Sexual and Social Behavior of Crustacea

A Way Forward

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Abstract and Keywords

The Crustacea represents one of the major branches in the tree of animal life, displaying diversity in form and lifestyle that rival those of the vertebrates and insects. But perhaps because of the primarily aquatic habits of crustaceans, they have received much less attention in evolutionary ecology than mostly terrestrial taxa. The chapters in this book make clear the richness of adaptations of crustaceans to social and sexual life, and their still largely untapped potential to test fundamental theory in behavioral ecology and evolution. Kinship, cooperation, and conflict play an important role in social evolution, modulated by extrinsic factors (resource competition, predation or parasitism), some of which have only recently begun to be studied. There are rich opportunities awaiting the student willing to pursue them, both in clarifying the social and sexual biology of individual crustacean species.
and in exploiting the Crustacea in broad comparative approaches to testing evolutionary theory.

*Keywords:* kinship, enemy pressure, parasites, macroevolution, innovative approaches, diversity, adaptations
The contributions in this book provide a sampling of the wide—and, we suspect, underappreciated—diversity of social and sexual systems among crustaceans, and they sketch the outlines of the range of environmental pressures and lifestyles that have molded that diversity. The chapters illustrate well both the value of Crustacea as models for addressing a range of general questions in evolutionary ecology, and the fascinating natural history and behavior of the group in its own right. Recurring throughout the book are tantalizing hints of novel social and sexual systems in crustaceans whose natural history and ecology remain otherwise little known. In several such cases, close relatives display quite different social or mating systems, the reasons for which are similarly poorly understood (e.g., chapters 11, 16, 18). Thus, these chapters raise at least as many questions as they answer.

A dominant theme that emerges is the pressing need for detailed, classical natural history research. Such research is necessary not only for advancing our basic understanding of crustacean sexual and social systems but also for using these animals effectively to test general theory in evolutionary ecology (e.g., chapters 2, 12). As Crespi notes in chapter 20, the historical neglect by evolutionary ecologists of crustaceans, compared with insects and vertebrates, means that crustaceans should provide high returns on research investment. Much progress could be made with creative new approaches to observing or inferring behavior in the field. Because of crustaceans’ small size and cryptic habitats, most previous studies of their social behavior have been conducted in the laboratory, which can provide only imperfect mimics of the complex natural environment. In particular, simulation of natural burrows or living habitats in the lab entails substantial logistical challenges. Clues to crustacean habits in nature may
be fostered by recent technological advances such as endoscopic tools (see, e.g., Richter et al. 2001) for peeking into their secret homes and biotelemetry via mounted electronic sensors or cameras to observe behavior of larger, mobile species in the field (Passaglia et al. 1997, Cooke et al. 2004). High-resolution molecular genetic markers may similarly be used to infer mating systems of animals that cannot be observed directly (e.g., Duffy 1996, Bilodeau et al. 2005, Gosselin et al. 2005).

In addition to a renewed focus on detailed natural history research, we see three promising general themes for advancing crustacean evolutionary ecology that are common to many of the disparate problems addressed in this volume: (1) closer linkage of general theory to empirical research, (2) better integration of modern molecular approaches, and (3) more phylogenetically explicit, rigorous comparative testing of evolutionary hypotheses. Combining these approaches offers much promise in addressing the more specific frontiers for understanding crustacean evolutionary ecology. In this concluding chapter, we summarize what we judge to be some of the most important open questions.

Relatedness, Conflict, and Cooperation
Family and Environment

The role of genetic relatedness in mediating the tension between conflict and cooperation among individuals has been a central theme of animal behavior since Hamilton’s (1964) pioneering, and deceptively simple, formulation of the concept of inclusive fitness, later known as kin selection. Hamilton recognized explicitly that the evolution of behavioral interactions depends both on genetic relatedness among individuals and on the ecological factors that define the costs and benefits of their interactions. This interplay of genetic relatedness and ecological constraints provides a bridge between social and sexual systems (Queller 1994; see chapter 20).

