8 Sociality in Shrimps

Kristin Hultgren, J. Emmett Duffy, and Dustin R. Rubenstein

Overview

The genus *Synalpheus* is a species-rich group of snapping shrimps (Alpheidae) common to coral-reef habitats worldwide. The informal "gambarelloides group" (Coutière, 1909; Dardeau, 1984) is a monophyletic clade (Morrison, *et al.*, 2004; Hultgren, *et al.*, 2014) of approximately forty-five currently known species of *Synalpheus* that live symbiotically within sponges and are mostly restricted to the tropical West Atlantic. Sponge-dwelling *Synalpheus* species exhibit a range of social systems, from the family's ancestral condition of pair-living, to social groups with varying numbers of queens and workers (Duffy, 1996a; Duffy & Macdonald, 1999; Duffy, *et al.*, 2000; Duffy, 2003; Duffy, 2007). This social diversity is evident in the distribution of social structures and patterns of reproductive skew among species of *Synalpheus*, which are qualitatively similar to those observed across the entire range of social vertebrate and invertebrate taxa. Eusociality has evolved independently multiple times within *Synalpheus* (Duffy, *et al.*, 2000; Morrison, *et al.*, 2004). Thus, this socially diverse group – including the only known eusocial species from the marine realm – offers a unique opportunity to study the evolution of sociality in the sea.

I SOCIAL DIVERSITY

8.1 How Common is Sociality in Shrimps?

The Crustacea is one of the most phylogenetically, morphologically, and ecologically diverse groups of organisms in the marine realm, with over 50,000 species living in nearly every conceivable ocean habitat (Martin & Davis, 2001). Crustaceans also exhibit a wealth of interesting behavioral variation, including a range of social systems

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as diverse as in their terrestrial relatives (Duffy & Thiel, 2007). Although crustacean social behavior has been less studied than that of insects or vertebrates, group living has been documented in a wide range of terrestrial, freshwater, and marine species (Linsenmair, 1987; Shuster & Wade, 1991; Diesel, 1997; Duffy, 2010). Crustacean social behavior has reached its apex in the diverse shrimp genus *Synalpheus*. Shrimp in the genus *Synalpheus* belong to the snapping shrimp family Alpheidae, whose common name derives from an enlarged claw – used primarily for communication, aggression, and defense against predators, conspecifics, and heterospecifics – that "snaps" upon closing to produce a powerful jet of water (Nolan & Salmon, 1970; Versluis, *et al.*, 2000). The vast majority of *Synalpheus* species and other alpheid shrimp live in pairs that are apparently monogamous, within a burrow or host (typically a sponge or a crinoid echinoderm in the case of species in the genus *Synalpheus*) that they defend vigorously against intruders (Duffy, 2007; Hughes, *et al.*, 2014). Within the single clade of approximately 45 West Atlantic *Synalpheus* species in the *Synalpheus gambarelloides* species group, eusociality has evolved multiple times (Duffy, *et al.*, 2000; Morrison, *et al.*, 2004; Duffy & Macdonald, 2010). Species within this highly social gambarelloides group dwell exclusively in the interior canals of sponges, which they depend upon as a long-lived, predator-free host and food source. Thus, all sponge-dwelling *Synalpheus* species – social or otherwise – meet the criteria of the "fortress defender" social insects that live inside their food sources (Queller & Strassmann, 1998). Specifically, the shrimps are engaged in a symbiotic relationship with their sponge host – a living and continually growing food source – much like some gall-dwelling insect species (Crespi & Mound, 1997; Stern & Foster, 1997; Chapter 6).

8.1.1 Instances of Social Behavior in Snapping Shrimps

Eusociality was first reported in the species *S. regalis*, which exhibits extreme reproductive skew (i.e. colonies with a single breeding female or "queen") and lives in large kin-based colonies of tens to a few hundred individuals, apparently the full-sib offspring of the queen and a single male (Duffy, 1996a). The original discovery of eusociality was based on demographic data showing only a single ovigerous queen (i.e. female with ovaries or eggs) within a sponge, allozyme evidence of close relatedness among colony members, and behavioral experiments demonstrating size-based division of defensive labor (Duffy, 1996a). Eusociality has since been reported from eight other species in this group, and comparative analyses suggest eusociality has arisen independently at least four times (Duffy, *et al.*, 2000; Morrison, *et al.*, 2004; Duffy & Macdonald, 2010) (Figure 8.1). However, group living is not confined to the eusocial species, but rather varies along an apparent continuum in the gambarelloides group, where it ranges from eusocial colonies with single or multiple queens, to communal groups with approximately equal sex ratios (i.e. mated pairs), to pair-living species.

Synalpheus is a globally-distributed lineage, and eusociality is not confined to the West Atlantic gambarelloides group. For example, large colonies of the sponge-dwelling species *S. neptunus neptunus* with a single ovigerous queen have been reported from Indonesia (Didderen, *et al.*, 2006), and colonies with two queens and more than

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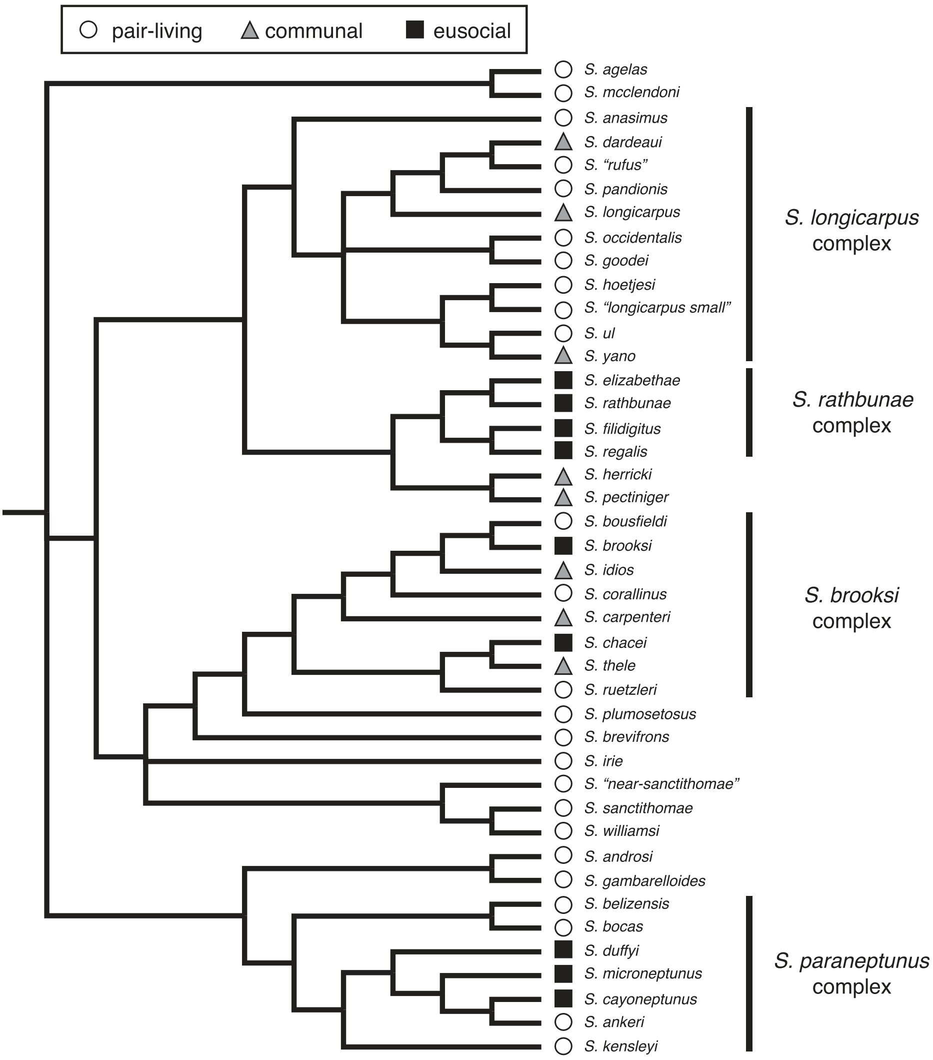

