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Crustacean Social Evolution

J. E. Duffy, Virginia Institute of Marine Science, Gloucester Point, VA, USA

Introduction

The Crustacea represent one of the most spectacular evolutionary radiations in the animal kingdom, whether measured by species richness or diversity in morphology or lifestyles. Its members range from microscopic mites of the plankton to fearsome giant crabs to sessile barnacles to amorphous parasites that are almost unrecognizable as animals. Crustaceans occupy most habitats on earth, from the deepest ocean trenches to mountaintops and deserts, and the dominance of the open ocean plankton by calanoid copepods makes them one of the most abundant metazoan groups on earth.

This ecological diversity suggests that the Crustacea should provide a wealth of interesting social and mating systems, and this is indeed true, as both classic and recent research has shown. Yet, despite their ubiquity and diversity, crustaceans have received surprisingly little attention from students of behavior compared with their younger siblings – the insects – or the vertebrates, no doubt due in large part to the aquatic habits of most crustacean species.

What are the ecological and behavioral consequences of the crustacean colonization of this range of habitats? What can they tell us about the generality of theory and the generalizations emerging from work on other, better studied taxa? Here, I highlight a few illustrative case studies of social systems in crustaceans, and discuss the broader implications of crustacean sociality for understanding some central issues in animal behavior and sociobiology.

A Primer in Crustacean Biology

Recent research in molecular systematics shows that the Crustacea is paraphyletic, with the insects (Hexapoda) nested within a pancrustacean clade that diverged in the Precambrian. Among the major branches in the crustacean family tree, the Malacostraca is the most diverse, both in morphology and in species, numbering tens of thousands. This group includes the large, ecologically and economically important crabs, shrimps, and lobsters familiar to the layperson. For all of these reasons, most of what is known about the social behavior of crustaceans comes from the Malacostraca.

Like their relatives, the insects, crustaceans share a basic segmented body plan divided into three regions: the head, thorax (pereon), and abdomen (pleon). The body is covered with a chitinous exoskeleton, which is shed periodically during growth. Each of the segments in the primitive ancestral crustacean body bore a pair of appendages, which have been modified during the evolution of the various crustacean groups into a wide range of structures used in feeding, locomotion, sensation, and communication. The bodies of most crustaceans are richly endowed with a wide variety of setae – stiff hair-like bristles of diverse form that are used for a wide range of functions. The two pairs of antennae, in particular, bear dense arrays of chemo- and mechanosensory setae, which are used in conjunction with directional currents of water generated by specialized appendages in the head region to distribute and collect chemical signals, and are important in social and mating interactions.

The mode of development strongly influences the potential for kin to interact, and thus the evolution of social systems in Crustacea. Most familiar decapods release microscopic larvae into the plankton, where they drift for some time – several months in some species – before settling to the bottom and transitioning to the adult lifestyle. In such species, populations are genetically well mixed and kin groups cannot form. In other species, however, eggs hatch directly into miniature versions of the adults in much the same way as eggs hatch into miniature adults (nymphs) in hemimetabolous insects such as grasshoppers and termites. This direct development is common to all peracarid crustaceans (isopods, amphipods, and their relatives) and is also found in some decapods. Crustaceans go through several molts as they grow, before reaching the adult stage.

Crustaceans display a wide range in reproductive biologies. While most species breed repeatedly during life and have separate sexes, brine shrimp and some *Daphnia* that inhabit temporary freshwater pools are cyclic parthenogens, and several shrimp are sequential or simultaneous hermaphrodites. Sex determination can be genetic, environmental, or involve some combination of the two.

Crustacean Mating Systems

The mating system is an important component of the social system in that it influences the size, composition, and kin structure of groups of interacting individuals. For example, establishment of monogamous relationships can lead to paternal care, and in some animals, avoidance of incest helps explain why adult helpers in social colonies do not breed. Crustaceans display a wide diversity of

mating systems that are molded by the variance in mate availability in time and space, variation in female life history, and behavior. These range from situations involving fleeting encounters to various forms of mate guarding, monogamous pair formation, to harems. Here, I describe a few examples that provide insights into the evolution of more advanced social systems.

