Ecology and Evolution of Eusociality in Sponge-Dwelling Shrimp

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DOI:10.1093/acprof:oso/9780195179927.003.0018

Abstract and Keywords

Sponge-dwelling Synalpheus shrimp comprises a clade of ~30 species that range from socially monogamous pairs to eusocial colonies of hundreds of individuals. Eusocial colonies have evolved at least three times independently within Synalpheus, and contain multiple cohabiting generations, with one or a few breeders of each sex, and non-breeders that defend the colony from intruders. Comparison of sponge-dwelling shrimp with other animal taxa reveals several shared characteristics of life history and ecology suggested to promote cooperative breeding and eusociality in insects and vertebrates: (i) direct development resulting in limited dispersal and kin association; (ii) specialization on a valuable, self-contained, and long-lived resource; (iii) strong competition for the host resource; and (iv) possession of a weapon (the snapping claw) effective in monopolizing it. Coincidence of these characteristics is rare within Crustacea and may explain why Synalpheus includes the only known eusocial marine animals.

Keywords: cooperation, defense, resource monopolization, dispersal, kin association
Eusociality refers to colonial life in which most individuals forgo reproduction to help raise and defend offspring of a lucky few of their kin. First described in ants, termites, and honeybees, eusociality is among the most striking phenomena in nature and has fostered spectacular evolutionary and ecological success in the several lineages of social insects (Wilson 1971, 1990).

Eusociality also poses an enduring puzzle—explaining its evolution has vexed biologists since Darwin (1859) famously observed that sterility in social insects posed “the one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory.” In essence, the question is how, in a world of Darwinian self-interest, a species in which most individuals behave altruistically can evolve, persist, and even thrive.

Historically, eusociality was defined by three criteria: cohabitation of different adult generations, reproductive “division of labor” (i.e., reproductive skew), and cooperative care of young (Michener 1969, Wilson 1971). The traditional concept of eusociality has been criticized for, among other things, being vague, arbitrary, and biased toward arthropods; hence, various alternative definitions have been proposed subsequently that either expand or restrict the definition (Gadagkar 1994, Sherman et al. 1995, Crespi and Yanega 1995). At one end of this spectrum is the concept of the eusociality continuum (Sherman et al. 1995), which emphasizes the similarities and intergrading social systems among the various social taxa of invertebrates and
vertebrates. At the other end, Crespi and Yanega (1995) emphasize the origin of irreversible sterility as a key transition that qualitatively changes the evolution of social organization, and restrict the term “eusociality” to lineages that have crossed that transition.

Efforts to solve Darwin’s fundamental puzzle have ranged from individual-based fitness analyses (e.g., Bourke and Franks 1995, Crozier and Pamilo 1996) inspired by Hamilton (1964), through broad-scale comparative analyses of sociality in different animal lineages (Alexander et al. 1991, Crespi 1994, 1996, Brockmann 1997, Helms Cahan et al. 2002, Hart and Ratnieks 2004). The latter approach exploits the fact that eusociality has arisen once each in the ancestors of ants and termites, several times among the bees and wasps, with a few scattered instances among other insects (Choe and Crespi 1997), and twice in the African mole-rats (Jarvis and Bennett 1993). The most recent addition to this group is the symbiotic marine shrimp genus *Synalpheus* (Duffy 1996a), in which eusociality has arisen independently at least twice and probably several times (Duffy 1998, Duffy et al. 2000). Wilson’s (1971) three criteria for eusociality have been demonstrated or inferred for at least five species of alpheids (Fig. 18.1): *Synalpheus regalis*, *S. filidigitus*, *S. rathbunae*, *S. “rathbunae A,” S. chacei*, and possibly *S. “paraneptunus small”* (Duffy 1996a, 1998, Duffy and Macdonald 1999, Duffy et al. 2000). Although behavior of most of these species is little known, all of them consist of colonies of tens to a few hundred individuals in which one or a very few females breed at any given time. Even a restrictive definition of eusociality based on irreversible caste differentiation (Crespi and Yanega 1995) would apply to *S. filidigitus*, in which the queen typically loses the large fighting claw and develops a second, minor-form chela, rendering her morphologically unique among members of the colony and presumably dependent on them for protection (Duffy and Macdonald 1999; see chapter frontispiece). There is currently no evidence of irreversible sterility in any *Synalpheus* species, as is also true of most eusocial lower termites and many wasps, although the complete reproductive skew and large colony size of several *Synalpheus* species strongly suggests that most individuals never breed in their lifetimes.
Consistent with the eusociality continuum of Sherman et al. (1995), colony size and reproductive skew both vary more or less continuously among species of *Synalpheus* (Duffy et al. 2000). Hence I use the term “eusociality” to refer to multigenerational, cooperative colonies with strong reproductive skew and cooperative defense.

The independent origins of quite similar social organizations in disparate taxa provide a valuable sample for comparative analysis of factors promoting the evolution of altruism.

