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Life in the colonies: Hierarchical demography of social organisms

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Abstract

Hierarchical population structure, where individuals are aggregated into colonies that themselves grow, survive or perish, and potentially produce offspring colonies, is an important feature of many biological systems, most notably eusocial organisms such as honeybees *Apis mellifera*. Despite this hierarchical structure, there is a paucity of analytical models and theory linking the dynamics of individuals within colonies to the dynamics of a population of colonies. We present an analytical model that provides a simple, robust, and predictive theory for the population dynamics of eusocial organisms. Our model explicitly describes and links demographic dynamics for the different levels in the hierarchy (individuals, colonies, population). We illustrate the application of the model by analyzing the effects of life history traits such as worker lifespan and size at swarming on the growth rate of populations. We conclude by discussing possible extensions of the model that increase its realism and expand its usefulness beyond swarm-founding, monogynous, eusocial insects.

Keywords

Apis mellifera; bees; demography; eusocial insects; hierarchical population; population model

Introduction

Eusociality, traditionally defined by colonial organization with overlapping generations, cooperative care of young, and non-breeding castes (Winston 1971), presents many apparent paradoxes to traditional ecological and evolutionary theories that focus on the primacy of individuals. A population of eusocial organisms is hierarchically structured with individuals aggregated in colonies containing one or more queens and attendant workers. The colonies

themselves go through growth cycles, survive or perish, and potentially produce offspring colonies. Thus, the dynamics of a population of colonies depends on colony-level survival and reproduction but these, in turn, are partially determined by the dynamics of individuals within a colony. For example, differences in growth rates of two populations can result from differences in intra-colonial birth and death rates or from differences in colony-level demography such as time to swarming. The scope and sophistication of ecological theory for eusocial organisms have increased dramatically starting with Oster & Wilson (1978), but little theoretical work explores the population consequences of hierarchical organization - individuals within colonies and colonies within a population.

Many previous models have focused on single colonies (Brian 1965, McClellan et al. 1980, Uchmaski & Pétal 1982, Degrandi-Hoffman et al. 1989, Fefferman & Starks 2006), or have described populations of colonies without referencing within-colony dynamics (Otis 1991, Matis et al. 1995). An exception is the work of Makela et al. (1993) linking within-colony dynamics to population growth in a complex, object-oriented simulation of the spread of Africanized honeybees *Apis mellifera*. While useful for specific applications, complex simulation models are not easily generalized to illuminate broader ecological and evolutionary questions. A general understanding of the population dynamics of eusocial organisms, especially honeybees, is also of practical importance because of ecosystem services (e.g., crop pollination) or public safety and ecosystem risks (e.g., Africanized honeybees or invasive fire ants). Additionally, the use of honeybees as model organisms for studying the genetic basis of aging (Rueppell 2004, Amdam and Page 2005) or learning (Beggs et al. 2005, Vergoz et al. 2007) will likely expand following the recent publication of the honeybee genome. But the mapping of phenotypic traits into fitness depends on the demography of the hierarchical population structure.

Here we present a simple yet robust analytical model for the dynamics of hierarchically organized populations. For concreteness we develop and apply the model for a monogynous, swarm-founding, eusocial organism, with particular reference to honeybees *Apis mellifera*, and indicate how the model can readily be generalized to describe other eusocial or hierarchical populations. We develop a renewal equation for “units” at an appropriate level in the hierarchy. The units of the population are colonies and individuals comprise these units. The growth rate r of the number of colonies satisfies an appropriate version of the Lotka equation (Wilson 1971, pg. 443)

$$1 = \int e^{-ra} l(a) m(a) da, \quad (1)$$

where $l(a)$ is the probability that a colony survives to age a , and $m(a)$ is the rate at which new colonies are produced by a colony at age a . Our key contribution is to show how colony-level survivorship and reproduction schedules are derived from within-colony change in which the “units” are individuals and colony-level events.

