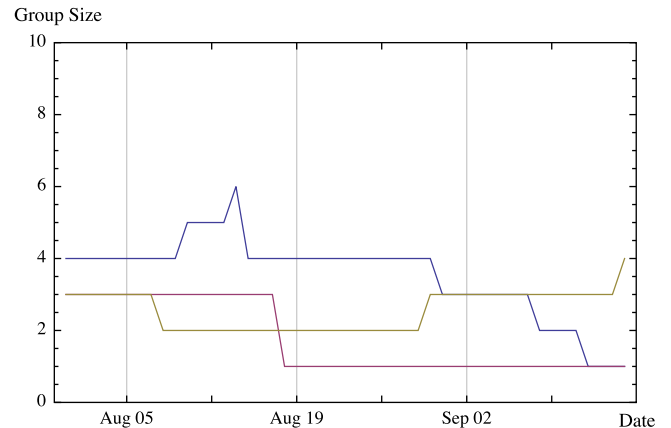


Fig. 1. Observed dynamics of a social queue of hover wasp over a 6 week period in 2001; Lines are representing the number of adults (the blue, the top line at Aug 19), larvae (the yellow, the middle line at Aug 19), and pupae (the red, the bottom line at Aug 19). Dynamics are reanalysed from the data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

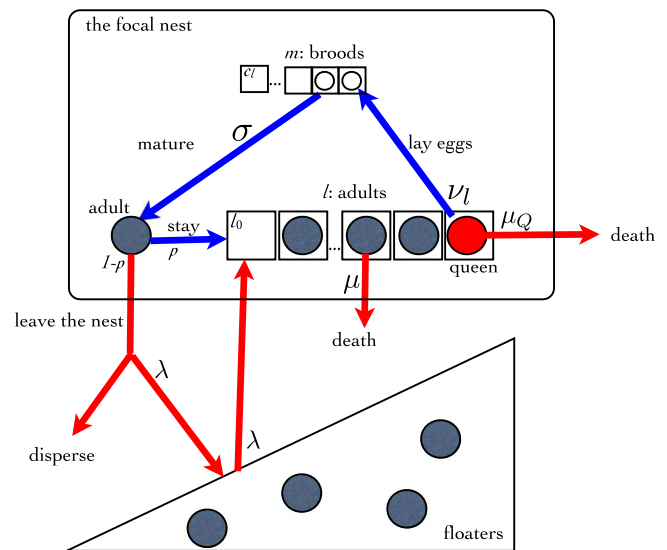


Fig. 2. Model of the social queue.

nests. At time 0, a founder individual builds the nest and starts the social queue. Let $L(t)$ be the number of adults and $J(t)$ be the number of brood in the social queue at time t . Note that we neglect males, which are not involved in nesting in wasps and bees. The dominant queen, who is the most senior (oldest) adult in the nest, produces her brood one at a time with the rate ν_l where l is the number of adults (including the queen herself) in the nest. When instantaneous productivity is linear with queue size (Shreeves and Field, 2002), $\nu_l = l\nu$. For mathematical simplicity, we ignore the age of brood, and each $J(t)$ brood becomes adult with the rate σ regardless of their age, which means that an individual brood need an independent exponential time to become an adult. Each adult forages and feeds brood. In a nest with l adults, at most c_l brood can be accommodated. When one of the adults dies, the number of brood may exceed the limit c_l , in which case the surplus of brood will be abandoned. We assume that c_l is an increasing function of l .

A new emerging adult has two options: (1) stay in the natal nest and become a helper with probability p or (2) leave the nest and disperse with the probability $1-p$. We assume that a maximum number of adults can reside on the nest, denoted by l_0 . When the adult population reaches l_0 , all subsequent emerging adults disperse until the adult population declines due to deaths. A dispersed individual has another two choices: (2a) become a floater or (2b) found a new nest somewhere else. The floater population can be regarded as a reservoir shared among all nests in the site, and floaters join a focal nest in the site according to Poisson process with the rate λ . To compensate for the influx at rate λ from the floater population, we assume that the emerging individual from the nest should join the floater population with the average rate λ , or the floater population will not be stable.

Helpers that forage have a death rate μ , but the dominant queen, who does not have to forage, has a different death rate μ_Q . At the time τ when the last adult on the nest dies, all the brood in the nest are abandoned and the nest is terminated.

The features of the social queue QBD model are summarized in Table 1.