Figure 8.1. Bayesian phylogenetic tree of West Atlantic *Synalpheus* (after Hultgren & Duffy, 2011). The original tree was built from thirty-three morphological characters and three genetic markers: (1) the mitochondrial cytochrome oxidase I gene (COI, ~600 bp of the 5' coding region); (2) the mitochondrial large-subunit ribosomal gene (16S, ~510 bp); and (3) the nuclear gene elongation factor 2 (EF2, ~700 bp). The social system of each of the 42 species depicted in the tree is indicated with symbols defined in the legend. Importantly, some normally pair-living species occasionally occur as communal groups. Identified but undescribed species are noted in quotations.

100 non-ovigerous individuals have been reported in the sponge-dwelling species *S. paradoxus* from the Red Sea (Banner & Banner, 1981). Similarly, large colonies with high reproductive skew have been found in several other species from Indonesia (*S. fossor, S. hastilicrassus*, and *S.* aff. *neomeris*: Didderen, *et al.*, 2006) and East Africa (*S. crosnieri*: Banner & Banner, 1983). In at least two other sponge-dwelling *Synalpheus*

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species, large colonies of non-ovigerous individuals with no queens have been reported, including *S. dorae* (Bruce, 1988) and *S. neptunus germanus* (Banner & Banner, 1975). Virtually nothing else is known about these putatively eusocial Indo-Pacific taxa, but interestingly, all reports of potential eusociality outside of the gambarelloides group also come from obligate sponge-dwelling species, suggesting that inhabitation of sponge hosts is a crucial component of sociality in these crustaceans.

8.1.2 Dimensions of Shrimp Sociality

Sociality in snapping shrimp varies in several dimensions. Three of these components – reproductive division of labor (i.e. reproductive skew), overlapping generations, and cooperative social behavior – comprise the classic criteria for eusociality (Wilson, 1971; Sherman, *et al.*, 1995). A fourth component, group or colony size, is also a crucial component of social diversity in snapping shrimp, as well as in other taxonomic groups (Bourke, 1999).

(1) Reproductive Skew. This describes the degree of asymmetry in distribution of direct reproduction among same-sex individuals within a group (Vehrencamp, 1983; Rubenstein, 2012). Reproductive skew among *Synalpheus* species varies from colonies in which nearly all females are ovigerous and breeding, to those in which only one is. Although we do not know how reproduction is shared among co-breeding females within a colony, they often appear to produce similarly sized clutches of eggs. Mature breeding females in *Synalpheus* can be easily distinguished by colored ovaries or eggs (and occasionally other morphological characteristics such as rounded pleura, i.e. the flaps surrounding the abdominal segments), but mature males and non-breeding females are morphologically indistinguishable under ordinary light microscopy (Duffy, 2007). However, identification of gonopores using scanning electron microscope studies showed that most non-breeders or “workers” of adult size class across several eusocial species consist of equal ratios of males and non-breeding females, although hermaphroditic (i.e. intersex) individuals occasionally occur in some species (Tóth & Bauer, 2007, 2008; Chak, *et al.*, 2015a).

(2) Overlapping Generations. This refers to the cohabitation of genetically related adults of different ages or cohorts (i.e. kin groups or family units larger than the mated pair) within a host sponge. Kin structure was first documented with allozymes in *S. regalis;* colonies in this species are composed primarily of full-sib offspring of a mated pair, the queen and an otherwise undifferentiated male (Duffy, 1996a). Similarly, microsatellite analysis in *S. brooksi* suggested cohabitation of family groups within a single host sponge (Rubenstein, *et al.*, 2008). Indirect evidence of overlapping generations in various *Synalpheus* species comes from co-occurrence of different size classes of a single species (i.e. juveniles, non-breeding adults, and breeding females) – often comprising visibly distinct cohorts – within a single sponge, and by behavioral responses of colony members to intruders. For example, whereas pair-living species generally do not tolerate individuals other than their mate, eusocial *Synalpheus* cohabit with large numbers of conspecifics (generally kin) and in some cases distinguish these colony members from heterospecific shrimp and sometimes from foreign (presumably non-kin) conspecifics (Duffy, *et al.*, 2002).

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(3) Cooperative Social Behavior. This refers to coordinated behaviors, engaged in by group members, that benefit others in the colony. Early studies of social insects focused upon cooperative care and feeding of young as a criterion of eusociality (Wilson, 1971), but since the underlying premise of cooperative social behavior is altruism and therefore encompasses more than just offspring care, such cooperation can also include coordinated defenses against predators (see below) or other altruistic behaviors. Direct care or feeding of juveniles has not been observed in *Synalpheus*, but we have frequently collected small juveniles in close proximity within a sponge to an ovigerous female and a large male in *S. brooksi*, suggesting some sort of parental care. Genetic analysis of these associations confirmed that the cohabiting adults were indeed the parents of both the eggs and juveniles, suggesting that in at least this species, families associate together for an extended period of time (D. Rubenstein & J. Duffy, *unpublished data*).

(4) Colony or Group Size. This refers to the number of individuals of a single species living together in an individual host sponge. Shrimp abundance within an individual sponge is strongly correlated to sponge volume (Hultgren & Duffy, 2010), and very small sponge fragments generally only host a single pair of shrimp. Many *Synalpheus* species inhabit small encrusting sponges that live in the spaces found in dead coral rubble, whereas others live in much larger, free-living sponges that grow on the reef. However, several different *Synalpheus* species can co-occur in a single individual sponge, with different, but species-specific, group sizes. In general, eusocial species are found in larger groups within an individual sponge, while pair-living species occur as one or occasionally a few heterosexual pairs, even in the largest sponges. It is possible that some large sponges might contain multiple eusocial colonies of the same species living together in distinct portions of the sponges, but current behavioral or molecular data are insufficient to test this hypothesis.

8.2 Forms of Sociality in Shrimps

Sociality in *Synalpheus* takes a number of forms that may be considered to span a continuum, with different species varying in patterns of reproductive skew, group size, coexistence of overlapping generations, and cooperative social behavior. Since sociality has been best studied in the gambarelloides group, our discussion focuses on this clade of sponge-dwelling, West Atlantic *Synalpheus* species. The approximately 45 species in this group exhibit a range of social systems from the family's ancestral condition of pair-living, to communal societies with a variable number of paired breeding males and females (low skew), to eusocial societies with one or, rarely, a few breeding queens and up to hundreds of non-breeders or workers (high skew) (Duffy, 1996a, 2003, 2007 Duffy & Macdonald, 1999; Duffy, *et al.*, 2000). Below we describe in detail these forms of social living in *Synalpheus* shrimps.