**Figure 18.1** Phylogenetic hypothesis for West Atlantic *Synalpheus* species in the gambarelloides group (after Morrison et al. 2004). The tree is based on six-parameter weighted-parsimony analysis of partial mitochondrial cytochrome oxidase subunit I and 16S rRNA sequences and 45 morphological characters. Numbers above branches are bootstrap proportions (N = 1,000). Eusocial taxa are indicated as black line segments. Boxes indicate known development modes based on observations of eggs hatching in the laboratory: open boxes, swimming larvae; black boxes, crawling juveniles (direct development); gray boxes, both types of larvae have been reported. Quotation marks denote provisional names of undescribed species diagnosed in Ríos (2003).
(Alexander et al. 1991, Crespi 1994, 1996, Hart and Ratnieks 2004). For example, exploring eusociality in a symbiotic, diploid marine arthropod with gradual (p.390) metamorphosis provides insights into the generality of proposed explanations for eusociality based on haplodiploid sex determination (Hamilton 1964), parental care (Wilson 1971), and food–shelter coincidence (Alexander at al. 1991). More specifically, the multiple, relatively recent origins of eusociality in Synalpheus and the broad range of social systems found among its species provide a promising model system for addressing such hypotheses at a finer taxonomic resolution (Duffy et al. 2000, Duffy 2003). In this contribution, I review the phenomenon of eusociality in sponge-dwelling alpheid shrimp (Synalpheus), and I examine its adaptive significance and ecological and evolutionary consequences.
Diversity and Natural History

*Synalpheus* is a species-rich and abundant component of cryptic coral-reef faunas worldwide. In the West Atlantic, most *Synalpheus* species belong to the monophyletic "gambarelloides group" (Coutière 1909, Ríos 2003, Morrison et al. 2004; Fig. 18.1), all species of which are obligate inhabitants of sponges, living their entire lives within the host and feeding on its tissues or secretions (Ruetzler 1976, Erdman and Blake 1987, Ríos and Duffy 1999). The host thus constitutes a self-contained, highly valuable, and often long-lived (Reiswig 1973, Ayling 1983) resource, providing habitat, food, and protection from predators. Unoccupied hosts are in short supply (Duffy 1996c, 1996d, Duffy et al. 2000), so shrimp likely experience habitat saturation like that proposed to favor cooperative breeding in some social vertebrates (see Emlen 1997, Hatchwell and Komdeur 2000).

The species richness of *Synalpheus* is accompanied by considerable diversity in social organization, with species ranging from the heterosexual pair formers typical of the family Alpheidae to eusocial species living in colonies of hundreds of individuals with a single breeding queen. The current phylogenetic hypothesis suggests that eusociality has arisen three times independently within the gambarelloides species group. Four of the eusocial species (*S. regalis*, *S. filidigitus*, *S. rathbunae*, and *S. “rathbunae A”*) comprise a single clade, the ancestor of which is parsimoniously reconstructed as eusocial (Morrison et al. 2004; Fig. 18.1). For each of the two remaining eusocial taxa, *S. chacei* and *S. “paraneptunus small,”* the strongly supported sister taxa are socially monogamous species (Morrison et al. 2004). Similar colony structures in Indo-Pacific species outside the gambarelloides group suggest additional origins of eusociality (Duffy 1998).

Alpheids are commonly called snapping or pistol shrimp because of their enlarged major chela or fighting claw, present in both sexes. Most alpheids are fiercely territorial, defending against any individual other than a familiar mate (Hazlett and Winn 1962, Nolan and Salmon 1970, N. Knowlton and Keller 1982, Nakashima 1987, Gherardi and Calloni 1993). Social sponge-dwelling *Synalpheus* species are a conspicuous exception in that they live in dense colonies. In these social
species, snapping is used to defend and maintain the integrity of the colony against intruders (Duffy et al. 2002, Tóth and Duffy 2005).

Like decapod crustaceans generally, most species of Synalpheus produce planktonically dispersing larvae. Several species of Synalpheus, however, exhibit “direct development” in which eggs hatch into crawling juveniles with very limited dispersal (p.391) potential (Dobkin 1965, 1969). These include, among others, all eusocial species (Fig. 18.1). In direct-developing social species, allozyme evidence of strong population subdivision (Duffy 1993, 1996b) suggests highly restricted dispersal. Yet dispersal clearly happens regularly as virtually all appropriate sponges are occupied in the field, at least for highly social species (Duffy 1996c, 1996d).

Reproductive Biology and Mating Systems
Mature female Synalpheus are easily identified by visible ovaries and morphology, whereas males show no external signs of maturity. Because sex is indistinguishable externally in individuals other than mature females, I refer here to nonovigerous individuals as either “juveniles” (small) or “adults” (large). Recent scanning electron microscopy revealed male and female gonopores in similar frequencies in social Synalpheus colonies across a range of body sizes, suggesting that sex is determined early in these species (E. Tóth and R.T. Bauer, personal communication), in contrast to some other alpheids that can change sex (Suzuki 1970, Gherardi and Calloni 1993). Thus, adult size classes in social Synalpheus appear to include both males and nonbreeding females. Allozyme studies confirm that both sexes are diploid (Duffy 1993, 1996b).

Most alpheids, including many Synalpheus species, exhibit social monogamy (Correa and Thiel 2003), in which adults live in heterosexual pairs but are intolerant of other individuals in a territory. Since female mating receptivity is limited to a short period after the molt (Rahman et al. 2003) and sperm storage is absent (R.E. Knowlton 1971, N. Knowlton 1980, Nakashima 1987), the female must mate each time she ovulates. Experiments suggest that social monogamy in pair-forming alpheids is maintained both by benefits to males of mate guarding (Mathews 2003, Rahman et al. 2003) and by
cooperation between mates in defending the common burrow (Mathews 2002).