In understanding the paradox of eusociality, in particular, kin selection has provided a key explanation and has stimulated four decades of highly productive research. That very success has led some authors recently to suggest that kin selection explanations have often been applied simplistically and to reemphasize the complex interplay of competition, cooperation, and sexual selection processes that mediate the
evolution of sociality (Alonso and Schuck-Paim 2002, Griffin and West 2002, Wilson and Hölldobler 2005). Although kin selection theory has incorporated both genetic relatedness and ecology since its inception (Hamilton 1964, Foster et al. 2006), important questions remain about the relative importance of direct fitness benefits versus indirect, kin-selected benefits in molding social behavior and, in particular, in mediating the evolution of group living. Thus, understanding both patterns of genetic relatedness and ecology is critical to understanding the evolutionary origins and maintenance of eusocial colonies. Several crustaceans discussed in this book would be ideal candidates for application of high-resolution markers to explore this interaction of genetic and ecological influences in molding evolution of social groups (see chapter 3). What is the extent of nest parasitism and multiple paternity in bromeliad crabs (chapter 17), and how do they influence levels of cooperation and group productivity? How are breeder number, colony genetic structure, and cooperative behavior related in phylogenetically controlled comparisons among species of sponge-dwelling shrimp (chapter 18)? In most social crustaceans studied to date, sociality appears to have arisen from parent–offspring groups with a high degree of kinship (chapter 14). Although close genetic relatedness in such families fosters group cohesion and cooperation, it also raises the risk of inbreeding. How do social colonies regulate the occasional incorporation of unrelated individuals into colonies? And how does their incorporation change the strength and nature of sexual selection within colonies? Social crustaceans offer promising, and perhaps unique, opportunities for understanding the interplay of ecology, kin selection, and sexual selection in the evolution of social systems.

Status and Individual Recognition

Behavioral strategies based on kinship presuppose some ability to distinguish kin from nonkin. But kin recognition is only one facet of the broader problem of distinguishing among conspecific individuals and the potential threats or benefits they represent. Studies of a diverse array of crustaceans suggest that recognition of dominance or aggressive status of conspecifics is widespread, because individuals can recognize, evaluate status, and remember their opponents during agonistic interactions. Color, size, and concentrations of
waterborne chemicals are used to obtain information about other individuals, often without the need to establish direct and potentially risky contact (e.g., Caldwell 1979, Gherardi and Daniels 2003, Bergman and Moore 2005; see also chapter 6).

Whether crustaceans are also capable of more finely tuned recognition of conspecific individuals, outside simple dominance or aggressive hierarchies, is less understood. Although individual recognition is often assumed to occur only in selected species (see, e.g., chapters 16, 18), it may be more common, particularly in species where cohabiting or neighboring individuals interact repeatedly. For example, in the monogamous shrimp *Hymenocera picta*, mates recognize one another via waterborne chemical cues (Wickler and Seibt 1972), and similar results have been reported for the shrimp *Stenopus hispidus* (Johnson 1977). Fiddler crabs also can recognize individual neighbors based on visual cues (Detto et al. 2006). Thus, there is good evidence that recognition of conspecific individuals is important in conflict resolution among crustaceans, and hints that individual recognition may also be important in facilitating cooperation. During social interactions, individuals obtain important information about potential opponents or partners, which influences their behavioral reaction toward these. Consequently, understanding the nature and sophistication of individual recognition is potentially important to interpreting social and mating systems. The Crustacea provide many species that are well suited to examine these phenomena through observation and experimentation.

Enemy Pressure and the Evolution of Social and Sexual Systems
Competition and Habitat Saturation

As discussed above, ecology is the other critical component of Hamilton's equation for understanding social interactions. Competition for limited habitat or nesting resources is thought to be a primary driver of social evolution in many cooperatively breeding birds (Selander 1964, Brown 1969, Emlen 1982, Arnold and Owens 1999, Hatchwell and Komdeur 2000) and some social insects (Lin and Michener 1972, Strassmann and Queller 1989, Brockmann 1997, Queller and Strassmann 1998, Wilson and Hölldobler 2005). Indeed, Wilson and Hölldobler (2005) argued that “the key adaptation that led to eusociality is defense against enemies, specifically predators, parasites, and competitors.” Similar selection pressures resulting from the difficulty of establishing new nests—or acquiring the “basic necessary resource” for sociality (Alexander et al. 1991)—have been invoked to explain sociality in sponge-dwelling shrimp (chapter 18), bromeliad crabs (chapter 17), desert isopods (chapter 16), and burrowing crayfish (chapter 15). This growing list suggests that general theories of environmental constraints and animal social evolution developed initially for vertebrates and insects may apply more broadly. Yet, in most of the crustacean cases studied to date, the influence of environmental constraints on social systems is largely conjecture based on indirect evidence. Experiments that manipulate the availability of limiting habitat resources, or removal or addition of breeders, have been conducted with several cooperatively breeding birds (Walters et al. 1992, Komdeur 1996, Komdeur et al. 1995, Russell and Hatchwell 2001) and fishes (e.g., Bergmüller et al. 2005) and should be similarly illuminating in certain crustaceans. The common correlation in insects and vertebrates between sociality and use of resources that are scarce, discrete, or difficult to exploit also provides clues to where new cases of sociality might be expected in crustaceans (Spanier et al. 1993, Duffy 2003). Symbiotic marine crustaceans in particular should provide fertile ground for such searches. In particular, phylogenetically controlled comparative studies of closely related crustaceans differing in social organization would be rewarding (e.g., Arnold and Owens 1999, (p.465) Duffy et al. 2000). We look forward to the day when crustaceans from a broad enough range of environments have been studied to rigorously test hypotheses.
on the environmental controls on social organization (e.g., Emlen 1982, Alexander et al. 1991; see also chapter 12).