8.2.1 Pair-Living Species

Formation of socially monogamous, heterosexual pairs is the ancestral form of sociality in the alpheid snapping shrimp (Knowlton, 1980; Mathews, 2002). More than half of

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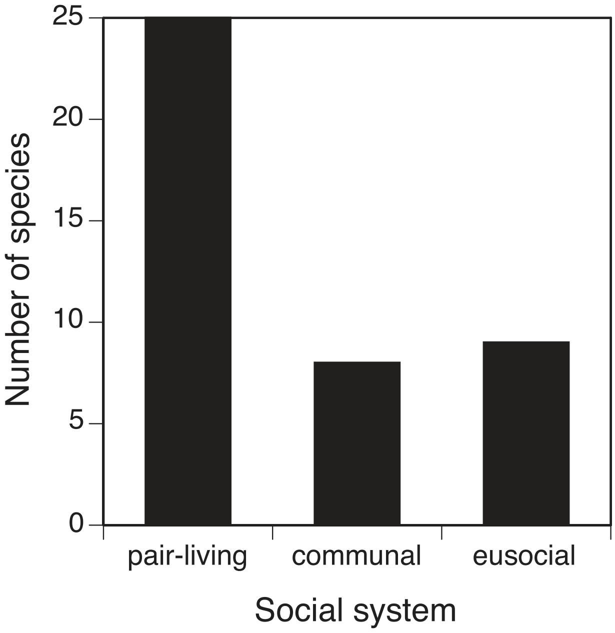

Figure 8.2. The number of pair-living, communal, and eusocial *Synalpheus* species in the gambarelloides group (N = 42 species). Some normally pair-living species occasionally occur as communal groups.

the sponge-dwelling *Synalpheus* in the gambarelloides group exhibit this pair-living lifestyle (Figure 8.2). In most alpheid shrimp, males and females form monogamous pairs, and cooperative behavior is limited to joint defense of their territory, burrowing, or hosting against other conspecific or heterospecific individuals (Mathews, 2002; Duffy, 2007). Although some pair-living *Synalpheus* species inhabit sponge species too small to house more than a pair of shrimp, other species occur occasionally in larger sponges (often with one or several other species of *Synalpheus)*, but nevertheless are reliably found in small assemblages of one or a few pairs, even in the largest sponges. Like other alpheids, females in most pair-living *Synalpheus* species typically brood a clutch of tens to a few hundred small eggs, which hatch directly into free-swimming larvae that leave the natal sponge to spend time in the plankton as is typical of decapod crustaceans (Dobkin, 1965; Duffy & Macdonald, 2010). This life history trait (i.e. free-swimming larvae) thereby precludes the opportunity for overlapping generations in the natal sponge or for any type of extended parental care in these pair-living species.

8.2.2 Communal Species

Approximately 20 percent of the species in the gambarelloides group can be classified as communal, meaning that they typically live in groups with most adults breeding in equal sex ratios and low reproductive skew (Figure 8.2). Thus, communal species fall somewhere on the social continuum between the highly eusocial species and the pair-living species. In these communal species, field collections have often yielded an adult male

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and female living together in the same sponge canal, suggesting that they are a mated pair. Most communal species produce free-swimming larvae that presumably disperse away from the natal sponge, suggesting that these groups of adults are unlikely to consist of kin. This hypothesis is supported by observations of communal species exhibiting aggressive snapping towards other conspecifics in the same sponge – typically tolerating only their mate – that form a striking contrast with the generally peaceful interactions among members of closely related eusocial colonies. These behavioral observations are also supported by evidence of low genetic relatedness among group members in the communal species *S. dardeaui* (D. Rubenstein & J. Duffy, *unpublished data*).

8.2.3 Eusocial Species

Eusocial *Synalpheus* species are characterized by high reproductive skew, overlapping generations, typically large colonies, and by cooperative defense of the host sponge in the few species where behavioral observations have been made. At least nine described species of *Synalpheus* have been characterized as eusocial, most with extreme reproductive skew (i.e. typically only a single queen) (Figure 8.2). However, the magnitude of reproductive skew varies among eusocial *Synalpheus*, ranging from species with invariably only a single breeding queen and often hundreds of workers (e.g. *S. regalis*), to colonies with typically only a few queens (e.g. *S. elizabethae*), to large colonies with occasionally more than a dozen queens (e.g. *S. brooksi*). Group size in eusocial species ranges from tens to hundreds of individuals, but can vary widely among and within species, and is likely limited by both age of the colony and the maximum size of the host sponge. For example, *S. cayoneptunus* is typically found in small colonies of 8 to 30 individuals, living in encrusting sponges within coral rubble (Hultgren & Brandt, 2015), while *S. regalis* forms colonies of a few hundred and sometimes more than 350 individuals in sponges more than 1000 ml in volume (Macdonald, *et al.*, 2009). In addition to exhibiting large colony sizes and high reproductive skew, all eusocial species of *Synalpheus* in which newly hatched juveniles have been observed undergo direct development, with eggs hatching directly into non-swimming, crawling larvae that remain in the natal sponge (Dobkin, 1965, 1969; Duffy & Macdonald, 2010); limited observations suggest that direct development is occasionally seen in one communal species (*S. idios*). In contrast, most communal and all pair-living species of *Synalpheus* release swimming larvae, which live in the plankton for days to weeks and have a much greater potential for long-distance dispersal. Thus, differences in larval development – specifically, direct development in eusocial species – appear to be the primary mechanism allowing for natal philopatry and the accumulation of close relatives and overlapping generations within a single host sponge, and thus a key prerequisite for the evolution of eusociality in *Synalpheus* (Duffy & Macdonald, 2010).

8.3 Why Shrimp Form Social Groups

Three years before the discovery of eusocial *Synalpheus* (Duffy, 1996a), Spanier & colleagues (1993) wrote a paper entitled “Why are there no reports of eusocial marine

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crustaceans?" The authors predicted that eusocial crustaceans, if they were to be discovered, would have a suite of traits predisposing them to living in family groups – including some form of parental care and non-dispersing juveniles – and that they would use a long-lived, predator-free domicile. With the exception of parental care, eusocial *Synalpheus* fulfill these conditions. However, it is not yet clear why some *Synalpheus* species form social groups and others do not. Indeed, eusocial species are often sister to pair-living and communal species, and eusocial species have evolved independently from pair-living ancestors at least four times (Duffy, *et al.*, 2000; Morrison, *et al.*, 2004; Duffy & Macdonald, 2010). Moreover, pair-living and eusocial species can be found inhabiting the same species of long-lived, predator-free host sponges, often even the same individual sponge. Thus, *Synalpheus* offers a rich opportunity to explore the traits that are most important in facilitating the evolution of eusociality using a phylogenetic comparative approach (e.g. Duffy & Macdonald, 2010). Of the numerous factors known to influence social behavior in other group living organisms, two have been particularly well-studied in *Synalpheus*: (1) the use of sponge resources (which is closely tied to predator avoidance, population size, and persistence); and (2) the variation in reproductive mode, specifically larval development. A variety of other factors could also influence sociality in snapping shrimp, and we briefly discuss them below.

