Comparative Evolutionary Ecology of Social and Sexual Systems

Water-Breathing Insects Come of Age

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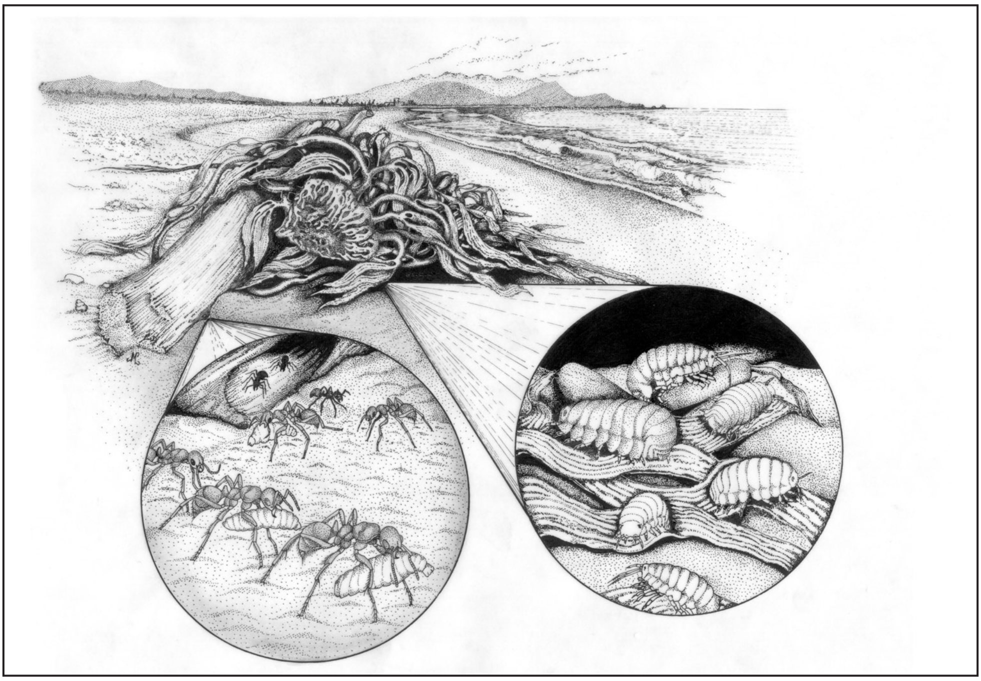

Food bounties washed up on sandy beaches rapidly attract dense aggregations of detritus-feeding amphipods and isopods; a colony of ants stranded in a wood log retreat in an organized manner, saving both their own lives and that of their brood.

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The evolutionary ecology of behavioral interactions is characterized by two great divides. The first divide is conceptual, in that some researchers focus on social systems and some focus on sexual selection and mating systems, and analyses of the two have seldom been combined (West-Eberhard 1983). Queller (1994) described how both types of system are characterized by competition between mutually dependent parties for limiting resources and generate complex mixtures of confluent and divergent interests. The evolution of both social and mating systems is also driven by variation in ecology (Emlen and Oring 1977, Crespi and Choe 1997, Queller and Strassmann 1998, Shuster and Wade 2003), and their evolutionary trajectories may involve complex webs of positive and negative feedback (Andersson 1994, 2004, Crespi 2004). However, this conceptual divide has seldom been crossed, except in some cases of biparental or alloparental care where cooperation and sex necessarily coincide to some degree.

The second divide in evolutionary ecology is taxonomic (Hart and Ratnieks 2005). The ever-burgeoning literature for every taxonomic group compels specialization, and indeed, in-depth analyses of particular species or clades may provide especially useful insights into microevolutionary and macroevolutionary processes (Grant 1999, Crespi et al. 2004). The main cost of specialization is limited perception of broad-scale, convergent patterns, patterns that unite the field conceptually and often lead to novel hypotheses (e.g., Hamilton 1967, 1978).

This book on crustaceans straddles both divides and brings into clear view the growing need to integrate research areas and taxa. My goal in this chapter is to draw together the concepts driving the study of sexual and social biology, and to use these "water-breathing insects" as a touchstone to reach across taxonomic groups, seeking convergences between crustaceans and other animals. Indeed, the diversity of studies represented in this volume may be considered a microcosm of evolutionary ecology as a whole, providing an ideal situation for surveying its landscape in current form.

Convergence and Divergence in Routes to Social and Sexual Inference

Analysis of the evolution per se of social and sexual behavior requires either phylogenies or studies that combine studies of selection with microevolutionary response. Phylogenetic studies have been conducted informally since Darwin (1871) began evaluating taxa for phenotypic similarities indicative of similar selective forces, and formally since Felsenstein (1985) devised the first statistically based comparative method. Informal methods are limited by their intrinsically heuristic nature, and statistical methods are limited by the difficulties of jointly analyzing far-flung taxa, such as dolphins and chimps (Connor et al. 1998), and by the loss of information in the mists of deep history for ancient clades. There are no solutions to this dilemma, only an optimality criterion of novel insight gained from any analysis.

