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When should honey bee (*Apis mellifera*) colonies swarm?

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Abstract

I used a mathematical model to calculate the optimal size of a honey bee (*Apis mellifera*) colony at swarming and the optimal number of offspring colonies produced during one swarming. The model indicates that in the stable population of European races the optimal size of a colony at swarming is 85% of its maximum size and the optimum number of offspring colonies is 3. In African races, which have a higher growth rate, the expected relative size at swarming and the expected number of offspring colonies is bigger. These predictions agree with empirical data. Another result of the model is that in growing populations the optimal relative size of a colony at swarming is smaller than in stable and declining populations and the optimal number of offspring colonies in growing populations is bigger than in stable and declining populations. These predictions cannot be verified because there is no data available. I suggest that the relative size of a colony is the major factor preceding the swarming of the honey bee.

Introduction

During honey bee swarming an old queen departs from the parental colony with prime swarm. In the following days issue afterswarms with young queens. In parental colony only one young queen and part of the workers stay. Despite a considerable amount of research it is still not clear what the factors preceding swarming are. Almost all research considering this problem investigated proximate factors [1,2,3,4]. There are only a few studies of ultimate factors preceding swarming [5,6] which are very general and give no predictions. In this paper I focus on natural selection which optimises all traits effecting fitness of individuals. Because the size at swarming and number of offspring colonies are very important traits they also are optimised. I use a mathematical model to calculate the optimal values of these two traits. The results of the model can help to indicate proximate factors preceding swarming.

The model

The fitness of a colony depends on the number and survival of offspring colonies and the time between following bouts of swarming. Survival of honey bee colonies is largely determined by their size. Bigger colonies survive winters better and are more resistant to predators [5]. But a colony can produce either many small offspring colonies or a few bigger ones. When a colony swarms earlier the amount of workers to divide between the offspring colonies is smaller. To calculate the optimal size at swarming and the optimal number of offspring colonies I used an optimisation model. For the sake of the simplicity of the model I assumed that all offspring colonies produced during one swarming are identical. It means that prime swarm, all afterswarms and the parental colony have the same size and the same probability of reaching maturity. These assumptions should not effect results significantly despite the fact that in reality prime swarm is larger than afterswarms, and the parental colony survives better than swarms. I assumed also that colonies live in an environment with one season. This seems reasonable because the honey bee derives from warm climates [7], and most honey bee races live in mild climates. As a measure of fitness I use Malthusian parameter r. With aforementioned assumptions it is equal

$$r = \frac{\ln(nl)}{\alpha} \tag{1}$$

where n number of offspring colonies produced during one swarming, l probability of surviving to maturity, α age of maturity of colony.

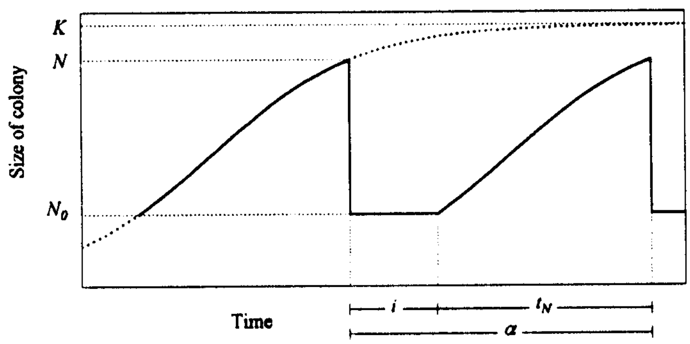

Fig. 1. Changes of size of a colony in time can be described by a logistic function (·····). The colony swarms after reaching size N and produces offspring colonies of size N_0. Between two bouts of swarming there is the time of maturation α which consists of the time of stagnation i and the time of growth t_N.

The age of maturity of a colony consists of the time of stagnation i and the time of growth t_N. The time of stagnation is constant and equals 25 days, it begins at swarming and ends at the emerging of the first workers in a new colony. Because the growth of honey bee colonies can be quite precisely described by logistic equation [8] time of growth t_N equals

$$t_N = \frac{1}{\rho}\ln\left[\frac{N(K-N_0)}{N_0(K-N)}\right] \tag{2}$$

where ρ coefficient of colony growth, N_0 size of offspring colony, N size of colony at swarming, K maximum size of colony. The maximum size of a colony is reached when all combs are occupied by brood and storage or when the queen has reached its maximum rate of egg laying. The size of a colony at swarming N and the size of offspring colonies N_0 can be expressed as a fraction of the maximum size of colony K

$$N = aK \tag{3}$$

$$N_0 = \frac{aK}{n} \tag{4}$$

where a relative size of colony.