While the details of our model pertain to honeybees and similar monogynous eusocial species, our main goal is to elucidate the interaction of individual and colony processes. By

linking all levels in the demographic hierarchy (individuals, colonies, population) we obtain novel insights not available from analyses that ignore the hierarchy. We illustrate these insights by analyzing how individual life history traits (such as worker lifespan) and colony level traits (such as size at swarming) affect the growth rate of populations. An earlier version of this model by two of the authors was outlined in the book by Carey (1993). We have revised and expanded that model and provided novel analyses and discussion.

The Model

Since monogynous eusocial insect colonies have a single queen, the units of the population can be thought of as queens (with their attendant colonies) instead of colonies, *per se* (Wilson 1971, pg. 424). The growth of the population can thus be indexed to the growth of the number of queens and the total number of individuals (workers plus queens) in the population asymptotically grows at the same rate as the number of queens (Appendix A). Thus, we formally explore the population dynamics by analyzing the life cycle (Figure 1) and renewal process of queens (but see Carey [1993] for a similar description focusing on colonies). The growth rate r satisfies the Lotka (equation 1 above), where $l(a)$ is the probability that a queen survives to age a , and $m(a)$ is the rate at which new queens are produced by a queen at age a .

To link the dynamics of queens (and their colonies) to the dynamics within single colonies, we assume, consistent with the biology of honeybees, that a new queen is produced when a colony reaches a size sufficient to issue a swarm. In fact, more than one potential queen may be produced but only one survives to take over the colony. The life cycle (Figure 1) thus begins with a newly emerged queen inheriting her natal colony (and nest site) after the resident queen (her mother) has departed in a swarm with some fraction of the worker population. After mating in one or more nuptial flights the newly emerged queen begins laying eggs and her colony grows. If her colony survives to reach a sufficient size, she departs in a swarm with many workers and a new queen is reared. The departing queen and her swarm seek a new nest location and may succeed in establishing a separate colony. This colony in turn starts a growth cycle leading to eventual swarming and colony fission. Therefore, a queen (and her colony) can recruit into the population single offspring queens (and accompanying colonies) at discrete time intervals (see Figure 1), the lengths of which depend on the cycle of colony growth followed by swarming. The survival probability of a queen over these discrete inter-swarm intervals depends on the number of workers present and on factors independent of worker number. Table 1 describes the variables of the model and the Table 2 summarizes the key equations; detailed model development is given in Appendix A.

Here we assume that a colony issues a swarm when the worker population reaches a threshold size N_s . Swarming undoubtedly occurs in response to many cues related to within-colony demographic factors (Winston 1987), such as worker population, worker age distribution, or the number of brood. Recently, Fefferman and Starks (2006) emphasized that all these cues for swarming are highly correlated. Their simulations showed that when a threshold for swarming was reached for one potential trigger mechanism, the other

mechanisms were also extremely close to their threshold values. Thus, it is reasonable to assume as we do that swarming is initiated in response to a single cue N_S .

During a growth cycle the number of workers in a colony depends on N_0 the worker number at the beginning of the growth cycle, μ the worker death rate, and the rate b at which the queen produces workers. The rate of change in worker number is described in equation 2 (see Table 2). Both the production and death rates may be functions of worker number, age, caste, resource availability, or other environmental variables. However, b must be bounded because of physiological limits on the queen and workers must die at some rate and therefore colony growth is intrinsically self-limiting, irrespective of density dependence in b and μ . Without swarming or death, a colony would reach a self-sustaining size N^* where the number of worker deaths is exactly balanced by the production of new workers. The swarming threshold N_S occurs at some fraction f of N^* . To illustrate the dynamics of the model we make the simplest assumption, that μ and b are constant, but the demographic structure of our model easily accommodates different functional forms. With this assumption, the number of workers in a colony during a growth cycle is given by equation 3 (see Table 2).