*Sympalpheus* is evidently unique among alpheids in that many species depart from this social monogamy. In addition to the ancestral pair forms, the genus includes communal species in which several to hundreds of pairs cohabit in a host with multiple females breeding (e.g., *S. longicarpus*, Erdman and Blake 1987; *S. brooksi*, Duffy 1992, 1996b) as well as fully eusocial species with colonies containing hundreds of individuals and only a single female breeding (Duffy 1996a, 1998, Duffy and Macdonald 1999). It is striking that these communal aggregations, with their strong reproductive skew, occur exclusively in sponges of moderate to large size (relative to the size of their shrimp inhabitants). In chapter 12, Baeza and Thiel (see also Thiel 2000) have suggested that the size of the host resource and constraints on movement among hosts strongly influence the expected mating system, and the unusual mating and social systems of many sponge-dwelling *Sympalpheus* seem consistent with this. Social monogamy appears to have been an important precursor to the evolution of eusociality in sponge-dwelling shrimp for at least two reasons: First, in conjunction with direct development, it fosters formation of close kin groups, and more specifically, long-term parent-offspring associations. Such families are otherwise rare among decapod crustaceans (but see chapter 17), although they appear common, if temporary, among peracarids (see chapters 14, 16). The second implication of social monogamy is that it provides opportunities for long-term cooperation among individuals, for example, in maintaining and defending the shared shelter.

(p.392) The Nature of Eusociality in *Sympalpheus*
Colony Organization

Of the several eusocial shrimp species, *Synalpheus regalis* has the largest colonies and strongest reproductive skew. Colony size (i.e., number of individuals within a sponge) ranges up to 350 individuals and colonies invariably contain only a single breeding female, the queen (Duffy 1996a). Relatedness among colony members calculated from allozyme data averaged 0.50 (Duffy 1996a), and several colonies showed strong heterozygote excesses (Duffy 2003). These data imply that *S. regalis* colonies consist largely of full-sib offspring of a single breeding pair and that outbreeding is the norm, since heterozygote excesses are expected where colony members are offspring of a single breeding pair homozygous for different alleles at the locus. Inbreeding, in contrast, produces heterozygote deficiencies, which were never found (Duffy 2003). Long-term reproductive monopoly by a single queen is also consistent with the strong correlation between queen body size and colony size in *S. regalis* (Duffy 1996a), which suggests coordinated growth of the breeding female and her colony. Thus, eusociality in *Synalpheus* has clearly arisen via the growth of nondispersing families, that

(p.393) is, through the subsocial route (*sensu* Wilson 1971), as appears true of most eusocial animals (Alexander et al. 1991). Experiments with captive colonies show that *S. regalis* discriminates between nestmates and other conspecifics entering the sponge, with even more pronounced aggression toward heterospecific intruders (Duffy et al. 2002). When faced with a nonnestmate conspecific, resident shrimp contacted it less and snapped more frequently than they did when faced with a nestmate (Fig. 18.2). Such discrimination presumably helps maintain integrity of the kin group, as it does in the remarkably sensitive kin discrimination system of social desert isopods (chapter 16).
**Figure 18.2** Behavioral differentiation among classes of individuals within colonies of *Synalpheus regalis*. Bars show mean numbers of contacts (left) and snaps (right) by resident small, large, and queen shrimp to each of three types of introduced intruders ($N=13$ independent experimental colonies). Top panels show colony totals; bottom panels show average numbers per individual resident. Resampling tests demonstrated that both foreign conspecific and heterospecific intruders elicited significantly fewer contacts and more snaps than did nestmate conspecifics (pooled across all individual classes), and that large males produced significantly more snaps per individual against heterospecific intruders than did other classes of individuals (after Duffy et al. 2002).
Caste and Division of Labor

The most fundamental feature of eusociality is “reproductive division of labor” between the queen and nonbreeding workers (Wilson 1971). In colonies of *S. regalis*, as in many eusocial insects, reproduction is restricted to the single queen and an apparently small number of male mates (Duffy 1996a). The queen also differs from other adults in being considerably less active and less aggressive (Duffy et al. 2002; J.E. Duffy, unpublished observations). In *S. filidigitus*, this reduced aggressiveness is manifested in a physical polymorphism in which mature queens lack a snapping claw, instead bearing two minor-form chelae (Duffy and Macdonald 1999). This polymorphism is the clearest example in eusocial shrimp of discrete morphological caste differentiation such as that found in social insects (Wilson 1971). Females with two minor chelae have also been reported in the eusocial *S. rathbunae* (Chace 1972) and in *S. crosnieri* (Banner and Banner 1983). This situation strongly implies that queens in these social species do not aggressively dominate other individuals and may indeed be protected by them.

Among nonbreeders in *S. regalis* colonies, the clearest evidence of division of labor involves colony defense. In captive colonies, small individuals were sedentary and often congregated in groups to feed, whereas large individuals moved more frequently around the sponge, were more aggressive, and spent more time near the sponge periphery where intruders would be first contacted (Duffy et al. 2002, Duffy 2003; Fig. 18.2). These size-based differences presumably reflect the ontogenetic development of aggressive behavior typical of most animals. Even within the large size class, however, a small proportion of individuals are responsible for most aggressive attacks against intruders, and these frequent attackers have proportionally larger major chelae than the others (E. Tóth and J.E. Duffy, unpublished observations). Thus, observations and experiments suggest that a group of behaviorally specialized and morphologically distinct large individuals in *S. regalis* shoulder the burden of colony defense, leaving small juveniles free to feed and grow and the queen free to feed and reproduce.

The Adaptive Significance of Sociality in Sponge-Dwelling Shrimp

Evolution of Shrimp Sociality: An Individual-Level Perspective
Hamilton (1964) revolutionized understanding of social behavior by putting interactions among individuals into an evolutionary context with the deceptively simple equation: \( rB - C > 0 \). Hamilton's rule states that natural selection will favor a gene (p.394) for altruistic behavior if the benefit (\( B \)) of the behavior to the recipient, weighted by relatedness (\( r = \) proportion of genes shared) between donor and recipient, is greater than the cost (\( C \)) to the donor. Hamilton's rule emphasizes that social systems arising from such interactions depend both on genetic structure of groups and on the ecological costs and benefits associated with membership. In practice, the origin of eusocial or cooperatively breeding groups can be analyzed as the outcome of a series of individual decisions (Emlen 1994, Brockmann 1997, Helms Cahan et al. 2002): (1) whether to disperse or stay on the natal territory; (2) given the decision to stay, whether to breed; and (3) given the decision not to breed, whether to help others in the group. The term "decision" is used loosely because these outcomes may reflect either individual choices or actions forced by other individuals. I consider each of these three decisions in turn.

