The ecology and evolution of eusociality in sponge-dwelling shrimp

J. EMMETT DUFFY

School of Marine Science & Virginia Institute of Marine Science, The College of William and Mary Gloucester Point, VA 23062-1346, USA. e-mail: jeduffy@vims.edu

INTRODUCTION

Recent evidence suggests that the Crustacea is the sister taxon to the Insects (Friedrich and Tautz 1995, Shultz and Regier, 2000). The two taxa share many similarities in morphology, physiology, and ecology, and just as insects dominate many terrestrial ecosystems, crustaceans often dominate those of the sea. The extraordinary ecological success of insects is due in part to the unparalleled efficiency and competitive ability resulting from highly organized cooperation found in the social taxa (Oster and Wilson 1978, Wilson 1990). Although the gigantic, superorganismal colonies of some ants and termites have no marine analog, there are nevertheless strong parallels between colonies of certain sponge-associated marine shrimp and those of both primitively social insects and cooperatively breeding vertebrates. For example, social *Synalpheus* are strikingly similar to termites in being diploid, generally monogamous animals with gradual development that live in cloistered environments that they must defend from competitors. One could substitute "*Synalpheus*" for "termite" or "Isoptera" throughout the abstract of Thorne's (1997) review of termite eusociality and it would remain quite accurate.

What can shrimp tell us about the ecology and evolution of social organization? At the broadest level, social shrimp offer a new data point in a small sample of higher taxa in which large, cooperative colonies with strong reproductive skew (eusociality in the traditional sense, Wilson, 1971) have evolved. In addition to the several clades of classically eusocial Hymenoptera and the termites, these include certain thrips (Crespi 1992, Crespi and Mound 1997), platypodid beetles (Kent and Simpson 1992), soldier aphids (Stern and Foster, 1996), African mole-rats (Bennett and Faulkes, 2000), and snapping shrimps. Given the wide disparity among these taxa in phylogenetic origins and ecology, any environmental or biological condition that is shared among them should offer intriguing insights into the enduring riddle of how and why eusociality has evolved

repeatedly among animals. The potential value of *Synalpheus* as a model system for studying social evolution is threefold. First, its social diversity ranges from species that live in isolated heterosexual pairs through eusocial colonies of several hundred individuals, including in particular the small, morphologically monomorphic eusocial colonies in which factors promoting the origin of eusociality should be most approachable. Second, the clade represents a manageable unit for comparative study, with ~30 species whose phylogenetic relationships are now emerging. Third, the species are broadly similar in general ecology (all are tropical sponge-dwellers), facilitating comparisons of the demographic and ecological factors fostering particular behavioral and social phenotypes. In this review I first summarize what is known of the natural history and ecology of sponge-dwelling shrimps. I then explore the possible adaptive significance of sociality in *Synalpheus*, comparing these animals with other eusocial taxa in search of clues to explain the convergence on this paradoxical social phenotype in such disparate animals as honeybees, termites, mole-rats, and coral-reef shrimp.

The definition of eusociality
The terminology for categorizing animal sociality has generated some debate. The traditional definition of eusociality entailed cohabitation of different adult generations, substantial reproductive skew (reproductive "division of labor"), and cooperative care of young (Michener 1969, Wilson 1971). More recently, several modified concepts have been suggested for the term eusociality (Gadagkar, 1994; Sherman et al., 1995; Crespi and Yanega, 1995) in attempts to remedy both vague wording and perceived taxonomic biases in its original formulations. Sherman et al. (1995), for example, emphasized the continuous nature of variation in social organization evident across the broad spectrum of social invertebrates and vertebrates, and proposed a "eusociality continuum" to recognize this pattern. At the other extreme are definitions more restrictive than the traditional one, which highlight the important distinction between colonies in which sterility is facultative versus irreversible (Crespi and Yanega 1995). Perhaps the most important point is that the concept used should be clearly defined for any particular case, and relevant to the particular problem addressed (Wcislo, 1997).

I use the term "eusociality" to refer to the syndrome of multigenerational, cooperative colonies with strong reproductive skew (usually a single breeding female) and cooperative defense of the host sponge found in several *Synalpheus* species. Our recent research (Duffy et al., 2000, 2002) explores the working hypothesis that large colony size and reproductive skew are correlates of cooperative behavior that enhances effectiveness of gaining and holding the host resource (Brown, 1987; Koenig and Pitelka, 1981; Emlen 1982, 1991; Andersson, 1984; Alexander et al., 1991). I use the term eusociality both as a simple semantic shorthand, and also to emphasize its similarity with the colony organization traditionally described as eusocial in various other animal taxa (Wilson, 1971; Crozier and Pamilo, 1996).

In *Synalpheus*, each of the three traditional criteria has been demonstrated or inferred for the social shrimp *Synalpheus regalis* (Duffy, 1996a) and several of its congeners (Duffy, 1998; Duffy and Macdonald, 1999), as discussed below. A definition based on irreversible caste differentiation might also be applied to *Synalpheus filidigitus*, in which the queen typically sheds her large snapping claw and regrows a second, minor-form chela, rendering her morphologically unique among members of the colony (Duffy and Macdonald, 1999). There is currently no evidence of irreversible sterility in any *Synalpheus* species, however, although data are insufficient to evaluate this rigorously. It should be emphasized that my usage of the term eusociality does not reflect a discrete state of social organization in *Synalpheus*, as is also true of many other animal taxa that historically have been termed eusocial (Sherman et al., 1995). Colony size and reproductive skew both vary more or less continuously among species of *Synalpheus* (Duffy et al., 2000), and sometimes among conspecific populations.

NATURAL HISTORY OF *Synalpheus*

Any effort to understand the social lives of sponge-dwelling shrimp immediately faces the paucity of information on their basic biology. Only a handful of papers were published on Caribbean *Synalpheus* in the century prior to 1990, the principal three of which were taxonomic monographs (Coutière, 1909; Chace, 1972; Dardeau 1984). Each of the latter made invaluable contributions to clarifying the still difficult (Duffy, 1996c; 1996d, 1998) taxonomy of the group, and Dardeau in particular presented a wealth of information on host associations. Nevertheless, there remain virtually no published data on mating, dispersal, behavior, interspecific interactions, and other aspects of basic demography and ecology that are available to students of many other social animals. This is due largely to the cryptic habits of *Synalpheus*, nearly all of which are specialist internal parasites or commensals of coral-reef sponges that are themselves taxonomically challenging and patchily distributed, often under 10s of m of water. Because published information on the natural history of these shrimp is scarce and scattered in specialized journals, I provide here a detailed summary of what is currently known. Some of this account is based on unpublished observations and data extracted from field collections made between 1988 and 2001, primarily in the vicinity of the Smithsonian Institution's field stations at Carrie Bow Cay, Belize, and the San Blas Islands of Caribbean Panamá, but also including a few collections from elsewhere. These collections include all but one of the 21 gambarelloides group species previously described from the region and ~10 new species. The great majority were obtained by carefully removing all shrimps from individual sponges collected using scuba, so that each sample provides data on shrimp assemblage structure, body size frequency distribution, population size structure, and adult sex ratio of each species present (Duffy, 1992; Duffy and Macdonald, 1999). Behavioral observations, primarily of *S. regalis*, were recorded in captive colonies occupying live sponge sections

in a flow-through seawater system (see Duffy et al., 2002 for details).

Diversity and systematics
Synalpheus (Decapoda: Alpheidae) is one of the most species-rich (>100 described species worldwide, Bruce, 1976; Chace, 1989) and abundant (Reed et al., 1982; Snelgrove and Lewis, 1989) genera of crustaceans, and is a dominant component of the cryptic coral-reef fauna throughout the world. Many species are symbiotic with sessile invertebrates, primarily crinoids (Indo-Pacific) and sponges (worldwide), and are generally highly host-specific. In the West Atlantic, the genus is represented primarily by the morphologically distinctive "gambarelloides group" (Coutière, 1909; Dardeau, 1984), a clade of ~30 sponge-dwelling species mostly endemic to this region (Figure 1). The species richness of the gambarelloides group is accompanied by considerable diversity in life history and social organization as well. Species range from the comparatively tremendous *S.* "*pandionis* giant" (length up to 30 mm), in which a few heterosexual pairs may defend an entire sponge and females release several hundred small, planktonically-dispersing embryos in a given clutch, to the tiny *S. filidigitus*, which lives in monogynous colonies of up to 120 individuals, the lone female measuring 2-3 mm in carapace length and carrying one to a few dozen large eggs that hatch directly into benthic juveniles (Duffy and Macdonald, 1999). In terms of social organization, the ~30 species in the gambarelloides group span the gamut from asociality, in which heterosexual pairs form but are intolerant of other adults (and generally juveniles as well) in a host, through 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), to eusocial species with colonies numbering in the hundreds and only a single female breeding (Duffy, 1996a, 1998; Duffy and Macdonald, 1999).

Nature of the shrimp-sponge relationship
The coral-reef environment in which *Synalpheus* species live is extraordinarily heterogeneous, consisting of a structurally complex framework of dead coral overgrown by invertebrates of nearly every phylum, as well as algae. These habitats typically contain 10s or even 100s of species of sponges (Wiedenmayer, 1977; van Soest, 1978, 1980, 1984). Amidst this chaos, *Synalpheus* in the gambarelloides group have adopted life in a highly predictable and constant microhabitat by living within specific sponges. These sponges are characterized by sinuous networks of narrow spaces, the aquiferous canals, through which the sponge pumps a continuous stream of water, providing oxygen and washing away wastes. Host specialization is typical in *Synalpheus*, most species having been recorded reliably from only one or a few sponge species at a given locality (Dardeau, 1984; Duffy, 1992, 1996c), and shrimp body width is closely related to width of the canals (Duffy, 1992). The shrimp apparently live their entire lives within their host sponges. In over 10 years of collecting we have rarely encountered any species in this