8.3.1 Resource Acquisition and Use

As far as is known, all *Synalpheus* species in the gambarelloides group live essentially their entire lives within the internal spaces of a single host sponge, which serves as both a stable, long-lived predator-free habitat (Duffy & Macdonald, 1999; Duffy, 2003; Hultgren, 2014) and a lifelong food source (Duffy, 1996b). Therefore, the importance of the sponge resource in *Synalpheus* ecology cannot be underestimated. The relationship between *Synalpheus* shrimp and their sponge appears to represent a mutualism. Although *Synalpheus* consume their sponge hosts (or at least the bacteria growing upon the sponge surface), experiments indicate that some species of *Synalpheus* also actively protect their hosts against sea star predators, enlarge sponge canals, and facilitate increased sponge growth under some conditions (Hultgren, 2014). Furthermore, surveys across multiple regions of the Caribbean suggest that the sponge habitat is saturated and available hosts are limiting; more than 95 percent of appropriate sponge habitat in Belize (i.e. the 20 species of sponges most commonly inhabited by *Synalpheus)* is typically occupied by shrimp (Macdonald, *et al.*, 2006). Thus, sponge hosts are essential to *Synalpheus* survival, but they are also in short supply.

Ecological constraints and the lack of available habitat are known to drive the evolution of sociality in vertebrates (Emlen, 1982; Koenig, *et al.*, 1992). Sponge use by *Synalpheus* appears to be consistent with this ecological constraints hypothesis because unoccupied sponges are rare (Macdonald, *et al.*, 2006). Furthermore, the few species of *Synalpheus* from outside of the gambarelloides group that have been characterized as eusocial are also reported as living in sponge hosts (Didderen, *et al.*, 2006). However, obligate sponge dwelling is a synapomorphy uniting all members of the gambarelloides group, from pair-living to communal to eusocial species. Thus, while

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sponge host use appears to be an important prerequisite for eusociality, it is not sufficient to explain the evolution of complex social behavior in this group (i.e. the “fortress defender” hypothesis alone does not explain sociality in shrimp; Queller & Strassmann, 1998).

8.3.2 Predator Avoidance

Predation avoidance in *Synalpheus* is tightly linked to sponge host use. Although formal studies have not been done on the effects of host sponge on predation risk, shrimp removed from their host sponge in the field are almost immediately consumed by fish (K. Hultgren & J. Duffy, *unpublished data*), and the majority of the sponge species inhabited by *Synalpheus* are chemically defended against fish (Pawlik, *et al.*, 1995). Although cooperative defense of the sponge habitat has been documented in some eusocial species (Tóth & Duffy, 2005), there has been no experimental work on relative rates of predation, colony failure, or colony turnover between host sponges dominated by pair-living, communal, or eusocial species of *Synalpheus*. In addition to the potential vulnerability of *Synalpheus* to predation, some species of sponge hosts are themselves susceptible to predation by fish or invertebrate enemies. While *Synalpheus* shrimps actively defend their sponge host against sea star predators (Hultgren, 2014), the magnitude of defense by species with different social systems has not been investigated.

8.3.3 Homeostasis

As all sponge-dwelling *Synalpheus* live underwater in tropical environments, group living should not have an appreciably large effect on regulation of temperature and other abiotic factors (i.e. physiological components of homeostasis). However, sponge hosts may provide a stable environment for shrimp. *Synalpheus* can be found inhabiting sponges from the intertidal zone to 30 m (or deeper) on some reefs (Macdonald, *et al.*, 2006, 2009, Hultgren, *et al.*, 2011). Although not yet tested, sponges could buffer shrimp from daily and annual changes in salinity, water temperature, and/or dissolved oxygen concentrations at shallower depths.

8.3.4 Mating

Little is known about mating in alpheid shrimp. In most alpheids, mating takes place after the female has molted, when her carapace is soft (Duffy & Thiel, 2007). Experimental work has shown that alpheids are not able to store sperm, suggesting that a female must mate every time she ovulates (summarized in Duffy, 2003). Laboratory studies of captive *S. brooksi* confirm that *Synalpheus* shrimp become receptive around molt, which occurs with the lunar cycle (D. Rubenstein, *unpublished data*). Moreover, limited observations of captive *S. regalis* colonies revealed rapid transfer of a spermatophore from male to female shortly after the female molts (E. Tóth & J. Duffy, *unpublished data*).

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Unlike the Hymenoptera, genetic and experimental data suggest that *Synalpheus* are not haplodiploid (Duffy, 1993; Duffy, 1996c). In fact, many *Synalpheus* in the gambarelloides have large genomes and were hypothesized to either be polyploid or have large genome duplications (Rubenstein, *et al.*, 2008). However, subsequent examination suggested that differences in genome size among *Synalpheus* species are related to differences in chromosome size rather than chromosome number (Jeffrey, *et al.*, 2016). It is not clear how sex is determined in *Synalpheus*; the several species studied in detail tend to show equal sex ratios (Chak, *et al.*, 2015a), but hermaphroditic (intersex) individuals have been identified by external morphology in some species (Tóth & Bauer, 2007; Tóth & Bauer, 2008). Preliminary examination of gonadal development suggests that most species with intersex individuals are sequentially hermaphroditic (Chak, *et al.*, 2015a), though it is not clear whether they are protandrous (i.e. male to female) or protogynous (i.e. female to male). It also remains to be determined if hermaphroditic species of *Synalpheus* can – or at least have at some time in the past – reproduce via selfing, as has been observed in malacostracan – but not decapod – crustaceans (Kakui & Hiruta, 2013).

8.3.5 Offspring Care

Extended parental care has evolved repeatedly in several other species of crustaceans (summarized in Duffy & Thiel, 2007), but direct parental care of juveniles in *Synalpheus* has never been documented. Newly-hatched crawling juveniles are evidently able to feed themselves and have been observed feeding from the surface of sponge canals in captive colonies (Duffy, 2007). The formation of family groups with multiple overlapping generations of offspring in *S. brooksi* (D. Rubenstein & J. Duffy, *unpublished data*) suggests that rudimentary parental care could exist in this group, but numerous observations of captive colonies have yet to produce any evidence of direct care. Further work is needed to determine whether cooperation extends to offspring care in *Synalpheus*.

8.4 The Role of Ecology in Shaping Sociality in Shrimp

Life in tropical coral reefs, though physically benign, can be biologically challenging for small invertebrates such as *Synalpheus*: predation rates on crustaceans in the tropics are extremely high relative to temperate regions (Bertness, *et al.*, 1981; Freestone, *et al.*, 2011; Ory, *et al.*, 2014). As suitable host sponges are a limiting resource, *Synalpheus* shrimps face challenges during dispersal to and colonization of sponge hosts, such as competition for space within the sponge and long-term defense of the sponge resource. The challenges associated with founding colonies, surviving predation, and interacting with heterospecific competitors (such as sponge-dwelling polychaete worms and brittle stars) likely played a strong role in selecting for reduction of these risks via direct development, natal philopatry, and perhaps the evolution of eusociality (Duffy, *et al.*, 2002; Tóth & Duffy, 2005; Macdonald, *et al.*, 2006).

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8.4.1 Habitat and Environment

Although *Synalpheus* shrimp are restricted to sponges in tropical marine habitats, the type of sponge habitats can vary greatly. Some shrimp species inhabit small cryptic sponges embedded in coral rubble or growing under rocks (e.g. the sponge *Hymeniacidon caerulea*), whereas others inhabit free-living sponges growing on more exposed reef surfaces (e.g. the sponge *Agelas clathrodes*). These host sponges can be found in reefs in shallow wave-exposed habitats (0 to 1 m depth), but also at much deeper depths (30 m). Cryptic host sponges occur in the interstices of live or recently dead coral rubble (predominantly *Madracis* spp.). Appropriate host sponges (and *Synalpheus*) are often uncommon in degraded reef environments (less than 10 percent coral cover) or extremely pristine reef environments (more than 80 percent coral cover) (Hultgren, *et al.*, 2010). Many *Synalpheus* species live in free-living sponges in protected seagrass beds (*Thalassia testudinum*) bordering coral reefs or mangroves; these areas tend to be more buffered than reefs from wave exposure (Macdonald, *et al.*, 2006). Although some shrimp species (e.g. *S. brooksi*) live in sponge hosts from a range of different habitats (e.g. exposed coral reefs and protected seagrass beds), little comparative work has been done on *Synalpheus* communities inhabiting different tropical marine habitats.