Comparative methods are based on two processes: selection-driven convergence to common phenotypes from ones that differ, and divergence from one lineage to multiple descendant lineages that show covarying phenotypic change indicative of selective forces. For robust studies of convergence, the greater the phylogenetic distance between forms the better, because this span maximizes the odds that all traits other than the covarying ones of interest are randomized. Such randomization reduces the odds that unobserved third variables underlie inferred associations (Ridley 1989). By contrast, analysis of divergence requires species-level or population-level studies with blanket taxonomic coverage—a so-called "model clades" approach (Crespi et al. 2004)—that ensures detection of all relevant microevolutionary changes that grade into differences between populations or species—as well as avoiding secondary effects of changes that may obscure selective origins (Wilson and Hölldobler 2005). Thus, for such divergence studies phylogeneticallycloser is better, which also leads to more robust tests via independent contrasts or other statistical methods (Pagel 1994, 1999, Crespi 1996, Martins 2000).

One important upshot of the convergence approach to analyzing social and sexual behavior is that each major taxonomic group may contribute similar analytic "weight" to any given study, regardless of its species diversity. For example, all Hymenoptera share a constellation of traits, such as haplodiploidy, that are likely to influence the evolution of social and sexual systems (Alexander et al. 1991), but analyzing the comparative role of such traits necessitates investigating other haplodiploid taxa, because each represents only one evolutionary experiment (Doughty 1996) with such genetic systems. A crucial implication of this line of argument is that each more or less major taxon in the idiosyncratic social bestiary, from microbes to spiders, insect orders, fish, birds, and mammals, may be equally useful for addressing particular questions, such as the origin of cooperative breeding from maternal care. Thus, intuition aside, mole-rats (Sherman et al. 1991, Jarvis et al. 1994), *Austroplatypus* beetles (Kent and Simpson 1992, Kirkendall et al. 1997), spiders (Whitehouse and Lubin 2005), social lizards (Chapple 2003), or snapping shrimp (chapter 18) may each be equally conceptually useful as all termites or all ants in some analyses of social evolution. With this viewpoint in mind, the Crustacea occupy a key position, as sister group to Hexapoda (Regier et al. 2004), with comparable phenotypic, ecological, social, and sexual diversity that this book brings to light.

The evolution of social and sexual behavior involves complex interplay of ecological selective factors with phenotypic and genotypic traits. In this chapter, I first describe a general conceptual framework for understanding the evolution of cooperation. Next, I discuss the phenotypic and genetic traits of crustaceans and other animals that I consider most salient to social and sexual evolution, and discuss how they affect evolutionary trajectories in this framework. Third, I evaluate the role of ecological and life-history factors in selecting upon phenotypic variation, leading to changes in social and mating systems. Finally, I integrate phenotype with ecology and describe hypotheses on how the determinants and components of social and sexual systems evolve together.

Social and Sexual Cooperation and Conflict

Sexual and social interactions each involves a mixture of cooperation, to fertilize eggs or to rear babies, and conflict, to control fertilization or to maximize inclusive fitness via avenues that differ from those of other group members. Social cooperation can be favored by three mechanisms: (1) kinship, (2) reciprocity, and (3) byproduct benefits (Sachs et al. 2004). Kinship-based cooperation can involve altruistic or mutualistic behavior, and cooperation is normally enforced or facilitated by forms of kin recognition, policing, or colony-level benefits. Reciprocity may involve relatives or nonrelatives, and cooperation is driven by the repeated, cumulatively beneficial nature of interactions, with cheater suppression or avoidance mediated by obligate cohabitation, partner recognition, or group-level benefits. Byproduct benefits involve behavior that is directly favored by selection for all parties, with no net gains possible from cheating (Connor 1995a, 1995b).

Under the kinship and reciprocity models, conflicts of interest are virtually ubiquitous, and such conflicts are ongoing or resolved via persuasion (providing benefits to cooperators), coercion (imposing costs on noncooperators), or force (taking control of behavior away) (W.D. Brown et al. 1997, Crespi and Ragsdale 2000, Frank 2003). Which of these three routes are followed depends in turn upon colony-level costs and benefits of the alternatives (e.g., Korb and Heinze 2004) and imbalances in power or information (Crespi and Ragsdale 2000, Beekman et al. 2003, Beekman and Ratnieks 2003).

Sexual interactions can also be interpreted in this framework. Males and females may in some cases exhibit confluence of interest, with fast, efficient mating and fertilization being optimal for both parties. However, in most species, males and females should exhibit conflicts of interest over mating, fertilization, premating or postmating associations, and any associated parental investment such as resource-rich spermatophores or nuptial gifts (West-Eberhard 1983, Alexander et al. 1997, W.D. Brown et al. 1997, Fincke 1997, Chapman et al. 2003, Arnqvist and Rowe 2005). As for sociality, conflict resolution may be persuasive, coercive, or forceful, with information, power, and mutual costs or benefits as key determinants of outcome. But incest aside, sexual cooperation must be based on short-term reciprocity (e.g., parceling; Connor 1995b) or mutualistic benefits, because a set of sexual interactions (from mate detection to fertilization; W.D. Brown et al. 1997) is seldom repeated for a given pair.

The challenge for students of sociality and sex is to explain interspecific and intraspecific variation in these systems as some function of ecology and life history, in the context of evolutionary histories, expressed as current phenotypes and genotypes that delimit behavioral trajectories (e.g., Crespi and Choe 1997, Cockburn 1998). For understanding the contributions of ecology and life history to behavior, tradeoffs are key. Tradeoffs between such fundamental traits as reproduction versus survival, mating effort versus parental effort, and helping versus reproduction thus differ among taxa at all levels and structure evolutionary trajectories. Ultimately, such tradeoffs reside in the genome and are expressed as reaction norms, but for now, phenotypes are our necessary units of analysis.