Precopulatory Mate Guarding and Its Consequences

A key trait influencing the mating system in many crustaceans is the limited time window of female receptivity, which results from the requirement that mating and ovulation take place immediately after a molt when her integument is soft. As a consequence, many crustaceans exhibit mate guarding, pair-bonding, and other behaviors that maximize a male's certainty of having access to a female when she is ready to mate. Precopulatory mate guarding (also called amplexus), in which the male carries the female for an extended period of time in anticipation of mating, is common in several groups of amphipods, including the familiar *Hyalella* species of North American lakes and *Gammarus* species of coastal marine waters, as well as many groups of isopods (**Figure 1**). Because of brief female receptivity, the operational sex ratio in such populations is highly male-biased, and this mate guarding allows the male to monopolize the female until she is receptive. In other species, including several crabs and lobsters, females can store sperm and so are not temporally restricted in mating time.

Mate guarding has been extensively studied in isopods and amphipods as a model system for understanding sexual selection and the resolution of intersexual conflict.

Figure 1 Precopulatory mate guarding in the estuarine isopod *Idotea baltica*. The larger male carries the smaller female for an extended period until she is receptive to mating. The initiation and duration of guarding often generates a struggle because of the conflicting interests of the male and female. Photo by Veijo Jormalainen, used with permission.

Males often do not feed while guarding so they incur a cost in exchange for the opportunity to mate. Females presumably also incur a cost in terms of reduced feeding, higher predation risk, and/or increased risk of being dislodged from the substratum. Indeed, experiments with the isopod *Idotea baltica*, conducted by Veijo Jormalainen and colleagues, showed that guarded females had lower glycogen (stored food) reserves and laid smaller eggs than females that had been mated but not guarded. Not surprisingly, female isopods often vigorously resist being guarded and the initiation of guarding tends to be a mutually aggressive affair. The proposed role of limited receptivity in selecting for mate guarding would seem to be proved by the exception to the rule: in terrestrial oniscoid isopods, females have extended receptivity and some can store sperm – using it for up to eight broods, reducing a male's ability to monopolize mating opportunities. Accordingly, these isopods lack prolonged guarding.

Sexual selection has molded the phenotypes of such mate-guarding species. Males are larger than females in several mate-guarding isopods, likely because larger male size is favored by both intrasexual selection, which favors larger size in competition among males, as well as intersexual selection generated by females resistant to guarding. Strong sexual dimorphism is also seen in some freshwater amphipods. Interestingly, among closely related species of the amphipod *Hyalella*, the dimorphism is reduced in species that inhabit lakes with fish, which impose strong size-selective predation on large individuals; in these populations exposed to predation, moreover, females show weaker preference for large males. Thus, phenotypic traits and behavioral preferences are molded by the trade-off between sexual selection for large male size and natural selection for reduced size to avoid predation.

Social Monogamy

Snapping shrimp (Alpheidae) are common and diverse animals in warm seas. Most live in confined spaces such as rock crevices, excavated burrows in sediment, or commensally within sessile invertebrates such as sponges, corals, or feather stars. Long-term heterosexual pairing, or 'social monogamy' is the norm among alpheids. Models predict that mate guarding can extend to long-term monogamous associations where male searching for mates is costly because of, for example, low population densities, male-biased operational sex ratios, or high predation risk outside the territory. All of these conditions are common among alpheids. As in the peracarids, pairing appears to have evolved partly as a male guarding response, as evidenced by the preference of males to associate with females close to sexual receptivity. But pairs of snapping shrimp also jointly defend a single territory, suggesting that other factors are also at play. Lauren Mathews conducted a series of experiments with

Alpheus angulatus testing the potential benefits of monogamy to the two partners. She showed that, in addition to its role in assuring males of mating opportunities, social monogamy is likely favored by benefits to both partners of sharing maintenance and defense of the joint territory. For example, females were less likely to be evicted from the territory by intruders when paired with a male than when unpaired, and males similarly were less frequently evicted when paired with a sexually receptive female. The tendency of both males and females to bring food back to the burrow may also have benefited their partners. Finally, paired females spent more time constructing the burrow than did paired males, possibly reflecting a division of labor in which males, with their larger snapping claw, took care of defense. As discussed below, the monogamous habit of these pair-living shrimp likely set the stage for the repeated evolution of multigenerational, cooperative societies in eusocial alpheids.