The number of workers at the beginning of a growth cycle N_0 depends on the parity of the queen (i.e., number of previous offspring queens). A newly emerged queen (parity zero) inherits her natal colony with $(1 - g)N_S$ workers; the departing queen (all higher parities) begins the growth cycle with a swarm of gN_S workers. A queen first produces an offspring queen after an interval of time T_1 and then produces offspring queens at intervals of length T_2 (see Figure 1). T_1 and T_2 are found by solving equation 3 with appropriate initial and final conditions.

The survival probabilities of a queen over the first and subsequent reproductive intervals are given by p and q , respectively. These probabilities have components p_0 and q_0 that are independent of the number of workers (e.g., surviving the nuptial flight) and a component s that depends upon the number of attendant workers. Queens are specialized for reproduction and, in honeybees at least, are incapable of surviving without workers to forage and maintain the nest. Colonies with more workers more successfully defend the nest site, locate and gather resources, thermoregulate, and perform other functions necessary for survival of the queen and colony. Thus, the survival of the queen is an increasing function of initial worker number (Winston, 1987), but subject to diminishing marginal returns (equation 7 in Table 2). The incremental benefit of each additional worker and the overall importance of workers to queen survival depends on the parameter v , which reflects environmental conditions. For example, in a relatively benign and constant climate the thermoregulatory function of workers may be less important and v would be lower than in harsher environments. Worker-independent survival constants p_0 and q_0 may also vary between environments.

It follows that the “fertility” $m(a)$ of a queen equals 1 when a swarm is issued at the exact ages T_1 , $T_1 + T_2$, $T_1 + 2T_2$, $T_1 + 3T_2$, etc., and is 0 at all other ages. The survivorship $l(a)$ of a queen to each of these discrete ages is equal to p , pq , pq^2 , pq^3 , etc. Thus, equation 1 reduces to a geometric series whose sum yields

$$1 = qe^{-rT_2} + pe^{-rT_1}, \quad (10)$$

which is to queens (and their colonies) what the Euler-Lotka equation is to populations in classical demography. It shows how individual and colony vital rates, by setting p , q , T_1 , and T_2 , determine growth in a population of colonies. As a fundamental demographic result equation 10 applies independently of many details about within-colony and colony-level events. Detailed specifications of worker production and death functions in equation 3, or the survival functions p and q , change the objects in equation 10 but not its structure. The population growth rate r is the only real solution of equation 10, and applies to both the number of queens (and colonies) and the total number of workers across all colonies (see Appendix A).

The Model in Action

Dynamic properties

Fitness, as measured by the population growth rate r , is determined by the balance between the inter-swarm intervals (T_1 and T_2) and the probability of a queen (and her colony) surviving those intervals (p and q , respectively). Note that T_1 and T_2 both scale with the swarming threshold size N_S , or equivalently with f . A large f makes every growth cycle long (see Figure 2a) because making more workers takes a longer time. However, large f also means that there are more workers when swarms are issued, which influences queen survival probability (equation 7, see Figure 2b). Figure 2c illustrates how r reflects this balance between survival and the time between reproductive swarms. Note that the maximum population growth rate occurs at a swarming threshold well below the self-limiting population size (i.e., $f < 1$). This is an important point as a recent analysis proposed that a colony swarms once it reaches the self-limiting population size as “the only way to satisfy the evolutionary goal of increasing the rate of production of bees related to the colony (Fefferman & Starks 2006).” However, we show here that natural selection would actually favor variants that swarmed before reaching their self-limiting colony size.

The population dynamics are also affected by the tradeoff between departing and newly emerged queens. As discussed above, both the inter-swarm interval and the survival probability depend on the number of attendant workers a queen has to support her. The swarming fraction g describes the partitioning of workers between the departing queen and the newly emerged queen. When g is large, the departing queen is accompanied by many workers and thus T_2 will be short (Figure 3a), allowing for a rapid production of subsequent offspring queens. However, the newly emerged queen will be poorly provisioned with workers and thus have a relatively low worker-dependent survival (Figure 3b) and a long reproductive maturation time (i.e., T_1 is long – Figure 3a). Fitness reflects this allocation tradeoff between the departing and newly emerged queens (Figure 3c).