group outside sponges, despite often high prevalence and abundance within them
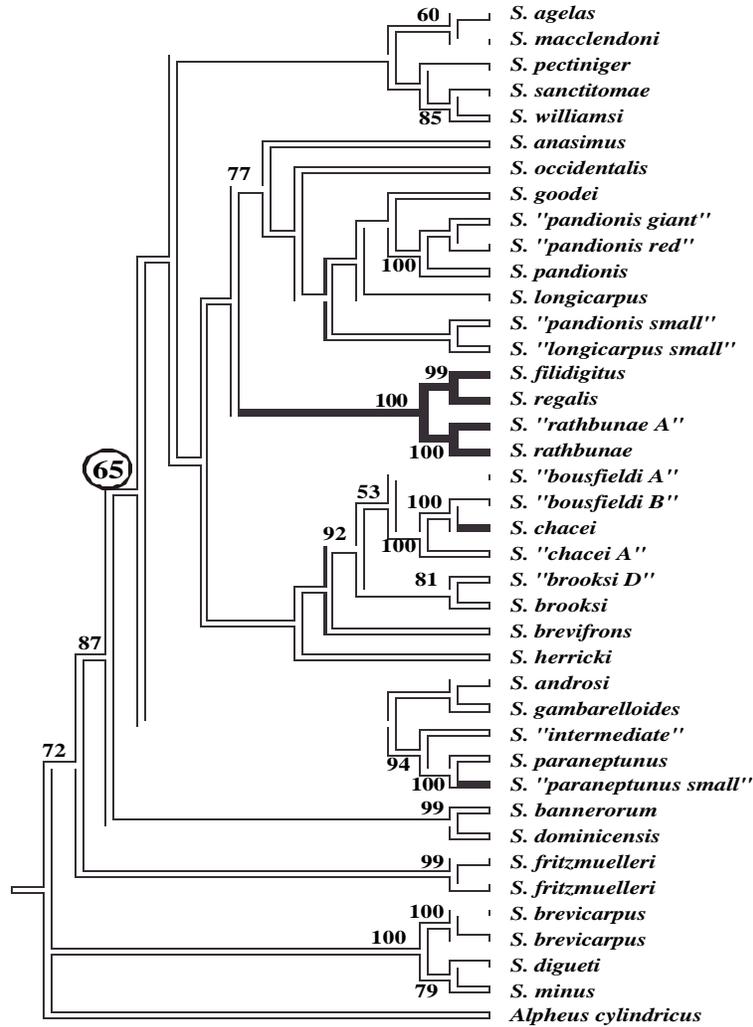
Figure 1. Phylogenetic hypothesis for West Atlantic *Synalpheus* species in the gambarelloides group and selected outgroups, based on 6-parameter weighted-parsimony analysis of partial mt COI and 16S rRNA sequences and 45 morphological characters (Morrison, Ríos, and Duffy in prep.). Numbers above or below branches are bootstrap proportions (N = 1000). Circled number indicates support for the gambarelloides clade. Eusocial species, as defined in the text, are indicated. Quotation marks denote provisional names of undescribed species.

(e.g., Figure 2). In the few species whose stomach contents have been examined, the major recognizable component is sponge spicules (Ruetzler, 1976; Erdman and Blake, 1987; Ríos and Duffy, 1999; J.Duffy unpublished). Because the canals occupied by shrimp are excurrent (water is drawn in through microscopic pores in the sponge surface), there is presumably little allochthonous food in them. Thus, it seems likely that shrimp feed primarily on organic matter produced by the sponge, whether in the form of tissues or mucoid secretions. Strictly speaking, then, these shrimp are parasites of sponges.

The prevalence of shrimp within host sponges (i.e., percentage of individual sponges occupied) varies considerably among both shrimp and host species, but is generally very high for the social species (Duffy et al., 2000). Moreover, these shrimp are often the most abundant macroscopic animals within their hosts. Because few predators can enter the narrow canals of the sponges, the most likely enemies of sponge-dwelling shrimp are conspecific and congeneric competitors for space. Whether shrimp have any effect, negative or positive, on the host sponge is unknown. Many authors have marveled at the density of alpheids in certain sponges (e.g., Pearse, 1932), noting for exa mple that "they were so numerous that it seems strange that they received sufficient oxygen" (McClendon, 1911). Potential impacts of shrimp on their hosts have not been tested experimentally, however. In summary, the host sponge is a self-contained resource for shrimps, providing both habitat and food, much as pieces of decaying wood serve for many termite taxa. In contrast to the wood habitat, however, living sponges are potentially very long-lived and grow rather than diminish in size.
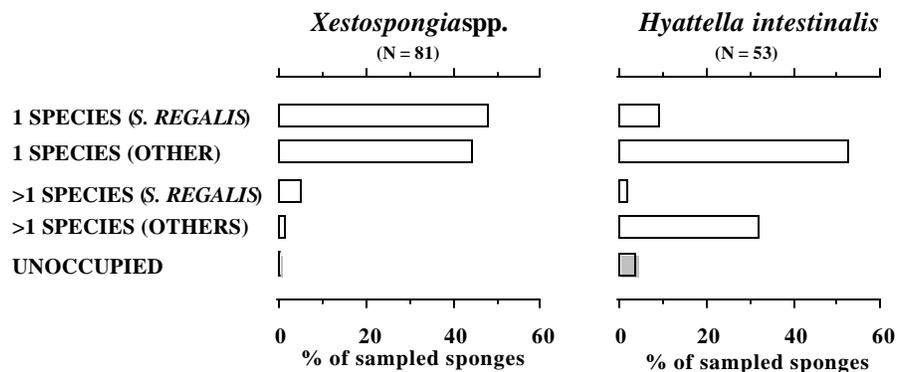
Figure 2. Patterns of occupancy for the two host sponges used by *Synalpheus regalis* at Carrie Bow Cay, Belize. Different bars denote the proportions of sampled sponges occupied by *S. regalis* alone, other species alone, more than one species (either including or not including *S. regalis*), or containing no *Synalpheus* species. Data from Duffy (1996d).

The distribution of host sponges in the field is patchy at all scales, from cm to 1000s of km. These distribution patterns have several potentially important consequences for social ecology and evolution. First, because sponges are discrete and patchily distributed, they force their symbionts into small, discrete demes. Since direct development in many *Synalpheus* species, including all social species (see below), strongly restricts dispersal potential, successful colonization of sponges is probably infrequent and the shrimp population within a sponge grows mostly by internal recruitment. Thus, the individuals within a sponge tend to be closely related (e.g., Duffy, 1996a), setting the stage for kin selection. Second, because unoccupied habitat is in short supply (Duffy, 1996c,d; Duffy et al., 2000, Figure 2), social *Synalpheus* likely experience habitat saturation like that proposed to favor cooperative breeding in some social vertebrates (see Emlen, 1997). I return to these points below. Finally, at the macroevolutionary level, the highly restricted dispersal of many *Synalpheus* species results in strong genetic subdivision among shrimp demes and regional populations (Duffy, 1993, 1996b, 1996c), undoubtedly contributing to the high species diversity and intraspecific regional differentiation in host use common in *Synalpheus.*

Reproductive biology, mating, and genetics
The reproductive biology of *Synalpheus* is poorly known. There is no sign of sexual dimorphism among juveniles, and in contrast to other alpheid genera in which mature males are recognizable by an appendix masculina on the second pleopod, there is no secondary sexual character that reliably distinguishes mature males from juveniles (Felder, 1982; Dardeau, 1984). Small, egg-bearing females in many *Synalpheus* species tend to have male-like morphology (large major chela, narrow abdomen, occasionally hooked first abdominal pleura). This situation probably indicates protandrous partial hermaphroditism, which is known in the alpheid genus *Athanas* (Suzuki, 1970; Nakashima, 1987; Gherardi and Calloni, 1993) and in several other caridean shrimp taxa (Bauer, 2000). Sexual biology has been studied in some detail in two species of *Athanas*, symbiotic with sea urchins (Suzuki, 1970; Nakashima, 1987; Gherardi and Calloni, 1993). In these species histological sectioning showed that all individuals matured first as males, after which some developed ovaries, while others remained males apparently throughout life. Individuals maturing as females retained sperm-filled testes for a time, and there was some evidence of ovarian regression in the largest individuals, which may possibly change sex again back to males (Suzuki, 1970, but see Nakashima, 1987). Social control of sex change was inferred in *A. kominatoensis* (Nakashima, 1987) and demonstrated experimentally in a hippolytid shrimp (Lin and Zhang, 2001). It is unknown whether similar processes occur in *Synalpheus,* but the invariant presence of only a single mature female in colonies of *S. regalis* (Duffy, 1996a) strongly suggests some sort of social control over sexual maturation. Although male maturity is difficult to discern externally

in *Synalpheus*, mature females are easily identified by the ovaries, which are visible from a relatively early state through the carapace and dorsal abdomen, and by several morphological modifications. Thus, large non-ovigerous individuals are presumably mature males, but may be sexually undifferentiated. Because sex is indistinguishable externally in all individuals other than mature females, I refer throughout this paper to non-ovigerous individuals as either "juveniles" (small) or "males" (large). The working hypothesis is that juveniles, and perhaps also some large "males", have the potential to mature as male, female, or perhaps both sequentially. Allozyme studies confirm that both sexes are diploid (Duffy, 1993, 1996b).

To my knowledge, mating has not been described in detail for any alpheid shrimp. In most crustaceans ovulation can occur only immediately after the female has molted, while her integument is soft, and mating takes place around this time. In most carideans whose mating has been studied, it involves the male attaching spermatophores to the female's abdomen (Bauer, 1976, 1979), followed by external fertilization when the female subsequently ovulates. Coutière's (1899) anatomical study of *Alpheus* illustrated a simple tubular oviduct without seminal receptacle, and in several species of *Alpheus* (R.E. Knowlton, 1971; N. Knowlton, 1980; Jeng, 1994) and the alpheid *Athanas kominatoensis* (Nakashima, 1987), females produced infertile eggs in the absence of males, indicating that they are unable to store sperm. The apparent absence of sperm storage in alpheids is important in implying that the female must mate each time she ovulates. This may explain the pair-bonding habit typical of many non-social alpheids, in which an adult male and female maintain a constant association. Eggs of *Synalpheus* are laid in the discrete clutches typical of crustaceans, rather than continuously as in some social insects, and the clutch is carried in the mother's brood pouch, sometimes with minor attrition, until the embryos hatch. Development has not been studied in *Synalpheus* but in *Athanas kominatoensis*, a symbiotic alpheid similar in size to many *Synalpheus* species, time from oviposition to hatching was 11 days at 25°C in the laboratory (Nakashima, 1987). A new clutch of eggs is laid very soon after the present clutch hatches. We have collected egg-bearing females of many *Synalpheus* species at all times of year, and mature females without eggs are extremely rare (personal observation), indicating that breeding is continuous in female *Synalpheus* in tropical habitats.

Development, "parental care", and dispersal

The majority of decapod crustacean species, including many species of *Synalpheus*, produce planktonic larvae that drift in the water column for days to weeks prior to settling back into benthic habitats. In these taxa, parents presumably have no contact with their offspring after eggs hatch. Several species of *Synalpheus*, however, exhibit "direct development" in which eggs hatch into crawling juveniles (Dobkin, 1965, 1969). These include the eusocial species *S. regalis, S. filidigitus*, and *S. chacei*, in which direct observations of captive colonies (unpublished observations), cohort structure of preserved

colonies (e.g., Duffy and Macdonald, 1999), and relatedness estimates (Duffy, 1996a) indicate that juveniles typically remain at least initially in the natal sponge. In addition to these eusocial species, we have documented direct development via observations of hatching in the lab in *S. agelas, S. "rathbunae A", S. brooksi, S. "bousfieldi A"* and *S. paraneptunus* (including S. "*paraneptunus small*"). In several of these species it is not uncommon to find small juveniles in the company of a heterosexual pair of adults, suggesting that offspring remain associated with their parents for some time after hatching. Insofar as such associations provide a safe place for the offspring to live they can be interpreted as a form of parental care. To date, however, we have seen no evidence of active parental care of small juveniles such as allofeeding, although detailed behavioral observations are limited and have been conducted only for *S. regalis* so far.