Sexual Selection and Alternative Male Mating Strategies

A more extreme case of mate monopolization occurs where males can assemble harems of females. This mating system is more common in situations in which female distribution is highly clumped, for example among habitat specialists, and in which males are capable of excluding other males from the habitat patch or group of females. An especially intriguing example from the Crustacea involves the isopod *Paracerceis sculpta*, which inhabits spaces within small intertidal sponges in the Gulf of California. Research by Stephen Shuster showed that large males may monopolize as many as 19 females in a given sponge. However, sexual selection driven by the intense competition among males for females has resulted in divergence of three alternative male mating morphs that coexist in the same populations. Alpha males are large and powerful and monopolize females by physically excluding other males. Beta males, in contrast, are similar to females in both morphology and behavior and gain access to sponges controlled by alpha males by mimicking females. Gamma males are very small and appear to mimic juveniles; although males attempt to exclude them, gammas can gain access to crowded sponges by slipping through male defenses unnoticed. Both beta and gamma males achieve some fertilizations in these highly competitive situations by subterfuge, providing an example of the 'sneaker' male morphs that co-occur with 'fighter' males in a range of animal taxa.

Larval Development, Parental Care, and Family Life

Social groups in most animals develop from nuclear or extended families. Thus, parental care and the concomitant aggregation of kin in families are important prerequisites to more advanced social organization in many animals, including vertebrates, insects, and crustaceans. For example, one of the classical criteria of eusociality is cohabitation of multiple adult generations, which generally arises as offspring extend a long period of parental care and remain with their parents after maturity.

Parental care and associated social behaviors are only possible, however, when parents and offspring remain in spatial proximity where they can interact. In most decapods such as lobsters, crabs, and shrimp, planktonic larvae result in broad dispersal. In these species, families cannot form and thus kin selection cannot operate. Among 'direct-developing' crustaceans, such as amphipods, isopods, and a few decapods, the situation is different. In these species, extended parental care is relatively common (Figure 2). Care is typically provided only by the mother, initially in the form of carrying, grooming, and ventilation of embryos. But males also contribute in several species by building and defending burrows or other nest sites. In extreme cases, including the highly social bromeliad crab *Metopaulias depressus* and certain sponge-dwelling shrimp (see below), other individuals – generally older siblings – also provide some care in the form of nest defense or even food provisioning to young offspring.

A primary function of parental care in crustaceans as in most other animals is protection of the vulnerable young from predators and harsh environmental conditions. Active 'shepherding' by mothers of small juveniles faced with danger occurs in several species of crabs and caprellid amphipods (skeleton shrimp); in some cases, a mother picks up her young offspring and carries them away from predators, whereas in others, some (generally unknown) signal from the mother causes juveniles to aggregate or to enter her brood pouch. Mothers also
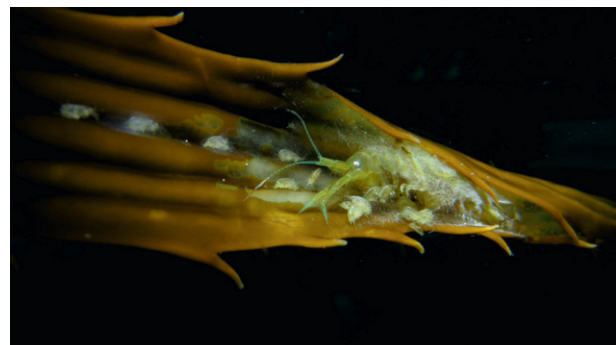
Figure 2   A mother of the Chilean marine amphipod *Peramphithoe femorata* with her young in their nest constructed on a frond of kelp. Ampithoid amphipods are common herbivores in coastal marine vegetation, where they build silken nests among algae and fouling material. Offspring of many amphipods remain with the mother for some time before dispersing, and in some species, are fed by the mother during this period. Photo by Iván Hinojosa, used with permission.

feed their offspring in several species of amphipods and, in desert isopods, even bring food back from extended foraging trips to provision offspring remaining at the nest, much as in birds, bees, and ants.

