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The number and age composition of queens (and colonies) in our model can be deduced by applying standard demographic methods (e.g., Keyfitz 1968) to the life cycle in Figure 2. Let $Q(a,t)$ be the number of queens (colonies) aged a at time t. Then we have

$$Q(a,t) = l(a)Q(0,t-a). \tag{B.1}$$

From the model derivation we see that the survivorship of queens $l(a)$ at the exact ages T_1, $T_1 + T_2$, $T_1 + 2T_2$, etc., is given by

$$l(a) = pq^m \quad \text{when} \quad a = (T_1 + mT_2), \quad \text{for} \quad m \geq 0. \tag{B.2}$$

While we have not made any assumptions about the shape of $l(a)$ within growth cycles, the detailed shape of $l(a)$ makes no difference to the characteristic equation nor to the subsequent theoretical development. At long times the population of queens will grow at the exponential rate r; thus, the number of queens born $Q(0,t)$ will become

$$Q(0,t) \sim Q_0 e^{rt}, \quad \text{as} \quad t \to \infty, \tag{B.3}$$

with the constant Q_0 determined by the initial distribution of colonies. Combining these results, it follows that the fraction of colonies aged a will become proportional to

$$e^{-ra} l(a), \quad \text{as} \quad t \to \infty. \tag{B.4}$$

Descending one level in the hierarchical structure of our model, consider a colony that begins a growth cycle at time $t = 0$. The colony starts with N_0 workers distributed by age a_w according to some function $n_0(a_w)$. As time progresses, the population in the colony will be given by equation (4) in the main text and the age distribution will be given by

$$n(a_w,t) = \begin{cases} be^{-\mu a_w}, & \text{for } a_w < t; \\ n_0(a_w - t)e^{-\mu t}, & \text{for } a_w > t. \end{cases} \tag{B.5}$$

The first line of the above equation describes workers born during the ongoing growth cycle. The second line describes workers that were present at the start of the growth cycle. For many social insects worker lifespans are shorter than the duration of a growth cycle. Thus, at the end of a growth cycle colonies of such insects will have a worker age distribution given by the first line of equation (B.5). In other words, a colony about to issue a swarm does not remember its initial age structure. Furthermore, since the characteristic age structure at swarming is the product of the worker production rate and worker survivorship, there will be a numerical predominance of young workers. Empirical evidence for honeybees (Winston 1987) qualitatively agrees with this theoretical prediction about the worker age structure at swarm issuance.

Note that the worker age distribution in individual colonies continually changes as the colony issues swarms and begins new growth cycles. However, the age of a colony's queen determines when the colony began its current growth cycle. Therefore, we can use equation (B.5) to calculate the age distribution $n(a_w \mid a)$ of workers in a colony whose queen is age a. Finally, note that the age distribution of queens approaches the stable distribution of equation (B.4). This implies that, although the worker age distribution in individual colonies continually changes with queen age, the population level age distribution of workers will approach a stable one,

$$n^*(a_w) = \int e^{-ra} l(a) n(a_w \mid a)\, da. \tag{B.6}$$

Literature cited

Keyfitz, N. 1968. Introduction to the mathematics of population. Addison-

Wesley, Reading, Massachusetts, USA.

Winston, M. L. 1987. The biology of the honey bee. Harvard University Press, Cambridge, Massachusetts, USA.