The Primacy of Phenotype

Analyzing the evolution of social and sexual systems has usually focused on ecology (as the agent of selective pressures) and genes (as the units of inheritance, the key to genetic relatedness, and the progenitors of phenotypic variation). To the extent that phenotypic traits are not just the outcome of evolution but also place limits on evolutionary trajectories, they also play a causal role in how behavior evolves (e.g., Wcislo 1989).

Ever since their universal common ancestor, animal lineages have differed in phenotypic traits that influence the evolution of their social and sexual systems. Traits most salient to social evolution include modes of foraging, feeding, defense, locomotion, and sensation; aspects of life history such as how offspring are produced also both direct and respond to selective pressures on social behavior. By contrast, traits most relevant to the evolution of mating systems include structures used in mate finding, courtship, sperm transfer, and fertilization (W.D. Brown et al. 1997).

Many common insect traits, such as high potential fecundity, air breathing, flight, diverse adaptations to defense, internal fertilization, and sperm storage, have undoubtedly contributed to how their social and sexual behavior can evolve, and similar arguments can be made for other taxa. Among crustaceans, traits that I hypothesize as crucial include the following:

1. The presence of gills or breathing water via the skin, and the existence of the aquatic larval stage, which makes crustaceans the equivalent of ferns and mosses among plants, or amphibians among tetrapods. As "water-breathing insects," the habitats and basic necessary resources essential to reproduction of crustaceans are fundamentally different from those of fully terrestrial creatures. Such habitats include, of course, the seas, where symbiotic relationships flourish, and localized aquatic habitats, such as wet burrows or small pools.
2. The absence of airborne flight, which limits searching for mates and other key resources, such as genetically related cooperators, and reduces ability to transport and concentrate food (e.g., Clark and Dukas 1994) or disperse long distances in a directed way—indeed, all eusocial insects exhibit flight at least at some life-cycle stage.
3. The common presence of claws, which provides opportunities for effective altruistic or mutualistic defense, and also armor, which may reduce the strength of selection for defense by making some crustaceans less profitable or accessible as prey (e.g., crabs, lobsters).
4. Hemimetabolous development in some crustaceans, such that juveniles above a certain size are like miniature adults, which makes helping possible by juveniles (e.g., chapter 17), as in termites, aphids, and some other taxa (Alexander et al. 1991), and molting, which increases vulnerability to predation during short periods and sometimes restricts mating opportunities (e.g., chapter 7).
5. All-at-one brood production, such that offspring develop in discrete cohorts, which may reduce the duration of mother–offspring overlap and lessen the odds of older offspring helping younger ones.
6. A habit in some lineages, such as snapping shrimp and some crabs, of feeding on food of relatively low nutritional quality, such as detritus or tiny animals, which reduces any possible benefits from paternal care that involves direct feeding (Hunt and Nalepa 1994) and may contribute to "capital" breeding via all-at-once brood production.

Assessing the impact of these traits on social and mating-system evolution requires comparison of sister lineages divergent for the presence or form of the trait, and comparisons of convergent taxa, in the context of the ecological selective pressures unique to each species and clade. Such comparisons are especially useful for traits with clear functional design, such as weaponry; indeed, effective weapons appear crucial both as a predaptation to complex social evolution and as a factor allowing social groups to enlarge, and sometimes flourish, in the context of between-species interactions. Such weaponry includes bacteriocins in microbes (Crespi 2001, Gardner et al. 2004); mouthparts, forelegs, and stings in insects (e.g., Kukuk et al. 1989); venom in spiders and scorpions (e.g., Binford 2001); teeth held in strong jaws for mole-rats and social carnivores (Sherman et al. 1991); and hunting tools in humans. Crustaceans demonstrate nicely how weapons play a key role in the evolution of "factory-fortress" eusociality, which may be the only form of complex sociality in this group given the constraints on their locomotion, form of brood production, and near restriction to wet or aquatic habitats.

The Ecological Nexus of Sex and Social Cooperation

The distributions of resources for breeding in space and time are considered central drivers of both sexual and social system evolution (Emlen and Oring 1977, J.L. Brown 1978). However, the conceptual divide between mating and helping has apparently thus far precluded the joint analysis of ecological factors in both contexts. By the Emlen and Oring (1977) scheme, extended by W.D. Brown et al. (1997), Shuster and Wade (2003), and others, the distribution of resources in space and time largely determines the distribution of females, which in turn drives optimal male mating tactics; other factors, such as tradeoffs between mating and parental effort, and sexual conflict (Arnqvist and Rowe 2005), mediate the ultimate outcome. The role of ecology in social evolution has been dominated by the ecological constraints model, which asserts that cooperation evolves in habitats that are especially valuable (J.L. Brown 1978, Emlen 1982, Andersson 1984), such that independent breeding via dispersal is relatively difficult. Staying at home (and perhaps helping) may also be facilitated by an evolutionary history of high adult survivorship (Arnold and Owens 1998, 1999) and the benefits of philopatry, most notably, a safe haven and possible inheritance (Ragsdale 1999, Hatchwell and Komdeur 2000, Pen and Weissing 2000, Kokko and Ekman 2002, Solomon 2003). These considerations linking ecology with behavioral interactions imply that social systems and mating systems should coevolve closely (Fig. 20.1), and indeed, for most social vertebrates, they are intricately mixed and centered around resources of especially high value (J.L. Brown 1978, Alexander et al. 1991, Faulkes and Bennett 2001, Koenig and Dickinson 2004).