Not surprisingly, parental care tends to be better developed in habitats or situations where offspring face strong challenges from the biotic or abiotic environment. For example, several species of Australian semiterrestrial crayfish inhabit burrows in soil, sometimes far from open surface water (**Figure 3**). Burrows provide shelter from predators and harsh physical conditions, and are also a source of food in some species. Particularly in crayfish species that live far from surface water, the burrow may be complex and extend for >4 m into the ground. In these drier areas, burrows can only be dug during a limited time of year, and thus represent a valuable, self-contained resource. Juveniles often face harsh conditions and strong risk of predation outside the burrow, and the life history of the crayfishes has adapted accordingly. Semiterrestrial crayfish have no free-living larval stage as most decapods do; instead, juveniles cling to the mother's pleopods (abdominal appendages) after hatching and remain there for 2–3 molts before graduating into independent miniature versions of the adults. In *Procambarus alleni*, juveniles at this stage make short excursions outside the burrow but usually remain close to the mother, who helps them back into the brood area by raising her body and extending the abdomen. Females in some semiterrestrial crayfish also produce pheromones that attract the juveniles. Mothers in *Procambarus clarkii* also defend their juveniles, even those that are already foraging independently, against large males. Extensive cohabitation of mother and offspring reaches its most extreme manifestations in Tasmanian species of *Engaeus*, in which four generations – including mother and three year classes of juveniles – have been observed cohabiting in the same burrow. The prolonged associations between mothers and young, and the difficulty of establishing new territories outside the parental burrow, in these species recall the situations believed to foster the evolution of eusociality in insects, and in snapping shrimp as discussed below.

Kin Recognition and Kin Discrimination

The aggregation of genetic relatives – family members – provides opportunities for kin selection to mold cooperative behaviors. Maintaining cohesive kin groups is facilitated by the ability to recognize kin from nonkin. In most crustacean species, experiments suggest that parents are incapable of distinguishing their own offspring from unrelated juveniles. In these cases, family cohesion can be maintained by simple rules of context in which interactions occur. For example, mothers in many crustacean species accept juveniles found in the nest area but are very aggressive toward individuals approaching the nest from the outside.

At the other end of the spectrum, kin recognition is highly developed in certain desert isopods, which are the dominant herbivores and detritivores over wide areas of arid North Africa and Asia. In one such species, *Hemilepistus reaumuri*, parent–offspring groups share burrows, with both parents caring for the young for several months, and adults must make long excursions outside the burrow to forage (**Figure 4**). The burrow provides protection from the harsh environmental conditions of the desert and from predators. Because it represents a highly

Figure 3 The Tasmanian endemic semiterrestrial crayfish *Engaeus orramakunna*. This species lives in deep burrows that may house a mother with up to three successive cohorts of offspring all living together. Photo by Niall Doran, used with permission.

Figure 4 Two desert isopods, *Hemilepistus reaumuri*, at the entrance to their burrow. These animals live in family groups and have finely tuned kin recognition based on complex chemical mixtures that allow them to discriminate family members from intruders approaching the burrow after wide-ranging foraging trips. Photo by Karl Eduard Linsenmair, used with permission.

valuable shelter, competition and invasion are common threats, and recognition of kin is critical to maintaining group cohesion in the face of foraging traffic in and out of the burrow.

Research by Karl Eduard Linsenmair has demonstrated that kin recognition is remarkably finely tuned in *H. reaumuri*. Individuals in this species recognize one another using nonvolatile, polar compounds that are transferred by contact. Because the compounds can be transferred by touch, contact between unrelated individuals could easily lead to contamination of the family signal that would lead to attack upon return to the family burrow, where an attentive guard stands at the burrow entrance (**Figure 4**). Thus, individuals are scrupulous about avoiding contact with nonkin. A large series of experiments showed that the chemical 'badge' worn by each family is unique and genetically determined, and arises from regular close contact among family members in the burrow, which mixes the individual signals into a family-specific odor. This process is strikingly similar to the way in which common family odor is distributed among eusocial naked mole-rats within their familial burrows. Interestingly, attacks on newborn isopods and family members that have just molted are inhibited by another (undefined) chemical substance, allowing these individuals to acquire the family odor without harm. As a result of this finely tuned kin recognition system, isopod families are able to maintain their strict kin structure despite high population densities and frequent long foraging excursions to and from the burrow.

Individual recognition among crustaceans is not confined to kin but extends to unrelated individuals and even other species. Stomatopods (mantis shrimp) in the genus *Gonodactylus* are common inhabitants of tropical reefs, where they live in cavities in coral rock, along with various other fishes and invertebrates. Experiments by Roy Caldwell and colleagues have shown that these stomatopods can learn to identify other individual stomatopods based on chemical cues and that they use these cues, along with memory of the fighting ability of the individual, to determine how to approach a cavity that might be occupied. Interestingly, the stomatopods are also able to learn the odor of individual octopuses, which compete for the same cavities. The shrimp are much more hesitant and defensive when approaching a cavity occupied by a conspecific or an octopus that they have fought previously. These examples demonstrate that certain crustaceans are capable of quite finely tuned discrimination among individual animals, both conspecifics and other species.