The means of dispersal in sponge-dwelling shrimp is an almost complete mystery. Species with swimming planktonic larvae presumably exit the natal sponge and disperse through the water column for some distance, although there is some evidence that even these may not go far (Knowlton and Keller, 1986). In species with direct development, the cohabitation of adults and small juveniles suggests that the latter frequently remain for some time in the natal nest, and allozyme evidence of strong population subdivision (Duffy, 1993, 1996b) is also consistent with this. Yet dispersal clearly happens with some regularity as virtually all appropriate sponges are occupied in the field, at least for highly social species (Duffy, 1996c,d, Figure 2). The high frequency of heterozygote excess in colonies of the eusocial *S. regalis* (Table 1) indicates outbreeding, which also suggests that at least one sex disperses in search of mates. In an anemone-associated alpheid, field observations indicate that males are the mobile sex (Knowlton, 1980).

Communication and interaction
In reviewing mating behaviors among animals, Darwin (1871) observed that "[t]he mental powers of the Crustacea are probably higher than might have been expected." Accordingly, individual recognition has been demonstrated experimentally in stomatopods ("mantis shrimp", Caldwell, 1979), lobsters (Karavanich and Atema, 1998), and a hippolytid shrimp (Rufino and Jones, 2001), and finely tuned kin recognition has been demonstrated in a social desert isopod (Linsenmaier, 1987). In most of these cases chemical cues were demonstrated or implicated. Communication in alpheid shrimps, as in many other crustaceans, involves visual, mechanical, and chemical modalities (Schein, 1975; Jeng, 1994; Hughes, 1996a,b; Herberholz and Schmitz, 1998, 1999, 2001), sometimes in combination (Hughes, 1996b).

Most alpheids are very aggressive toward both heterospecific and conspecific individuals other than familiar mates (Hazlett and Winn, 1962; Nolan and Salmon 1970, Knowlton and Keller, 1982; Nakashima, 1987; Gherardi and Calloni, 1993). Social *Synalpheus* species are a conspicuous exception, as they live in dense colonies and are in

Table 1. Inbreeding coefficients (F_{IS}) calculated for ten colonies of *Synalpheus regalis* based on genotypes at three allozyme loci. Asterisks denote estimates showing significant heterozygote excesses at the Bonferonni-adjusted P = 0.00167. Significance determined by comparison with randomized data (N=3000) using the Fstat program (Goudet, 2000). No colony showed a significant heterozygote deficiency at any locus.

Colony	F_{IS} estimates			
	Pgi	*Tpi*	*Pep*	All
04	-0.900*	-0.356	--------	-0.619*
13	---------	-0.462	--------	-0.462
15	-0.576*	--------	-0.188	-0.444*
16	-0.355	--------	-0.739*	-0.566*
23	--------	--------	-0.043	-0.043
24	-0.400	-0.909*	-0.088	-0.475*
28	--------	--------	0.782	0.782
29	-0.143	--------	--------	-0.143
32	-0.379	-0.565	--------	-0.478*
33	-0.810*	0.000	--------	-0.728*

almost continuous contact with other individuals. Aggression in alpheids is most frequently manifested in defending a territory, whether a burrow (Nolan and Salmon, 1970), host anemone (Knowlton and Keller, 1982), or host sponge (Duffy, 1996a; Duffy et al., 2002). The major chela, or snapping claw, figures prominently during such aggressive interactions among alpheid shrimp. Both sexes in *Synalpheus* typically bear two asymmetric chelae on the first pair of legs (Figure 4). The heavy major chela, which

makes up a large fraction of the body mass, particularly in adult ma les, is used in both threat displays and physical attacks (Hazlett and Winn, 1962; Nolan and Salmon, 1970; Schein, 1977; Conover and Miller, 1978; Knowlton and Keller, 1982; Hughes, 1996a, 1996b). A plunger and socket mechanism in the fingers of the major chela, when closed rapidly, produces a focused, high-velocity jet of water anteriorly and results in a loud snap, hence the common name "snapping shrimp". The much smaller, more delicate minor chela is used in feeding. The snaps and associated water jets produced by the major chela are directed at opponents during aggressive interactions, and larger alpheid species have even been reported to stun small prey thereby without contacting them (MacGinitie and MacGinitie, 1949; Schultz et al., 1998). When contests escalate, the major chela is used to grapple with or pinch opponents, sometimes inflicting serious damage. In the alpheids *Athanas kominatoensis* and *A. indicus*, many individuals in the field have mutilated or lost claws (Nakashima, 1987; Gherardi and Calloni, 1993), and we commonly find signs of wear on the snapping claw of *Synalpheus* species as well. As the claw is used primarily if not exclusively during aggressive interactions, these observations suggest that such interactions are frequent and often intense in natural populations.

Although the behavior of *Synalpheus* has received comparatively little attention, that of the large, pair-bonding *Alpheus* species common in shallow water is fairly well-studied. In both genera, interaction between two conspecifics generally starts with mutual contact of the antennules, experimental removal of which greatly impedes sex recognition and pair formation in *A. edwardsii* (Jeng, 1994). In *Alpheus* spp., encounters often escalate to aggressive posture in which the snapping claw is cocked open (Nolan and Salmon, 1970). This posture is a threat display and *A. heterochaelis* responds aggressively to even isolated claws when open (Hazlett and Winn, 1962; Hughes, 1996a), confirming that the chela provides an important visual cue during interaction. In males of this species, aggressive response is enhanced by simultaneous presentation of chemical cues. These chemical cues are focused specifically toward an opponent by the anterior gill current, which operates primarily during aggressive interactions and serves to direct chemical signals efficiently toward the opponent (Herberholz and Schmitz, 2001). Size of the snapping claw is strongly correlated with body size, which significantly predicts the outcome of aggressive contests among individuals (Nolan and Salmon, 1970; Schein, 1977; Hughes, 1996a). Shrimp whose snapping claw has been immobilized experimentally lose out to intact individuals in contests for shelters (Conover and Miller, 1978).

Although the snap is conspicuous to human observers, alpheids have no known auditory receptors so it is unclear whether shrimp actually detect its sound. In a series of elegant experiments Herberholz and Schmitz (1998, 1999, 2001) demonstrated that *Alpheus heterochaelis* directs its snap fairly precisely toward a dense field of mechanosensory setae on the opponent's snapping claw, concluding that the water jet produced represents a threat display. Experimental occlusion of the setal field resulted in the receiver of snaps more often retreating and in a longer latency of response (Herberholz

and Schmitz, 1998). Shrimp with larger snapping claws produce louder snaps (Schein, 1975) and faster, wider water jets that travel farther, and the latter effect is more pronounced in males (Herberholz and Schmitz, 1999). Thus, snaps provide a reliable signal of the snapper's claw size and fighting ability.

SOCIALITY IN *SYNALPHEUS*

Phylogenetic distribution of eusociality

Because the species of *Synalpheus* are quite similar in morphology and general ecology, this group provides an unusual opportunity to test the correlates of social system evolution unconfounded by the many lineage-specific factors complicating comparative analyses at higher taxonomic levels (e.g., Andersson, 1984; Alexander et al., 1991; Crespi, 1996). As in any comparative analysis, however, exploiting the potential of sponge-dwelling shrimps to explore social evolution depends critically on a well-supported phylogenetic tree on which hypotheses of character evolutionary history can be traced. We have recently conducted a phylogenetic analysis that includes 20 of the ~24 described species of *Synalpheus* in the gambarelloides group, 10-11 undescribed species in the group, and eight outgroup *Synalpheus* taxa. The character data set includes sequence data from ~540 bp of the mt COI gene, ~520 bp of the mt large-subunit (16S) rRNA gene, and 45 morphological characters. Analysis of the combined data set using 6-parameter weighted parsimony produced one tree (Figure 1, Morrison, Ríos, and Duffy in prep.). The analysis provides fair support (bootstrap = 65%) for monophyly of the geographically circumscribed and socially diverse gambarelloides group, making it a promising unit for comparative studies. The new tree also corroborates the conclusion from an earlier analysis of only 13 ingroup taxa (Duffy et al., 2000) that eusociality has evolved two to three times independently within the gambarelloides group. Interestingly, collections of large numbers of small-bodied shrimp with few or no ovigerous females have also been reported in several Indo-Pacific species of *Synalpheus* outside the gambarelloides group (Banner and Banner, 1981, 1983; Bruce, 1988). It is likely that these records represent incomplete collections of monogynous colonies, suggesting that at least one additional independent origin of eusociality within the genus is possible.

Within the gambarelloides group, six taxa currently can be recognized as eusocial, based on the presence of a single breeding female in most colonies and evidence that adult offspring remain in the colony without breeding. Four of these species comprise a single clade, the ancestor of which is parsimoniously reconstructed as eusocial (Figure 1); they are *S. regalis* (see Duffy, 1996a; Duffy et al., 2002), *S. filidigitus* (see Duffy and Macdonald, 1999), *S. rathbunae* (see Duffy, 1992), and the undescribed species *S. "rathbunae A"*. Colonies of *S. regalis* and *S. filidigitus* almost always contain only a single female; those of the other two species sometimes contain a few, but always have

marked reproductive skew. As borders between adjacent conspecific sponges are often difficult to discern in the field, it is possible that occasional findings of multiple-queen colonies in *S. rathbunae* (Duffy, 1992) and *S. filidigitus* (Duffy and Macdonald, 1999) reflect pooling of separate colonies. Moreover, additional collections made since those reported by Duffy et al., (2000) produced several monogynous colonies of *S*. "*rathbunae* A". Thus, we now consider this entire clade of four species as eusocial. The social organization of *S. rathbunae* and *S*. "*rathbunae* A" has otherwise been little studied.

The two remaining eusocial taxa are *S. chacei* (discussed below) and a divergent population of *S. paraneptunus* in the Florida Keys that we refer to as *S*. "*paraneptunus* small". Our phylogenetic analysis strongly supports two recently discovered, undescribed species as the closest relatives of *S. chacei* (Figure 1). Although few specimens of these undescribed species are available, they all were found in heterosexual pairs. Thus, eusocial colony structure in *S. chacei*, though superficially similar to that in *S. regalis*, appears to represent an origin entirely separate from that of *S. regalis*. In our collections of *S. paraneptunus* from Belize and Caribbean Panamá, a sponge usually contains one (rarely more) heterosexual pair of adults, often with a small number of juveniles (Duffy et al., 2000). In Florida, however, *S. paraneptunus* is noticeably smaller, slightly different morphologically, and a sponge usually contains several apparently adult individuals (median colony size = 9, range = 2-23, Duffy et al., 2000) with usually a single breeding female. Thus, if such small colonies can be considered eusocial, they represent a third independent origin of eusociality within the gambarelloides group.