The core ecological feature of social and sexual systems is what I call the "basic necessary resource": a habitat, be it burrow, territory, nest, gall, social group members, or other requirement for successful breeding. Aspects of this resource that are crucial for its role as an arena of selection include whether or not it is created, how hard it is to acquire and defend, whether it can be replaced if lost, whether food is available in the habitat, and the longevity of the habitat in relation to generation time (Alexander et al. 1991, Crespi 1994). For any given species, these aspects of the basic necessary resource, plus ecological interactions involving competitors, predators, parasites, and mutualists, strongly affect male mating opportunities (Fig. 20.1). Mating and social systems interact in the context of the male promiscuity–care tradeoff; as this tradeoff evolves, both systems are affected. Moreover, mating system evolution influences social evolution via incest avoidance, genetic relatedness effects, and mate guarding as a predisposition to male care, and social evolution may change the distribution of receptive females, as well as the operational sex ratio and sexual selection intensity (Fig. 20.1). Empirical analysis of such predicted effects requires microevolutionary, "microphylogenetic" studies of joint changes in sociality and mating systems, as described above.

The ecological interface of social and sexual systems is structured by four main axes. First, tradeoffs between mating effort and parental effort, mediated by the scope

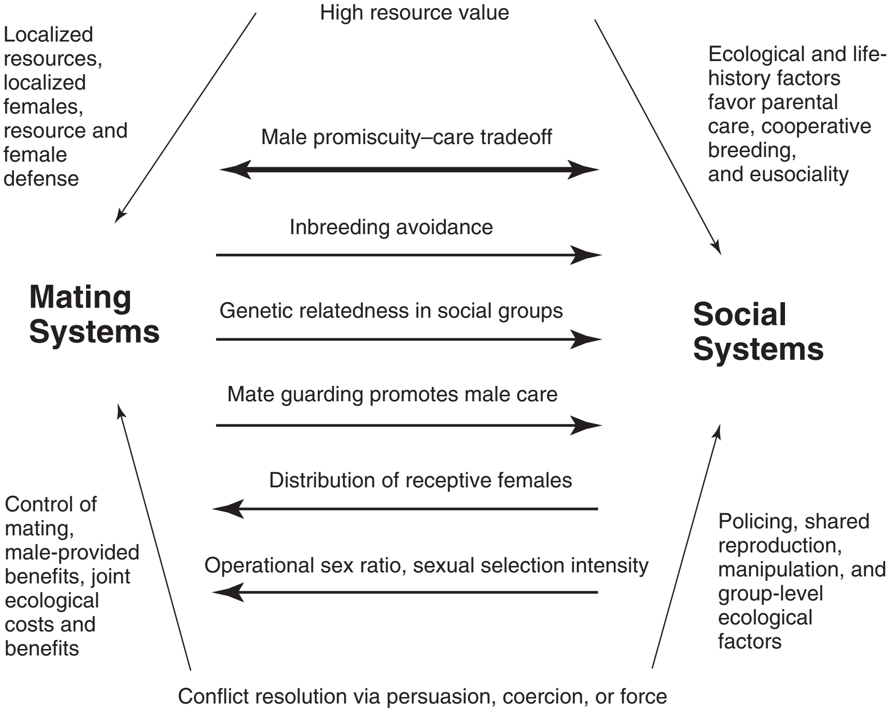

Figure 20.1 Coevolution of social and mating systems. This figure illustrates two main points. First, the evolutionary interactions between aspects of social and sexual systems are shown by the arrows at the center of the figure. These effects may be bidirectional (as with the promiscuity–care tradeoff) or unidirectional, such that changes in either mating or sexual systems can influence the evolutionary trajectory of the other. Second, both social and sexual systems are ultimately determined by (1) ecological and life-history factors, with a central role for high resource value, and (2) the nature of cooperation, conflicts and conflict resolution, which may involve provision of benefits to others ("persuasion"), imposition of costs on others ("coercion"), or force imposed on others.

for promiscuity and the benefits of helping, influence the presence and form of parental care, maternal, paternal, or biparental (e.g., Clutton-Brock 1991, Black 1996) (Fig. 20.1). Second, female foraging effort may trade off strongly with parental effort, as in some insects where females are mobile, predacious, and food limited; this tradeoff may select for exclusive paternal care, with males gaining both paternity and protection of young via guarding of eggs (Tallamy 2000, Owens 2002). Third, the tradeoff between staying, and perhaps also helping, in one's natal habitat versus dispersing to breed independently drives the initial evolution of cooperative breeding from paternal care (Fig. 20.2). This tradeoff applies to both sexes, and for males a higher intensity of sexual selection may favor staying and helping (Alexander et al. 1991). Finally, for helpers there is a tradeoff between helping and engaging in personal reproduction, within ones' social group (Fig. 20.2). This tradeoff may be energetic and physiological or social, with "cheaters," who lay eggs or engage in surreptitious matings, suffering imposed costs from dominants, including eviction at worst (Johnstone and Cant 1999).