**Whether to Disperse**

The relative fitness benefits of dispersal versus remaining in the natal territory depend on ecological constraints on independent breeding and on any benefits that accrue from remaining in the natal group (Koenig et al. 1992, Emlen 1994). A primary ecological constraint on independent breeding in many social vertebrates is habitat saturation, that is, shortage of available territories (Emlen 1984, 1994, Koenig et al. 1992, Hatchwell and Komdeur 2000). Similarly, in several social insects, evidence suggests that low success of independent breeding has selected for delayed dispersal (Lin and Michener 1972, Strassmann and Queller 1989, Brockmann 1997).

In decapod crustaceans, the option to disperse is constrained in part by development mode. Species with swimming larvae seemingly have little choice but to disperse (although some terrestrial decapods have ingeniously circumvented this constraint; see chapter 17), precluding formation of kin groups. Thus, cooperative behavior and strong reproductive skew are not known from those *Synalpheus* species with swimming larvae (Fig. 18.1), even though some such species
occur in large groups (e.g., *S. longicarpus*; Duffy 1992, Duffy et al. 2000). In contrast, species with direct development, including all social *Synalpheus* species, may disperse as juveniles or stay in the natal sponge.

In social sponge-dwelling shrimp, colony cohort structure (e.g., Duffy and Macdonald 1999) and relatedness estimates (Duffy 1996a) indicate that most juveniles remain for extended periods, probably permanently, in the natal sponge. Moreover, field evidence indirectly supports the hypothesis that suitable habitat is saturated in that nearly all host sponges are occupied by shrimp (Duffy 1992, 1996d). Thus, independent breeding opportunities appear limited by shortage of territories (hosts). Forgoing dispersal may also confer direct benefits in that juvenile shrimp likely benefit from the larger size and more effective defensive capabilities of resident adults. Thus, individual shrimp remaining in the natal sponge as juveniles may often have higher inclusive fitness than those that disperse.
Whether to Breed

Once an individual has chosen to remain in its natal group, it faces the decision whether to attempt breeding. In eusocial colonies, by definition, most individuals do (p.395) not breed. Understanding what controls this inequity is the central problem of eusociality and is addressed formally by reproductive skew models (Keller and Reeve 1994, Johnstone 2000, Reeve and Keller 2001). The main factors hypothesized to influence reproductive skew include the severity of ecological constraints on independent breeding, genetic relatedness among individuals, and the relative power of individuals to control reproduction by others. Although genetic and behavioral data are currently insufficient to test reproductive skew models rigorously in Synalpheus, some tentative conclusions are possible. Transactional concession models (Reeve et al. 1998) predict that skew will be pronounced in colonies of close relatives living under strong ecological constraints, which is consistent with data from social shrimp. In small colonies of social animals such as some wasps (Michener and Brothers 1974, Jeanne 1980, Fletcher and Ross 1985), cooperatively breeding vertebrates (Emlen 1997), and the eusocial naked mole-rat (Reeve and Sherman 1991), this reproductive skew is maintained by behavioral dominance. But in eusocial Synalpheus, observations of captive colonies found no evidence of aggression or behavioral dominance by the queen (Duffy et al. 2002; J.E. Duffy, unpublished observations). And in S. filidigitus, the queen's lack of a fighting claw further implies that she cannot maintain her sole breeding status through aggression.

In large social colonies such as those of S. regalis and S. filidigitus, reproductive monopoly might be explained by the "worker policing" (Ratnieks 1988) or "majority-rules" model (Reeve and Jeanne 2003). This model predicts that a single individual—the "virtual dominant"—can come to monopolize a colony's reproduction even without being behaviorally dominant, simply by being the individual to which other colony members have the greatest average genetic relatedness (Reeve and Jeanne 2003). This situation is most likely in mother–offspring associations. In such colonies, nonbreeding workers are more closely related to the current queen's offspring (their siblings; r =0.50 in diploids) than they would be to offspring of a sibling worker (their nieces/nephews; r =0.25), so selection will favor subordinates ("workers")
preventing one another from breeding in favor of reproduction by their mother, the queen. The majority-rules model is supported by progeny sex ratios in some social Hymenoptera that are consistent with control by workers rather than the queen (Ratnieks 1988, Queller and Strassmann 1998). Worker policing is also an attractive, albeit yet untested, hypothesis for reproductive skew in social Synalpheus, in which colonies appear to consist mainly of the resident queen's offspring. Finally, the large colony size and complete reproductive skew (single breeding female) typical of social Synalpheus suggest that many colony members never reproduce. Explaining such lifetime sterility is the most difficult problem of social biology—and indeed, of evolution generally, as recognized by Darwin. A recent model (Jeon and Choe 2003) finds that evolution of sterile castes occurs only under very restrictive conditions, namely, saturated (large), asymmetrical relatedness (parent–offspring) groups with complete reproductive skew. These conditions describe Synalpheus regalis colonies well and are consistent with Jeon and Choe's (2003) model.