8.4.2 Biogeography

Synalpheus shrimp are distributed widely across the globe. Species in the gambarelloides group are largely restricted to the tropical West Atlantic, except for *S. occidentalis* and *S. gambarelloides*, which are endemic to the Mediterranean. Over the past two decades, sampling for sponge-dwelling *Synalpheus* has largely been restricted to fewer than a dozen sites or islands in the Caribbean, and largely at relatively shallow depths. Despite these limitations, these efforts have yielded a database of more than 60,000 specimens and relatively complete species lists for several regions. Although we have not rigorously quantified the effects of sociality on species' ranges, in general, eusocial species do not appear to have wider or narrower geographic distributions than pair-living or communal species. Rather, some shrimp species are distributed widely across the Caribbean, while others are endemic to certain regions, and geographic distribution in some cases is related to sponge host use (J. E. Duffy & K. Hultgren, *unpublished data*). For example, several widespread shrimp species (e.g. the pair-living species *S. agelas*) are specialists in common, cosmopolitan sponge species (*Agelas* spp.), whereas others (e.g. the pair-living species *S. bousfieldi*) live in a range of different sponge hosts in different regions. Some endemic species of shrimp live in what appear to be rare or endemic sponge hosts (e.g. *S. irie* has been found only in a white tube-like sponge observed only in Jamaica, Macdonald, *et al.*, 2009), while other endemic shrimp species live in cosmopolitan sponges (e.g. the eusocial *S. microneptunus* has only been found in *Xestospongia* spp. in Barbados, Hultgren, *et al.*, 2011). Rigorous sampling of additional Caribbean locations will be necessary to more comprehensively examine how

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sociality, sponge host use, and larval dispersal mode interact to affect *Synalpheus* biogeography.

The biogeographic distribution of species and genetic connectivity of populations is likely to be affected by larval developmental mode (i.e. direct development versus swimming larvae). Allozyme studies comparing a eusocial species with direct development (*S. brooksi)* to a communal species with swimming larvae (*S. pectiniger*) demonstrated significantly higher genetic structuring within and between regions in the eusocial species with direct development, suggesting population structure is correlated with the potential for larval dispersal (Duffy, 1993). Because eusocial species have direct-developing larvae that do not disperse from the natal sponge, we might expect eusocial species to have a lower colonization potential, and consequently a smaller geographic range, than pair-living or communal species. Although comparative studies on biogeography and host ranges have not been conducted, exhaustive surveys in some regions of the Caribbean (e.g. Curaçao) indicated a complete absence of eusocial species, despite the presence of appropriate host sponges and a wide diversity of pair-living and communal species (Hultgren, *et al.*, 2010). Curaçao is upstream to most other Caribbean regions via prevailing surface currents and larval exchange is generally low in Curaçao for many taxa (Roberts, 1997; Vollmer & Palumbi, 2007; Kough, *et al.*, 2013). It is possible that direct development in eusocial *Synalpheus* impedes dispersal to this region, suggesting that ecological constraints beyond simply host limitation might influence the evolution of social diversity in this group.

8.4.3 Niches

Social species or populations have been suggested to occupy a wider niche breadth than non-social species (Sun, *et al.*, 2014). In *Synalpheus*, a wider niche breadth would be a greater range of host species. Comparative work, based on decades of field surveys in Belize, has demonstrated that eusocial *Synalpheus* species are far more abundant in terms of frequency of occurrence and abundance, and occupy a greater range of sponge hosts than pair-living and communal species (Macdonald, *et al.*, 2006; Duffy & Macdonald, 2010; but see Duffy, *et al.*, 2013). Together, these data suggest that eusocial species may be able to competitively exclude pair-living and communal species from host sponges. The large colony sizes of eusocial species, paired with their cooperative defense behaviors (Tóth & Duffy, 2005), likely allow them to successfully dominate and defend large sponges that would be difficult for a single pair or a small group to hold on their own. Furthermore, with sponge habitat saturated (i.e. nearly all sponges are occupied by *Synalpheus*) and unoccupied hosts in short supply, it may be a less risky strategy for juveniles to remain in the natal sponge, as they do in eusocial species, than to disperse and colonize a new sponge. Thus, while sponge host use appears to be necessary for eusociality to evolve in snapping shrimp, and eusocial species are generally more ecologically successful at defending (and possibly acquiring) sponge resources in the field, sponge use alone is insufficient to explain the evolution of sociality in *Synalpheus*. However, by being able to exploit a wider niche, eusocial species appear to maintain a significant competitive advantage over pair-living and communal species.

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8.5 The Role of Evolutionary History in Shaping Sociality in Shrimps

Evolutionary history likely plays an important role in explaining social diversity in *Synalpheus* and interacts with other life history and ecological factors. For example, direct larval development (in which newly hatched juveniles remain in the natal sponge) is almost perfectly phylogenetically correlated with eusociality (Duffy & Macdonald, 2010). In previous phylogenetic studies on this group, eusociality has been quantified using a modified version of the eusociality (E) index (Keller & Perrin, 1995) that takes into account both reproductive skew and group size (Duffy, *et al.*, 2000; Duffy & Macdonald, 2010). These data suggest that eusociality has evolved independently at least four times in the gambarelloides group (Figure 8.1), although the phylogenetic clustering of eusocial species clearly suggests strong phylogenetic signal. For example, four of the nine eusocial species come from the *S. rathbunae* complex, a group of four morphologically and ecologically similar species that together account for nearly half of the overall shrimp abundance recorded from three decades of surveys across the Caribbean (Duffy, *et al.*, 2000; Morrison, *et al.*, 2004; Hultgren & Duffy, 2012). Three other eusocial species – the recently described *S. microneptunus*, and *S. duffyi*, and a newly discovered eusocial species, *S. cayoneputunus*, from Florida (Hultgren & Brandt, 2015) – occur in the morphologically homogeneous *S. paraneptunus* complex, while the remaining two (*S. chacei* and *S. brooksi*) are closely related to several other communal (*S. idios, S. carpenteri*) and pair-living species (*S. bousfieldi*) in the *S. brooksi* complex (Figure 8.1).

II SOCIAL TRAITS

Vertebrate and social insect biologists often take for granted the wealth of information about the basic biology and life history that is known from their study organisms. Studies of social shrimps do not enjoy this advantage. Early workers on the genus *Synalpheus* (Coutière, 1909; Chace, 1972; Dardeau, 1984) established an invaluable foundation for the taxonomy of this large and difficult group over the last century, but it has only been in the last two decades that research has progressed beyond taxonomy and general distribution to begin revealing the remarkable behavior and life history of *Synalpheus*. *Synalpheus* snapping shrimp have been little studied in the wild, largely because they spend nearly their entire lives inside particular species of sponges, which are themselves very challenging taxonomically, and often at deep depths where doing direct observations is difficult. Therefore, what we know about *Synalpheus* life history traits is limited, and much of it comes from observations in the lab.