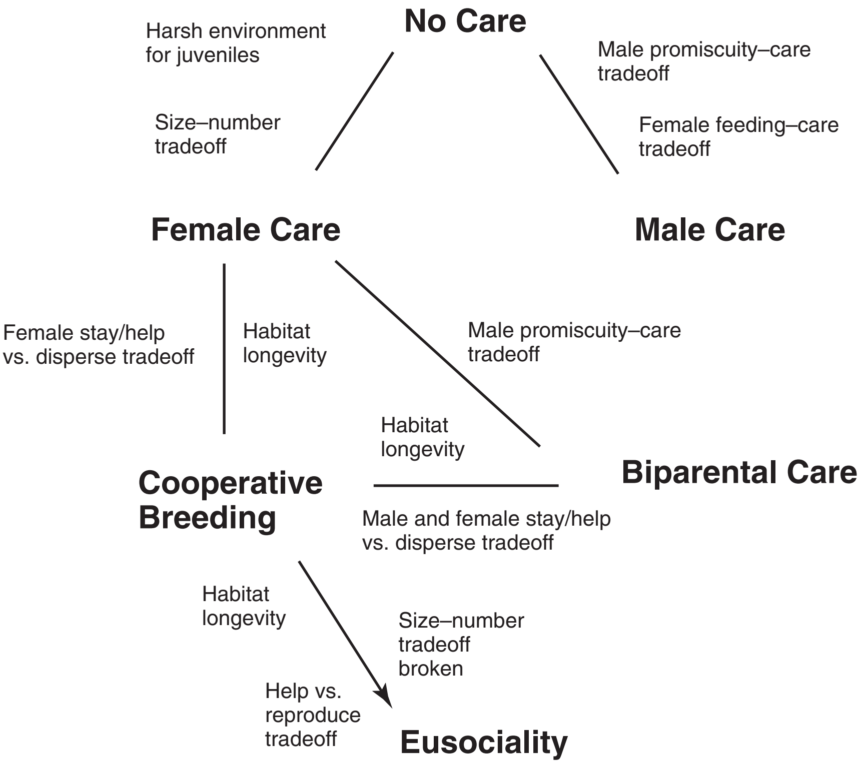

Figure 20.2 The hypothesized evolutionary transitions between different forms of social system (the lines connecting the social systems), and the most important selective factors and tradeoffs involved in each specific transition (the phrases adjacent to the lines). Only the transition from cooperative breeding to eusociality is presumed to be unidirectional; other transitions may occur in either direction. These evolutionary transitions between social systems are mediated by ecological factors and tradeoffs involving life-history and mating-system characteristics. The form of such tradeoffs is expected to differ among species, mainly as a function of their food source and the regimes of predation and competition to which they are subjected.

Each of these tradeoffs may differ in strength between species, in some cases being strong, as for the latter two tradeoffs in naked mole-rats; weak, as for helper reproduction in some factory-fortress species such as thrips (Chapman et al. 2002); or essentially nonexistent, as for some social mammals such as the Damaraland mole-rat where within-group matings must involve incest and so are precluded (Jarvis and Bennett 1993, Jarvis et al. 1994). The strength of tradeoffs for any given species depends strongly on ecological factors, including the nature of the basic necessary resource, life-history, and other phenotypic traits, as well as aspects of social power asymmetries and kinship, as exemplified in skew models (Johnstone 2000).

The ecology of crustacean social and sexual systems is dominated by several themes. As described in chapters 14 and 16, maternal care is common in this group, especially in the relatively "harsh" terrestrial environment of some isopods with desiccation risk, food provisioning, and a valuable, relatively safe microhabitat as major selective contexts. In some situations, such as that of the isopod *Hemilepistus*, such maternal care has apparently evolved into biparental care, as in many insects, many birds, and some mammals (Reynolds et al. 2002). This transition apparently involves reductions in benefits from promiscuity to males, as well as increased benefits from joint care such as division of labor in defense of especially valuable reproductive resources such as burrows (Fig. 20.2), although to what relative degree mating-system, social, and life-history factors (e.g., semelparity) are involved remains unclear. Finally, either maternal care or biparental care has evolved into cooperative breeding and eusociality in at least two clades of the Crustacea, snapping shrimp (chapter 18), bromeliad crabs (chapter 17), and possibly burrowing crayfish (chapter 15). Biparental care may provide an evolutionarily smooth route to cooperative breeding because broods of potential helpers will very likely be full sibs, and the ecological situation already involves benefits from having two helper-parents present, suggesting that additional help may be even more advantageous. Moreover, in this case both sexes have already been shown to be ecologically or sexually constrained enough (from greater fecundity with less care, or greater promiscuity) to engage in extensive parental care, such that offspring of both sexes serve as potential helpers even after they reach adulthood or breeding age. The transition from exclusive maternal care to cooperative breeding may be relatively less likely, based on these arguments, so it may require stronger effects from a basic necessary resource that constrains breeding opportunities of female dispersers.

Crustaceans provide some of the best evidence for the factory fortress model for the evolution of eusociality. Thus, social snapping shrimp (chapter 18) and bromeliad crabs (chapter 17) meet the criteria described in Crespi (1994), a claustral habitat that combines food and shelter, strong selection for defense, and ability to defend via weaponry. "Primary burrower" crayfish may also approach this situation (chapter 15), although these species must presumably forage outside of the burrow—though perhaps relatively safely. Consideration of the life histories of these three crustacean taxa also suggests that helping by juveniles, exclusively or in conjunction with helping by adults, often coincides with the factory fortress mode of sociality. Thus, in snapping shrimp and bromeliad crabs, as well as some termites, aphids with soldiers, naked mole-rats, *Austroplatypus* beetles with apparent helping by larvae (Kent and Simpson 1992, Kirkendall et al. 1997), and some social spiders (Aviles 1997, Whitehouse and Lubin 2005), juveniles engage in some degree of helping, presumably due to a combination of hemimetaboly or its equivalent in noninsects, the relatively safe nature of the habitat, and inclusive fitness gains from helping relatively soon after birth (Queller 1996). This pattern reaches its apex in some termites where all helpers senesce as juveniles (Thorne 1997, Thorne et al. 2002), and indeed, such divergence in life span between helpers and reproductives suggests that the self-reinforcing nature of senescence has helped to drive the evolution of complex sociality (Alexander et al. 1991). Helping by juveniles in cooperative vertebrates may be more or less limited to humans, which also enjoy relatively safe habitats and benefit from extensive alloparental care (Alexander 1989). Has such helping favored in part the greatly extended juvenile period of humans (because children help to raise siblings), and is it also reflected at the other end of the life cycle, with the evolution of sterility, and helping, via menopause (Foster and Ratnieks 2005)?

