Possible Importance of Relatedness in the Fire Ant, *Solenopsis invicta*
Buren (Hymenoptera: Formicidae) in the United States

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ABSTRACT The fire ant was accidentally introduced from southern Brazil to Mobile, Ala., some time between 1933 and 1940 and has spread throughout the southeastern United States. The coefficient of genetic relationship of female fire ants was calculated on the assumption that only one or a few females was originally introduced and that each was mated with one to several males. The model shows that relatedness stabilizes in fewer than 10 generations and that the ultimate relatedness is more strongly affected by the number of females in the original inoculum than by the number of males mating with each female. The results are discussed in light of the potential effect of relatedness on the social biology of the fire ant in the United States.

Degree of genetic relatedness is at the very base of one of the major theories of sociality (Wilson 1975). Closely related animals are thought to be more likely to cooperate with or to show altruism toward one another. Thus, factors which affect genetic relatedness may affect the social biology of animals. When a small inoculum (perhaps a single female) of an exotic species is introduced into a new habitat, the resulting population, however large, carries only a fraction of the genetic variation of the parent population, and genetic relatedness is consequently high (Dobzhansky 1970, Futuyma 1979).

The fire ant, *Solenopsis invicta* Buren, represents a classic case of the expansion of a small inoculum into a large population. Although the exact nature of its accidental introduction is unknown, it was first noticed in the Mobile, Ala., harbor area around 1940, probably having been introduced 5 to 7 years earlier (Buren et al. 1974). The inoculum probably consisted of one or a few females, and all North American fire ants are descendants.

A substantial literature on fire ant biology exists (Wojcik and Loofgren 1982), but practically all of it relates only to the North American population. Several unusual biological features suggest that the probable higher genetic relatedness in the United States may be of importance to the fire ant’s social biology. We therefore set out to calculate the average relatedness of female fire ants in the United States. Because we know neither the number of introduced females nor the number of males with which each was mated, relatedness was computed for 1 to 10 females each mated with 1 to 10 males.

Methods

The ‘‘coefficient of relationship’’ is the fraction of genes in two individuals that are identical by descent, averaged over all loci. By the algorithm given by Wilson (1971, 1975), this coefficient, with modification for haplo-

diploidy, was programmed and computed for 20 generations for each male/female combination. The general procedure was as follows. For a single locus, frequency of male and female gametes of each genotype was calculated for the parent generation. The frequency of each male by female combination resulting from random mating was then calculated and these frequencies were summed for each genotype (combination) resulting in the genotype frequency distribution. The fraction of shared alleles (0, 0.5, or 1.0) for each pairwise comparison within this distribution was multiplied by the frequency of each genotype and summed over all genotypes to yield the average fraction of genes identical by descent (coefficient of relationship). The computation was then reiterated for the next generation.

Assumptions of the model were: (1) mating was completely random; (2) each allele of a single locus was different in the founding genomes represented; (3) in multiply mated females, sperm of each male had an equal probability of fertilizing eggs; (4) the males/female mating pattern is the same in each subsequent generation; (5) each female contributes the same proportion of offspring to the next generation; (6) generations do not overlap; (7) there is no selection over the 20 generations; and (8) sampling effects due to finite population size are negligible. While several of these assumptions are probably not true, the effect would be primarily on the rate at which the final average relatedness is approached, rather than its value. Violation of assumptions 2 and 8 would increase relatedness.

Results and Discussion

No matter what combination of males and females is initially “introduced,” the coefficient of relationship of females declines to a steady value within fewer than 10 generations. Fig. 1 shows the progress of this decline for an inoculum of a single female mated with 1 to 10 males. There is very little change after 6 or 7 generations. As the number of males increases from 1 to 10, the ultimate relatedness declines from 0.43 to 0.28, but most of this change occurs between 1 and 5 males.