Colony organization and social biology of Synalpheus regalis
    Colony structure. Of the several social species of *Synalpheus*, *S. regalis* has the largest colonies, the strongest reproductive skew, and is the best studied. This species has been found only in the vicinity of Carrie Bow Cay, Belize, and almost exclusively in the sponges *Xestospongia* cf. *subtriangularis* and *Hyattella intestinalis* (Duffy, 1996c, 1996d, Figure 2). Colony size (i.e., number of individuals within a sponge) ranges up to 350 individuals (Figure 3) and colonies invariably contain only a single breeding female, the queen (Duffy, 1996a). Genetic data and reproductive allometry together indicate that *S. regalis* colonies consist largely of full-sib offspring of a single breeding pair which "reigns" for most or all of the colony's life– simple, biparental families in Emlen's (1997) terminology. First, relatedness among large, non-ovigerous colony members (queen and juveniles were not genotyped) calculated from allele frequencies at three allozyme loci averaged 0.50, consistent with full sibs (Duffy, 1996a). Second, reexamination of this same data set reveals strong heterozygote excess at several of the ten colonies (Table 1). For example, in colony 4, 19 of 20 individuals scored had the genotype AB at the *Pgi* locus, and in colony 24, 21 of 22 individuals had the genotype AB at the *Tpi* locus. No locus showed a lower than expected frequency of heterozygotes in any colony.
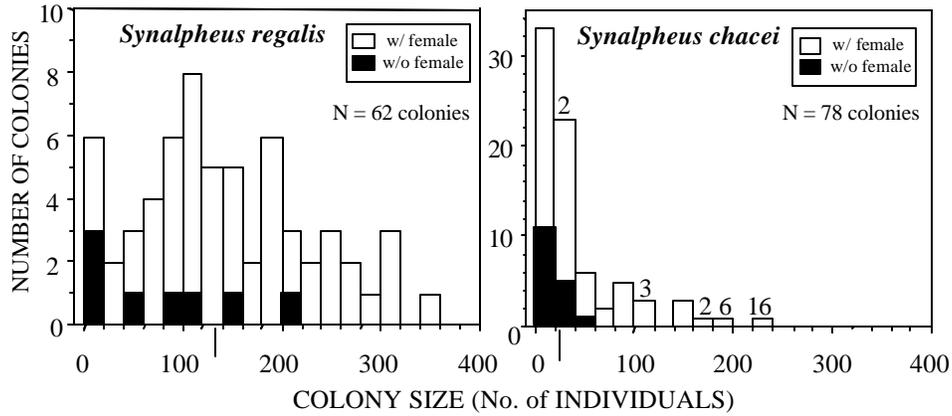
Figure 3. Distribution of colony sizes (number of individuals per sponge) in two eusocial shrimp species from Belize. Arrows below abscissa show median colony size. Five colonies of *S. chacei* contained more than one female; each is indicated by a numeral above the bar for the appropriate colony size, the numeral indicating the number of breeding females in that colony.
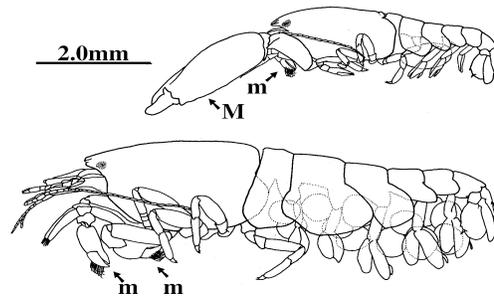
Figure 4. Morphological transformation of the queen in *Synalpheus filidigitus*. Top: a smaller female (carapace length = 1.81 mm) from a colony of 4 individuals; this specimen carried a single egg, and a normally developed major chela (M), or snapping claw. Bottom: the largest female found in our collection (carapace length = 3.13 mm), from a colony of 121 individuals. This specimen carried 29 eggs and bore two minor chelae (m). Note the enlarged abdomen, and replacement of the major chela by a second minor-type chela (m) in the larger queen. Both specimens drawn to same scale. After Duffy and Macdonald (1999), used by permission.

The heterozygote excesses are reflected in calculated values of F_{IS}, which were significantly negative at the Bonferonni-adjusted P value of 0.00167 in six of the ten sampled colonies (Table 1). Weir and Cockerham's (1984) f, an estimator of F_{IS}, averaged -0.443 across all loci and colonies. These heterozygote excesses also imply that *S. regalis* colonies, at least the larger size classes, are full-sib families as heterozygote excesses are expected where colony members are offspring of a single breeding pair homozygous for different alleles at a locus. Inbreeding, in contrast, would produce heterozygote deficiencies, which were not found. 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. In several other *Synalpheus* species, heterosexual pairs are occasionally or regularly collected with small juveniles. Taken together these data indicate that eusociality in this genus has evolved through the subsocial route (sensu Wilson, 1971) as appears true of most eusocial animals (Alexander et al., 1991).

The behavioral repertoire of Synalpheus regalis. We have made detailed macrovideo observations on captive colonies of *S. regalis* occupying living sponge slices in a flow-through seawater system in Belize. Although these videotapes have not yet been scored completely, first impressions indicate that *S. regalis* spend the great majority of their time resting and grooming, interspersed with short bouts of feeding. Shrimp fed either by picking at the surface of the sponge canal, using the small chelae on the second pair of legs, or by rapidly sweeping the setal brush on the dactyl of the minor first chela against the canal surface. In both cases, collected material was transferred rapidly to the mouth after each movement. As in other *Synalpheus* species, microscopic examination of stomach contents from freshly field-collected adults revealed only sponge spicules and flocculent material, confirming that *S. regalis* feeds primarily or exclusively on sponge tissue and/or secretions.

In contrast to the more accessible and better studied *Alpheus* and *Athanas* species, which typically live singly or in heterosexual pairs, social *Synalpheus* species are in frequent contact with nestmates, and indeed appear to seek out such contact, often climbing over one another and huddling closely with several other individuals. Initial interactions with other shrimp involve the mutual antennulation typical of carideans. My impression from observing captive colonies is that colony members actively seek contact with the queen, which is supported by the finding that, on a per-individual basis, the queen is more likely to be contacted by intruders than are large males and juveniles (Duffy et al., 2002) despite her general sluggishness. In captive colonies we also regularly observe a large male in association with the queen, behaving aggressively (e.g., with cocked chela) when other large males approach her. It is not yet clear whether or how long mate guarding occurs, although the inference of monogamy from genetic data (Duffy, 1996a, Table 1) suggests that the queen associates with a single male for a prolonged period.

Finally, I have observed several times *S. regalis* handling dead nestmates. Generally,

the carcasses are dragged and pushed to an out-of-the-way place and over the course of time the carcass is picked free of accessible flesh. Eventually, the picked carcass is worked and pushed toward an opening in the sponge surface and pushed out of the sponge entirely. Other more specifically social behaviors are discussed below.

Nestmate recognition, colony cohesion, and communication. Aggregation and interaction among relatives is an important prerequisite for social evolution involving kin selection (Hamilton, 1964), and some ability to distinguish kin from non-kin broadens the conditions under which altruism can evolve (Perrin and Lehmann, 2001). Experiments introducing intruders to captive colonies of *S. regalis* provide evidence for discrimination between nestmates and other conspecifics, and even more pronounced aggression toward heterospecific intruders (Duffy et al., 2002). When faced with a non-nestmate conspecific, resident shrimp contacted it less and snapped more frequently than they did when faced with a nestmate. As nestmates are generally close relatives in *S. regalis*, this behavior effectively results in kin discrimination (although whether it involves kin recognition per se remains uncertain) and should help maintain the integrity of kin-structured social colonies. Water-borne chemical cues, which are important in other alpheids (Schein, 1975; Jeng, 1994; Hughes, 1996b), presumably explain the finding that residents contacted non-nestmate conspecifics and heterospecifics less frequently than nestmates. But the mutual antennulation that initiates nearly all contacts in alpheids (Nolan and Salmon, 1970; Knowlton and Keller, 1982; Jeng, 1994), including social *Synalpheus*, suggests that contact chemical signals are of central importance in mediating recognition in these shrimp, as they are in many social insects (Hölldobler and Wilson, 1990; Blum, 1996).

Our observations of captive colonies of *S. regalis* have revealed a preliminary but intriguing case of apparent communication I refer to as "mass snapping": a sudden initiation of simultaneous, repeated snapping by multiple colony members. The phenomenon begins with rhythmic snapping by one individual, followed by rapid recruitment of many others, and lasts for a few seconds. It is quite clear that the other colony members are responding to the signal of the initial snapper, as many of them join in immediately, producing a startling, simultaneous crackling sound. Thus, the phenomenon appears to be a form of communication. Although we have observed this several times, we could discern neither what caused the initial signal nor its message. It is difficult to reconcile this phenomenon with the conclusion (Herberholz and Schmitz, 1998, 1999) that the snapping signal in alpheids is perceived primarily via mechanical sensing of the water jet at close range, although it is conceivable that snapping transmits a mechanical signal through the substratum.

Division of labor. Most adaptive explanations for eusociality depend fundamentally on some form of division of labor, which results in enhanced reproductive output of breeders and inclusive fitness benefits for non-breeding helpers (Wilson, 1975; Oster and Wilson, 1978; Seger, 1991; Emlen, 1991). The most fundamental aspect of division of

labor is in reproduction, which is restricted to a single queen in colonies of *S. regalis*. The queen in this species also appears considerably less active and less aggressive than adult males (Duffy et al., 2002, unpublished). Indeed, in the closely related eusocial *S. filidigitus*, the reduced aggressiveness of queens is manifested in a physical polymorphism in which mature queens lack a snapping claw, apparently having shed it and regenerated a second minor-form chela (Duffy and Macdonald, 1999, Figure 4).

Apart from reproduction the clearest evidence of behavioral differentiation that might be construed as division of labor in *S. regalis* involves behaviors associated with colony defense, an activity with probable strong consequences for colony fitness in the space-limited environment (Duffy, 1996c; Duffy et al., 2000). Because evidence from host occupation patterns (Duffy, 1992, 1996c, 1996d) and aggressive behavior (Duffy, 1996a) indicate strong competition for hosts among sponge-dwelling *Synalpheus*, our investigations of putative helping behavior and division of labor accordingly have focused on colony defense against intruders. Observations of captive colonies (Duffy et al., 2002) showed that small individuals were sedentary and often congregated in groups to feed, whereas large males more frequently moved boldly around the sponge, cocking the chela upon contacting another individual. When we recorded positions of colony members during such observations, large males were significantly more likely to be crawling on the outside surface of the sponge than were smaller individuals ($P < 0.0001$, bootstrapped data for 11 colonies). In experiments where intruders were introduced into colonies, large males were more aggressive on a per-individual basis than juveniles or the queen when facing heterospecific intruders and, at the level of the colony, large males were responsible for most contacts and snaps against all types of intruders. Thus, our observations and experiment show that large males 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. This shielding of the queen and juveniles from contact with danger is likely to translate into important fitness advantages as aggressive encounters between alpheid shrimp can cause serious injuries or even death (Knowlton and Keller, 1982; Nakashima, 1987; Gherardi and Calloni 1993, Duffy 1996a).