We assume that $(L(t), J(t))$ forms a QBD process with the level $L(t)$ and its phase $J(t)$. The process has $\sum_{l=1}^{l_0} (c_l + 1)$ states:

$$\left\{ \underbrace{(1, 0), (1, 1), (1, 2), \dots, (1, c_1)}_{l=1}, \underbrace{(2, 0), (2, 1), \dots, (2, c_2)}_{l=2}, \dots, \underbrace{(l_0, 0), (l_0, 1), \dots, (l_0, c_{l_0})}_{l=l_0} \right\}. \tag{3.1}$$

The termination time τ of the nest can be regarded as the hitting time to the boundary state $\{L(t) = 0\}$, and the social queue process $(L(t), J(t))$ is the taboo process. Define the state probability of the social queue:

$$p_{(l,j)} = p_{(l,j)}(t) = P\{(L(t), J(t)) = (l, j), t \leq \tau\}. \tag{3.2}$$

We use the following convention to map the two-dimensional state probabilities $\{p_{(l,j)}(t)\}_{(l,j)}$ to the vector $\mathbf{p}(t)$:

$$\mathbf{p}(t) = (\mathbf{p}_1(t), \mathbf{p}_2(t), \dots, \mathbf{p}_{l_0}(t)) = \left(\underbrace{P_{(1,0)}, P_{(1,1)}, P_{(1,2)}, \dots}_{l=1}, \underbrace{P_{(2,0)}, P_{(2,1)}, P_{(2,2)}, \dots}_{l=2}, \dots, \underbrace{P_{(l_0,0)}, P_{(l_0,1)}, P_{(l_0,2)}, \dots}_{l=l_0} \right). \tag{3.3}$$

The founder starts the nest at time 0 and $(L(0), J(0)) = (1, 0)$, so the initial probability vector is

$$\mathbf{p}(0) = (1, 0, 0, \dots, 0, 0, \dots, 0, 0, 0). \tag{3.4}$$

The dynamics of social queue QBD processes are described by the

following Kolmogorov equation:

$$\frac{d}{dt} \mathbf{p}(t) = \mathbf{p}(t)\mathbf{Q}, \tag{3.5}$$

where \mathbf{Q} is the infinitesimal generator of QBD process and defined by

$$\mathbf{Q} = \begin{pmatrix} \mathbf{A}(1) & \mathbf{B}(1) & \mathbf{0} & \dots & \mathbf{0} \\ \mathbf{D}(2) & \mathbf{A}(2) & \mathbf{B}(2) & \mathbf{0} & \dots & \mathbf{0} \\ \mathbf{0} & \mathbf{D}(3) & \mathbf{A}(3) & \mathbf{B}(3) & \dots & \mathbf{0} \\ & & \ddots & & & \\ \mathbf{0} & \dots & \mathbf{D}(l_0-2) & \mathbf{A}(l_0-2) & \mathbf{B}(l_0-2) & \mathbf{0} \\ \mathbf{0} & \dots & \mathbf{0} & \mathbf{D}(l_0-1) & \mathbf{A}(l_0-1) & \mathbf{B}(l_0-1) \\ \mathbf{0} & \dots & \mathbf{0} & \mathbf{0} & \mathbf{D}(l_0) & \mathbf{A}(l_0) \end{pmatrix}. \tag{3.6}$$

Here $\mathbf{B}(l)$, $\mathbf{A}(l)$, $\mathbf{D}(l)$ and $\mathbf{0}$ are submatrices, and each represents a specific movement of social queue dynamics summarized in Table 2 (see also Fig. 3 and Appendix A for the detailed mathematical model).

Since the matrix \mathbf{Q} has the two-layered coordination system, its element is expressed as $Q_{(l,j),(m,i)}$. Eq. (3.5) can be solved formally, and

$$\mathbf{p}(t) = \mathbf{p}(0) \exp\{\mathbf{Q}t\}, \tag{3.7}$$

Table 1
Features of the QBD social queue model.

Features	Notation	Remark
Large group size (2+)	$l_0 \geq 2$	Upper limit of group size
Separation of adults and broods	$(L(t), J(t))$	No distinction among eggs, larvae and pupa
Linearity of Reproduction	$\nu_l = l\nu$	Eggs laid at a rate proportional to the group size
Long maturation time	$1/\sigma$	Exponential time, with no ageing effect
Brood capacity	c_l	Maximum number of brood allowed with l adults
Staying ratio	p	Random decision
Floaters	λ	The rate of Poisson arrival of floaters
Division of labour	μ and μ_Q	Mortality difference between queens and helpers
Progressively feed brood	τ	Part-reared offspring abandoned at the termination of a nest

Table 2
Transition rate matrices.