A final potential explanation for reproductive skew in social shrimp colonies involves incest avoidance. Where social colonies consist of close relatives, such as full-sib offspring of outbred parents, avoidance of incest often can explain why offspring of the breeding pair do not attempt to breed (Emlen 1995). This hypothesis is supported, in part, by an elegant series of experiments in the eusocial Damaraland mole-rat, which lives in colonies consisting of a breeding pair and one or more cohorts of its adult offspring (Bennett et al. 1996, Cooney and Bennett 2000, Greeff and Bennett 2000). Nevertheless, recent genetic analyses show that Damaraland mole-rat colonies often contain unrelated, nonbreeding individuals, suggesting that reproductive skew cannot be maintained solely by incest avoidance (Burland et al. 2004). Maintenance of reproductive skew by incest avoidance is also consistent with some data from eusocial termites (Shellman-Reeve 2001). Incest avoidance is an attractive possibility for the strong reproductive skew in S. regalis, in which colonies consist mostly of full-sibs descended from a single breeding pair (Duffy 1996a, 2003). In such situations, unrelated potential mates would appear scarce. On the other hand, the heterozygote excesses common in colonies of S. regalis (Duffy 2003) clearly indicate that the queen breeds with an unrelated mate, which in turn implies sufficient dispersal to avoid
inbreeding. If dispersal indeed brings unrelated individuals to a sponge frequently, some mechanism must prevent most of them from breeding since S. regalis colonies maintain strong reproductive skew. The frequency of immigration to colonies, conditions under which it occurs, and mechanisms suppressing immigrant (and resident) breeding are important frontiers for future research.
Whether to Help

Given that an individual has chosen to stay in its natal group without breeding, the final decision in the “social trajectory” (Helms Cahan et al. 2002) is whether to help, that is, participate in activities that entail individual investment and that benefit other group members. In social insects and vertebrates, helping most commonly involves provisioning young and defending the nest or territory. Currently, we have no evidence of provisioning of young in social shrimp. Even very small juvenile shrimp appear capable of feeding on their own. Thus, foraging outside the sponge is unnecessary, and our admittedly limited observations of captive colonies have found no evidence that nonbreeders care directly for the queen or her young. Instead, the principal work of social Synalpheus appears to be defense from competitors, and perhaps predators. In this sense, social shrimp are similar to “fortress defender” social insects (Queller and Strassmann 1998), such as gall-forming aphids and thrips that live inside their food source and have independent young (Choe and Crespi 1997, Aoki 2003). Insofar as social aggregations provide a safe place for offspring to live, colony defense might be interpreted as a form of parental care.

The most direct evidence that nonbreeding individuals help in shrimp colonies is that large individuals regularly engage in dangerous defense of the colony, despite genetic evidence (Duffy 1996a) that most of them do not breed. Experiments show how this cooperative defense enhances effectiveness of social colonies at repelling intruders, and thus of holding and dominating the host resource (Tóth and Duffy 2005). Conspecific intruders attempting to enter a sponge elicited vigorous snaps from resident S. rathbunae inside. Frequency of snaps by residents increased sharply after intruders were introduced (Fig. 18.3a), but sometimes these individual snaps failed to repel intruders, which caused many residents suddenly to begin snapping in unison, producing a distinctive crackling noise lasting up to tens of seconds. Up to 60% of the visible colony members were involved in these “coordinated snapping” events, which were observed exclusively after introducing intruders (Fig. 18.3b) and usually (p.397)
Figure 18.3 Defensive responses to nest intruders by eusocial *Synalpheus rathbunae* in intact sponges in the laboratory. (a and b) Numbers of single snaps (a; $N=8$) and coordinated snap events (b; $N=8$) for 30 minutes before (open symbols) and 30 minutes after (solid symbols) introduction of conspecific intruders in each of eight colonies. (c and d) Frequency distributions of numbers of snaps required to repel an intruder when the intrusion failed (c; $N=70$) versus succeeded (d; $N=27$) in eliciting a coordinated snapping event. Arrows above histograms show the mean across colonies of the median value per colony. Coordinated snapping was an escalated response that occurred after single snaps were unsuccessful at repelling the intruder. From Tóth and Duffy (2005, used by permission).
occurred only after intruders ignored repeated snaps by single defenders (Fig. 18.3c,d). Coordinated snapping effectively repelled intruders when repeated snaps by single defenders did not (Tóth and Duffy 2005), supporting the conclusion that nonbreeding helpers enhance defensive capability of eusocial shrimp colonies. Finally, patterns of field abundance are also consistent with superior defense by eusocial colonies.

**Figure 18.4** Ecological consequences of eusociality in sponge-dwelling shrimp. (a and b) Dominance of the host sponge is positively related to degree of social organization (eusociality index; Keller and Perrin 1995) among species of *Synalpheus*; phylogenetically controlled comparisons (not shown) are significant for percentage of individuals in sponge (a) and marginally nonsignificant for number of cohabiting congener species (b) (after Duffy et al. 2000). Symbols show median ± 95% confidence interval. (c and d) Relative abundance of eusocial versus noneusocial *Synalpheus* species in samples of sponge-infested coral rubble from shallow patch reefs in Belize (after Macdonald et al. 2006). (c) Mean (± standard error) proportions of sampled shrimp that belonged to eusocial versus noneusocial gambarelloides-group species and to non-gambarelloides species ($N = 13$ samples). (d) Mean (± standard error) proportional abundance per species for eusocial, noneusocial, and non-gambarelloides species.