Such size- or age-related polyethism is a common component of labor specialization among social insects (Wilson, 1971; Oster and Wilson, 1978; Robinson, 1992) and vertebrates (Emlen, 1991) as well, although the link between age and task may not be causal (Bourke and Franks, 1995). In many primitively eusocial insects such as paper wasps and lower termites, and in most cooperatively breeding vertebrates, behavioral differentiation tends to be facultative, changing with social and dominance context, ontogeny, and position in the nest (Strassmann and Queller, 1989; Emlen, 1991). In more derived, large-colony eusocial insects such as certain ants and termites, division of labor is often accompanied by irreversible morphological specialization and sterility (Crespi and Yanega, 1995). One general process that may generate the frequently described correlation between age and task is the tendency of workers to begin working near their

birthplace at the nest center and move progressively outward, a process described by Wilson (1985) as temporal polyethism. The spatial structure of social shrimp colonies is too poorly known to assess whether a similar phenomenon occurs therein, but three observations suggest it is a possibility. First, in our field collections, the queen is often among the last individuals to be removed from a sponge, suggesting that she resides near the center of the sponge. Second, in a captive colony in which we observed the hatching of a clutch of newborn *S. regalis*, the newborns congregated in close proximity to the queen for the several days during which the colony was watched. Third, the individuals found most commonly on the outside of the sponge in captive colonies were overwhelmingly large males (see last paragraph).

Maintenance of reproductive skew.
The formation of kin aggregations in poorly dispersing animals such as *Synalpheus* is easy to understand. But why, in the extreme case of eusociality, do only a single female and sometimes a single male breed? Several hypotheses are available (Emlen, 1996). First and perhaps most straightforward is dominance asymmetry: the breeder aggressively suppresses reproduction in subordinates. This mechanism explains, at least in part, maintenance of reproductive skew in several primitively eusocial 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). Two lines of behavioral evidence suggest that queen aggression does not maintain her reproductive monopoly in *S. regalis*. First, observations of interactions among individuals in captive colonies produced no evidence of aggression or behavioral dominance by the queen that might maintain her reproductive monopoly over other colony members (Duffy et al., 2002, unpublished). Indeed the queen was relatively inactive. Second, in preliminary analyses of colonies experimentally split into queenright and queenless halves for a period of 9 days, we found no evidence in the queenless half of increased aggression, contests for dominance, attempted mating, nor indeed any detectable differences in behavior between the two treatments (Duffy, Morrison, and Macdonald, in prep.). Lack of aggressive dominance by the queen is also implied for the eusocial *S. filidigitus*, in which the queen routinely sheds her snapping claw, replacing it with a second minor-form chela (Duffy and Macdonald, 1999); this phenomenon has also been reported in populations of *S. rathbunae* (Chace, 1972) and *S. crosnieri* (Banner and Banner, 1983), both of which also show strong reproductive skew. As the major chela is crucial to defense and aggressive encounters, this situation strongly implies that females in social *Synalpheus* cannot maintain their sole breeding status through aggression and harassment of other potential breeders. Loss of the snapping claw, which constitutes a substantial fraction of body mass, may be an adaptation to achieving higher fecundity in the cloistered queen, who is defended by her colony, can divert the resources from chela to egg production, and gains a second feeding appendage.

A second potential mechanism maintaining reproductive skew in social taxa involves relatedness asymmetry (Emlen, 1982; Keller and Reeve, 1994), causing sibling workers to police one another's reproduction because they are less related to prospective nieces than to prospective sisters (Ratnieks, 1988), the "constitutional monarchy" of Queller and Strassmann (1998). In large-colony eusocial insects, where the queen is incapable of aggressively dominating all colony members, monogyny may nevertheless be maintained where the queen is multiply mated, as workers are selected to suppress one another's breeding because they are more closely related to the queen's (i.e., their mother's) offspring than to that of other workers, who will on average be their half-sisters (Ratnieks, 1988; Bourke, 1999). This hypothesis is supported indirectly by progeny sex ratios in some social Hymenoptera that are consistent with control by workers rather than the queen (Queller and Strassmann, 1998). In a diploid animal such as *Synalpheus*, if colonies consist of full sibs as they appear to in *S. regalis* (Duffy, 1996a, Table 1), non-breeding colony members should also resist allowing their siblings to mate with unrelated intruders since they will be related to the progeny thus produced by 0.25 whereas they will be related to offspring of their parents (the reigning breeders) by 0.50. Currently we have no experimental evidence to evaluate this hypothesis for *Synalpheus.*

Finally, a third hypothesis to explain strong reproductive skew, with considerable support from some social vertebrates, is incest avoidance. Mating with close relatives generally carries a cost in the form of reduced fitness (i.e., inbreeding depression, Pusey and Wolf, 1996). If eusocial colonies consist of close relatives, such as full-sib offspring of outbred parents, the avoidance of incest that is common in many animals might explain why offspring of the breeding pair do not attempt to breed (Emlen, 1995). This hypothesis is supported by an elegant series of experiments in the Damaraland mole-rat, in which colonies consist of an unrelated breeding pair and its adult offspring. When a breeder was removed from the colony, its members would not attempt to breed unless an unrelated individual was introduced (Bennett et al., 1996). Conversely, addition of an unrelated adult to an intact colony initiated breeding activity even in the presence of the original breeders (Cooney and Bennett, 2000). These results, together with evidence of strong inbreeding depression in this species (Greeff and Bennett, 2000) support the hypothesis that monogyny in colonies (families) of this eusocial species is maintained by inbreeding avoidance. Maintenance of reproductive skew by incest avoidance is also consistent with some data from eusocial termites (Shellman-Reeve, 2001). Incest avoidance is an attractive explanation for strong reproductive skew in *S. regalis* , in which average relatedness (Duffy, 1996a) and heterozygote excesses (Table 1) suggest that colonies are full-sib families of a single breeding pair. Nonetheless, the hypothesis has not yet been tested experimentally in social *Synalpheus.*

A different kind of eusociality in Synalpheus chacei?

Like *S. regalis* and its close relatives, *S. chacei* lives in multigenerational colonies with usually only a single female breeding. *S. chacei* has been found in Panamá, Belize, and the US Virgin Islands in at least 7 species of sponges (Duffy, 1998), although it generally uses only a small number of host species at a given site. Available data provide several lines of evidence that the structure and dynamics of colonies in *Synalpheus chacei*, and specifically the frequency of queen replacement, differ substantially from those of *S. regalis*. The most obvious differences between *S. regalis* and *S. chacei* lie in colony size and the degree of reproductive skew. Sampled colonies of *S. chacei* from Belize were considerably smaller on average than those of *S. regalis*, ranging in size from 2 to 238 individuals, with a median of 23 (Figure 3). Seventeen of 78 sampled colonies (22%) lacked a mature female (queen) and the frequency of such queenless colonies was substantially greater in colonies smaller versus larger than the median size ($P = 0.0050$, Fisher's exact test). Of those colonies containing a queen, the majority had only one. However, multiple breeding females were found in each of five colonies, all of which were larger than the median colony size. The extreme case was the largest colony of *S. chacei* collected, which contained 238 individuals and 16 ovigerous females (Figure 3). Females from these multi-queen colonies were smaller, less fecund, and had larger snapping claws than single queens from colonies of similar size, hinting that they may recently have matured as females from the population of non-breeders in the colony.

We have obtained preliminary genetic data from two microsatellite loci that are consistent with frequent queen turnover in *S. chacei* (J.E. Duffy and L. Bilodeau, in prep.). We screened a total of 46 individual shrimp (5 queens, 8 adult males, 17 juveniles, 16 embryos) from four colonies for variation at two loci. Variability was relatively low for microsatellite loci and most alleles were shared among the four colonies screened. Of the five clutches of embryos we screened each was compatible with a single father (not the same among colonies), although variation is too low to test this rigorously. Despite the relatively low variability at these loci, our preliminary data unambiguously demonstrate that queen turnover is frequent in *S. chacei* colonies: in three of four colonies most of the juveniles screened had two-locus genotypes incompatible with parentage by the resident queen, i.e. that shared neither of her alleles at one or both loci.

In summary, the available data suggest that *S. regalis* colonies are large, stable, nuclear families with consistently high relatedness, whereas *S. chacei* colonies are smaller, more dynamic, and genetically heterogeneous. Compared with the large (median 135.5 individuals) colonies of *S. regalis*, the much smaller colonies of *S. chacei* (median 23 individuals) more often contained multiple queens, or no queen, suggesting that social control of reproduction is weaker in *S. chacei*, a hypothesis supported by the microsatellite evidence for frequent queen turnover. The greater genetic heterogeneity in *S. chacei* colonies also suggests that incest avoidance may be a less likely explanation for reproductive skew in this species. Thus, in *S. chacei* colonies, an individual's average

chance of attaining breeder status and inheriting the nest should be considerably higher than in *S. regalis*, leading to a higher predicted level of aggression, weaker kin selection, and weaker cooperative behavior in the former species. Future experimental studies of behavior will be required to test this prediction.

ADAPTIVE BASIS OF EUSOCIALITY IN *SYNALPHEUS*

A number of general hypotheses have been proposed to explain the origin and maintenance of eusociality and cooperative breeding among animals. These can be grouped broadly into hypotheses emphasizing kin selection, ecological constraints, or life history. This pigeonholing is of course artificial as these features work together to determine benefits of particular behaviors (Hamilton, 1964; West-Eberhard, 1981; Andersson, 1984; Alexander et al., 1991; Bourke and Franks, 1995; Strassmann and Queller, 1998). Nevertheless, it is convenient to categorize them by main emphasis for discussion. Similarly, several authors have stressed that no single factor is sufficient in itself to explain eusociality and that hypothesized general promoters of eusociality will only be effective given certain environmental situations and phenotypic traits (Andersson, 1984; Alexander et al., 1991; Crespi, 1994). An explicitly hierarchical approach to this complexity, which identifies nested occurrences of conditions promoting sociality within clades, recently has proven successful in explaining the distribution of cooperative breeding in birds (see below).

Kin selection and unusual relatedness
Relatedness among interactants is fundamental to most social interactions, as first developed formally by Hamilton (1964) and amply demonstrated empirically in social insects (e.g., Bourke and Franks, 1995; Queller and Strassmann, 1998) and vertebrates (Emlen, 1997). Beyond this general importance, discussion of the evolution of eusociality historically placed much emphasis on mechanisms producing unusually high genetic relatedness among interactants, notably haplodiploidy in Hymenoptera (Hamilton, 1964). Despite the demonstrated importance of genetic asymmetries in influencing social and sex ratio evolution in hymenopteran colonies, numerous authors have emphasized that haplodiploidy is neither necessary nor sufficient for the evolution of eusociality (Lin and Michener, 1972; Alexander, 1974; Andersson, 1984; Alexander et al., 1991; Crespi, 1994) as is clear from the occurrence of similar eusocial colony organization in termites, mole-rats, and now shrimp, all of which are diploid. Inbreeding can also produce high relatedness within colonies, and this has been suggested as important in promoting and maintaining eusociality in termites (Bartz, 1979) and naked mole-rats (Reeve et al., 1990; Jarvis et al., 1994). More recent work suggests that cyclic inbreeding is not characteristic of most termites (Myles and Nutting, 1988; Thorne, 1997) and that naked mole-rats,

despite generally high inbreeding, seek unrelated mates when they are available (Braude, 2000; Ciszek, 2000).