Another way to think about this allocation tradeoff is to consider the fact that $r > 0$ only when the queen net reproductive rate $R > 1$. This condition is only satisfied when $p + q > 1$. At the extremes of $g = 0$ and $g = 1$ the survival of the departing queen and the newly

emerged queen, respectively, are equal to 0, implying that populations can only persist at intermediate values of g where both the departing queen and newly emerged queen have non-zero survival probabilities (Figure 3c). Within the range of g where populations are viable, a slight change in either direction might increase p or q , but only at the expense of the other. Thus there is a maximum population growth rate at some intermediate value of g , but it occurs on a broad fitness plateau rather than at a sharp peak.

In conventional life history theory, two central issues are the timing of reproduction and the quality of offspring produced (e.g., Stearns 1992). For eusocial insects like honeybees, these are interrelated issues concerning the timing of swarm issuance and the size of the swarm. The curves in figures 2 and 3 illustrate the life history tradeoffs inherent in colonial organization: reproductive cycle time is balanced against the probability of survival and parental success is balanced against the success of offspring. The result is that the fitness landscape (Figure 4) is like a mesa with many nearly optimal combinations of f and g ; fitness only declines steeply at low values of f and extreme values of g .

From individuals to populations

We now focus on the interplay between levels in the hierarchy. How do individual level traits, like worker mortality μ and the queen's rate of worker production b , affect population growth? The impact of a queen's rate of worker production is relatively straight forward to understand. Worker dependent survival of both the departing and newly emerged queens increases monotonically with N_S , the size of the colony when a swarm is issued (equation 7). Assuming f is fixed, N_S increases monotonically with b (equation 4). Thus, p and q both increase monotonically with a queen's ability to produce workers and equations 11 and 12 translate this increase to r . Figure 5 (both panels) shows this pattern for any given μ .

The relationship of μ to population growth rate is more complicated. Both the time until a queen first swarms T_1 and the time until subsequent swarming T_2 are inversely proportional to worker mortality (equations 5 and 6). Increasing worker lifespan (decreasing worker mortality) for fixed f actually increases the time between swarms. However, longer worker lifespan also means that N_S is larger, and thus, there are more workers available to swarm or to provision the newly emerged queen, which positively impacts their survival. Thus, the net effect on population growth rate of reducing worker mortality could be positive or negative due to the balance of impacts on queen survival and inter-swarm intervals, as illustrated in Figure 5. In the top panel, population growth rate increases with worker mortality at high rates of worker production, but decreases with increasing worker mortality at lower rates of worker production. At high worker production rates the modest reduction in queen survival accompanying high worker mortality is more than compensated for by the decreased inter-swarm intervals. At lower worker production rates, the decreases in queen survival associated with high worker mortality outweigh the positive effects of decreasing the inter-swarm intervals.

Differences in the strength of worker dependence v can shift the balance between the effects on inter-swarm interval length and impacts on queen survival. At relatively low values of v the survival of a queen is high and changes little over a relatively large range of initial colony sizes. This would be the case in benign environments where few workers are needed

to gather sufficient resources, defend against predators, or otherwise maintain the colony. In a relatively harsh environment where a large cadre of workers (large v) is needed to support and maintain the colony, the survival of the queen increases rapidly with initial colony size. In the bottom panel of Figure 5 the worker dependence v is much greater than in the top panel, reflecting a more demanding environment. Here decreasing worker mortality increases the population growth rate over the entire range of worker production rates.

Understanding how individual and colony-level traits interact to determine population growth rate is an important, but open, question about bees and other social insects. For example Dyer and Seeley (1991) noted marked differences in average worker lifespan among *Apis* species, and lacking a general model relating worker traits to population fitness, “assumed that worker longevity potentially constrains colony growth rate (pg. 168),” where colony growth rate is defined as $\frac{dN_t}{dt}$ as in our equation 2. By reasoning that selection would optimize the colony growth rate, they posited that differences in worker lifespan offset suspected differences in the worker production rates achievable by the different species. Our model makes clear that the effect of worker longevity on population growth rate is mediated by the ecological context. Increased worker lifespan might offset constraints on worker production but could also lead to lower population growth rates by increasing the inter-swarm intervals.