Phylogenetically controlled comparisons among *Synalpheus* species show that, whereas noneusocial species typically share their host sponge with congeners, eusocial species tend to dominate numerically the sponges they occupy; indeed, eusocial species are typically found in dense, monospecific groups in their hosts (Duffy et al. 2000; Fig. 18.4).
These data support the hypothesis that defense by nonbreeders enhances fitness at the colony level. But what are the benefits of helping to the helper? Defensive behavior in eusocial shrimp colonies has both direct benefits, in protecting oneself against intruders, and indirect fitness benefits in protecting close relatives. Nonbreeders in *S. regalis* colonies are defending primarily their parents and siblings (p.399) (Duffy 1996a, 2003), with whom they share the same genetic relatedness as to their own offspring. Moreover, the defense may have low costs in terms of average offspring production: field surveys of *S. regalis* colonies showed that total colony egg production (i.e., clutch size of the resident queen) was strongly and linearly related to colony size, whereas average per capita egg production (i.e., queen clutch size divided by number of colony members) declined little as colony size grew to 350 individuals (Duffy et al. 2002).

In summary, data from eusocial shrimp offer considerable circumstantial support for the hypothesis that ecological constraints are a fundamental driver of cooperative breeding: (1) host sponges appear to be a limiting resource for sponge-dwelling shrimp species; (2) offspring of eusocial colonies generally do not disperse, thus forming families of close genetic relatives; (3) these families develop strong reproductive skew, probably as a result of both incest avoidance and the collective interest of most colony members in maintaining their parents as sole reproductives; and (4) nonbreeding individuals engage in group defense that enhances the colony's productivity and dominance of the host sponge resource. By doing so, nonbreeders gain both direct benefits of enhanced protection and inclusive fitness benefits of enhancing survival and productivity of nondescendent kin.

Evolution of Shrimp Sociality: A Comparative Perspective

The preceding discussion examined the adaptive significance of shrimp eusociality from the perspective of a nonbreeding individual. But why has eusociality evolved in *Synalpheus* and not in other crustacean taxa? Here I ask whether sociality in shrimp might be explained by two models for the evolution of eusociality/cooperative breeding, one based primarily on insects (Crespi 1994) and one on birds (Hatchwell and Komdeur 2000).

The Fortress Defense Hypothesis
Crespi (1994; see also Alexander et al. 1991) proposed that three conditions are sufficient, though not necessary, to explain most known cases of eusociality in that all taxa that met the criteria in his judgment are eusocial. (1) Coincidence of food and shelter in an enclosed habitat creates a highly valuable, often long-lived resource that promotes accumulation of kin and frees juveniles from foraging to accomplish other tasks. (2) Strong selection for defense arises from the high value of food-habitat resources, which are vulnerable to attack by competitors and/or predators and puts a high premium on cooperative defense. (3) Ability to defend the resource creates opportunities for nonbreeding individuals to specialize in protecting kin, thus gaining large indirect fitness by defending the colony. Queller and Strassmann (1998) termed eusocial colonies of this type “fortress defenders.”

Eusociality in sponge-dwelling shrimp (Duffy 1996a) independently supports Crespi’s (1994) hypothesis. First, the near absence of unoccupied sponges in the field (Duffy 1996d, Duffy et al. 2000) and the aggressive defense of host resources (Duffy et al. 2002, Tóth and Duffy 2005) indicate that habitat is saturated. Food and habitat are clearly coincident for sponge-dwelling shrimp generally, and some sponges reach sizes that can support thousands of shrimp (Pearse 1932) and live for decades (p.400) (Reiswig 1973, Ayling 1983). Genetic and morphometric differentiation among shrimp demes in individual sponges (Duffy 1996b, 1996c) suggests long-term occupation by particular genetic lineages of shrimp with little exchange among sponges. Thus, the sponge resource is both valuable and long-lived, fosters formation of kin groups, and provides a shrimp family with the potential for resource inheritance (Myles 1988). Second, selection for defense is supported indirectly by the evidence that suitable hosts are in short supply and by the ubiquity of aggression and territoriality among alpheids. Together, these factors suggest that pressure from enemies is likely strong and persistent for sponge-dwelling alpheids. Third, sponge-dwelling shrimp are clearly well endowed for defense by the powerful snapping claw, used in aggressive contests, and in social species by cooperative defense of the host sponge (Tóth and Duffy 2005). Andersson (1984) and Starr (1985) similarly emphasized that the transition from group living to eusociality has occurred only in taxa with effective weapons, notably, the sting of...
aculeate Hymenoptera. Thus, eusocial *Synalpheus* appear to meet each of Crespi's (1994) three criteria. The puzzle is that *all* sponge-dwelling *Synalpheus* appear to meet these criteria. Yet these species range from pair forming (the majority of species), through communal, to eusocial. It thus appears that additional criteria are necessary to explain eusociality in shrimp. The clearest of these involves life history.
Turnover of Breeding Opportunities

Life history has fundamental consequences for social organization and evolution. For example, parental care is an important prerequisite for eusociality in insects and cooperative breeding in vertebrates (Alexander 1974, Andersson 1984, Alexander et al. 1991), as well as crustaceans (chapter 14). Long periods of offspring dependence (Queller 1989) and delayed age of reproduction (Gadagkar 1991) appear important to social evolution in insects. In birds, recent analyses have used phylogenetically controlled comparisons to assess the importance of life history and ecology in evolution of sociality (Arnold and Owens 1998, 1999). Cooperative breeding was concentrated in particular families characterized by low fecundity and high adult survival, and within these families, ecological factors—specifically, sedentariness and a warm, stable environment—significantly predicted the incidence of cooperative breeding among species. These results were interpreted as showing that life history features predisposed lineages toward sociality, after which ecological factors influenced which species within lineages evolved cooperative breeding. This interaction of life history and ecology limits the turnover rate of breeding opportunities, which appears to be the best predictor of the distribution of cooperative breeding among species of birds (Hatchwell and Komdeur 2000).