Colonies consist of close kin in eusocial *Synalpheus* (Duffy, 1996a; Duffy and Macdonald, 1999) as they do in all insects and vertebrates with strong, life-long reproductive skew. There is currently no evidence, however, of any mechanism creating relatedness skew or asymmetry in social shrimp. *Synalpheus* are diploid and *S. regalis* colonies showed heterozygote excesses (Table 1) indicative of regular outbreeding. Nor were colony members in this species heterozygous at all loci, as might be expected under the cyclic inbreeding hypothesis of Bartz (1979). Thus, inbreeding seems unlikely to be a significant part of a general explanation for eusociality. Genetic relatedness is undoubtedly central to maintaining strong reproductive skew and cooperation in social shrimp but appears to involve the same basic relationships common to all biparental families.

The role of life history
Life history has fundamental consequences for social organization and evolution. Indeed, one of the three classical criteria for eusociality is overlap in generations (Wilson, 1971). Many reviews have noted that parental care is an important prerequisite for eusociality in insects and cooperative breeding in vertebrates (Alexander, 1974; Andersson 1984; Alexander et al., 1991). Theory and empirical data from social Hymenoptera show that high adult mortality and long periods of offspring dependence (Queller, 1989) and delayed age of reproduction (Gadagkar, 1991) can favor the non-breeding helper strategy.

Recent analyses of cooperative breeding in birds, using phylogenetically controlled comparisons of a large sample (Arnold and Owens, 1998, 1999), have taken an innovative approach to assessing the relative importance of various life history and ecological factors in evolution of sociality by analyzing hierarchical patterns in their phylogenetic distribution. These authors found that cooperative breeding was concentrated in particular families characterized by low fecundity and high adult survival, and that within these families (but not in a broader among-family comparison), ecological factors – specifically sedentariness and living in a warm, relatively stable environment – significantly predicted the incidence of cooperative breeding. These results were interpreted as showing that life history features, which in birds are conserved at higher taxonomic (i.e., deeper cladistic) levels, evolved earlier and predisposed lineages, after which ecological factors influenced which species within such predisposed lineages evolved cooperative breeding. These life history and ecological factors act in concert to limit the turnover rate of breeding opportunities, which appears to be the best predictor of cooperative breeding in birds (Hatchwell and Komdeur, 2000).

At this stage such a hierarchical approach can only be used informally for *Synalpheus* due to limited knowledge of most species. Nonetheless, preliminary results are intriguing. In many 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). At a broad level, data from crustaceans show that family and social groups occur almost exclusively in taxa with direct development. Post-hatching parental care and family structure occur in several amphipods (e.g., Conlan and Chess, 1992; Aoki, 1997; Thiel, 1997, 1999; Thiel et al., 1997), isopods (Linsenmaier, 1987), bathypelagic mysids (Childress and Price, 1983), and certain *Synalpheus* species, all of which have direct development. 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 snails shells or leaf axils (Diesel, 1989, 1992; Diesel and Horst, 1995), i.e., in restricted spaces that prevent dispersal. Thus, life history traits (or, in the last case, a unique form of parental care) that restrict dispersal are an important prerequisite for family living in crustaceans.

The gambarelloides species group provides an interesting contrast with birds in that life history in these shrimp is less conserved than the fundamental ecological constraint of life in sponges. That is, all species in the group are obligate sponge-dwellers, and share the sedentary lifestyle in warm, relatively 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, in principle, 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. Development mode is known for only a subset of species within the gambarelloides group but there is some evidence that it is conserved within subclades of the gambarelloides group. For example, all species in the clade containing *S. filidigitus* through *S. rathbunae* (Figure 1) are direct developers (and all are eusocial), as apparently are species in the clade *S. "bousfieldi A"* through *S. chacei*, and the two *S. paraneptunus* taxa, whereas species in the clade *S. goodei* to *S. longicarpus* have swimming larvae. Interestingly, eusociality occurs in three subclades with direct development and in none with swimming larvae, supporting direct development as a prerequisite for eusociality in this group.

High adult survival also 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 predators, abundant with food, and thus relatively free of danger, compared with the rock crevices in which most congeners outside the gambarelloides group live. The very low fecundity of some *Synalpheus* species (e.g., *S. filidigitus*, median 4.5, range 1-29 eggs per clutch, Duffy and Macdonald, 1999) also indirectly suggests high survival, which is necessary to balance low fecundity in a population at equilibrium.

Ecological constraints: the mutualism hypothesis

As the potential power of kin selection mediated by relatedness became widely recognized as a force in social evolution, several authors reemphasized that the other terms in Hamilton's (1964) equation – the costs and benefits of altruism dictated by the ecological arena are of equal or sometimes greater importance (Lin and Michener, 1972; Alexander, 1974; Evans, 1977; West-Eberhard, 1981). Chief among these was the proposed importance of enemy pressure in fostering cooperation (Lin and Michener, 1972), later referred to as the mutualism hypothesis. In essence, the argument is that where nest founding is dangerous and individuals often fail, cooperation among individuals in construction and defense may benefit all parties, at least until reproduction begins. Field studies show that pairs and small colonies indeed have higher probabilities of death or disappearance than larger colonies in social wasps, bees, and spiders (Strassmann and Queller, 1989; Itô, 1993; Avilés and Tufiño, 1998), and several authors have concluded that the risk of reproductive failure in individuals and small groups has been a primary factor selecting for eusociality (Lin and Michener, 1972; Evans, 1977; Strassmann and Queller, 1989). More generally, Wenzel and Pickering (1991) showed that, in wasps, variance in average per capita reproduction decreased with colony size, providing a more stable environment and, thus, more predictable fitness prospects in larger colonies.

There is some evidence that mutualism, in combination with kin selection, may be important in the organization of social shrimp colonies. The survival advantage of group founding cannot be tested rigorously with available data on static colony structure because such collections do not include data on failed colonies. Nevertheless, of the 17 sampled colonies of *S. chacei* that lacked females, and thus were at risk of reproductive failure, 14 were below median colony size, a highly significant difference (P = 0.005, Fisher's exact test), with a similar, non-significant trend for *S. regalis* (Figure 3). These patterns suggest that reproductive failure in social *Synalpheus* is more frequent in smaller colonies, as it is in many other social animals, and that selection may favor remaining in (or joining) a social group to minimize this risk.

Mutualistic cooperation, and more specifically behavioral division of labor with respect to defense, could contribute to the previously documented dominance of host sponges by social shrimp species compared with less social taxa (Duffy et al., 2000). Two general mechanisms for such dominance, not mutually exclusive, are possible: enhanced average survival of individuals within the colony (mutualism, see last paragraph), and enhanced reproductive rate of the breeders (involving kin selection). Indirect evidence from field data is consistent with enhanced reproduction in that reproductive output of the lone queen in *S. regalis* colonies increased steadily with colony size (Duffy, 1996a; Duffy et al., 2002). Queen body size is also correlated with colony size (Duffy, 1996a), however, so larger colony size could be a consequence, rather than a cause, of breeder reproductive success, for example through high territory quality or breeder experience. The mechanism for this relationship remains an open question. Nonetheless, as competition for sponges

(Duffy, 1996c, 1996d) likely places a fitness burden on individuals and small groups, and aggressive activities of large males demonstrably reduce the queen's need to defend against such competitors (Duffy et al., 2002), there is a plausible mechanism for a link between such defense and colony reproductive output.

Ecological constraints: the fortress defense hypothesis
Queller and Strassmann (1998) drew a distinction between two modes of eusociality: "life insurers", including most Hymenoptera, in which cooperation yields benefits primarily in reducing the risk of total reproductive failure, and "fortress defenders", including the more recently discovered eusocial thrips, beetle, shrimp, and aphids, in which cooperation enhances defense of a commonly held, valuable resource. Focusing on the fortress-defense type, Crespi (1994, see also Alexander et al., 1991) argued that three conditions are sufficient to explain most known cases of eusociality. First, coincidence of food and shelter in an enclosed habitat represents a highly valuable, often long-lived resource that fosters accumulation of closely related kin and frees juveniles from foraging for other tasks. Second, the high value of many such food-habitat resources should render them vulnerable to attack by competitors and/or predators and thus select strongly for effective defense. Third is the ability to defend the resource effectively: strong selection from enemies on such kin-structured aggregations may promote evolution of specialized defenders that raise their own and the breeders' inclusive fitness by defending the colony. Evidence is available to evaluate each of Crespi's criteria for *Synalpheus*, as follows.
The nest as a valuable resource.
　　Food and habitat are clearly coincident for sponge-dwelling shrimp, which live and feed exclusively within their hosts. Although sponges vary widely in morphology, size, and life history, many reach large sizes (10s - 100s of cm in largest dimension) and can live for decades or centuries (Reiswig, 1973; Ayling, 1983). A single large sponge may harbor thousands of shrimp (Pearse, 1932). Demographic rates have not been studied in *Synalpheus* but it seems safe to conclude that these small crustaceans might easily pass 10s - 100s of generations within a single large sponge. Evidence indeed confirms that social shrimp colonies are close kin aggregations with both high genetic relatedness (Duffy, 1996a) and clear cohort structure (Duffy and Macdonald, 1999), and genetic and morphometric differentiation among demes in different sponges (Duffy, 1996b, 1996c) suggests long-term occupation with little exchange among sponges. Thus, the sponge is not only a valuable resource but a long-lived one, setting up the potential for resource inheritance as an alternative strategy to risky dispersal and independent nest-founding (Myles, 1988).
Selection for defense.
　　Many authors have emphasized the fundamental importance of defense in selecting for cooperation among social insects (Lin and Michener, 1972; Wilson, 1971, 1975; Oster and Wilson, 1978). In *Synalpheus*, data from field collections suggest that host

sponges are in short supply and subject to strong competition (Figure 2, Duffy, 1996d). For the two main host species used by *S. regalis* in Belize, fewer than 5% of sponges sampled were unoccupied by shrimp. Moreover, in those sponge species used by more than one shrimp species, individual sponges are nearly always occupied by only one shrimp species (Figure 2), suggesting competitive exclusion of other species. Indeed, the data shown in Figure 2 actually underestimate the degree of segregation in that those few sponges occupied by more than one shrimp species invariably contained only one or a few individuals of the second species.

Effectiveness of defense.