Predation

Predation is a pervasive threat, and consequently a strong selective pressure, in the lives of most organisms. Predation has been suggested as an important selective factor favoring cooperative breeding and sociality in birds (Hoogland and Sherman 1976), mammals (Alexander 1974, Clutton-Brock et al. 1999), cichlid fishes (Heg et al. 2004), and insects (Lin and Michener 1972, Strassmann and Queller 1989, Wilson and Hölldobler 2005). The central role of predation in social and sexual evolution of crustaceans is emphasized in several of the chapters in this book (chapters 7, 10, 12, 13). Predation appears commonly to influence the balance between sexual selection and viability selection. Its evolutionary consequences have been illuminated through comparative analyses of conspecific populations, particularly in freshwater crustaceans distributed across water bodies that differ strongly in predation pressure (e.g., Strong 1972, deMeester 1996; see also chapter 7). The ability of freshwater Daphnia to form “resting eggs” that accumulate in sediments has been exploited ingeniously to trace the microevolutionary history of behavioral and physiological responses of these important zooplankters to changing predation regimes (e.g., Cousyn et al. 2001, Kerfoot and Weider 2004). It would be fascinating to use this approach to ask whether mating systems have also been influenced by the changes in predation pressure. Evolutionary consequences of predation on crustaceans have also been approached more indirectly through phylogenetically controlled comparisons among species (e.g., Harrison and Crespi 1999). As the phylogenetic relationships among species become better documented, such comparative approaches should prove fruitful in discerning evolutionary impacts on mating and social systems in a wide range of crustacean taxa.
Parasitism and Its Consequences

Social groups are prime targets for parasites because they concentrate host individuals and often other vital resources such as food and shelter (Schmid-Hempel 1998). Defense against parasites and disease is thought to be a primary selection pressure maintaining, and perhaps originally giving rise to, sex (Lively 1996) because sexual recombination breaks up gene combinations in each generation and thus presents parasites with a “moving target,” interfering with adaptation to the host. Persistent kin groups such as social colonies lose some of this advantage of sex because they present a temporally stable, genetically homogeneous resource that is attractive to parasites and pathogens. Defense against these enemies appears to provide an important selective pressure for multiple mating in social insects, and genetic data, experiments, and phylogenetically controlled comparisons all suggest that polyandry can reduce the impact of parasites in several social insects (e.g., Brown and Schmid-Hempel 2003, Hughes and Boomsma 2004, Tarpy and Seeley 2006). Polyandry may have similar fitness benefits and consequences for social and sexual life in crustaceans. There is also evidence from birds that parasitism and disease can be important engines of sexual (p.466) selection, favoring ornaments that honestly advertise an individual's vigor and freedom from disease (Saino et al. 1997, Horak et al. 2001, Faivre et al. 2003).

