HOT TOPICS IN MARINE BIOLOGY 6.2

When Shrimp Socialize in the Extreme

George Williams's classic 1966 book *Adaptation and Natural Selection* emphasized the role of individuals and genes in the process of natural selection. Selection paid little attention to groups of individuals but rather to the functioning of individuals that might leave different numbers of offspring into the next generation. A gene has no loyalty but to itself, so the individuals carrying a given gene may or may not increase in frequency, depending upon that gene's contribution to fitness. Owing to this crucial individuality, Williams argued that selection would not go on for the "good of the group," especially because the genes in individuals were not confined to specific groups.

This generalization applies to most populations in which individuals are at best distant cousins of each other. But what happens if all individuals in a population are closely related, as in the case of siblings? If so, they will share on average 50 percent of their genes. In social bees, workers are sterile and defend the colony, often dying in the process. But, if individual fitness always prevails, why this apparently altruistic behavior? William Hamilton first explained this seeming anomaly in terms of the relatedness of members of a colony. The workers are extremely close relatives of the queen; their role in doing the work of the colony, therefore, increases not only the genes of the queen but also their own. The evolutionary force leading to the evolution of cooperative behavior among close relatives to proliferate similar genes is known as **kin selection.**

The extreme case of an entire colony of individuals behaving in cooperative fashion is known as eusociality. This behavior usually is found in a group of individuals that serve a queen's reproduction. It is extremely rare beyond social ants, bees, wasps, and a few other groups of insects. Naked mole rats (*Heterocephalus glaber*) are also eusocial: there is one "queen," plus several mating males and numerous other closely related nonmating siblings or very close relatives that gather resources and take care of the tunnels in which the mole rats live.

The key to eusociality is the ability to construct a functioning integrated colony, which is often enclosed in a structure built or occupied by the eusocial organisms. Naked mole rat colonies, for example, maintain an elaborate system of burrows, which must be defended. The queen does all the reproduction for the colony, whereas the reproducing males and nonreproducing members all perform communal roles in tunnel maintenance and defense. If the colony lives for a long time in one place, then there is an obvious advantage for closely related individuals to maintain and defend the colony, occasionally producing queens to found new colonies.

Some marine environments lend themselves to discrete colonies of animals. If you cut a large sponge in the tropics, you will immediately encounter a large number of invertebrates that live in the interstices of the sponge colony. Indeed, marine biologists have been showing their students such assemblages for many years. Large numbers, often of a single species of crustacean, were found commonly, especially species of snapping shrimps of the family Synalpheidae. These sponge-associated populations are liable to be separated from those in other sponges because movement between sponges would expose them to predators.

After cutting open many sponges in Belize, Emmett Duffy* came upon a discovery that had probably been overlooked by many others. Groups of individuals of the shrimp *Synalpheus regalis* were found in sponges of Belize, averaging 150 individuals per sponge. Usually a large female (Box Figure 6.4) was found with many smaller males or immature animals. A simple experiment demonstrated altruistic behavior. When species of other snapping shrimp

* See Duffy, 1996a, in Further Reading, Hot Topics in Marine Biology.

BOX FIGURE 6.4 A mature queen of the eusocial shrimp *Synalpheus regalis*. The clutch of late-stage embryos, some with visible eyes, can be seen in the brood chamber beneath the queen's abdomen. Normally, shrimp would rarely be found on the exterior of the sponge. (Courtesy of J. Emmett Duffy.)