The absence in crustaceans of "life-insurance" forms of sociality (Queller and Strassmann 1998) or large complex societies as found in ants, wasps, bees, and termites that forage outside the nest may be due to their lack of flight, the fact that their foods are less energy dense than meat or pollen, the "low fecundity" life history of fully terrestrial species, or the lack of easy expansibility of the habitat. These hypotheses are, however, notably difficult to test, except in the context of sister-taxon comparisons of Hymenoptera and Isoptera lineages with and without complex sociality (e.g., Hunt 1999).

Joint consideration of the factory-fortress and life-insurance models and models developed for cooperative breeders suggests that one of the key variables in the evolution of helping is the degree to which helping influences mortality rates (Fig. 20.3). Thus, increased helping under cooperative breeding, as exemplified best by birds, appears to normally coevolve with decreased adult mortality. Such reduced mortality leads to increased habitat saturation, increased constraints on independent breeding, higher relatedness (Taylor and Irwin 2000, Le Galliard et al. 2005), increased chances of inheritance, and delayed senescence, all of which should further favor staying and helping and drive populations toward the "slow" end of the life-history spectrum (e.g., Härdling et al. 2003, Oli 2004, Russell et al. 2004). Indeed, under this view, ecological constraint may be a consequence and not a simple cause of cooperative breeding.

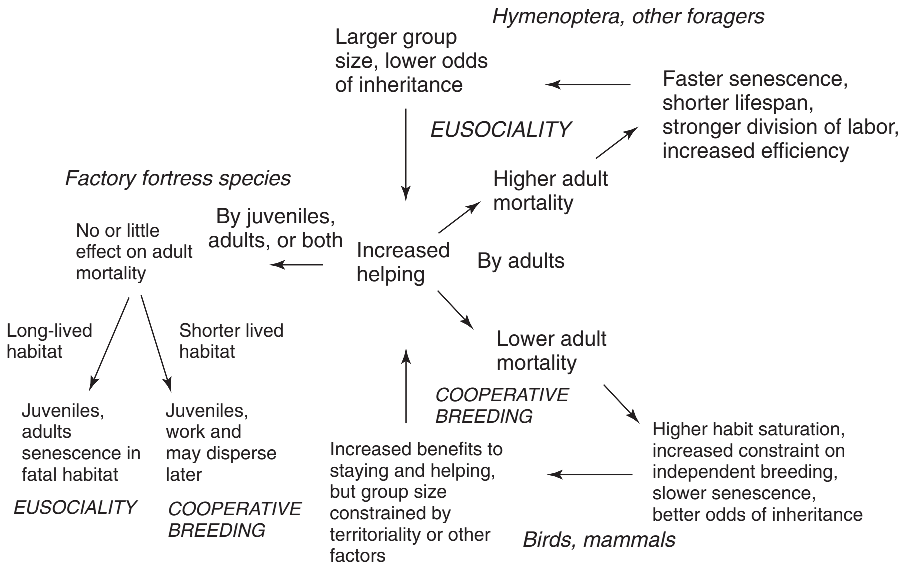

Figure 20.3 Cooperative breeders and eusocial species appear to comprise three main groups with regard to two factors: (1) their habitat (combined food and shelter "factory fortresses" vs. foraging outside the nest) and (2) whether helping involves increased versus decreased adult mortality of helpers. In Hymenoptera and other foragers, higher adult mortality and increasing group sizes lead to eusociality via a positive feedback loop. In birds and mammals, lower adult mortality follows from staying and helping and leads to habitat constraints, group sizes constrained by territoriality, and cooperative breeding. In factory fortress species, mortality rates are low in the enclosed natal habitat, and the evolution of cooperative breeding versus eusociality may be largely a function of habitat duration relative to life span.

By contrast, increased helping in many invertebrates, such as Hymenoptera that forage outside the nest, is expected to raise mortality rates of helpers, leading to accelerated senescence and shorter life span, but also enhanced efficiency via division of labor, larger groups, lower chances of inheritance, and further helping via a positive feedback cycle (Alexander et al. 1991, Keller 1997, Bourke 1999); this route thus leads directly from cooperative breeding to eusociality (Jeon and Choe 2003). Factory-fortress lineages such as snapping shrimp and bromeliad crabs may follow a life-history route whereby juveniles enjoy low mortality and gain inclusive fitness via helping full sibs; groups can increase in size until limited by density dependence in their special food–shelter habitat, after which altruistic dispersal is increasingly favored (Crespi and Taylor 1990). Under this model, individuals may remain totipotent if habitat duration is not unduly long compared to generation time, or eusociality may evolve if nepotistic effort or personal reproduction leads to senescence and death at home.