Andersson (1984) and Starr (1985) emphasized that the transition from group-living to eusociality has only occurred in taxa with effective weapons, notably the sting of aculeate Hymenoptera. In alpheid shrimp the primary agent of defense is the snapping claw, which can be a potent weapon. Large alpheids have been reported to break the glass of aquaria with the snapping claw, and there is laboratory evidence that some species can use the water jet produced by snapping to stun small animal prey (MacGinitie and MacGinitie, 1949, Schultz et al., 1998). We have observed social *Synalpheus* species inflict serious injuries on one another with the snapping claw. Thus, social *Synalpheus* appear to meet each of Crespi's (1994) three criteria. The emphasis on competition for valuable nesting resources in Crespi's (1994) argument echoes the proposed role of ecological constraints, and more specifically "habitat saturation", in selecting for cooperative breeding in social vertebrates (Selander, 1964; Emlen, 1982), the principal difference being Crespi's emphasis, for insects, on the importance of active defense against strong enemy pressure. It is interesting in this context that non-breeding defenders in social *Synalpheus* are male. In contrast, workers in eusocial Hymenoptera are usually exclusively female, which has been attributed by several authors to the absence of the sting (a modified ovipositor) in males, rendering them ineffectual as defenders of the nest (Andersson, 1984; Starr, 1985). The dominance of males among non-breeding defenders in social shrimp might be similarly explained, as the snapping claw is proportionally larger and heavier in male than in female alpheids (Schein, 1975; Knowlton, 1980; Nakashima, 1987)

EUSOCIALITY IN THE SEA

Prior to the report of eusociality in *S. regalis*, Spanier et al. (1993) asked "why are there no reports of eusocial Crustacea?" Building mostly on the arguments of Andersson (1984) and Alexander et al., (1991), they reasoned that several conditions suggested to favor eusociality -- including cavity nesting, overlapping generations, restricted dispersal, and some form of parental care – are reasonably common in crustaceans and should have

selected for eusociality in one or more of its component taxa. Spanier et al. can be congratulated for correctly predicting the occurrence of eusociality in this group. Their question can now be refined to ask (1) why are there not more eusocial crustaceans? And (2) more particularly, why are some but not all *Synalpheus* species eusocial? These questions can be addressed in the context of Crespi's (1994) three criteria for eusociality.

Among the Crustacea there are many taxa that meet one or more of Crespi's criteria but few that met all of them. Several groups of crustaceans, particularly on coral reefs, associate with discrete, long-lived, valuable resources that provide both shelter and food. In addition to *Synalpheus*, these include pontoniine shrimp in Indo-Pacific sponges (Bruce, 1976), and various shrimps and crabs in Indo-Pacific corals (Patton, 1974; Bruce, 1976; 1998). The alpheids and crabs, in particular, are aggressive and well-equipped with powerful claws to defend their host resource. To my knowledge, however, all of these groups produce planktonically dispersing larvae, preventing the formation of kin groups. Among the more promising potential candidates for crustacean eusociality may be the leucothoid or anamixid amphipods. These animals have direct development (like all amphipods) and live within sponges or ascidians, generally on tropical reefs. They are sometimes found in what appear to be family groups (Thomas, 1997; Thiel, 1999), and males bear hypertrophied gnathopods (claws), presumably used in sexual contests, that could perhaps be employed in cooperative defense of a host sponge. It is tempting to speculate that one factor foiling the evolution of eusocial colonies in these amphipods is competition with *Synalpheus*, which dominate the fauna of many sponges in the West Atlantic.

Thus, from a marine perspective, I would add an additional criterion for eusociality to Crespi's three, namely life history that allows restricted dispersal. Planktonic, moderately long-distance dispersal is the rule among marine invertebrates and fishes, and works against kin-structured sociality in many taxa by stirring the gene pool more or less vigorously. Thus, sociality will likely be found only in taxa with sufficiently restricted dispersal, at least among invertebrates. The association between direct development and kin association in crustaceans generally and among species of *Synalpheus* particularly is consistent with this hypothesis. Alternatively, even widely ranging animals may maintain kin associations through behavioral mechanisms, as in certain cetaceans that typically live in family groups similar in organization to those of other social mammals on land.

In summary, then, I hypothesize that eusociality in sponge-dwelling shrimps has been fostered by a combination of four characteristics that are shared with many social insects but appear to be unique in the Crustacea, and perhaps in marine animals, namely (1) direct development resulting in limited dispersal and kin association, (2) ecological specialization on a valuable, long-lived resource (the host sponge), (3) strong competition for the host resource, and (4) possession of weaponry (the snapping claw) effective in monopolizing it. These factors foster long-term occupation of specific nest sites by multigenerational family groups, conditions which result in low turnover of breeding

opportunities and persistence of dynastic lineages headed by one or a few breeders of each sex, with non-breeding adults defending the colony from intruders. Explaining the distribution of eusociality among species within the genus *Synalpheus* is more challenging. Life history (criterion 1 above) clearly seems to be a "filter", as it is in cooperatively breeding birds (Arnold and Owens, 1998, 1999), determining which groups are able to form kin aggregations. Yet all species in the gambarelloides group meet criteria 2 and 4. Variance among species in the strength of competition for hosts (criterion 3) may be the key to explaining which species or populations evolve eusociality, but this is a difficult factor to quantify without experimentation. Clearly there is much work remaining to be done.

ACKNOWLEDGMENTS

SUMMARY.

Within the tropical shrimp genus *Synalpheus*, the monophyletic gambarelloides species group contains ~30 species of internal symbionts of sponges, most of which specialize on a small number of host species. These shrimp are diploid, probably sequential hermaphrodites, with sedentary adults, and the group includes both direct developers and species with planktonic larvae. Social organization ranges from heterosexual pairs to eusocial colonies with strong reproductive skew, multiple adult generations, and cooperative nest defense. Phylogenetic analysis strongly supports at least three independent origins of eusociality within the gambarelloides group. Comparisons among species of *Synalpheus*, and with other animal taxa, suggest that coincidence of four characteristics has fostered eusociality in these *Synalpheus* taxa: (1) direct development resulting in very limited dispersal and kin association, (2) ecological specialization on a valuable, long-lived resource (the host sponge), (3) strong competition for the host

resource, and (4) possession of weaponry (the snapping claw) effective in monopolizing it. These factors foster long-term occupation and defense of specific nest sites by multigenerational family groups, resulting in low turnover of breeding opportunities in social *Synalpheus* species. In the best studied species, *S. regalis*, such dynastic lineages are headed by one or a few breeders of each sex and non-breeding adults defend the colony from intruders. The coincidence of these four characteristics in certain lineages of *Synalpheus* appears to be unique within Crustacea and may explain why they are the only known eusocial marine animals.

The characteristics of social shrimp are similar to those previously suggested to foster cooperative breeding and eusociality in insects and vertebrates, bolstering support for general explanations of eusociality based on the interplay of life history and ecological constraints. First, social shrimp share with cooperatively breeding birds the combination of low fecundity (associated with direct development), probably high adult survival in the protection of the host sponge, sedentariness, and life in a warm climate with relatively stable environment. In opposition to birds, however, habitat association is conservative within *Synalpheus*, whereas life history is more labile. Social shrimp also share the three more specific conditions (criteria 2-4 above) hypothesized to explain the distribution of "fortress defense" eusociality in insects, namely coincidence of food and shelter, strong enemy pressure, and ability to defend the resource. Whereas the general conditions favoring sociality in *Synalpheus* seem evident, the specific conditions that distinguish eusocial *Synalpheus* species from their less social, but direct-developing sister taxa remain elusive.

REFERENCES

Alexander, R.D., 1974. The evolution of social behavior. *Annu. Rev. Ecol. Syst*. 5:325-38.

Alexander, R.D., K.M. Noonan, and B.J. Crespi. 1991. The evolution of eusociality. In: *The biology of the Naked Mole-rat.* (eds. Sherman, P.W., J.U.M. Jarvis, and R.D. Alexander). pp. 3-44. Pinceton University Press, Princeton, N.J.

Andersson, M., 1984. The evolution of eusociality. *Annu. Rev. Ecol. Syst 15*:165-189.

Aoki, M., 1997. Comparative study of mother-young association in caprellid amphipods: Is maternal care effective? *J. Crust. Biol*. *17*: 447-458.

Arnold, K.E. and I.P.F. Owens, 1998. Cooperative breeding in birds: a comparative test of the life history hypothesis. *P. Roy. Soc. Lond. B 265*: 739-745.

Arnold, K.E. and I.P.F. Owens, 1999. Cooperative breeding in birds: the role of ecology. *Behavioral Ecology. 10*: 465-471.

Avilés, L. and P. Tufiño, 1998. Colony size and individual fitness in the social spider *Anelosimus eximius. Am. Nat. 152*: 403-418.

Ayling, A.L., 1983. Growth and regeneration rates in thinly encrusting Demospongiae

from temperate waters. *Biol. Bull. 165*: 243-352.

Banner, A.H., and D.M. Banner. 1983. Annotated checklist of the alpheid shrimp from the Western Indian Ocean. Travaux Documents l'ORSTOM 158: 164.

Banner, D.M., and A.H. Banner. 1981. Annotated checklist of the alpheid shrimp of the Red Sea and the Gulf of Aden. *Zool. Verhandelingen 190*: 1-99.

Bauer, R.T., 1976. Mating behaviour and spermatophore transfer in the shrimp *Heptacarpus pictus* (Stimpson) (Decapoda: Caridea: Hippolytidae). *J. Nat. Hist. 10*: 415-440.

Bauer, R.T. 1979. Sex attraction and recognition in the Caridean shrimp *Heptacarpus paludicola* Holmes (Decapoda: Hippolytidae). *Marine Behav. Physiol. 6*:157-174.

Bauer, RT., 2000. Simultaneous hermaphroditism in caridean shrimps: a unique and puzzling sexual system in the Decapoda. *J. Crust. Biol. 20*: 116-128.

Bartz, S. H., 1979. Evolution of eusociality in termites. *Proc. Nat. Acad. Sci. USA 76*: 5764-5768.

Bennett, N.C. and C.G. Faulkes. 2000. *African mole-rats: ecology and eusociality*. Cambridge Univ. Press, Cambrudge, UK.

Bennett, N.C., C.G. Faulkes, and A.J. Molteno. 1996. Reproductive suppression in subordinate non-breeding female Damaraland mole-rats: two components to a lifetime of socially induced infertility. *P. Roy. Soc. Lond. B 263*: 1599-1603.

Blum, M.S., 1996. Semiochemical parsimony in the Arthropoda. *Annu. Rev. Entomol. 41*: 353-374.

Bourke, A.F.G., 1999. Colony size, social complexity and reproductive conflict of social insects. *J. Evol. Biol. 12*: 245-257.

Bourke, A.F.G. and N.R. Franks. 1995. *Social evolution in ants*. Princeton University Press, Princeton, N.J.

Braude, S., 2000. Dispersal and new colony formation in wild naked mole-rats: evidence against inbreeding as the system of mating. *Behavioral Ecology. 11*: 7-12.

Brown, J.L., 1987. *Helping and communal breeding in birds*. Princeton Univ. Press, Princeton, N.J.

Bruce, A.J., 1976. Shrimps and prawns of coral reefs, with special reference to commensalism. In*: Biology and Geology of Coral Reefs*. (eds. O.A. Jones and R. Endean) Volume III: Biology 2. pp. 37-94. Academic Press, New York, New York.

Bruce, A.J., 1988. *Synalpheus dorae*, a new commensal alpheid shrimp from the Australian Northwest shelf. *Proc. Biol. Soc. Wash. 101*: 843-852.

Bruce, A.J., 1998. New keys for the identification of Indo-West Pacific coral associated Pontoniine shrimps, with observations on their ecology (Crustacea: Decapoda: Palaemonidae). *Ophelia 49*: 29-46.

Caldwell, R.L., 1979. Cavity occupation and defensive behaviour in the stomatopod *Gonodactylus festai*: Evidence for chemically mediated individual recognition. *Anim. Behav. 27*: 194-201.