Matrix	Transition	Meaning
\mathbf{Q}	$(l, j) \rightarrow (m, i)$	Generator of social queue QBD process
$\mathbf{B}(l)$	$(l, j) \rightarrow (l+1, i)$	Emergence of an adult or joining of a floater
$\mathbf{A}(l)$	$(l, j) \rightarrow (l, i)$	Birth of a brood or dispersal of an adult
$\mathbf{D}(l)$	$(l, j) \rightarrow (l-1, i)$	Death of an adult
$\mathbf{0}$	$(l, j) \rightarrow (m, i)$	No transitions

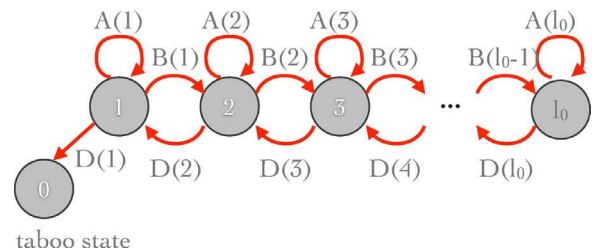


Fig. 3. Transition diagram of the matrix \mathbf{Q} .

where the exponential should be interpreted as the matrix exponential and

$$\exp\{\mathbf{A}\} = \sum_{n=0}^{\infty} \frac{\mathbf{A}^n}{n!}. \tag{3.8}$$

We estimate the total productivity of the social queue by r_{nest} , which is the net rate of growth in the number of individuals that disperse and produce new nests. Since one original nest is terminated at the end and some dispersed individuals join the floater population with the average rate λ , we have

$$r_{nest} = \frac{E[H]-1}{E[\tau]} - \lambda, \tag{3.9}$$

where $E[H]$ is the expected number of adults dispersing from the focal nest, and can be obtained by transient QBD analysis (see Appendix B). If r_{nest} is positive, the number of nests increases, and the larger the value of r_{nest} the more rapidly the population grows.

Now we check a simple analytically tractable but interesting example, which will be the basis of our analysis. When $l_0 = 1$, $c_1 = \infty$, $\nu_1 = \nu$, $\lambda = 0$ and $p=0$, the system represents a population of lone breeders with no brood capacity limit, no helpers and no floaters. All emerging wasps will disperse. In this case, the brood population process $J(t)$ turns out to be a transient $M/M/\infty$ queue with the arrival rate ν and the departure rate σ starting from

$J(0)=0$. It is well-known that the marginal distribution of a transient $M/M/\infty$ queue is a Poisson distribution, and

$$P\{J(t)=j\} = \frac{\rho(t)^j}{j!} e^{-\rho(t)}, \tag{3.10}$$

where $E[J(t)] = \rho(t) = \nu(1 - e^{-\sigma t})/\sigma$. Because the nest termination time τ is simply the lone breeder's exponential lifetime with the death rate μ independent of $J(t)$, $E[H]$ can be calculated directly as

$$\begin{aligned} E[H] &= E\left[\int_0^\tau \sigma J(t) dt\right] = \sigma \int_0^\infty E[J(t)1_{\{t \leq \tau\}}] dt \\ &= \sigma \int_0^\infty E[J(t)]P\{t \leq \tau\} dt = \int_0^\infty \nu(1 - e^{-\sigma t})e^{-\mu t} dt = \frac{\nu}{\mu} - \frac{\nu}{\sigma + \mu}. \end{aligned}$$

Since $E[\tau] = 1/\mu$, the growth rate of nests in a population of lone breeders is

$$r_{nest} = \nu \left(1 - \frac{\mu}{\mu + \sigma}\right) - \mu. \tag{3.11}$$

For example, let $\mu = 1$, $\nu = 2$ and $\sigma = 1/2$. On average, over the period of her unit life time, the lone breeder will produce 2 brood. At first sight, r_{nest} should be $\nu - \mu = 1$. However, on average, it takes two units of time for brood to mature, and those brood that fail to mature before the death of the lone breeder (the ratio $\mu/(\sigma + \mu) = 2/3$) will be “wasted”. Thus the net growth rate is

Table 3
Social queue models with linear brood capacity $c_l = 5l$ and linear reproduction rate $\nu_l = 2l$.

Model	$1/\sigma$	p	$1/\mu$	$1/\mu_Q$	λ	$E[\tau]$	$E[H]$	r_{nest}
Lone breeder ($c_l = \infty$)	2	0	1	1	0	1	2/3	-1/3
Simple social queue	2	1/2	1	1	0	1.28801	0.759516	-0.18671
Social queue with DOL	2	1/2	1	3	0	1.61677	1.63728	0.394169
With floater (FLT)	2	1/2	1	1	1/10	1.40143	0.961348	-0.12758
With DOL+ FLT	2	1/2	1	3	1/10	1.88688	2.33406	0.607017
All stay	2	1	1	1	0	4.26263	8.28762	1.70965