Probability of surviving to maturity is usually [9] defined as

$$l = \exp\left(-\int_0^a j \mathrm{d}t\right) \tag{5}$$

I assumed that the instantaneous mortality rate j equals

$$j = \frac{\gamma}{N_t} \tag{6}$$

where γ coefficient of mortality and N_t instantaneous size of colony. Coefficient of mortality γ can be expressed as a fraction of maximum size of colony K

$$\gamma = \lambda K \tag{7}$$

where λ relative coefficient of mortality.

I found numerically the optimal size of a colony at swarming and the optimal number of offspring colonies for various values of coefficient of colony growth and the relative coefficient of mortality. I was particularly interested in such a combination of values of these two coefficients for which the Malthusian parameter equals zero, which is the case in stable populations.

Results and discussion

In stable populations with a higher growth rate the expected relative size at swarming and the expected number of offspring colonies is bigger than in those with a lower growth rate. In case of European races where colony growth rate is 0.03 [10,11] optimal relative size at swarming is 0.85 and optimal number of offspring colonies is 3.

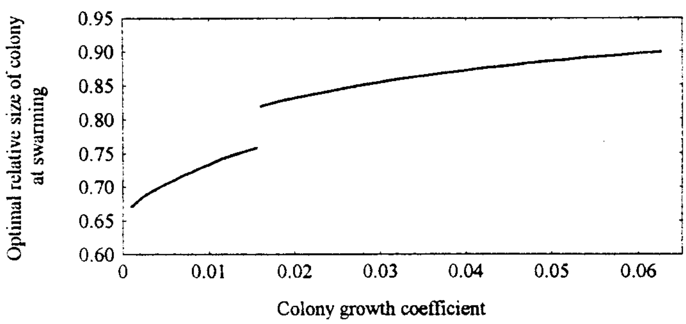

Fig. 2. The optimal relative size of a colony at swarming in stable populations with different coefficients of colony growth.

There is no direct empirical data which can be used to verify this prediction. However when the growth of a colony is restricted by the size of cavity, the satisfactory measure of the relative size of a colony is the proportion of combs occupied by brood and storage. In African races colony growth rate is higher than in European races [7] so African races should swarm after reaching a bigger relative size of colony and produce more offspring colonies. These predictions are consistent with observations as African races produce on average 3.9 offspring colonies when 86% of combs are occupied by brood and storage and European races produce on average 3.5 offspring colonies when 72% of combs are occupied by brood and storage [12]. The predicted relative size of a colony at swarming in the stable population of European races (0.85) approximates the proportion of combs occupied at swarming (0.72). The predicted number of offspring colonies (3) also approximates observed value (3.5) [12].

In growing populations the expected relative size at swarming is smaller than in stable and declining populations and the expected number of offspring colonies in a growing population is bigger than in stable and declining populations.

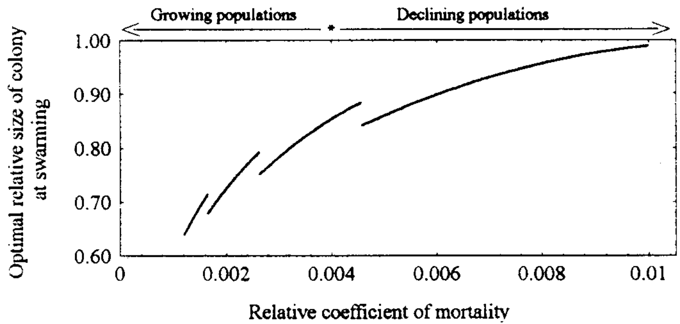

Fig. 3. The optimal relative size of a colony at swarming in growing, stable and declining populations of European races (ρ=0.03). Stable population is marked by *.

There is a unique opportunity to verify these predictions in North America where the population of the Africanized honey bee is still growing. In order to achieve this the proportion of occupied combs in relatively small cavities should be measured during swarming on the border of a growing population and in its centre, where the number of colonies is stable. On the border of a growing population the proportion of occupied combs at swarming should be smaller than in the centre.

The model indicates that the relative size of a colony at swarming has a big influence on its fitness. That is why I expect that workers can perceive prospects of the further growth of their colony and use this information in order to start swarming at an optimal moment. Of course workers do not assess directly the maximum size of their colony and do not compare it with the actual size. Probably they perceive other signals, intensity of which changes as the colony approaches its maximum size. These signals have to be equally efficient when colony growth is restricted by cavity size and the ability of the queen to lay eggs.

The optimal strategy of colony reproduction is an alternative to the colony demography hypothesis [4], which assumes that swarming is initiated by many factors. These factors include colony size, patterns of comb utilisation, congestion of brood and workers in the brood nest area, and worker age distribution. The colony demography hypothesis assumes that swarming starts when all these factors reach their threshold value. The experiment presented to confirm this hypothesis showed small variability of many demographic traits of swarming colonies. However all these traits are strongly correlated with each other. In this situation one other trait correlated with those measured in the experiment can be responsible for the starting of swarming. I argue that relative size of colony is this trait.

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