Violation of certain of the model’s assumptions would increase the time to stabilization. For example, if mating within and between pedigrees were not similar (non-
random mating), it would take longer for the average relatedness to stabilize. The greater the preference for inbreeding, the longer it would take. The final relatedness, however, would be identical and would depend only on the make-up of the initial inoculum. Similarly, the number of males mating with each female is likely to have dropped during the early phase of the real-life invasion because populations would have been small. This could slow the stabilization rate, or increase it due to the chance effects of sampling, but would not affect the final value.

The age of fire ant colonies at first reproduction appears to be 1½ to 2 years under favorable conditions (Markin et al. 1973). While fire ants are iteroparous, producing sexuals over a number of years, it seems reasonable to assign a value of about 2 years to a genera-

**Fig. 1.** Coefficient of relationship as a function of the number of males mated with a single female and the number of generations of random matings. Relatedness stabilizes within six or seven generations. Results for multiple queen introductions are generally similar.

**Fig. 2.** Ultimate coefficient of relationship as a function of the number of females in the original inoculum and the number of different males with which each was mated. Relatedness declines more rapidly with an increase in females than males.
tion. The time elapsed since *S. invicta* was introduced at Mobile, Ala, thus allows for about 20 generations. Overlap of successive generations would probably decrease the rate of stabilization somewhat.

Fig. 2 shows the ultimate relatedness of females after 20 generations as a function of the number of females in the original inoculum, and the number of different males with which each was mated. Relatedness declines much more rapidly as the number of females in the inoculum increases and less rapidly as the number of males per female increases. This is the consequence of the haplo-diploid mode of sex determination, in which males carry only a single set of genes.

It might be possible to estimate the number of females in the Mobile inoculum by determining the average relatedness of fire ants in the United States over a number of loci. If a single female, mated with fewer than five males had been introduced, the present relatedness ought to be between 0.28 and 0.43. This limiting case (introduction of a single female) would be distinguishable from almost all others. With two or more females, each mated with up to five males, the relatedness would be less than 0.30 but specific combinations of females and males would not be readily distinguishable.

Whatever the case may be, it seems likely that fire ants in the United States are more related than their counterparts in South America. This could possibly lead to differences in the social biology. A partial list of phenomena which might be affected follows: (1) In the United States, several queens often cooperate during colony founding (Tschinkel and Howard 1983). Such mutual tolerance could be increased by mutual recognition of relatedness, although relatedness is not necessary to rationalize such cooperative founding. (2) Fire ant colonies in the United States are reported to be territorial and distinct (Wilson et al. 1971). Yet, relatedness could easily affect the degree of distinctness, perhaps even abolishing it in the limiting case, with widespread cooperation and exchange among colonies. Exchange of workers among colonies has been reported. (3) Fire ants are generally monogynous, or functionally monogynous (a single laying queen) (Tschinkel and Howard 1978), yet in certain parts of its range, colonies are commonly polygynous, often with very large numbers of queens (Glancey et al. 1973, Fletcher et al. 1980). This change, which must have occurred after introduction, could be the result of generally higher relatedness or it could be associated with isolated outlier populations whose relatedness is still higher as a result of a second founder effect and still higher inbreeding. (4) A consequence of polygyny might be a radical change in the mode of reproduction. Currently, fire ants are thought to found entirely independently (i.e., unaccompanied by workers), but polygynous colonies could well reproduce by colony fission, and this in turn would probably have far-reaching effects on the potential range of habitats which the ant can colonize. (5) Fire ant workers attack and kill newly mated queens landing in their territory after mating flights, yet inseminated, nonlaying queens are common in mature colonies (Glancey et al. 1973, Tschinkel and Howard 1978). Are these survivors of multiple-queen founding (all but one foundress are normally killed by the first worker brood), or are they queens accepted into colonies after mating flights? In either case, the chance of survival of such queens is likely to be affected by relatedness.

These examples will suffice. Probably almost any aspect of fire ant social biology involving recognition between offspring of different queens could be affected.

It would clearly be of great interest to (1) determine the degree of relatedness of fire ants in the United States and in Brazil, and (2) to identify the aspects of social biology which differ between the two populations. The results would be of interest not only to the biology of the fire ant, but to the question of the importance of relatedness in social insects in general.

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REFERENCES CITED