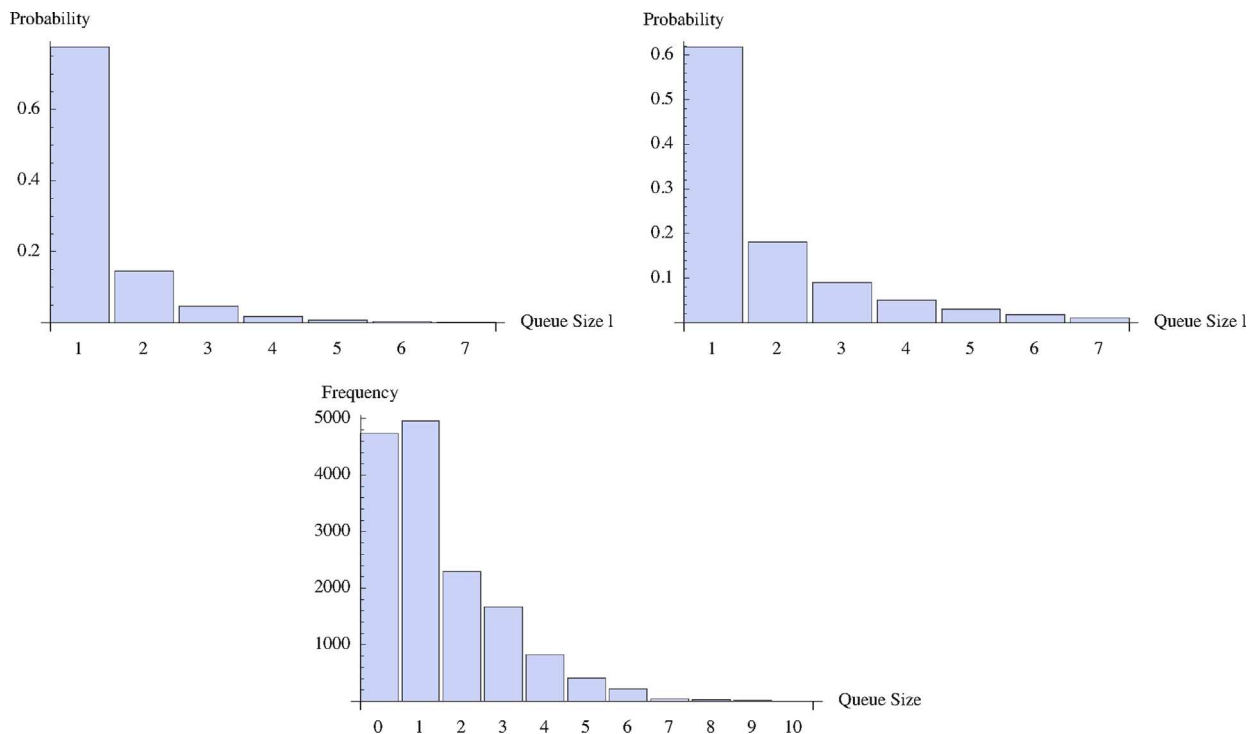


Fig. 4. Distribution of the group size of adults in the nest. The upper left-hand and upper right-hand graphs show the distributions derived by QBD models of simple social queues and social queues with DOL, respectively. The lower graph shows the real distribution of group sizes observed during censusing of 96 nests over 6 week period (Field et al., 2006), including the number of vacant nests observed (queue size 0).

negative and $r_{nest} = -1/3$. The population of lone breeders will not survive in this environment and will go extinct. Note that when $\sigma \rightarrow \infty$ (no need for progressive feeding), we have a mass provisioning model (Field, 2005), and its productivity is $r_{nest} = \nu - \mu$.

4. Numerical examples of social queue models

A population of lone breeders faces extinction because of the long maturation time of brood, as seen above. Now we determine whether extinction is still inevitable under social queueing. The results are summarized in Table 3 and Figs. 4 and 5(a). In these numerical analyses, parameters such as $p = 1/2$, $\sigma = 1/2$, $\mu_Q = 1/3$, $l_0 = 7$ and $\lambda = 1$ (the unit time is set to have $\mu = 1$) are in line with the natural social queues of hover wasps, and derived from the observational data collected by Field et al. (2006). The group size

distributions in Fig. 4 are based on the ratio of the expected times spent in the state $L(t) = l$.

By changing the key parameters, we can analyse and compare the impacts of various potential strategies of hover wasps, which cannot be observed in real world.

4.1. Simple social queue

In the simple social queue, emerging helpers rear the brood of the queen even after her death. Thus, we take into account the effect of EPC (extended parental care), but not the effect of longer lifespans due to DOL (division of labor). There is a positive impact on r_{nest} , which improves by 0.14659 ($= -0.18671 - (-1/3)$), but this impact is limited and r_{nest} is still negative. This is because the time for rearing adult helpers is longer than the lifetime of the initially lone queen. In other words, a simple social queue cannot solve the problem of long offspring maturation time.