The swarming threshold parameter f and the allocation parameter g may be evolutionarily constrained, or they may vary to reflect the ratios achievable given environmental conditions. The latter implies that the size at swarming N_S and the size of the swarm may be evolutionarily constrained. Unfavorable environmental conditions might result in a reduction in b and an increase in μ . Faced with such harsh environmental conditions, would a colony lower its swarming threshold N_S (implying f is constrained) or would it simply fail to swarm, reaching a self-limiting population size N^* lower than N_S ? Anecdotal evidence of enormous colonies in very favorable environments suggests that N_S does scale with demographic conditions; however, Winston *et al.* (1981) reported that European honeybee races in Kansas and Africanized honeybees in French Guiana had nearly identical colony sizes when issuing swarms ($19,993 \pm 1,973$ versus $20,378 \pm 1,447$, respectively) suggesting that N_S might be constrained. This is an open empirical question that has been brought into focus by our hierarchical model.

Discussion

In developing a relatively simple model for the population dynamics of swarm-founding, monogynous, eusocial insects, we have illustrated a potentially general approach to explicitly incorporating hierarchical demographic structure. Our model illuminates how fitness depends on both intra-colonial birth and death rates as well as colony-level characteristics. This has provided new insights not available from analyses that ignore hierarchical structure. As an example, we found that increasing the worker mortality rate could actually increase the population growth rate in some circumstances due to its negative relationship to both queen survival and time between swarming. Similarly, our results clearly

indicate, in contrast to previous work (Fefferman & Starks 2006), that swarming well before the colony growth rate $\frac{dN_t}{dt}$ declines to zero would be evolutionary advantageous.

As discussed previously, changing the functional form of worker mortality, production rate of workers, or queen survival to reflect density, resource, or age dependence does not change the fundamental structure of the model. There is great flexibility in this framework to change the specification of parameters to address particular questions of interest. For example, to explore the role of worker tempo in shaping life history strategies one could model worker mortality as a function of energetic expenditures (cf., Novoseltsev et al. 2002). Seasonality could likewise be introduced to the basic model structure by allowing parameters to vary with season. Most temperate populations are essentially univoltine with rather high colony mortality during winter periods. This would sharply constrain the set of feasible f and g values that would allow colonies to swarm during the growth period yet attain sufficient population size prior to the onset of winter (Al-Khafaji et al., *unpublished*).

The model may also be extended to include additional life stages and more realistic details about their roles and interactions. There has been extensive interest in age polyethism in workers, the change in behavioral repertoire with age. Of particular interest is the transition from hive-based activities to foraging (Page *et al.* 1992, Huang & Robinson 1996, Rueppell *et al.* 2004), which is influenced by resource availability (Schulz *et al.* 1998), and entails exposure to different mortality hazards. Thus, a promising direction for future work is to integrate the within-colony caste demography of Oster & Wilson (1976) with resource transfer-mediated survival and reproduction (Lee 2003, Amdam & Page 2005) in the hierarchical context of the population dynamics.

While we developed the model in reference to honeybees and similar species, it could likely be adapted to apply to other eusocial insects such as termites and ants. In this context, g might represent the fraction of females in a nest committed to becoming colony-founding queens, rather than the fraction of workers that swarm. The survival of newly emerged queens to age at first reproduction could be specified as a small constant or explicitly written in terms of a mortality hazard function that decreases with colony size. The production of workers by the queen could likewise depend on colony size up to a physiological maximum. It would be straightforward to extend the model to accommodate finitely many queens in a colony and drone numbers could be described by equations essentially identical to equations 2–4 and reflecting the resource allocation to drone production (Page & Metcalf 1984, Henderson 1994).