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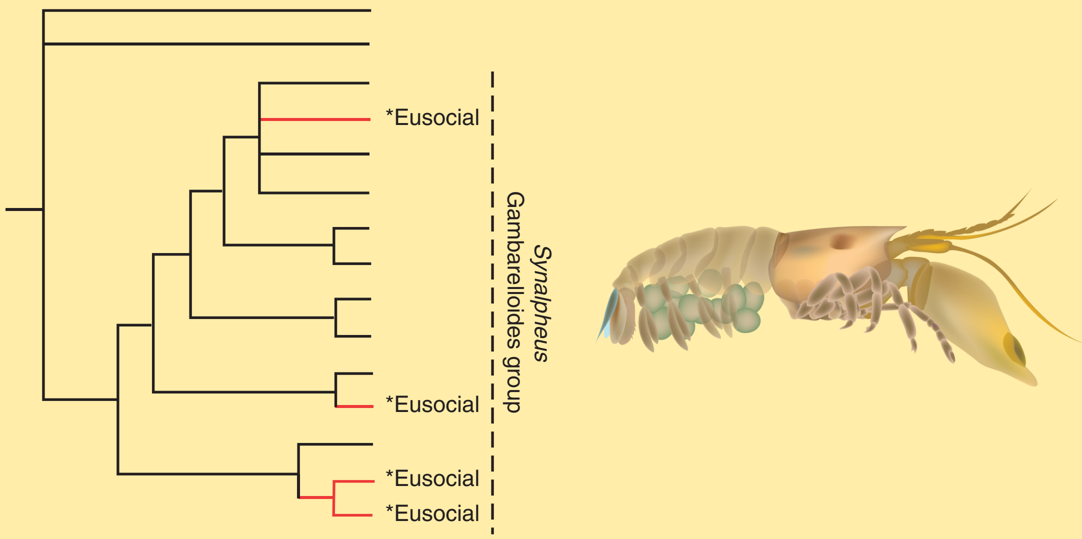

BOX FIGURE 6.5 An evolutionary tree for synalpheid shrimp species, based upon DNA sequence and morphological characters. Note the starred eusocial species, which apparently arose several times in independent lineages. (Courtesy of J. Emmett Duffy.)

were introduced into colonies of *S. regalis*, groups of resident shrimp used their powerful major claws to attack the intruders, eventually killing them. If resident shrimp were removed and then reintroduced, however, defense behavior evaporated, suggesting the existence of a recognition system among colony members. Shrimp in a colony also produce an alarm signal. When an intruder appears, a sentinal shrimp reacts by snapping, and soon shrimp throughout the colony snap in concert for several minutes, which is enough to repel the intruder.[†]

Genetic analyses further add evidence for eusociality in these synalpheid shrimp. Using enzyme genetic polymorphisms as markers, Duffy demonstrated that the average difference between shrimp in a colony was close to that expected for siblings. One large individual was a female, and she is probably analogous to the queen of mole rat colonies. Such a colony and its sponge cavity habitat fit well with the nesting areas of many other eusocial species, including many ants, termites, naked mole rats, and other species. Sponges are long-lived, and shrimp colonies could similarly persist over many years. Selection for eusocial behavior is strongly favored in such cases, and Duffy has now found a number of species of eusocial synalpheid shrimp.[‡]

Because there are many species of apparently eusocial synalpheids, the question immediately arises: Did eusociality evolve only once in this group, or is selection and the response to selection strong enough that this behavior may have arisen in a number of species associated with sponges? An evolutionary tree,[§] combining data from DNA sequences and morphological characters, demonstrated that three eusocial species were scattered among the tips of the tree. Eusociality had apparently evolved several times from noneusocial ancestors (Box Figure 6.5). The association with the interstices of discrete and long-lived sponge colonies is the driving force for the several evolutionary appearances of eusociality. More generally, specialization for living in specific sponge hosts has been a general driving force in the evolution of the Synalpheidae,[||] and this group radiated very rapidly. Speciation in the whole group may be very rapid because of the isolating force of adopting new sponge hosts.

[†] See Toth and Duffy, 2005, in Further Reading, Hot Topics in Marine Biology.

[‡] See Duffy, 1998, in Further Reading, Hot Topics in Marine Biology.
[§] See Duffy and others, 2000, in Further Reading, Hot Topics in Marine Biology.
[||] See Duffy, 1996b, in Further Reading, Hot Topics in Marine Biology.

to several thousand individuals. All derive from a single colonizing larva that repeatedly divides asexually. At any time, it is usually possible to catch some individuals in the middle of fission. Lisbeth Francis[16] found that contacts between individuals of different clones result in a stereotyped aggressive response. The affected anemones raise their tentacles and expose acrorhagi, which sting individuals from the other clone. No such aggression occurs between individuals within the same aggregation. This behavior can be interpreted as the defense of a communal territory, but it is not known what benefit is obtained from the defense.

[16] See Francis, 1973, in Further Reading, Sex, Fertilization, and Life Cycles.