4.2. Social queue with division of labor

A social queue with DOL in addition to EPC can have positive r_{nest} . Even though obtaining helpers is still rare, as seen in the second graph of Fig. 4, once the queen gets helpers, the nest has a longer time span and the social queue can be productive. The impact of DOL is 0.580879 ($= 0.394169 - (-0.18671)$), which is considerably higher than the effect of simple social queue with EPC only. See also Fig. 5(a) which compares r_{nest} for various maturation rates σ . Note that lone breeders have negative r_{nest} unless the brood maturation time is shorter than the expected adult life span.

4.3. Effect of floaters

Floaters might represent a backup for existing nests. Thus, we checked the effect of floating on r_{nest} . As seen in Table 3, floaters have an impact on improving r_{nest} especially for social queues with DOL.

4.4. Staying decision

From the perspective of nest productivity, all individuals should stay in the nest until the nest reaches its full capacity l_0 , when the nest then has the maximum adult dispersal rate (see the column "All Stay" in Table 3). However, in nature almost half of the emerging individuals disperse even from shorter queues (the observational data collected for Field et al., 2006). This might be explained by the balance between fitness benefits for individuals and nests.

4.5. Other parameters

Because the expected maturation time $1/\sigma$ has a substantial impact on queue dynamics, we illustrate the nest productivity for various σ in Fig. 5(a). It clearly indicates that the longer maturation time $1/\sigma$ will have a large negative impact on nest productivity, but a social queue with DOL can compensate for this to some degree.

The lifespan of the queen $1/\mu_Q$ and the number of adult residents in the nest l_0 will also have some impact on r_{nest} , which is shown in Fig. 5(b) and (c). They show the robustness to perturbations around the empirically estimated parameters such as $1/\mu_Q = 3$ and $l_0 = 7$, which we used in previous analyses.

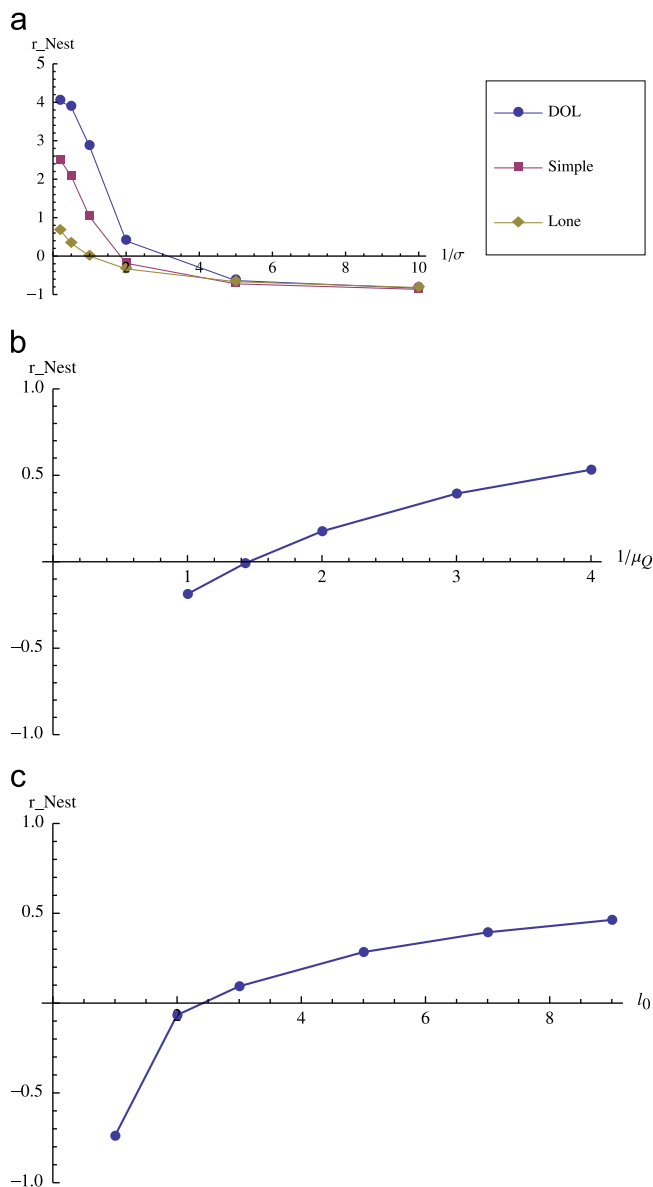


Fig. 5. Comparison of the nest productivities for various parameters. Lone, simple and DOL represent the nest productivity r_{nest} of lone breeders, simple social queues and social queues with division of labor, respectively. The other parameters are as in Table 3. (a) The nest productivity and the maturation rates σ , (b) the nest productivities and the life span of queen $1/\mu_Q$, and (c) the nest productivities of social queue with DOL and the maximum number of adults l_0 .