The hierarchical concept represents a new innovation in demography that could be extended to an arbitrary number of levels and potentially has broad applications beyond eusocial organisms. For example, early humans are thought to have lived in small hunter-gatherer groups (i.e. colonies) of relatively constrained size. A hunter-gatherer group, in response to its internal demographic or social conditions might have split into smaller groups that could then grown in size. Similarly, an entire group might have perished due to conflict with neighboring groups, failed dispersal attempt, or other event. Thus, the groups themselves potentially reproduced, grew, and died, as did the individuals within those groups. The

mapping from individual vital rates and group properties to population growth requires a theory of population dynamics that explicitly incorporates the hierarchy of individuals within groups and groups within a population.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.
Life cycle of queens.

Figure 2.

Effects of f on inter-swarm interval, worker-dependent survival, and population growth. $g = 0.5$ therefore $T_1 = T_2$ and worker dependent survival is $s(0.5N_S)$ for both the departing queen and the queen inheriting the colony. $\mu = 1/30$, $b = 1350$, $p_0 = 0.9$, $q_0 = 0.81$, and $v = 5000$

Figure 3.

Effects of g on inter-swarm interval, worker-dependent survival, and population growth. In 3a the solid line is T_1 and the dashed lines is T_2 . In 3b the solid line is $s((1-g)N_S)$ and the dashed line is $s(gN_S)$. $\mu = 1/30$, $b = 1350$, $p_0 = 0.9$, $q_0 = 0.81$, and $v = 5000$

Figure 4.

Effects of f and g on population growth rate. The contours present values of r in increments of 0.0025. The darker line indicates $r = 0$; for contours above it $r > 0$ and for contours below it $r < 0$. $\mu = 1/30$, $b = 1350$, $p_0 = 0.9$, $q_0 = 0.81$, and $v = 5000$

Figure 5.

Effects of μ and b on population growth rate. In the top panel $v = 5000$. In the bottom panel $v = 15000$. In both panels $f = 0.9$, $g = 0.6$, $p_0 = 0.9$, and $q_0 = 0.81$

Table 1.

Key parameters in model

Parameter	Description
N_t	number of workers in colony at time t
μ	death rate of workers
b	rate of worker production by the queen
N^*	self-sustaining maximum colony size in absence of fission or death
N_s	swarming threshold size
f	ratio N_s/N^*
g	proportion of workers departing in swarm
T_1	time until a newly emerged queen produces an offspring queen and swarms
T_2	inter-swarm interval for departing queens
p	survival of newly emerged queen over an interval of length T_1
q	survival of departing queen over an interval of length T_2
p_0	worker-independent component of survival for newly emerged queen
q_0	worker-independent component of survival for departing queen
$s(N_0)$	worker-dependent component of survival of queen
V	strength of worker dependence of queen survival
R	net reproductive rate
r	population growth rate

Table 2.

Key equations

Equation	Description	Number
$\frac{dN_t}{dt} = b - \mu N_t$	within-colony growth rate	(2)
$N_t = N_0 e^{-\mu t} + \frac{b}{\mu} (1 - e^{-\mu t})$	number of workers in colony at time t	(3)
$N^* = \frac{b}{\mu}$	maximum colony size	(4)
$T_1 = \frac{1}{\mu} \log \left(\frac{1 - (1-g)f}{1-f} \right)$	time until a newly emerged queen first swarms	(5)
$T_2 = \frac{1}{\mu} \log \left(\frac{1-gf}{1-f} \right)$	inter-swarm interval for departing queens	(6)
$s(N_0) = \frac{N_0}{v + N_0}$	worker dependent survival	(7)
$p = p_0 s(N_0 = (1-g)N_S)$	survival of newly emerged queen	(8)
$q = q_0 s(N_0 = gN_S)$	survival probability of departing queen	(9)
$1 = qe^{-rT_2} + pe^{-rT_1}$	characteristic equation for monogynous eusocial insects	(10)
$R = \frac{p}{1-q}$	net reproductive rate	(11)
$r \approx \frac{\log R}{T_1 + \frac{qT_2}{1-q}}$	approximation for population growth rate	(12)