Demography of the Worker Caste of *Leptothorax allardycei* (Hymenoptera: Formicidae)

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ABSTRACT The demography of workers of *Leptothorax allardycei* was studied by marking and monitoring individuals within colonies maintained in the laboratory. The maximum lifespan for a worker in this study was 300 d, with an average life expectancy, at eclosion, of 145 d. The workers showed a type I survival curve. Life expectancy declined slowly until an age of ≈100 d, after which there was a marked decrease in the rate of change of life expectancy. The probability of survival decreased exponentially with age. Workers that eclosed in the field, and were, therefore, of unknown age, survived longer than predicted on the basis of the survival of ants of known age. This is probably because workers collected in nature are, on average, substantially younger than *L. allardycei* workers in the laboratory. This is almost certainly because older workers, who forage for the colony, are at a great risk of predation.

KEY WORDS *Leptothorax*, demography, survival

Despite the fact that ants are one of the most studied groups of arthropods, there is relatively little information on the demography of ant workers. The number of species for which there are data on the life expectancy and probability of death of workers is small. This information is important for understanding the ecology and social behavior of ants. First, the demography of workers within colonies provides a context for the evolution of social behavior. Potential payoffs for altruistic behavior are a function of the cost of the altruistic act, which will be determined partially by the probability of surviving. The demography of workers also influences the growth of colonies and, therefore, the rate at which a colony can achieve a size sufficient for reproduction. Finally, the demography of workers will influence competitive interactions between other colonies and, thus, the amount of food necessary to support a colony.

The demography of worker ants has been studied in *Solenopsis invicta* (Porter & Tschinkel 1985, Calabi & Porter 1989), and the demography of the foraging caste has been studied in *Pogonomyrmex barbatus*, *P. rugosus* (Gordon & Hölldobler 1987), *P. owyheei* (Porter & Jorgensen 1981), and *Cataglyphis bicolor* (Schmid-Hempel & Schmid-Hempel 1984). The demography of the foragers, and other workers who leave the nest, is easier to study and is relevant to studies of foraging and to the interactions with other colonies. Data on the survival of foragers do not provide a complete picture of the pattern of survival among the workers, because foragers are typically older workers. Furthermore, it may be revealing to study the pattern of age-related mortality in the absence of predation because it may illustrate intrinsic limits to lifespan. If the survival of the younger workers is to be measured, it is almost inevitable that the studies will be done in the laboratory. Only in the laboratory is it feasible to mark individually those workers that remain within the nest without disturbance to the nest. The drawback is that the laboratory is much safer, particularly for the foragers, and the lifespan in the laboratory, under a similar temperature regime to the field, is probably much greater.

We report data here on the laboratory survival of workers of the myrmicine ant, *Leptothorax allardycei* (Mann). This ant is an inhabitant of hollow sawgrass stems in the Florida Keys, tropical mainland Florida, and the Bahamas. The behavior and ecology of this species have been described by Cole (1986; 1988; 1991a, b). Two observations motivate the study of worker demography in *L. allardycei*. First, the workers of this species assemble themselves into a dominance hierarchy based on differential reproductive potential (Cole 1986). High ranking workers, who are typically of the younger caste, are aggressive toward one another, have more highly developed ovaries and, even in queenright colonies, lay eggs that develop into males. The survival curve of workers has never been completely determined and will influence the

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potential payoff for attaining behavioral dominance. Second, the level of spontaneous activity of workers is a function of the age of the worker (Cole 1992). Younger workers have a higher probability of becoming active than do older workers. The survival curve of the workers will influence the age-structure of the colony, which may then affect the production of short-term activity cycles within the colony (Cole 1992).

Materials and Methods

Complete colonies of *L. allardycei* were collected in late May 1992 from Big Pine Key, FL. They were housed in glass observation nests (Cole 1986) and censused upon being brought into the laboratory. Ten colonies were selected for complete study. The colonies averaged about 40 workers and each had a single queen. Laboratory temperatures ranged from 24–27°C. All workers in each colony were spray painted with two colors of spray enamel paint. The random pattern of dots generated a unique and recognizable pattern for each ant. Workers were photographed for future reference. During the course of the study, 328 ants of unknown age retained their initial markings. We will refer to these as the *unknown age group*. They represent workers of mixed age that eclosed in the wild. Each colony was monitored at approximately weekly intervals for the next 300 d, until all marked individual ants had died. At each weekly census interval, any newly eclosed workers, who were unmarked, were marked with a different color combination of paints. Workers who emerged to adulthood over the next 90 d were included in the study, and a total of 84 ants of known ages were followed. They will be referred to as the *known age group*. We calculated the survival curve, discarding each colony in turn, to obtain jackknifed confidence intervals of the probability of survival.