Crustaceans host many parasites, some of which (e.g., bopyrid isopods, rhizocephalid barnacles) are themselves crustaceans. Bopyrids, in particular, are conspicuous large external parasites, which allows easy recognition of infected host individuals. Parasite-induced changes in crustacean behavior and physiology are well documented (Moore 1984, Bakker et al. 1997, Cezilly et al. 2000) and may indirectly affect mating interactions and thus the strength of sexual selection in crustaceans. Castrating parasites shut down sexual function in female crabs, distorting the operational sex ratio more strongly toward males and increasing the potential for mate competition among the latter (Brockerhoff 2004). Conversely, infestation with Wolbachia causes feminization in many crustaceans (Juchault et al. 1993, Bouchon et al. 1998), thereby distorting the operational sex ratio in the direction of females.
A reduction in proportion of males also may result from
trematode parasitism of male amphipods, which increases
their activity at the sediment surface and thus their predation
risk (McCurdy et al. 2000). Such indirect effects of parasites
on sexual selection, mediated via changing operational sex
ratios, have not yet been studied in crustaceans. Several
questions would repay future study in crustacean host-
parasite systems. How does parasitism affect an individual’s
matting prospects, and the population’s operational sex ratio?
How, in turn, do parasite-induced changes in reproductive
success influence phenotypic evolution? Has parasitism
fostered or foiled the evolution of sociality in crustaceans? Is
parasitism more frequent in social than in nonsocial
crustaceans? Among species, or among populations within
species, of social crustacean hosts, does frequency of
parasitism correlate with genetic relatedness or with mate
numbers? Does the risk of parasite infection favor monogamy
or positive interactions among social partners (e.g.,
grooming)?

Finally, it is worth noting that crustacean parasites themselves
may provide fascinating subjects for studying evolution of
matting systems. Parasitic bopyrid isopods, for example,
represent an extreme case of sexual dimorphism, with highly
modified females that amount to little more than a large egg
sac, and minute dwarf males. The small male, which itself lives
as a parasite on the female, may produce sperm just sufficient
to fertilize all the females’ eggs, approaching a case of optimal
adjustment of gamete numbers between the male and female
partners. This intimate association between the female and
male also reflects an extreme form of lifelong monogamy,
which may result from the very low population densities of the
parasites and the premium on finding and retaining a mate
(Andersson 1994).

Crustacean Mating Systems and Sexual Selection
Consequences of Sperm Competition

Sexual selection, and sexual conflict, may also be exacerbated when both sexes mate multiply, as occurs in many crustacean species (chapters 2, 12). What are the consequences for fertilization success of different sperm donors in such cases? How has sperm competition influenced evolution of male and female behavior and morphology? How do patterns differ for species with sperm storage and internal fertilization? It has been suggested that females of some of these crustacean species are capable of choosing (p.467) among sperm donations from different males (Jensen et al. 1996), but the exact mechanisms remain elusive.

Males have different mechanisms to counteract the risk of sperm competition, by (1) monitoring the reproductive status of female partners and fending off competitors (Wirtz and Diesel 1983, Murai et al. 2002), (2) reducing the number of male competitors (e.g., by mate guarding; see chapter 7), (3) sealing off the female's reproductive tract or sperm packages, or (4) diluting sperm masses from competitors with large sperm donations (Rondeau and Sainte-Marie 2001). Whether crustacean males actively remove sperm from previous males is not known at present. However, the sperm transfer apparatus of many decapod crustaceans (the modified male pleopods) contains numerous bundles of setae that give this appendix a brushlike appearance. It is very similar in appearance to that of male insects known to remove sperm of competitors from the female reproductive tract (Eberhard 1996) and may serve a similar purpose.
Female Control

As is true of animals generally, studies on mating behavior of crustaceans historically have focused on male behaviors and assumed male control of mating interactions. But recent studies in a variety of animal taxa have underscored the role of female behaviors in controlling mating interactions (Eberhard 1996). One of the most important such mechanisms of female control involves timing. In some crustaceans females appear capable of controlling the moment of the reproductive molt, physiological receptivity, ovulation, and finally fertilization (e.g., Cowan and Atema 1990, Brockerhoff and McLay 2005). Concealment of reproductive status also is employed by females in some crustaceans, allowing them to gain control over the mating process (see also chapter 16). While female control of mating interactions clearly occurs in several crustaceans, little is known of the mating behavior of social species. For example, do queens of social crustaceans mate multiply? If so, what are the consequences for relatedness of the offspring, interactions among colony members, male competition for mating, and the evolution of social behaviors generally?