5. Conclusion

We show that a transient QBD model can be applied to estimate the productivity of complex dynamic systems such as social queues. Applying QBD analysis to the social queue, we can analyse various potential strategies of hover wasps: lone breeding, simple social queueing and social queueing with DOL. It is apparent that the productivity of the strategies increases in this order.

Our analysis shows that lone breeding and simple social queueing that includes EPC fail to maintain a viable population with realistic parameter values. On the other hand, DOL, which extends queen lifespan, will significantly increase the productivity of a simple social queue. The numerical analysis shows that the impact of DOL on nest productivity is slightly greater than the impact of simple social queueing itself. Thus, DOL might be one of the main benefit of social queues.

Appendix A. The matrices of QBD

Here we summarize the definitions of matrices our QBD model.

The matrix $\mathbf{B}(l)$ is $(c_l + 1) \times (c_{l+1} + 1)$ -submatrix and represents the increase of adult population (transition $l \rightarrow l + 1$) and is defined by

$$\mathbf{B}(l) = \begin{matrix} & \begin{matrix} 0 & 1 & 2 & \dots & c_l & c_{l+1} & \dots & c_{l+1} \end{matrix} \\ \begin{matrix} 0 \\ 1 \\ 2 \\ \vdots \\ c_l - 1 \\ c_l \end{matrix} & \begin{pmatrix} \lambda & 0 & 0 & & \dots & 0 & 0 & \dots & 0 \\ p\sigma & \lambda & 0 & & \dots & 0 & 0 & \dots & 0 \\ 0 & 2p\sigma & \lambda & & \dots & 0 & 0 & \dots & 0 \\ & & & \ddots & & & & & \\ 0 & \dots & 0 & (c_l - 1)p\sigma & \lambda & 0 & 0 & \dots & 0 \\ 0 & \dots & 0 & 0 & c_l p\sigma & \lambda & 0 & \dots & 0 \end{pmatrix} \end{matrix} \tag{A.1}$$

The diagonal element λ is the inflow rate from the floater population following a Poisson process, and the term $jp\sigma$ in the lower off-diagonal is the maturation rate of adults (an immature brood becomes an adult) which decide to stay on the nest (with probability p), resulting in the number of brood on the nest decreasing by one ($j \rightarrow j - 1$). The matrix $\mathbf{A}(l)$ represents the dynamics of brood that mature to produce adults which then leave the nest (the transition inside the level l), and is defined by

$$\mathbf{A}(l) = \begin{pmatrix} a_{l,0} & \nu_l & 0 & 0 & \dots & 0 \\ (1-p)\sigma & a_{l,1} & \nu_l & 0 & \dots & 0 \\ 0 & 2(1-p)\sigma & a_{l,2} & \nu_l & \dots & 0 \\ & & & \ddots & & \\ 0 & \dots & 0 & (c_l - 1)(1-p)\sigma & a_{l,c_l - 1} & \nu_l \\ 0 & \dots & 0 & 0 & c_l(1-p)\sigma & a_{l,c_l} \end{pmatrix}, \tag{A.2}$$

for $l = 1, 2, \dots, l_0 - 1$. The diagonal terms represent aggregated outbound flow (transition $(l, j) \rightarrow$ other states) and when $l = 2, \dots, l_0 - 1$,

$$a_{l,j} = \begin{cases} -\lambda - (l - 1)\mu - \mu_Q - \nu_l - j\sigma & \text{for } j \neq c_l, \\ -\lambda - (l - 1)\mu - \mu_Q - j\sigma & \text{for } j = c_l, \end{cases} \tag{A.3}$$

and when $l = 1$

$$a_{1,j} = \begin{cases} -\lambda - \mu - \nu_1 - j\sigma & \text{for } j \neq c_1, \\ -\lambda - \mu - j\sigma & \text{for } j = c_1. \end{cases} \tag{A.4}$$