To compare the survival curves of the known age and unknown age groups, a simulation study was performed. Using the survival data from the group of known age ants, we constructed assemblages of individuals who were sampled randomly from a group of ants that survived like the known age ants. These randomly constructed groups, which simulate the construction of the unknown age groups, were followed for 150 d. The simulation was repeated 200 times to obtain an estimate of the standard error of the predicted survival curve for the unknown age group.

Results

The survival curve (±2 SEM from jackknifed estimates) for the ants of known age (Fig. 1) was a type 1 curve with an initial life expectancy upon eclosing to adulthood of 145 d. The probability that the worker died during any 10-d interval increased exponentially with age (Fig. 2; $r^2 = 0.66$, $P < 0.001$). Life expectancy declined gradually from 145 to 73 d at an age of 120 d. Life expectancy remained relatively constant, declining only form 64 to 55 d between the age of 120 and 190 d. Thereafter, life expectancy declined fairly rapidly.

The survival rates of the 328 ants of unknown age were consistently lower than that of the ants of known age. The life expectancy of an average

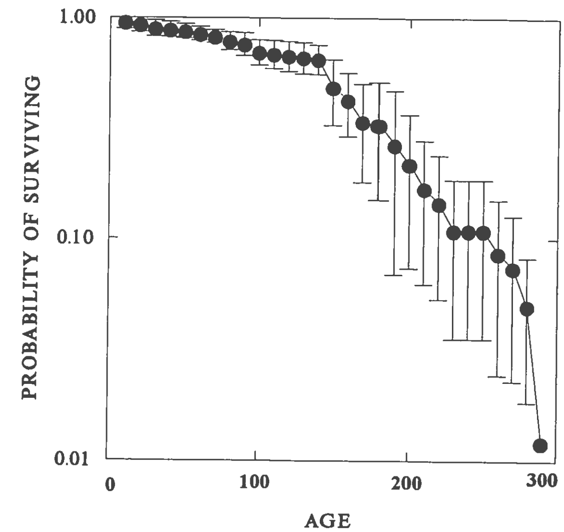

Fig. 1. Probability of surviving (±2 SEM) for a worker of *L. allardycei* as a function of age (in days). Note that the probability of surviving is plotted on a logarithmic axis. Curve is a type I survivorship curve with a life expectancy, at eclosion, of 145 d. The standard errors are calculated by jackknifing survivorship across colonies.

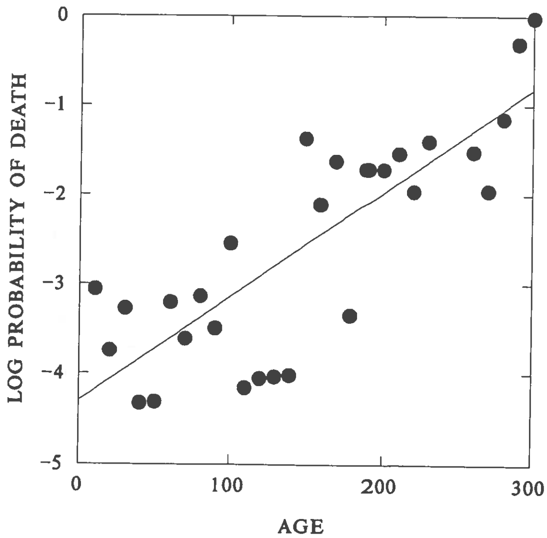

Fig. 2. Probability of dying (natural logarithm) during any given 10-d interval as a function of age (in days).

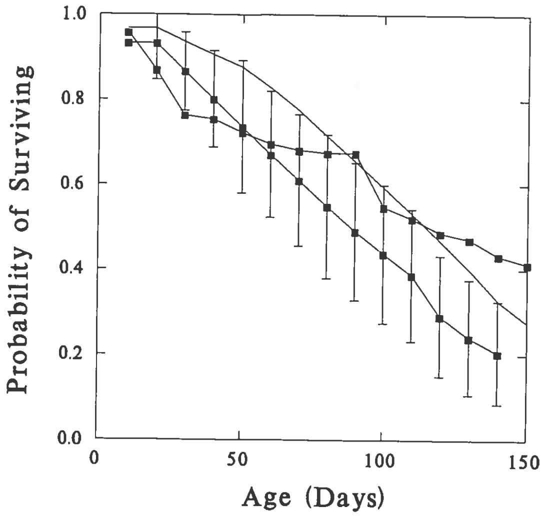

Fig. 3. Probability of survival of ants of unknown age from wild collected colonies (solid squares). Probability of survival is consistently lower than that of ants of know age in Fig. 1. Hollow squares represent the predicted (±2 SEM) probability of surviving of a randomly constructed group of ants which survive in the manner of ants of known age. Consistent underestimate of the survival of wild collected ants is probably caused by wild ants that are, on average, younger than ants from the laboratory. Other line describes the predictions of simulations based on a life history in which ants in the field survive identically for their first 100 d of life and then all of them die. Standard errors are omitted in the last curve for the sake of clarity.

ant taken from the wild and placed into the laboratory was 114 d. The survival curve of the unknown age ants can be compared with the simulated survival curve derived from the known age ants. The predicted survival curve (±2 SEM of the simulation) is shown in Fig. 3 for the first 150 d in comparison to the observed mixed age survival curve and in comparison to the survival curve for the known age ants. The simulation agrees relatively well with the observed mixed age survival curve up to about 60–70 d. After this time, the simulation consistently predicts that the survival of mixed age ants should be markedly lower that the actual survival curve.