8.6 Traits of Social Species

8.6.1 Cognition and Communication

Alpheid shrimp are known to use both visual and chemical signals in conspecific interactions, including mate and competitor recognition (Nolan & Salmon, 1970; Hughes,

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1996a; Hughes, 1996b; Obermeier & Schmitz, 2003; Bauer, 2011; Chak, *et al.*, 2015c). Moreover, alpheid shrimp that live symbiotically with gobies use a complex series of signals to communicate with their goby partners (Karplus & Thompson, 2011). Work on cognition and communication in the gambarelloides group has primarily focused upon group recognition and communication in the eusocial species. For example, experimental work in *S. regalis* and observations of other eusocial species demonstrate that individuals can discriminate colony members from conspecific and heterospecific intruders (Duffy, *et al.*, 2002). Individual contacts typically are initiated by antennal palpations, which can then be followed by bouts of snapping. Snapping bouts are typically higher in response to heterospecific than conspecific intruders, whereas colony members are often accepted into the colony without snapping (Duffy, *et al.*, 2002). In addition to individual communication, snapping also facilitates an important form of group communication and cooperative defense in eusocial *Synalpheus.* This so-called coordinated snapping typically occurs when initial warning snaps fail to repel intruders, and consists of multiple colony members snapping in unison for several seconds, causing a distinctive, escalating crackling sound that serves as an intense warning signal towards intruders (Tóth & Duffy, 2005).

8.6.2 Lifespan and Longevity

We know very little about individual lifespan or colony longevity in *Synalpheus* since individuals have not been kept for extended period of times in the lab and long-term field studies have not yet been initiated, largely because many sponge hosts are embedded in coral rubble, making it difficult to monitor colonies repeatedly in the field. Limited experimental data suggest that shrimp colonies may be able to grow along with the sponge host. During short-term experiments in the field (3 weeks), *Synalpheus*-inhabited sponges grew more slowly than empty sponges, but most sponges experienced positive net growth (Hultgren, 2014). However, sponges are typically slow-growing organisms, and it is unknown whether slow sponge growth limits colony growth or keeps pace with colony expansion.

In terms of individual lifespan, *S. brooksi* individuals have been housed successfully in self-contained aquaria in the lab for up to a year (D. Rubenstein, *unpublished data*), and the safe, long-lasting nature of their host sponges (some of which can live for decades or more) suggests by analogy with social insects (Keller & Genoud, 1997) that the lifespans of some social shrimp may be much longer. Colony longevity will be much longer than individual lifespan, since sponges are extremely slow-growing, long-lived organisms; the largest specimens of the sponge *Xestospongia muta* – a close relative of the sponge genus *Neopetrosia* that hosts *Synalpheus* – have been estimated from growth rates to have been alive for more than 2,300 years on reefs in the Florida Keys, where *Synalpheus* are common (McMurry, *et al.*, 2008).

8.6.3 Fecundity

Fecundity varies greatly within and among *Synalpheus* species, with average clutch size ranging from a few to hundreds of eggs (Duffy, 2007; Ríos & Duffy, 2007;

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Hernáez, *et al.*, 2010). Some eusocial species with crawling larvae have very low fecundity (e.g. *S. filidigitus*, median clutch size is 4.5), suggesting high offspring survival (Duffy, 2007). However, correlations among fecundity, egg size, and sociality have not been explored across different species. Within a species, the number of eggs a female can produce is related to body size. In the eusocial species *S. regalis*, queen clutch size, as well as queen body size, are positively correlated with colony size (Duffy, 1996a; Duffy, *et al.*, 2002). These data suggest either that non-breeding colony members may enhance queen fecundity, or that fecundity simply increases steadily with size and age of the queen and colony (see above). Females in many species are often externally parasitized by bopyrid isopod parasites, which occur in either the branchial cavity or the abdominal area, and abdominal parasites have been shown to significantly suppress clutch size in infected females (Hernáez, *et al.*, 2010).

8.6.4 Age at First Reproduction

Due to the challenges of rearing sponges and breeding shrimp in the laboratory, little is known about when reproduction commences in *Synalpheus*. Experiments in which empty sponge fragments were colonized by the eusocial species *S. rathbunae* indicate that after 45 days, sponges were inhabited by a male-female pair of shrimp, with the female showing some signs of ovarian development but no embryos (Tóth & Bauer, 2007). Moreover, after queen removal in lab colonies of *S. elizabethae*, female workers developed mature ovaries within 33 days (Chak, *et al.*, 2015b). Although little is known about age of first reproduction, we do know that like most caridean shrimp, *Synalpheus* show continuous (indeterminate) growth throughout their lives, with no terminal molt (Hartnoll, 2001). Species with swimming larvae exhibit distinct larval stages that metamorphose into adults, whereas those with larvae that exhibit gradual development do not (Dobkin, 1965, 1969).

8.6.5 Dispersal

Differences in larval development and consequent mode of dispersal appear to be the primary mechanism underlying the formation of kin-based colonies and thus the evolution of eusociality in *Synalpheus*. As discussed earlier, eggs of all pair-living and communal species studied (with a single possible exception) hatch directly into free-swimming larvae and are released into the water column (Dobkin, 1965; Duffy & Macdonald, 2010), reducing the opportunity for overlapping generations in the natal sponge, any type of extended parental care, or association of kin. In contrast, in all eusocial species that have been studied, eggs undergo direct development, hatching into non-swimming, crawling larvae that remain in the natal sponge (Dobkin, 1965, 1969; Duffy & Macdonald, 2010).

Despite the role of dispersal mode in *Synalpheus* social evolution, few direct experimental studies of colonization and dispersal have been conducted, and basic questions (e.g. how eusocial species establish new colonies) have yet to be fully investigated. Tóth & Bauer (2007) used scanning electron microscopy to determine the sex of individuals

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of the eusocial species *S. rathbunae* that had colonized unoccupied sponge fragments after 45 days in the field. In most cases, colonists of these small fragments consisted of a single heterosexual pair, often with a sexually immature female, suggesting that eusocial species may colonize available sponges as juveniles or subadults. In another set of field experiments in Panama examining how *Synalpheus* impact sponge growth, unoccupied sponge fragments were rapidly colonized by multiple *Synalpheus* species (50 percent recolonization within approximately 17 days) (Hultgren, 2014). Colonists in empty sponges consisted primarily of newly settled postlarval juveniles of two communal species with swimming larvae, *S. dardeaui* and *S. yano*, and occasionally juveniles of the eusocial species *S. elizabethae* (K. Hultgren, *unpublished data*). Finally, limited evidence from the eusocial species *S. brooksi* demonstrated that males are more genetically related to each other than are ovigerous females, suggesting that dispersal in this eusocial species could be sex-biased (D. Rubenstein, *unpublished data*). That is, *S. brooksi* may exhibit male-biased philopatry and female-biased dispersal, as in most cooperatively breeding birds (Greenwood, 1980). Together, these studies suggest that pair-living and communal species have the ability to rapidly recolonize empty sponges via swimming larvae, but that eusocial species may colonize sponges on a longer time scale as sexually immature juveniles or subadults.