Testing these ideas requires a broad perspective from life-history theory in social evolution, models that incorporate coevolutionary dynamics, and focused study of invertebrates with small colonies and vertebrates with large ones, especially in clades with some species exhibiting totipotency (Crespi and Yanega 1995, Hart and Ratnieks 2005) but others crossing the threshold to eusociality.

Vagaries of Social and Sexual Conflict

Ecological factors exert largely deterministic effects on the evolution of social and sexual systems. By contrast, some forms of behavioral interaction that involve conflict are expected to generate antagonistic coevolution (Rice 1996, Rice and Holland 1997, Rice and Chippindale 2001) whose resolution, or ongoing nature, appears relatively difficult to predict (Arnqvist and Rowe 2005). The magnitudes of conflicts over mating and fertilization and conflicts over postzygotic investment in offspring depend on the degree of divergence of the optima for males versus females, or parents versus offspring, or intrasexual interactions (Chapman et al. 2003). For example, male–female confluence of interest can arise when harsh ecological conditions compel having two helpers raise young (Clutton-Brock 2001[a]) or when male mating opportunities via mate searching are few and females are predatory or otherwise constrained in food acquisition, leading to exclusive paternal care (Tallamy 2000). By contrast, conflicts may persist and dominate behavioral interactions where males gain by promiscuity, females suffer costs, and neither party can fully control the mating sequence from contact until fertilization (W.D. Brown et al. 1997).

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In general, the resolution of conflicts will depend on the set of strategies available (e.g., one party being able to forcibly achieve its optimum), the strength of selection on different parties, and the forms and extent of genetic variation that underlie the interactions. A key factor in conflict resolution is whether or not one party can adjust the behavior of the other via the provision of benefits, in contrast to the imposition of costs. For example, males may persuade females to mate via the offering of nuptial resources, or coerce them to mate by making them more vulnerable to predation via precopulatory guarding, and females in social groups may allow cooperators to have higher personal reproduction, or punish and evict noncooperators (e.g., Cant et al. 2001). The success of such varying strategies will depend on ecological factors as well as phenotypic and genetic asymmetries, and assessing how ecological factors interact with aspects of conflict and its resolution is a crucial challenge for future analyses of social and mating-system evolution. Moreover, whereas ecological selective pressures always generate adaptation, at least in the context of tradeoffs, antagonistic coevolution driven by behavioral conflict will often result in phenotypic traits that are maladaptive in males, females, or juveniles; moreover, such phenotypes may be difficult to recognize as maladaptive without a clear understanding of mechanisms and microevolutionary trajectories (Crespi 2000, Nesse 2005).

In crustaceans, studies of social evolution have mainly focused on cooperative behavior, which is still being characterized. Future studies of factory-fortress–inhabiting crustaceans may usefully investigate conflicts among juveniles between mother and offspring over parental investment, and female–female conflict, especially over new breeding opportunities. Analyses of sexual interactions have, by contrast, already demonstrated complex interplay between cooperation, conflict, and ecology, especially in species with biparental care or elaborate systems of mate searching, courtship, and female choice. Thus, in fiddler crabs, predation regimes and local population density can tip the balance between different mating systems even within species, by adjusting the costs and benefits of alternative male and female strategies (chapter 10); this group nicely exemplifies how the divergence approach to analyzing evolutionary changes works best at the lowest levels. At the most divergent taxonomic levels, *Hemilepistus* isopods appear convergent with humans in exhibiting extensive biparental care, few but huge offspring, habitation of highly valuable resource, high survivorship, concealment of ovulation, control of mating largely by females, a complex system of interindividual recognition, and strong intraspecific competition (chapter 16). These traits apparently form a coadapted set, grounded in life history, at the "slow" extreme of the slow–fast continuum as has been described in mammals (Oli 2004). Indeed, the combined mating/social system involving biparental care with female control of mating and a highly valuable basic resource appears to be convergent across diverse taxa, perhaps driven by feedbacks between sexual and social system evolution.

Transitions and Feedbacks in the Evolution of Social and Sexual Systems

How do social and sexual systems coevolve? At the broadest scale, each is influenced by phenotypic and ecological factors and also drives the evolution of the other. First, consider selection on social cooperation, perhaps due to ecological change, from no parental care, to maternal care, to cooperative breeding, to eusociality. How might mating systems change in response? The origin of maternal care may localize receptive females, making them more defensible by males. Depending on the nature of any male promiscuity–care tradeoff, postcopulatory mate guarding may provide a preadaptation to biparental care (e.g., Mathews 2003), or even paternal care, depending on the female foraging–care tradeoff. Exclusive paternal care may preclude the evolution of cooperative breeding, but as noted above, biparental care may, in principle, facilitate it. How the transition from parental care to alloparental care affects mating systems must depend on which sex helps. Exclusive female helping essentially removes young females from the pool of receptive mates, which may increase the intensity of sexual selection (Andersson 1994). Exclusive male helping, as found in many birds, may have the opposite effect, unless it is driven in the first place by sharply limited mating options for young males (Alexander et al. 1991).

Finally, the transition from cooperative breeding to eusociality, as seen in some arthropods and naked mole-rats, further limits male mating opportunities in time and space. This transition has led convergently to swarming or lekking in many bees, ants, and termites with flight and foraging outside the nest, but in factory-fortress species the situation may be quite different due to their claustral habitat. Here, mating and breeding opportunities may arise within the fortress if a founder or foundress dies, leading to intense struggles given the high reproductive skew that characterizes such societies. Alternatively, inbreeding may normally occur among helpers, as in some thrips and spiders (Aviles 1997, Chapman et al. 2000, 2002), or selection against incest may effectively enforce cooperation and a lack of supersedure, as in Damaraland mole-rats (Jarvis and Bennett 1993, Jarvis et al. 1994). Such inbreeding effects may also structure the behavior and life histories of social shrimp, crabs, and crayfish.