Discussion

Relatively few studies provide life-table data on ants. The most desirable data would be data from ants followed, in the field, from eclosion to death. No studies provide these data, although several studies have examined the lifespan of marked foragers in the wild (*Cataglyphis*, Schmid-Hempel & Schmid-Hempel 1984; *Pogonomyrmex*, Gordon & Hölldobler 1987; Porter & Jorgensen 1981). In each of these studies, the marked individuals were of unknown age, but the mortality rate of foragers was so high (the life expectancy is 6 d for *C. bicolor* and 12 d for *P. owyheei*) that uncertain age at marking probably did not make much difference. Field studies of mortality are usually limited to studies of foragers. While this is an important portion of the lifespan of the ants, it does not provide a complete picture of the demography of a colony.

Temperature, which has been shown to influence longevity of fire ants (Calabi & Porter 1989), is not responsible for the changes in survival reported in this study. First, all the ants were not the same age at the same time. Although the probability of surviving changed markedly with age, it did not change simultaneously in ants who were at different ages. Second, there were consistent differences between the survival of the known age and unknown age groups who would be exposed to identical environmental conditions.

Laboratory studies provide the opportunity to study ants of known age, both during the age when they are found within the colony and after they become foragers. However, such studies, including the current one, are limited because mortality, especially of the forager caste, is not comparable in the lab and in the field. These studies do provide relevant information on the potential life history characteristics, in the absence of predation. Haskins & Haskins (1980) studied the lifespan of several individuals from several species of *Myrmecia*. These data are not extensive enough to provide information on the pattern of survival in any one species, but they suggest that workers live an average of more than one year. Porter & Tschinkel (1985) examine the survival of *Solenopsis invicta* in relation to a number of variables, including size, and found that longevity could be >1 yr. Plateaux (1986) studied several species of *Leptothorax* in the laboratory and showed that the average longevity was 2–3 yr.

Colony size will depend on the interaction between worker lifespans and the rate of queen egg-laying. Because colony size in *L. allardycei* is ≈60 workers in nature, egg production to maintain this colony size may be fairly low. It is necessary for a queen to lay about one egg that produces an eclosing worker every 2–3 d. Even allowing for mortality among eggs and larvae, a low egg-laying rate is required to maintain colony size. We can make the simple postulate that, across species, the life expectancy of a worker divided by the interval between egg laying should be proportional to colony size.

During the lifespan of *Leptothorax allardycei*, the probability that a worker dies during any given time interval increases exponentially with age. Thus, they follow the Gompertz assumption concerning the relation between mortality rates and age (Sohal 1985). Most theories of aging either explicitly assume this relationship or attempt to explain this relationship. Although this pattern has often been regarded as universal in aging, the connection of traditional theories of aging to the worker caste of a social insect is not clear. For example, it is not at all obvious how the evolution of senescence pertains to a nonreproductive caste of a social insect.

The relation between the pattern of longevity of known age and unknown age workers in *Leptothorax* allows us to make a simple prediction concerning the survival of the foragers in the wild. The survival of unknown age workers exceeds that predicted by the simulation based on the survival of known age workers. In nature, the survival of an ant declines markedly when it begins foraging outside of the nest. Therefore, the age structure of natural colonies probably differs from that of laboratory-maintained colonies in that there will likely be a larger fraction of older ants in the laboratory. The average age of workers in colonies in nature is less caused by the higher mortality of the older workers. This fact must be kept in mind when interpreting the results of laboratory experiments, on foraging or activity patterns, which may be influenced by the age of the workers.

The average age of workers from colonies recently collected should be less than predicted from the survival curve; therefore, the predicted survival rate of a mixed age group of ants will be less than the actual survival. We can construct simulated colonies with any starting age structure, subject them to the observed pattern of lab survivorship, and ask whether we can reconstruct the observed pattern of survival of unknown age workers. If we assume that, in the field, the survivorship curves are identical to lab survivorship curves over the first 100 d and then all ants die (mimicking extremely high forager mortality), then the survival curves that are produced provide a better fit to the observed survival over 150 d (Fig. 3).

An important aspect in understanding the ecology and behavior of ants are demographic studies of colonies (Tschinkel 1991, 1993). Worker lifespan influences a large number of colony attributes and is important in determining the growth and size of colonies, their behavioral interactions with other colonies, and their ecological interactions with other species.

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