It seems clear that a similar interaction of life history and ecology influences evolution of sociality in shrimp. In many marine invertebrate groups, direct development is associated with lower fecundity and higher juvenile survival (predictors of cooperative breeding in birds), compared with planktonic dispersal (Strathmann 1985). Among crustaceans, family and social groups occur almost exclusively in taxa with direct development (chapter 14). Indeed, the most striking exception proves the rule: terrestrial crabs of Jamaica raise and care for their planktonic larvae in carefully prepared and managed pools of rainwater in leaf axils (reviewed in chapter 17), that is, in restricted spaces that prevent dispersal. Thus, life history traits that restrict dispersal are an important prerequisite for family living in crustaceans.

In the gambarelloides species group of Synalpheus, unlike in birds, life history is less conserved than the fundamental ecological characteristic of life in sponges. That is, all species in the group are obligate sponge dwellers, sharing the
sedentary lifestyle in warm, stable environments that fosters cooperative breeding in birds (Arnold and Owens 1998). Life history, in contrast, varies among Synalpheus species, which include both direct developers and species with planktonically dispersing larvae. Thus, the role of life history in promoting eusociality should be especially clear in Synalpheus because dispersal potential varies among species while general ecology is fairly constant. As expected, eusociality occurs only in Synalpheus species with direct development, supporting low dispersal as a prerequisite for eusociality in this group (Fig. 18.1).

Finally, high adult survival correlates with cooperative breeding in birds (Arnold and Owens 1998) and seems likely in sponge-dwelling Synalpheus, as well. The interior of sponges is well insulated from enemies and abundant with food, compared with the rock crevices in which most other alpheids live. The very low fecundity of some Synalpheus species (e.g., S. filidigitus; median, 4.5 eggs per clutch; range, 1–29; Duffy and Macdonald 1999) also indirectly suggests high survival, which is necessary to balance low fecundity in a population at equilibrium.

**Comparative Analysis of Shrimp Social Evolution: Synthesis**

Many crustacean taxa meet one or more of Crespi's criteria, but few meet all of them. For example, several crustaceans associate with valuable hosts that provide both shelter and food, and some of these are well equipped with powerful claws to defend their host resource (Patton 1974, Bruce 1976, 1998). But, to my knowledge, all of these groups produce planktonically dispersing larvae, precluding formation of kin groups. Other promising candidates for crustacean eusociality include the leucothoid or anamixid amphipods, which have direct development and live within sponges or ascidians. Some species are found in apparent family groups (Thomas 1997, Thiel 1999, 2000; see also chapter 14), and males bear hypertrophied gnathopods (claws), presumably sexually selected, that might be employed in cooperative defense. To date, however, I know of no reports of multigenerational colonies with strong reproductive skew (eusociality) in amphipods. Thus, for marine crustaceans, I would argue that Crespi's three criteria for eusociality must be supplemented by an additional one: life history that allows restricted dispersal.
and long-term kin interaction. The association between direct development and kin grouping in crustaceans generally, and among species of *Synalpheus* specifically, is consistent with this hypothesis.

In summary, eusociality in sponge-dwelling shrimps appears to have been favored by a combination of four characteristics shared with several social insect lineages but possibly unique in the Crustacea: (1) direct development resulting in limited dispersal and kin association (2) ecological specialization on a valuable, long-lived resource; (3) strong enemy pressure associated with occupation of the host resource; and (4) possession of weaponry (the snapping claw) effective in defending it. Together, these factors promote long-term occupation of specific nest sites by multigenerational family groups, conditions that result in low turnover of breeding opportunities and persistence of dynastic lineages headed by one or a few breeders of each sex, with nonbreeding adults defending the colony from intruders. The first filter in the process of social evolution among sponge-dwelling shrimp appears to have been evolution of direct development, in that eusociality has evolved in none of the clades characterized by pelagic swimming larvae but has evolved independently in at least two or three clades containing direct-developing species (Fig. 18.1). Explaining the variation in sociality among direct-developing species of *Synalpheus* is more challenging because all such species have weapons and coincident food and shelter. It remains for future research to determine whether variance among species in availability of host resources and/or the strength of enemy pressure can explain which species or populations evolve eusociality.

Ecological and Evolutionary Consequences of Eusociality in Shrimp
Ecological Dominance

Eusocial insects are prominent members of most terrestrial ecosystems, dominating not only the insect fauna but also animal biomass generally (Wilson 1990). This dominance is due largely to the superior ability of organized cooperative colonies to obtain and process resources and to defend themselves against both enemies and harsh environmental conditions. Among sponge-dwelling marine animals, a parallel trend is evident. Using phylogenetically independent contrasts, Duffy et al. (2000) showed that eusocial species had higher relative abundance within sponges than did less social congeners. Eusocial species also use a larger number of host species, on average, than do noneusocial species (Macdonald et al. 2006). In quantitative samples of sponge-encrusted reef rubble from Belize, the average eusocial shrimp species was 17 times more abundant than the average noneusocial species (Fig. 18.4d), and eusocial species made up 68% of the shrimp collected (Fig. 18.4c; Macdonald et al. 2006). Thus, eusocial shrimp species appear to be more productive and more effective competitors for the limited sponge resource than are their noneusocial congeners.