Cooperative Breeding in Jamaican Bromeliad Crabs

About 4.5 Ma, a marine crab colonized the Caribbean island of Jamaica and moved up into the forests, radiating into at least ten endemic species of freshwater and terrestrial crabs. Among the most unique of this group is *Metopaulias depressus*, which lives exclusively in the small bodies of water that collect in leaf axils of bromeliad plants in the forested mountains (**Figure 5**). These small pools provide most everything the crabs need: water required to moisten the gills, molt, and reproduce; food in the form of plant matter, detritus, and small arthropods; and protection from predatory lizards and birds. Individual plants can live for several years and their leaf axils represent a reliable and stable water source that collects dew as well as rain and thus persist even through extended droughts. But because suitable bromeliads are scattered, in short supply, and surrounded by hostile habitat, finding and maintaining these nests presents challenges. As in many social insects, birds and mammals, these environmental challenges appear to have selected for a cooperatively breeding or even eusocial lifestyle in which delayed dispersal results in accumulation of large family groups that cooperate in raising the young. The story of the Jamaican bromeliad crab has been documented in an elegant series of studies by Rudolf Diesel.

Life History and Maternal Care

Bromeliad crabs breed once a year, during December and January, producing clutches of 20–100 eggs. When the eggs hatch, the larvae are released into the water in a leaf axil. Here, the larvae develop rapidly – within about 2 weeks – into small juvenile crabs. The young crabs then remain in the mother's territory for up to 3 months during which the mother provides extensive care for them, defending them against predatory spiders

Figure 5   A mother and young of the Jamaican bromeliad crab *Metopaulias depressus*. Mother crabs raise their larvae in pools of water that collect in the leaf axils of bromeliads and fastidiously manage the water chemistry by removing leaf litter and adding empty snail shells that raise the pH and concentration of calcium ions required by growing larvae. Older siblings also provide care in this cooperatively breeding species. Photo by Rudolf Diesel, used with permission.

and aquatic insect larvae, and provisioning them with food. But what is most remarkable about these crabs is the mother's extreme care in maintaining water quality in the leaf axils. By actively removing leaf litter and collecting and placing empty snail shells in the nursery pools, mothers more than doubled nighttime dissolved oxygen in the nursery pools, and raised pH and concentrations of calcium necessary for proper larval development. Indeed, mother crabs introduced more shells into nursery pools in which calcium concentrations had been experimentally reduced, confirming that they manage water quality actively and with a high degree of sophistication. Then, around the age of 3 months, the juvenile crabs begin to disperse from the nursery pool into other leaf axils on the same plant. They reach maturity after a year or more, and females live for up to 3 years.

Field studies have shown that the colony of crabs living on a single plant can consist of up to 84 individuals, but invariably harbors only a single breeding female. Generally, distinct annual cohorts of juvenile crabs are visible in a colony, and many colonies contain at least a few individuals of reproductive size that nonetheless do not breed. The size distributions of colony members suggest that most juveniles stay with the mother for at least a year.

In addition to maintaining good water quality and providing food for the larvae, experiments showed that mother crabs aggressively defended their nest against intruding crabs, even when the intruders were large, and sometimes even killed them. Mothers were also able to distinguish larger juveniles living in their own nests (presumably their offspring) from unfamiliar juveniles of the same size when both types of individuals were introduced experimentally into the nest; small juveniles were not attacked, regardless of whether they were familiar or not. Thus, Jamaican bromeliad crabs appear able to distinguish kin from nonkin.

Cooperative Brood Care and Social System

While a wide range of animals exhibit parental care of varying degrees of sophistication, what distinguishes cooperatively breeding or eusocial species is alloparental care, that is, care of young by individuals other than parents. Several lines of evidence confirm alloparental care in Jamaican bromeliad crabs. First, nonbreeding adult females from earlier cohorts that remained in the nest helped the mother defend the nest against unfamiliar intruders. Second, when the mother was removed, young ones in the nest survived and grew better in the presence than in the absence of nonbreeding adult siblings, presumably because the older individuals helped defend the nest and maintain good water quality.

Jamaican bromeliad crabs appear to be unique among crustaceans in the sophistication of brood care by both mothers and nonbreeding adult helpers, particularly in

comparison with other crabs, most of whom release larvae to face their fate in the plankton and provide no care afterwards. Indeed, Jamaican bromeliad crab colonies meet the criteria traditionally defining the most advanced social system, eusociality: overlapping adult generations, reproductive division of labor, and cooperative care of young.