8.6.6 Other Traits: Body Size

Body size is a master trait of sorts among organisms, with pervasive effects on ecological interactions, life history, and distribution (Woodward, *et al.*, 2005). Eusocial *Synalpheus* species tend to be smaller in size on average than pair-living species (Duffy & Macdonald, 2010). Since size is a strongly phylogenetically conserved trait in *Synalpheus* (Hultgren & Duffy, 2012), it is unclear whether small body size is directly related to evolution of eusociality, or a byproduct of the close phylogenetic relationships of many eusocial species. Regardless, given the pervasive inverse relationship between size and abundance in many animal communities, smaller body size could partially explain many of the ecological traits more common in eusocial *Synalpheus*, such as increased abundance. However, comparative analysis examining the dual effects of eusociality (E index) and body size on these ecological traits suggested that eusociality is a stronger correlate of sponge host range and percentage of sponges occupied than body size; body size alone was significantly correlated only to relative abundance (Duffy & Macdonald, 2010). Thus, increased abundance and sponge host breadth in eusocial species appear to be a direct result of social life, rather than of small body size.

8.7 Traits of Social Groups

8.7.1 Genetic Structure

Despite ongoing genetic work, currently there exist few quantitative data on genetic structure in *Synalpheus* colonies. Allozyme studies of eusocial *S. regalis* showed that

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colonies exhibited high relatedness and consisted primarily of full-sib offspring of a mated pair (Duffy, 1996a). Similarly, microsatellite analysis in eusocial *S. brooksi* suggested cohabitation of family groups within a single host sponge (Rubenstein, *et al.*, 2008; D. Rubenstein & J. Duffy, *unpublished data*). In contrast, microsatellite analyses of communal *S. dardeaui* colonies indicate very low genetic relatedness within colonies (D. Rubenstein, *unpublished data*). These patterns accord with the presence of crawling juveniles in *S. brooksi* versus swimming larvae in *S. dardeaui*. Thus, high genetic structure is expected in other eusocial species with crawling larvae, and similarly low genetic structure in communal species with swimming larvae.

Genetic relatedness among colony members can depend not only upon dispersal mode but also upon mating patterns. Lifetime monogamy has been hypothesized to underlie the evolution of eusociality in social insects because it produces full-sib offspring (Boomsma, 2007, 2009, 2013), as suggested by allozyme data for *S. regalis* (Duffy, 1996a). Preliminary microsatellite-based molecular work in five *Synalpheus* species shows no evidence of multiple paternity (i.e. polyandry) in broods of eggs (D. Rubenstein & J. Duffy, *unpublished data*). This is likely to be the case for all *Synalpheus* species because of the absence of sperm storage in alpheids (Knowlton, 1980) and the constraint that females only mate immediately after they molt and males generally guard them aggressively during this short period of receptivity (Duffy & Thiel, 2007). However, while pairs are genetically monogamous in each reproductive event, females are unlikely to exhibit lifetime monogamy. For example, parentage analysis of family groups and ovigerous females in *S. brooksi* suggest that females can mate sequentially with different males (D. Rubenstein & J. Duffy, *unpublished data*).

8.7.2 Group Structure, Breeding Structure and Sex Ratio

Sociality in *Synalpheus* is defined by the structure and sex ratio of the group. Group living species, within which most adult-sized females breed, are defined as communal. In most of these communal species, a female and male are found together in the same sponge canal, and are likely to be a mated pair. In contrast, eusocial species are typically defined by the highly unequal numbers of ovigerous (i.e. queens) and non-ovigerous individuals (i.e. workers). Determining the exact sex ratios of *Synalpheus* colonies is difficult because non-ovigerous *Synalpheus* lack obvious external sexual characteristics. Based upon external morphology under a scanning electron microscope, Tóth & Bauer (2007) found that worker sex ratios in four eusocial species (*S. regalis, S. rathbunae, S. chacei*, and *S. filidigitus*) generally conform to a 50:50 sex ratio. However, preliminary evidence from histological analysis of gonads in five species of *Synalpheus* suggests that sex ratios in some colonies can vary considerably in both directions from 50:50 among eusocial species (Chak, *et al.*, 2015a). Nonetheless, the ratio of ovigerous to non-ovigerous members of a colony provides a reasonable approximation of the degree of reproductive skew within a group and can be used to differentiate pair-living from communal from eusocial species.

Eusocial species vary considerably in their group structure and degree of reproductive skew. Most social species in the *S. rathbunae* and *S. paraneptunus* complexes are

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characterized by a single queen. Indeed, rarely is more than a single ovigerous female found in these colonies, despite a range of group sizes. Species like *S. microneptunus* are always found in small colonies, whereas its sister species, *S. duffyi*, can be found in much larger groups. This may be partially due to the size of the host sponges that these species use. In contrast to these obligately eusocial species, a variety of species in the *S. brooksi* complex have multiple queens and much lower reproductive skew. For example, *S. chacei* typically has a single queen, but can be found in colonies with multiple queens. In many parts of its range where it inhabits the large sponge *Spheciospongia vesparium*, *S. brooksi* is almost always found in large colonies with multiple queens (D. Rubenstein & J. Duffy, *unpublished data*). However, in other parts of its range where it lives in the small sponge *Hymeniacidon caerulea, S. brooksi* is found in small groups or even heterosexual pairs (J. Duffy, K. Hultgren & D. Rubenstein, *unpublished data*). It is not yet clear whether this social plasticity occurs because *S. brooksi* social structure varies in different hosts, since this species inhabits a range of sponge species.

8.7.3 Other Traits: Competitive Ability

The primary cooperative benefit that non-breeding colony members provide to the colony (including offspring in species with crawling larvae) is defense against other shrimp. As discussed earlier, evidence for this cooperative “coordinated snapping” in eusocial *Synalpheus* comes from behavioral and morphological data (Tóth & Duffy, 2005). Several eusocial species exhibit size-based and likely individual-level variation in behavior or morphological defense, constituting a kind of division of labor (Duffy, *et al.*, 2002; Tóth & Duffy, 2008). Although the division of labor seen in *Synalpheus* is not as extreme as that seen in social insects, it is a topic that warrants further study. In *S. regalis*, larger, non-breeding colony members spend more time defending the colony than do the queen and smaller juveniles (Duffy, *et al.*, 2002), and larger individuals also are more likely to occupy the peripheral parts of the sponge where intruders are first met (Duffy, 2003). In *S. chacei* and *S. regalis*, queens have smaller major chela (relative to body size) than non-reproductive workers (Tóth & Duffy, 2008). Allometric studies indicate that in larger eusocial colonies, the largest non-breeding individuals have disproportionately large major (fighting) chela, suggesting the formation of a “fighting” caste in some species (Tóth & Duffy, 2008). The most extreme example of this defensive division of labor is seen in *S. filidigitus*, in which the queen typically loses her primary weapon – the major chela – and instead bears two minor-form chelae (Duffy & Macdonald, 1999). Interestingly, this morphological pattern has been noted in the eusocial species *S. rathbunae* (Chace, 1972), as well as a putatively eusocial species from outside of the gambarelloides group, *S. crosnieri* (Banner & Banner, 1983). Coordinated social behavior has not been well-studied in communal species, but data suggest that allometry of fighting claw size (relative to body size) in communal and pair-living species is significantly less steep than in eusocial species, suggesting little morphological (and presumably behavioral) division of labor in larger individuals within a communal group (Tóth & Duffy, 2008).