Importantly, this advantage of eusociality is realized only in the highly specialized niche within living sponges, whereas free-living alpheids that inhabit rock crevices or burrow in sediments are universally monogamous pair formers. Again, this pattern supports the argument that coincidence of food and shelter selects for the fortress-defense type of eusociality (Crespi 1994). Thus, while eusociality appears to confer advantages in the specialized symbiotic niche within sponges, it appears not to have been selected in more open marine habitats. Consequently, the ecological impacts of eusocial shrimp are much more limited than those of widely foraging eusocial insects (Queller and Strassmann 1998).
Morphological Evolution

Among some eusocial insects, the specialization of worker groups on different tasks is accompanied by morphological differentiation into discrete castes. In certain large-colony ants and termites, this caste specialization has led to spectacular morphological differentiation among groups within a colony (Wilson 1971, Hölldobler and Wilson 1990). Although such dramatically different castes are not found in shrimp (or in (p. 403) most social insects), eusocial shrimp species do show evidence of morphological evolution compared with less social relatives (E. Tóth and J.E. Duffy, unpublished observations). Allometry of social species differed consistently from that of pair-forming species in each of two lineages in which eusociality has arisen independently. First, queens in social colonies had smaller fighting claws than did females in pair-forming species. Second, allometry of fighting claw size among other colony members was steeper in social than in pair-forming species. Finally, social species showed a change in allometry with increasing colony size; large but not small colonies exhibited a biphasic allometry of fighting claw and finger size (i.e., slope of the relation changes abruptly between smaller and larger individuals), indicating a distinctive group of large individuals possessing relatively larger weapons than other colony members (E. Tóth and J.E. Duffy, unpublished observations). These patterns are similar to those seen in some eusocial insects and naked mole-rats and emphasize that social life has had similar evolutionary consequences in disparate lineages.

Future Directions

Many challenges remain to understanding eusociality in snapping shrimp, but some solutions should soon be within reach. For example, reproductive skew models make testable predictions about how reproductive skew and cooperation arise as a function of genetic relatedness, disparities in fighting ability among individuals, and ecological constraints on independent breeding (e.g., Keller and Reeve 1994, Reeve et al. 1998, Reeve and Jeanne 2003). Testing these predictions will require high-resolution genetic markers to measure relatedness among interacting individuals and methods for observing and manipulating shrimp interactions under quasi-natural conditions. Progress is being made: shrimp have been observed for periods up to a few weeks in captivity (Duffy et
al. 2002, Tóth and Duffy 2005), and microsatellite markers are currently under development.

Some specific questions for future research include the following: Do habitat saturation and other ecological constraints foster reproductive skew and cooperation in sponge-dwelling shrimp? Similarly, do the rarity and size of host sponges influence mating systems as predicted (chapter 12)? Now that a phylogeny is available for the gambarelloides species group (Morrison et al. 2004), these hypotheses should be testable via a comparative approach. What is needed are quantitative field data on distribution and demography of host sponge populations. Similarly, more complete data on development mode will allow a rigorous comparative test of the hypothesis that restricted dispersal is the first “filter” determining which species can form social kin groups (Fig. 18.1).

Does a “majority-rules” model of social evolution explain the extreme reproductive skew typical of eusocial shrimp? Given the evidence that queens are incapable of enforcing their dominance by aggression (Duffy and Macdonald 1999), the majority-rules prediction should be testable simply by measuring whether colony members are indeed more closely related to the queen than to anyone else. Experimental manipulations of queen presence, potential chemical signals, and relatedness in captive (or wild) colonies would also yield valuable insights into mechanisms maintaining reproductive skew.
Summary

Sponge-dwelling *Synalpheus* shrimp comprise a clade of approximately 30 species that range from socially monogamous pairs to eusocial colonies of hundreds of individuals. Eusocial colonies have evolved at least three times independently within *Synalpheus* and contain multiple cohabiting generations, with one or a few breeders of each sex and nonbreeders that defend the colony from intruders. Similarly to social insects on land, eusociality in sponge-dwelling shrimp has resulted in numerical ecological dominance within their niche and in consistent changes in allometry suggestive of morphological caste evolution. Comparison of sponge-dwelling shrimp with other animal taxa reveals several shared characteristics of life history and ecology suggested to promote cooperative breeding and eusociality in insects and vertebrates. First, social shrimp share with cooperatively breeding birds a constellation of factors that lead to low turnover of breeding opportunities, including low fecundity, high adult survival, sedentariness, and life in a warm, stable climate. Second, social shrimp share three conditions hypothesized to explain the distribution of “fortress defense” eusociality in insects: coincidence of food and shelter, strong enemy pressure, and ability to defend the food–shelter resource. Combining these two approaches, I hypothesize that coincidence of four conditions favored evolution of eusociality in certain *Synalpheus* lineages: (1) direct development resulting in limited dispersal and kin association; (2) specialization on a valuable, self-contained, and long-lived resource; (3) strong competition for the host resource; and (4) possession of a weapon (the snapping claw) effective in monopolizing it. These factors allow multigenerational occupation of nest sites, resulting in low turnover of breeding opportunities and selecting for cooperative defense by philopatric offspring that lack breeding opportunities. Coincidence of these characteristics is rare within Crustacea and may explain why *Synalpheus* contains the only known eusocial marine animals. Nevertheless, explaining why certain direct-developing sponge dwellers within the genus are social and other species are not remains a challenge.

Acknowledgments
I am grateful to the National Science Foundation (DEB-9201566, DEB-9815785, IBN-0131931) and the Smithsonian Institution’s Caribbean Coral Reef Ecosystem (CCRE) program for long-term support of my research on sponge-dwelling shrimps; Klaus Ruetzler, Mike Carpenter, the late Brian Kensley, and the staff of the Pelican Beach resort for facilitating work in Belize; and Tripp Macdonald, Cheryl Morrison, Rubén Ríos, and Eva Tóth, whose collaboration and camaraderie have been critical to this work. I thank Jae Choe, Martin Thiel, and an anonymous reviewer for comments that improved the manuscript. This is contribution #2800 from the Virginia Institute of Marine Science and contribution #789 from the CCRE.

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