What factors explain such advanced social organization in the bromeliad crab? As is true of many other social animals, both insects and vertebrates, the answer appears ultimately to involve ecological pressures that make independent reproduction difficult. In the case of bromeliad crabs, these pressures include the scattered nature of water-filled microhabitats, which are surrounded by unsuitable habitat, making dispersal dangerous. Moreover, because the bromeliad microhabitats are relatively rare, they are also in high demand and subject to invasion by competitors. Theory and data from other animals suggest that such ecological pressures favor delayed dispersal, which allows kin groups to form, and also provide an opportunity for the nonbreeding older offspring to help raise younger siblings, which provides inclusive fitness benefits. Moreover, field observations suggest that staying at home eventually pays off for some of the daughters either in inheriting the mother's territory when she dies, or colonizing an adjacent territory as the bromeliad sprouts new plants from the same rhizome. Such territory inheritance has similarly been suggested as a selective advantage to helping at the nest in eusocial termites.

Eusociality in Sponge-Dwelling Shrimp

Eusociality ('true sociality') is the most extreme manifestation of altruistic cooperation in the animal kingdom. Eusocial colonies historically have been defined on the basis of three characteristics: (1) presence of multiple adult generations living together, (2) reproductive division of labor, meaning that only a subset of colony members reproduce, and (3) cooperative care of young. This definition unites the familiar social bees, ants, wasps, and termites, which typically live in colonies headed by a single queen (and, in the case of termites, also a king) and containing many nonbreeding workers that cooperate in raising the queen's offspring, foraging for food, maintaining and defending the nest, and so on.

In 1996, social colonies were reported in the Caribbean coral-reef shrimp *Synalpheus regalis*, which consisted of a single breeding female – the queen – and tens to hundreds of other individuals, including many nonbreeding adults. Genetic analyses confirm that colonies of these eusocial shrimp consist of close relatives, and likely full siblings, the offspring of a single breeding pair, which evidently dominates reproduction for an extended period. Similar eusocial colonies have subsequently been discovered in several other species of *Synalpheus* (**Figure 6**). The colonies

Figure 6 The Caribbean eusocial shrimp *Synalpheus regalis*. These shrimp occupy the internal canals of sponges on coral reefs. Several eusocial species, like this one, live in colonies of 10s to a few 100s of individuals with a single breeding female, the queen. Large nonbreeding individuals aggressively defend the colony against intruders. Photo by Emmett Duffy, used with permission.

consist of several generations living together, and the non-breeding colony members contribute to colony welfare by defending the nest, qualifying them as eusocial by the traditional definition. Eusocial colonies form only in certain species of *Synalpheus* that produce crawling offspring that typically remain in the same sponge where they were born, allowing kin groups to accumulate.

Eusociality poses a fundamental paradox for evolution by natural selection, as Darwin famously recognized: If adaptive evolution proceeds via differential survival and reproduction of individuals, how can a species arise in which most individuals never breed at all? As the only known case of eusociality in a marine animal, snapping shrimp have become valuable subjects for understanding general features of the evolution of advanced social organization in animals via comparisons with social insects and vertebrates. Why have a few species of sponge-dwelling shrimp, alone among marine animals, adopted this cooperative lifestyle? The search for an answer illuminates some key questions in understanding animal social life generally.

Natural History and Social Behavior in Sponge-Dwelling Shrimp

Shrimp in the genus *Synalpheus* are mostly symbiotic or parasitic, living their entire lives within the internal canals of living sponges and feeding on the tissues and secretions of their hosts. The common name snapping shrimp or pistol shrimp refers to the large claw carried on one side of the body, which produces a powerful jet of water and a loud snap when closed, and is used in aggressive interactions and fights. Unlike most alpheid shrimp, which

are aggressive toward all individuals other than their mate, eusocial *Synalpheus* species live in dense aggregations and are in nearly constant contact with other colony members.