The upper off-diagonal terms ν_l represent the rate of brood production when there are l adults, resulting in an increase in the number of broods ($j \rightarrow j + 1$). The term $j(1 - p)\sigma$, which is the lower off-diagonal of $\mathbf{A}(l)$, is the maturation (emergence) rate of adults

that disperse, again resulting in a decrease in the number of brood ($j \rightarrow j - 1$). The matrices $\mathbf{A}(1)$ and $\mathbf{A}(l_0)$ correspond to boundary of the state space (the brink of termination and the saturated nest), and they have slightly different elements from the other $\mathbf{A}(l)$, because they represent the extremes (boundaries) of the maximum and minimum possible adult population. In the case of $\mathbf{A}(1)$, only the diagonal elements are different and represented in (A.4), since a lone dominant queen ($l = 1$) has to forage for herself. Note $a_{1,j}$ includes the outflow μ to the taboo state $\{l = 0\}$. On the other hand, for $\mathbf{A}(l_0)$, at the maximum adult group size,

$$\mathbf{A}(l_0) = \begin{pmatrix} a_{l_0,0} & \nu_{l_0} & 0 & 0 & 0 & \dots & 0 \\ \sigma & a_{l_0,1} & \nu_{l_0} & 0 & 0 & \dots & 0 \\ 0 & 2\sigma & a_{l_0,2} & \nu_{l_0} & 0 & \dots & 0 \\ & & & \ddots & & & \\ 0 & 0 & \dots & 0 & (c_{l_0} - 1)\sigma & a_{l_0, (c_{l_0} - 1)} & \nu_{l_0} \\ 0 & 0 & \dots & 0 & 0 & c_{l_0}\sigma & a_{l_0, c_{l_0}} \end{pmatrix}, \tag{A.5}$$

where the diagonal terms,

$$a_{l_0,j} = -(l_0 - 1)\mu - \mu_Q - \nu_{l_0} - j\sigma, \tag{A.6}$$

reflecting the fact that no further floaters can join, and the lower off-diagonal elements $j\sigma$ reflect the fact that all emerging adults must disperse. The matrices $\mathbf{D}(l)$ represent deaths (the transition $l \rightarrow l - 1$) for $l \geq 2$. The death rate of dominant queen (μ_Q) is less than the death rate of helpers and lone queens (μ): helpers and lone queens have the same death rate (Shreeves and Field, 2002; Field et al., 2000). Thus,

$$\mathbf{D}(l) = \{(l - 1)\mu + \mu_Q\} \mathbf{I}_{l \rightarrow l - 1} \quad \text{for } l \geq 2, \tag{A.7}$$

where $\mathbf{I}_{l \rightarrow l - 1}$ is defined by

$$\mathbf{I}_{l \rightarrow l - 1} = \begin{matrix} & \begin{matrix} 0 & 1 & \dots & c_{l-1} \end{matrix} \\ \begin{matrix} 0 \\ 1 \\ \vdots \\ c_{l-1} - 1 \\ c_{l-1} \end{matrix} & \begin{pmatrix} 1 & 0 & \dots & 0 \\ 0 & 1 & \dots & 0 \\ & & \ddots & \\ 0 & \dots & 0 & 1 \\ 0 & \dots & 0 & 1 \\ \vdots & & & \vdots \\ 0 & \dots & 0 & 1 \end{pmatrix} \end{matrix}. \tag{A.8}$$

Appendix B. Evaluation of $E[\tau]$ and $E[H]$

First we estimate $E[\tau]$, the expected time to the termination of the nest. Since $P\{L(t) = l, J(t) = j, \tau \geq t | L(0) = m, J(0) = i\} = (\exp\{\mathbf{Q}t\})_{(m,i),(l,j)}$, we have

$$P\{\tau \geq t\} = \mathbf{p}(0) \exp\{\mathbf{Q}t\} \mathbf{1}, \tag{B.1}$$

where $\mathbf{1} = (1, 1, \dots, 1)$. Since \mathbf{Q} is a sub-stochastic matrix, it has its inverse, and we have

$$E[\tau] = \int_0^\infty P\{\tau \geq t\} dt = \int_0^\infty \mathbf{p}(0) \exp\{\mathbf{Q}t\} \mathbf{1} dt = \mathbf{p}(0) (-\mathbf{Q})^{-1} \mathbf{1}. \tag{B.2}$$

Here we used the relation of integral of matrix exponential and the inverse: $(-\mathbf{Q})^{-1} = \int_0^\infty \exp\{\mathbf{Q}t\} dt$. Let $T(l, j)$ be the cumulated time spent in (l, j) until the termination of the nest. Similarly, we can calculate its mean $E[T(l, j)]$ as

$$E[T(l, j)] = E \left[\int_0^\tau \mathbf{1}_{\{(L,J) = (l,j)\}}(t) dt \right] = \mathbf{p}(0) (-\mathbf{Q})^{-1} \mathbf{1}_{(l,j)}, \tag{B.3}$$

where $\mathbf{1}_S(t)$ is the indicator function of the set S and $\mathbf{1}_{(l,j)}$ is the vector whose elements are all 0 but only (l, j) -element is 1.