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The competitive advantage of eusociality that we discussed earlier is also consistent with distributional and ecological evidence. First, comparative analyses demonstrate that eusocial *Synalpheus* species constitute the majority of sponge-dwelling *Synalpheus* abundance in localities where quantitative sampling has occurred (Macdonald, *et al.*, 2006). Moreover, eusocial species use a significantly higher number of host sponge species than pair-living or communal species (Macdonald, *et al.*, 2006). Stronger competition in eusocial species has also been supported by studies of phylogenetic community ecology, or the phylogenetic relatedness of co-occurring species in a community. Hultgren & Duffy (2012) examined phylogenetic relatedness of hundreds of *Synalpheus* communities (defined as the community of different species inhabiting a single sponge host) and found striking differences between sponge communities containing eusocial species and those lacking them. Specifically, shrimp communities containing only pair-living or communal species tended to be phylogenetically closely related and similar in body size, consistent with a strong effect of habitat filtering on community assembly. However, shrimp communities containing eusocial species showed a contrasting pattern: communities were less phylogenetically related and more dissimilar in size, suggesting that competitive exclusion is an important determinant of community structure in *Synalpheus* communities, but only when eusocial species were present (Hultgren & Duffy, 2012). Strikingly, survey data collected over nearly three decades across six Caribbean regions failed to find a single instance of two different eusocial species co-occurring in a sponge (Hultgren & Duffy, 2012). Thus, the stronger competitive abilities of eusocial species, paired with data indicating lower dispersal potential of direct-developing eusocial species, suggest that competition-colonization trade-offs may shape *Synalpheus* community assembly within and between regions.

Finally, despite being more competitive, eusocial species may be more susceptible population collapse than communal and pair-living species. Evidence from long-term field surveys throughout the Caribbean suggest a drastic and recent decline in eusocial species along with an associated increase in the relative abundance of pair-living species, due in part to changes in the coral assemblages and associated sponge community (Duffy, *et al.*, 2013). These changes, which could be environmentally-driven, human-induced, or represent natural cycles of population collapse similar to those seen in other non-classically eusocial species (reviewed in Aviles & Purcell, 2012), have led to the local extinction of some (e.g. Panama) or all (e.g. Belize) eusocial species in some regions of the Caribbean, and hint towards furthered extinction in other areas (e.g. Jamaica) (Duffy, *et al.*, 2013).

III SOCIAL SYNTHESIS

8.8 A Summary of Shrimp Sociality

Despite having fewer species than nearly any other taxonomic lineage with highly social representatives (e.g. Hymenoptera), the *Synalpheus gambarelloides* species group exhibits a wide range of social behavior and numerous evolutionary transitions

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between social states. Nearly half of the species in this clade live in groups of more than two individuals, some forming eusocial colonies with extreme reproductive skew and the beginning of behavioral caste formation. However, snapping shrimp lack sterile castes (Chak, *et al*., 2015a, 2015b) and therefore have not reached the degree of reproductive specialization as many social insects (Boomsma, 2013). Nonetheless, *Synalpheus* in the gambarelloides group represent the pinnacle of social evolution not only in crustaceans, but also in the sea.

Although we have divided *Synalpheus* into three discrete social categories (pair-living, communal, and eusocial), social structure varies widely and continuously in this group. Nearly all species that typically live as heterosexual pairs are occasionally found in small groups. Several species that we characterize as eusocial because colonies typically have a single queen and high reproductive skew, nevertheless occasionally have colonies with several queens. Moreover, some of these multi-queen colonies are demographically similar to those of the communal species. However, fundamental differences in larval dispersal mode (i.e. swimming larvae that disperse in the water column versus crawling larvae that remain in the host sponge) underlie key differences in kin structure between eusocial and communal species. Although we do not yet know the colony genetic structure of all species, for those that have been studied, eusocial species tend to live in kin groups and communal species do not. All species are likely to be monogamous in a single breeding event – like alpheid shrimp generally (Nolan & Salmon, 1970; Knowlton, 1980; Mathews, 2002) – so variation in genetic structure must be the result of either mate-switching (i.e. sequential polyandry), queen replacement, or reproduction by multiple females within a single colony (i.e. polygyny). Together, these results strongly suggest that kin selection plays an important role in the evolution and maintenance of sociality in this group. The life history differences that mediate kin structure may also have consequences for biogeography and even diversification patterns within this group. We might expect eusocial species to have a lower colonization potential, and consequently smaller geographic ranges, than pair-living and communal species. Interestingly, the same pattern has been observed in cooperatively breeding birds. Non-cooperative breeders tend to have greater capacity for colonization than cooperative breeders, which results in broader ranges and more species-rich clades in the non-cooperative lineages (Cockburn, 2003).

All *Synalpheus* shrimp live symbiotically with other organisms, and species in the gambarelloides group associate only with sponges. Since all species in this group are obligate sponge users, ecological differences are unlikely to fully explain the evolution of eusociality (Duffy, 2007). This does not mean, however, that ecology is unimportant in the discussion of social evolution in snapping shrimp. Several lines of evidence show that eusocial species appear to have a competitive advantage over communal and pair-living species; eusocial species use a significantly higher number of host sponges (Macdonald, *et al.*, 2006), they tend to exclude ecologically similar species from co-occurring in the same sponges (Hultgren & Duffy, 2012), and they cooperatively defend their host sponges (Tóth & Duffy, 2005). Although eusocial species occur at a higher abundance than communal and pair-living species on some reefs (Macdonald, *et al.*, 2006), recent evidence suggests that they may be more susceptible to factors that drive

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population decline, having gone locally extinct in a number of regions of the Caribbean (Duffy, *et al.*, 2013). This could be due in part to the slower colonization potential of eusocial species with non-dispersing larvae than pair-living or communal species with free-swimming larvae.

8.9 Comparative Perspectives on Shrimp Sociality

Synalpheus species share key life history traits with both social vertebrates and insects, and hence could serve as a model system to bridge the gap between them. Like vertebrates and termites, all eusocial *Synalpheus* species exhibit gradual development (i.e. not discrete larval and adult stages), though eusocial species bear young that look like miniature adults and grow by molting, whereas pair-living species have distinct, swimming larval stages that do not resemble miniature adults and live and mature in a distinct environment (i.e. open water vs. sponge). At least one species of eusocial *Synalpheus* appears to have female-biased dispersal, like many birds (Greenwood, 1980). Conversely, these small-bodied arthropods most resemble social insects in the way they form large colonies and inhabit and defend valuable protective host "fortresses" (Queller & Strassmann, 1998). Like vertebrates, there appears to be minimal morphological and physiological caste specialization in eusocial *Synalpheus*, and the most likely specialization for non-breeding workers in *Synalpheus* involves defense of host sponges against competitors (Tóth & Duffy, 2008), almost like a specialized fighting or defender class such as that seen in termites (Shellman-Reeve, 1997; Korb, 2008), aphids (Stern & Foster, 1997), and thrips (Crespi & Mound, 1997) (see also Chapters 5 and 6). Also like termites, some thrips, and most vertebrates – but unlike most Hymenoptera – the queen in all social *Synalpheus* species must cohabit with her mate. Thus, eusocial *Synalpheus* species are perhaps most similar to the wood-dwelling termites that also live inside their food sources (Chapter 5), as well as the gall-dwelling aphids and thrips (Chapter 6).

8.10 Concluding Remarks

Of the more than 50,000 crustaceans in the oceans worldwide, only a handful of species in the *Synalpheus gambarelloides* group are highly social. Yet, this group of approximately 45 species of obligate sponge-dwellers is extremely socially diverse, ranging from eusocial colonies, to cooperatively breeding groups, to communal associations, to simple pairs of males and females. Despite being poorly studied compared to most other vertebrate and invertebrate social lineages, we are beginning to learn a great deal about the biology, life history, and behavior of snapping shrimps. In particular, many eusocial species share both individual and group traits with other social vertebrates and insects, making them an ideal system to study social evolution in a comparative context.

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