The canals of host sponges provide a valuable resource in the combination of safe shelter and constant food, and shrimp populations fill nearly all suitable sponges on the reef, such that available habitat is 'saturated.' Because the host sponge combines food, living space, and a safe haven, there is a high premium on obtaining and defending it, and that necessity is clearly reflected in the aggression of resident shrimp against intruders, which sometimes ends in fights to death. Indeed, homeland defense appears to be the primary job of the nonbreeding helpers. Experiments with *S. regalis* reveal that, compared with juveniles or the queen, large helpers are more active, more aggressive, and more likely to be found near the periphery of a sponge, where intruders are a threat. In contrast, juveniles are sedentary and often congregate in groups to feed. Thus, shrimp show behavioral differentiation among classes of individuals reminiscent of the caste roles of certain social insects.

Social shrimp colonies also show coordinated activity. For example, in captive laboratory colonies, groups of shrimp have been observed cooperating to remove dead nestmates from the sponge. But the most striking example involves 'coordinated snapping,' during which a sentinel shrimp reacts to some disturbance by recruiting other colony members to snap in concert for several to tens of seconds. Experiments suggest that coordinated snapping in social shrimp is a specific and effective group warning signal to nest intruders, produced when individual defenders meet an unfamiliar shrimp and are unable to chase it away. The function of coordinated snapping as a specific warning to intruders is supported by its occurrence only after introductions of intruders, and its effectiveness at repelling them even after single snaps fail to do so. Coordinated snapping can also be considered an honest warning signal because the few intruders unable to flee in experiments were subsequently killed. Coordinated snapping in social shrimp thus represents a mass communication among colony members, a fundamental characteristic of highly social insects and vertebrates.

Genetics and Ecology in the Evolution of Shrimp Eusociality

Genetic relatedness between interacting individuals has occupied a central role in explaining the tension between conflict and cooperation since William Hamilton's seminal formulation of the concept of inclusive fitness (or kin selection). According to Hamilton, the evolution of behavioral interactions depends on both genetic relatedness among individuals and on the ecological factors that define the costs and benefits of their interactions.

In understanding the paradox of eusociality, in particular, kin selection has provided a key explanation and has stimulated four decades of highly productive research. Recently, it has been argued that kin selection is a consequence rather than a cause of eusociality, and that the ecological context driving competition and cooperation are the dominant pressures selecting for cooperation. Research on sponge-dwelling shrimp contributes to resolving this debate.

One powerful, albeit indirect, approach to evaluating evolutionary hypotheses is via phylogenetic comparative methods, which statistically separate the influence of recent common ancestry from that of ecological factors in shaping evolutionary change in a lineage. For example, comparative analyses among sponge-dwelling shrimp species in Belize controlled statistically for the close phylogenetic relatedness and the small body sizes of social shrimp, and supported the hypothesis that eusociality evolved as a result of both ecological benefits of group living and of close genetic kin structure. Eusocial shrimp species were more abundant and had broader host ranges than nonsocial sister species, supporting the basic hypothesis that cooperative groups have a leg up in ecologically challenging environments. But ecological advantages of eusocial colonies are not the whole story: eusociality arose only in species with nondispersing larvae, which form family groups subject to kin selection. Thus, superior ability to hold valuable resources favors eusociality in shrimp, but close genetic relatedness is nevertheless key to its origin, as in most social insects and vertebrates.

Adaptive Demography

In addition to the three classical criteria described above, eusociality is often recognized by the loss of totipotency, i.e., a transition to irreversible sterility or other form of specialization within a colony. In this sense, eusocial colonies are qualitatively different than other cooperatively breeding animal societies and evolution of sterility represents a threshold, which, once crossed, allows new evolutionary processes to act. Once workers are freed from selection for personal reproduction, their behavior, physiology, and body form can be molded by colony-level selection toward specialized phenotypes that benefit the colony as a whole, such as the soldiers, nurses, and other specialized castes that reach sometimes bizarre extremes in certain large-colony ant and termite species.

Among shrimp, the division of labor between reproduction and defense reaches its clearest manifestation in *Synalpheus filidigitus*, in which the queen's irreversible dependence on her colony is reflected in a physical metamorphosis. Queens of this species lack the typical large snapping claw, having replaced it with a second minor-form chela. This is strong indirect evidence for organized division of labor in the colony, since an alpheid lacking its

fighting claw is helpless on its own. It also presents an interesting parallel with the advanced social insects, in which queens typically become nearly helpless egg-laying machines.