Next, we estimate the productivity of the nest. Let H be the number of adults dispersing from the focal nest. Since adults mature at the rate $\sigma J(t)$, and stay in their natal nest with probability p until $L(t)$ reached l_0 , the conditional dispersal rate given $(L(t), J(t)) = (l, j)$ is defined by

$$r(l, j) = \begin{cases} \sigma j & \text{for } l = l_0, \\ (1-p)\sigma j & \text{otherwise.} \end{cases} \quad (\text{B.4})$$

Using this, we define the dispersal rate vector \mathbf{r} whose elements are of the form $r(l, j)$. Since

$$E[r(L(t), J(t))1_{\{t \leq \tau\}}] = \mathbf{p}(0) \exp(\mathbf{Q}t)\mathbf{r}, \quad (\text{B.5})$$

we have

$$\begin{aligned} E[H] &= E\left[\int_0^\tau r(L(t), J(t)) dt\right] = \int_0^\infty E[r(L(t), J(t))1_{\{t \leq \tau\}}] dt \\ &= \int_0^\infty \mathbf{p}(0) \exp(\mathbf{Q}t)\mathbf{r} dt = \mathbf{p}(0)(-\mathbf{Q})^{-1}\mathbf{r}. \end{aligned} \quad (\text{B.6})$$

References

- Field, J., 2008. The ecology and evolution of helping in hover wasps (hymenoptera: Stenogastrinae). *Ecol. Soc. Evol.*, 85–107.
- Field, J., 2005. The evolution of progressive provisioning. *Behav. Ecol.* 16 (4), 770–778, URL <http://beheco.oxfordjournals.org/content/16/4/770.abstract>.
- Field, J., Cronin, A., Bridge, C., 2006. Future fitness and helping in social queues. *Nature* 441, 214–217, URL <http://dx.doi.org/10.1038/nature04560>.
- Field, J., Shreeves, G., Sumner, S., Casiraghi, M., 2000. Insurance-based advantage to helpers in a tropical hover wasp. *Nature* 404 (6780), 869–871, URL <http://dx.doi.org/10.1038/35009097>.
- Gadagkar, R., 1990. Evolution of eusociality: the advantage of assured fitness returns. *Philos. Trans.: Biol. Sci.* 329 (1252), 17–25, URL <http://www.jstor.org/stable/76892>.
- Hamilton, W., 1964. The genetical evolution of social behaviour II. *J. Theor. Biol.* 7 (1), 17–52.
- Kokko, H., Johnstone, R.A., 1999. Social queuing in animal societies: a dynamic model of reproductive skew. *Proc. R. Soc. Lond. B* 266, 571–578, URL <http://www.journals.royalsoc.ac.uk/openurl.asp?genre=article&id=doi:10.1098/rspb.1999.0674>.
- Kokko, H., Johnstone, R.A., Clutton-Brock, T.H., 2001. The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. B: Biol. Sci.* 268 (1463), 187–196, URL <http://www.journals.royalsoc.ac.uk/content/en6x5dgrht76ulhw>.
- Latouche, G., Ramaswami, V., 1999. *Introduction to Matrix Analytic Methods in Stochastic Modeling*. SIAM.
- Nonacs, P., Liebert, A., Starks, P., 2006. Transactional skew and assured fitness return models fail to predict patterns of cooperation in wasps. *Am. Nat.* 167 (4), 467–480.
- Queller, D., 1994. Extended parental care and the origin of eusociality. *Proc.: Biol. Sci.* 256 (1346), 105–111.
- Queller, D., 1996. The origin and maintenance of eusociality: the advantage of extended parental care. In: *Natural History and Evolution of Paper Wasps*. Oxford University Press, Oxford, pp. 218–234.
- Queller, D.C., 1989. The evolution of eusociality: reproductive head starts of workers. *Proc. Natl. Acad. Sci.* 86 (9), 3224–3226, URL <http://www.pnas.org/content/86/9/3224.abstract>.
- Shen, S.-F., Kern Reeve, H., 2010. Reproductive skew theory unified: the general bordered tug-of-war model. *J. Theor. Biol.* 263 (1), 1–12, URL <http://www.sciencedirect.com/science/article/B6WMD-4XRYTBM-3/2/15051acaa41548cf09231c01f66303a5>.
- Shen, S.-F., Kern-Reeve, H., Vehrencamp, S.L., 2011. Parental care, cost of reproduction and reproductive skew: a general costly young model. *J. Theor. Biol.* 284 (1), 24–31, URL <http://www.sciencedirect.com/science/article/pii/S0022519311002803>.
- Shreeves, G., Field, J., 2002. Group size and direct fitness in social queues. *Am. Nat.* 159 (1), 81–95.