Now consider selection on mating systems and how it may affect social evolution (Figs. 20.1, 20.2). Many mating system transitions will engender changes in the degree of multiple paternity in broods, which should affect relatedness and the likelihood that helping evolves, and the degree to which broodmates cooperate. Increases in the intensity of sexual selection may make male parental care less likely, at least by the most successfully promiscuous males, but less dominant males may be selected to care more for a female's offspring if they have some confidence of parenthood. Alternatively, stronger sexual selection on both sexes could lead to a situation where males fight for breeding resources and females compete for males, or the sexes fight jointly for resources, leading to biparental care. Increased control of mating and fertilization by females may also, in some cases, lead to increased paternal care, if females can essentially trade fertilizations for help; this may be less likely with all-at-once brood production, as in crustaceans.

It should be clear from this exercise that sexual and social systems must evolve together via mutual feedbacks, both negative feedbacks with constraining effects and positive feedbacks leading to runaway evolution and rapid shifts (Andersson 1994, 2004, Crespi 2004). The evolution of sociality may involve four main forms of positive feedback loops: (1) between the degree of helping and senescence (Alexander et al. 1991); (2) among colony size, worker reproductive potential, and queen–worker dimorphism (Bourke 1999) (Fig. 20.3), (3) among decreased adult mortality, increased habitat saturation, and increased helping (Fig. 20.3), and (4) among increased helping, increased socially generated resource, increased selection for resource usurpation via cheating or other means, and increased cooperation involving resource defense—a social arms race such as may have led to the evolution of the human psyche (Alexander 1989). The evolution of mating systems involves at least four such processes: (1) Fisherian positive feedback loops in the evolution of mate choice (Kokko et al. 2002, Mead and Arnold 2004), (2) the self-reinforced evolution of leks from other mating systems (Sutherland 1996, Bro-Jorgensen 2003), (3) coevolution between parental investment and sexual selection (Andersson 1994, 2004), and (4) runaway processes driven by other genetically covariant aspects of male and female mating phenotypes, such as promiscuity (West-Eberhard 1983, Shuster and Wade

2003). One of the main coevolutionary loops connecting social and sexual systems involves changes in the strength for sexual selection affecting the mating system and parental investment levels, which affects male and female potential reproductive rates, which feeds back to the opportunity for sexual selection via the life history (Andersson 1994). Thus far, the processes involved in this loop have been analyzed primarily in the context of the tradeoffs between parental effort and mating effort for species with biparental care, with a focus on vertebrates. Extending such analyses to species with cooperative breeding and eusociality, and to invertebrates, should lead to recognition of novel convergences, such as those between *Hemilepistus* and some vertebrates.

The degree to which feedback loops operate is an empirical matter that can only be resolved via analyses of fine-scale divergence among populations and closely related species, with a focus on the key tradeoffs involved in social and sexual behavior, and the central roles of ecology and phenotype. This is not an easy task, but it is essential to our understanding of how sex and cooperation actually evolve—theoretical models, studies of convergence, and "model species" (Dugatkin 2001) can take us only so far.

Conclusions

The two great divides of evolutionary ecology, conceptual and taxonomic, must be crossed for the study of mating systems and social systems to reach maturity. Conceptual unification should, I think, hinge on recognition that both sex and sociality involve conflict between mutually dependent parties over limiting resources, and yield complex mixtures of cooperation and conflict over different prezygotic and postzygotic processes. For any lineage, the balance of cooperation and conflict depends on how different life-history tradeoffs are expressed and how well persuasion, coercion, or force may be used by the interacting parties, as a function of their phenotypes, the strength of selection, and the ecological benefits and costs of alternative resolutions to conflict (W.D. Brown et al. 1997, Arnqvist and Rowe^b 2005). These considerations imply that further conceptual progress requires synthesis of two approaches: (1) the optimization analyses of behavioral ecology and (2) analyses of the evolutionary rules regarding how conflicts are resolved or ongoing, usually in ways nonoptimal to one or both parties (Beekman et al. 2003, Beekman and Ratnieks 2003). In general, I would expect that ecological "harshness" and resource limitation select for increased within-group cooperation in the evolution of sociality and for increased between-sex cooperation in the evolution of mating systems. Such cooperation is, however, coupled with enhanced between-group conflict in sociality and within-sex conflict in mating systems. Moreover, successful within-sex or between-sex cooperation creates new resources, be they "basic necessary" ones or a social group itself, which can generate new forms of intense conflict within and between species.

AQ: Please check the reference Arnqvist and Rowe^b 2005 is not include in reference list.

Taxonomic and phylogenetic divides create opportunities for recognizing convergences. Groups such as the Crustacea are highly diverse yet understudied compared to vertebrates and insects, and as such, they provide especially high returns on research investment. In particular, the presence of cooperative, claw-defended factory fortresses provides stunning comparisons with other animals, the presence of molting yields opportunities to dissect sexual conflict in precopulatory guarding and postcopulatory behavior, and their status as "water-breathing insects" means that a complex mosaic of shared and divergent traits drive the social and sexual evolution of Insecta, Crustacea, and other taxa and remain to be elucidated. This book is a crucial first step.

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