Colony-level selection may produce not only specialized individual phenotypes but also adaptive demography, that is, changes in the relative proportions of different types of colony members that benefit the colony by increasing its efficiency. Social shrimp also show trends suggestive of such adaptive demography. Growth allometry and body proportions of three eusocial shrimp species differed in several respects from that of their pair-forming relatives: allometry of fighting claw size among males and nonbreeding females was steeper, and queens had proportionally smaller fighting claws, in eusocial species. Shrimp are thus similar to other eusocial animals in the morphological differentiation between breeders and nonbreeders, and in the indication that some larger nonbreeders might contribute more to defense than others.

Eusocial shrimp species also tend to be smaller bodied than less social relatives, and this trend remains even after phylogenetic relationships are controlled for, as also reported for social wasps. This situation may result from selection for improved colony performance, that is, adaptive demography. Oster and Wilson argued that reduced body size could allow a colony to have a larger number of individuals and thus maintain more efficient operations, providing some redundancy, and maintaining a higher 'behavioral tempo' that enhances productivity. Whether this explains the patterns of smaller body size in social shrimp remains to be tested.

Conclusions and Comparisons with Other Animals

Evidence from crustaceans supports models based on study of insects and vertebrates that evolution of cooperative social systems is strongly influenced by ecological pressures and, in particular, the difficulty of obtaining and defending a 'basic necessary resource' in the parlance of Alexander, Crespi, and colleagues. For social snapping shrimp, this resource is the host sponge, which is in short supply and generally fiercely defended by competitors. For Jamaican bromeliad crabs, it is a host plant with a sufficient number and sizes of leaf axils to provide food, shelter, and a nursery for larvae. In desert isopods, and perhaps also Australian semiterrestrial crayfish, the resource is the burrow, which can only be built during a limited time after rain and is essential for survival under harsh conditions. In all of these cases, the aggregation of parent(s) with multiple cohorts of offspring creates kin groups that are presumably also essential to the evolution of cooperative behavior. Indeed, in sponge-dwelling shrimp, phylogenetically controlled comparisons confirm

that eusocial groups evolved only in species with crawling larvae, which allow formation of close kin groups. Thus, these examples add to the list of examples from other taxa that show that advanced cooperative social life evolves in situations where cooperation leads to superior ability to hold valuable resources, and that cooperation is especially favored in kin groups, where helpers can receive inclusive fitness rewards for their efforts.

See also: Cooperation and Sociality; Group Living; Kin Selection and Relatedness; Mate Choice in Males and Females; Reproductive Skew; Social Recognition; Social Selection, Sexual Selection, and Sexual Conflict; Termites: Social Evolution.

Further Reading

Caldwell RL (1979) Cavity occupation and defensive behaviour in the stomatopod *Gonodactylus festai*: Evidence for chemically mediated individual recognition. *Animal Behavior* 27: 194–201.

Correa C and Thiel M (2003) Mating systems in caridean shrimp (Decapoda: Caridea) and their evolutionary consequences for sexual dimorphism and reproductive biology. *Revista Chilena de Historia Natural* 76: 187–203.

Crespi BJ (1994) Three conditions for the evolution of eusociality: Are they sufficient? *Insectes Sociaux* 41: 395–400.

Diesel R (1997) Maternal control of calcium concentration in the larval nursery of the bromeliad crab, *Metopaulias depressus* (Grapsidae). *Proceedings of the Royal Society of London, Series B* 264: 1403–1406.

Duffy JE (1996) Eusociality in a coral-reef shrimp. *Nature* 381: 512–514.

Duffy JE and Thiel M (eds.) (2007) *Evolutionary Ecology of Social and Sexual Systems: Crustaceans as Model Organisms.* Oxford: Oxford University Press.

Jormalainen V (1998) Precopulatory mate guarding in crustaceans: Male competitive strategy and intersexual conflict. *Quarterly Review of Biology* 73: 275–304.

Linsenmair KE (1987) Kin recognition in subsocial arthropods, in particular in the desert isopod *Hemilepistus reaumuri*. In: Fletcher D and Michener C (eds.) *Kin Recognition in Animals.* Chichester: John Wiley and Sons.

Shuster SM and Wade MJ (1991) Equal mating success among male reproductive strategies in a marine isopod. *Nature* 350: 608–610.

Thiel M (1999) Parental care behaviour in crustaceans – A comparative overview. *Crustacean Issues* 12: 211–226.

Thiel M and Baeza JA (2001) Factors affecting the social behaviour of crustaceans living symbiotically with other marine invertebrates: A modeling approach. *Symbiosis* 30: 163–190.

VanHook A and Patel NH (2008) Primer: Crustaceans. *Current Biology* 18: R547–R550.