Preference, Coercion, and Intersexual Conflict

Sexual selection has traditionally been understood to result from intrasexual competition (usually among males) for matings and intersexual choice (usually by females) among suitors (Darwin 1871). But interactions between the sexes can also generate antagonistic coevolution when genes at different loci enhance fitness in one sex but reduce it in the other (reviewed by Parker 2006). Under such circumstances, evolution at one locus selects for counterrevolution at the other locus in a runaway chain reaction analogous to the Red Queen model of arms-race coevolution among different species (van Valen 1973). Rice and Holland (1997) argued that much of the evolution of mating and courtship signals, ornaments, and other sexual differences are driven by such antagonistic intersexual conflict evolution (ICE) and, indeed, suggested that ICE is “the dominant mode of evolution for genes controlling social behavior.” They argued that many traits previously interpreted as evolving in response to female preference may actually reflect evolution in response to female resistance (p.468) to mating, and that genes for sexual and social interactions, and the phenotypes they produce, should evolve much more rapidly than other genes not involved in
ICE. Distinguishing preference from coercion in mating and other social behaviors is not simple, however (Kokko 2005), as shown by detailed studies of amphipod and isopod crustaceans in which female resistance to mating is well documented (e.g., chapters 7, 8). These mate-guarding crustaceans offer promising opportunities for further quantifying direct and indirect costs and benefits of mating, thus disentangling the several interacting influences on mating system evolution.

Macровolutionary Consequences

In addition to its effects on individual morphology and behavior, sexual selection also has important macroevolutionary consequences because it tends to drive rapid coevolution between the sexes, often involving antagonistic coevolution, which results in rapid evolution of reproductive isolation among populations. In montane jumping spiders, for example, allopatric populations show strong phenotypic differentiation in male courtship-related traits and in courtship behavior (Masta and Maddison 2002). Interpopulation differentiation in these traits, in female responsiveness, and in postzygotic viability were stronger than divergence in neutral genetic markers, confirming that evolution of sexually selected characters has been much faster than that of neutral control, and suggesting that sexual selection enhanced divergence rate. Sexual conflict may similarly enhance speciation rate. Multiple mating creates strong competition among sperm of different males to maximize fertilization, often with negative consequences for female fitness. Counterselection by the female to maximize her own fitness can set up an arms race of sexually antagonistic coevolution of reproductive traits. In contrast, when females mate singly, the interests of the male and female are basically the same. Thus, polyandry should speed up evolution of reproductive isolation and speciation. Confirming this hypothesis, Arnqvist et al. (2000) found that species richness averaged four times higher in polyandrous clades of insects than in their monandrous sister clades. Such comparisons have not yet been attempted for crustaceans, but their wide range of mating systems suggests that sexual selection and sexually antagonistic coevolution might be important drivers of speciation and diversification in crustaceans, as well.

Evolutionary Ecology and Conservation
Social and sexual phenomena are central to population dynamics. Harvesting and habitat destruction clearly have many direct impacts on animal populations but may also have indirect impacts by disrupting social or sexual interactions. Many animals that historically lived at high population density do not breed effectively at low population density either because of difficulty in mate finding or because of disrupted social interactions. This “Allee effect” creates the phenomenon known in fisheries as depensation—a decrease in per capita population growth rate at low density. Sex-specific harvesting may also change mating interactions with important consequences. Several crustacean fisheries have targeted males on the reasonable assumption that female fecundity limits population growth and that “sperm is cheap.” But strong male-specific harvesting pressure has led to sperm limitation in several exploited crustaceans (chapter 9), which may disrupt normal social and mating systems. For example, in heavily exploited Canadian populations of American lobster, microsatellite data indicate higher levels of multiple paternity than in less exploited populations, suggesting that sperm limitation fosters female promiscuity (Gosselin et al. 2005). Understanding how social interactions influence mating systems is recognized as critically important in managing finfish stocks (e.g., Alonzo and Mangel 2004, Heppel et al. 2006) and is likely to be important to effective conservation and management of exploited crustaceans, as well.

Concluding Thoughts
The Crustacea represents one of the major branches in the tree of animal life, displaying diversity in form and lifestyle that rival those of the vertebrates and insects. But perhaps because of the primarily aquatic habits of crustaceans, they have received much less attention in evolutionary ecology than mostly terrestrial taxa. We hope that the chapters in this book make clear the richness of adaptations of crustaceans to social and sexual life, and their still largely untapped potential to test fundamental theory in behavioral ecology and evolution. There are rich opportunities awaiting the student willing to pursue them, both in clarifying the obscure social and sexual biology of individual crustacean species and in exploiting the Crustacea in broad comparative approaches to testing evolutionary theory. Our hope is that vigorous pursuit of these opportunities will soon render this book out of date.
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