Chace, F.A.,1972. The shrimps of the Smithsonian-Bredin Caribbean Expeditions with a summary of the West Indian shallow-water species. (Crustacea: Decapoda: Natintia) *Smithsonian Contr. Zool. 98*: 1-179.

Chace, F.A., 1989. The Caridean shrimps (Crustacea: Decapoda) of the *Albatross* Philippine expedition, 1907-1910, Part 5: Family Alpheidae. *Smithsonian Contr. Zool 46*: 1-99.

Childress, J.J. and M.H. Price, 1983. Growth rate of the bathypelagic crustacean *Gnathophausia ingens* (Mysidacea: Lophogastridae). 2. Accumulation of material and energy. *Mar. Biol. 76*: 165-177.

Ciszek, D., 2000. New colony formation in the "highly inbred" eusocial naked mole-rat: outbreeding is preffered. *Behavioral Ecol. 11*:1-6.

Conlan, K.E. and J.R. Chess, 1992. Phylogeny and ecology of a kelp-boring amphipod, *Peramphithoe stypotrupetes*, new species (*Corophioidea*: Ampithoidae). *J. Crust. Biol. 12*: 410-422.

Conover, M.R. and D.E. Miller, 1978. The importance of the large chela in the territorial and pairing behaviour of the snapping shrimp *Alpheus heterochaelis*. *Mar. Behav. Physiol. 5*: 185-192.

Cooney, R. and N.C. Bennett. 2000. Inbreeding avoidance and reproductive skew in a cooperative mammal. *P. Roy. Soc. London B 267*: 801-806.

Coutière, H. 1899 Les Alpheidae. Morphologie externe et interne, formes larvaires, bionomie. *Annales de Sciences Naturelles*, *8e série, Zoologie 9*: 1-560.

Coutière, H . 1909. The American species of snapping shrimps of the genus *Synalpheus. Proc. United States Natl. Museum 36*: 1-93.

Crespi, B.J. 1992. Eusociality in Australian gall thrips. *Nature 359*: 724-726.

Crespi, B.J., 1994. Three conditions for the evolution of eusociality: are they sufficient? *Insectes Soc. 41*: 395-400.

Crespi, B.J., 1996. Comparative analysis of the origins and losses of eusociality: causal mosaics and historical uniqueness. In: *Phylogenies and the Comparative Method in Animal Behavior.* (eds. E.P. Martins). pp.253-287 Oxford University Press, New York.

Crespi, B.J. and L.A. Mound, 1997. Ecology and evolution of social behavior among Australian gall thrips and their allies. pp.166-180 *in* Choe and Crespi 1997.

Crespi, B.J. and D. Yanega,. 1995. The definition of eusociality. *Behavioral Ecology. 6*: 109-115.

Crozier, R.H. and P. Pamilo, 1996. *Evolution of Social Insect Colonies*. Sex allocation and kin selection. Oxford Univ. Press, Oxford.

Dardeau, M.R., 1984. *Synalpheus* shrimps (Crustacea: Decapoda: Alpheidae). I. The Gambarelloides group, with a description of a new species. *Memoirs Hourglass Cruises* 7, Part 2: 1-125.

Darwin, C., 1871. *The descent of man, and selection in relation to sex*. J. Murray, London.

Diesel, R., 1989. Parental care in an unsual environment: *Metopaulias depressus* (Decapoda: Grapsidae), a crab that lives in epiphytic bromeliads. *Anim. Behav. 38*: 561:575.

Diesel, R., 1992. Maternal care in the bromeliad crab, *Metopaulias depressus*: protection of larvae from predation by damselfly nymphs. *Anim. Behav*. 43: 803-812.

Diesel, R. and D. Horst, 1995. Breeding in a snail shell: Ecology and biology of the Jamaican Montane Crab *Sesarma jarvisi* (Decapoda: Grapsidae). *J. Crust. Biol. 15*:1: 179-195.

Dobkin S.R. 1965. The first post-embryonic stage of *Synalpheus brooksi* Coutière. *Bull. Mar. Sci. 15*: 450-462.

Dobkin S.R. 1969. Abbreviated larval development in caridean shrimps and its significance in the artificial culture of these animals. *FAO Fish. Rep. 57*: 935-946.

Duffy, J.E. 1992. Host use patterns and demography in a guild of tropical sponge-dwelling shrimps. *Mar. Ecol. Prog. Ser.* 90: 127-138.

Duffy, J.E., 1993. Genetic population structure in two tropical sponge-dwelling shrimps that differ in dispersal potential. *Mar. Biol. 116*: 459-470.

Duffy, J.E., 1996a. Eusociality in a coral-reef shrimp. *Nature 381*: 512-514.

Duffy, J.E., 1996b. Resource-associated population subdivision in a symbiotic coral-reef shrimp. *Evolution 50*: 360-373.

Duffy, J.E., 1996c. Specialization, species boundaries, and the radiation of sponge-dwelling alpheid shrimp. *Biol. J. Linn. Soc. 58*: 307-324.

Duffy, J.E., 1996d. *Synalpheus regalis*, new species, a sponge-dwelling shrimp from the Belize Barrier Reef, with comments on host specificity in *Synalpheus. J. Crust. Biol. 16*: 564-573.

Duffy J.E., 1998. On the frequency of eusociality in snapping shrimps (Decapoda: Alpheidae), with description of a second eusocial species. *Bull. Mar. Sci. 63*: 387-400.

Duffy J.E. and K.S. Macdonald, 1999. Colony structure of the social snapping shrimp, *Synalpheus filidigitus*, in Belize. *J. Crust. Biol. 19*:283-292.

Duffy J.E., C.L. Morrison, and R. Rios, 2000. Multiple origins of eusociality among sponge- dwelling shrimps (*Synalpheus*). *Evolution. 54. 2*: 503-516.

Duffy, J.E., C.L. Morrison, and K.S. Macdonald. 2002. Colony defense and behavioral differentiation in the eusocial shrimp Synalpheus regalis. *Behav. Ecol. Sociobiol.*, 51:488-495.

Emlen, S.T., 1982. The evolution of helping. I. An ecological constraints model. *Am. Nat. 119*: 40-53.

Emlen S.T., 1991. Evolution of cooperative breeding in birds and mammals. In: *An Evolutionary Approach.* 3rd Edition (eds. J.R. Krebs and N.B. Davies) pp 301-337. Behavioural Ecology. Blackwell, Oxford.

Emlen, S.T., 1995. An evolutionary theory of the family. *Proc. Natl. Acad. Sci. USA. 92*:

8092-8099.

Emlen, S.T., 1996. Reproductive sharing in different types of kin associations. *Am. Nat. 148*: 756-763.

Emlen, S.T., 1997. Predicting family dynamics in social vertebrates. In: *Behavioural ecology: An evolutionary approach*, Fourth Edition. (eds. J.R. Krebs and N.B. Davies) pp. 228-253. Blackwell Science Ltd.

Erdman, R.B. and N.J. Blake, 1987. Population dynamics of the sponge-dwelling alpheid *Synalpheus longicarpus*, with observations on *S. brooksi* and *S. pectiniger*, in shallow-water assemblages of the eastern Gulf of Mexico. *J. Crust. Biol. 7*: 328-337.

Evans, H.E., 1977. Extrinsic versus intrinsic factors in the evolution of insect eusociality. *BioScience 27*: 613-617.

Felder, D.L., 1982. Reproduction of the snapping shrimps *Synalpheus fritzmuelleri* and *S. apioceros* (Crustacea: Decapoda: Alpheidae) on a sublittoral reef off Texas. *J. Crust. Biol. 2*: 535-543.

Fletcher, D.J.C. and K.G. Ross, 1985. Regulation of reproduction in eusocial Hymenoptera. *Annu. Rev. Entomol. 30*: 319-343.

Friedrich, M and D. Tautz, 1995. Ribosomal DNA phylogeny of the major extant arthropod classes and the evolution of myriapods. *Nature*, 376: 165-167.

Gadagkar, R., 1991. Demographic predisposition to the evolution of eusociality: A hierarchy of models. *Proc. Natl. Acad. Sci. USA. 88*: 10993-10997.

Gadagkar, R., 1994. Why the definition of eusociality is not helpful to understand its evolution and what we should do about it. *Oikos 70*:485-487.

Gherardi, F., and C. Calloni. 1993. Protandrous hermaphroditism in the tropical shrimp *Athanas indicus* (Decapoda: Caridea), a symbiont of sea urchins. *J. Crust. Biol. 13*: 675-689.

Goudet, J. 2000. FSTAT, a program to estimate and test gene diversities and fixation indices (v. 2.9.1). Available from http://www.unil.ch/izea/softwares/fstat.html.

Greeff, J.M. and N.C. Bennett. 2000. Causes and consequences of incest avoidance in the cooperatively breeding mole-rat, *Cryptomys darlingi* (Bathyergidae). *Ecology Letters 3*: 318-328.

Hamilton, W.D., 1964. The genetical evolution of social behavior I, II. *J. Theor. Biol. 7*: 1-52.

Hatchwell, B.J. and J. Komdeur, 2000. Ecological constraints, life history traits and the evolution of cooperative breeding. *Anim. Behav. 59*: 1079-1086.

Hazlett, B.A. and H.E. Winn. 1962. Sound production and associated behavior of Bermuda crustaceans (*Panulirus, Gonodactylus, Alpheus,* and *Synalpheus*). *Crustaceana 4*: 25-38.

Herberholz, J. and B. Schmitz, 1998. Role of mechanosensory stimuli in intraspecific agonistic encounters of the snapping shrimp (*Alpheus heterochaelis*). *Biol. Bull.*

195: 156-167.

Herberholz, J. and B. Schmitz, 1999. Flow visualisation and high speed video analysis of water jets in the snapping shrimp (Alpheus heterochaelis). *J. Comp. Physiol. A. 185*: 41-49.

Herberholz, J. and B. Schmitz, 2001. Signaling *via* water currents in behavioral interactions of snapping shrimp (*Alpheus heterochaelis*). *Biol. Bull. 201*:6-16.

Hölldobler, B. and E.O. Wilson, 1990. *The ants*. Harvard University Press, Cambridge, Massachusetts.

Hughes, M., 1996a. Size assessment via a visual signal in snapping shrimp. *Behav. Ecol. Sociobiol. 38*: 51-57.

Hughes, M., 1996b. The function of concurrent signals: visual and chemical communication in snapping shrimp. *Anim. Behav. 52*: 247-257.

Itô, Y., 1993. *Behaviour and social evolution of wasps.* The communal aggregation hypothesis. Oxford Univ Press, Oxford UK

Jarvis, J.U.M., M.J. O'Riain, N.C. Bennett, and P.W. Sherman, 1994. Mammalian eusociality: a family affair. *Trends Ecol. Evol. 9*: 47-51.

Jeanne, R.L. 1980. Evolution of social behavior in the Vespidae. *Ann. Rev. Entomol. 25*: 371-396.

Jeng, M-S. 1994. Effect of antennular and antennal ablation on pairing behavior of snapping shrimp *Alpheus edwardsii* (Audouin). *J. Exp. Mar. Biol. Ecol. 179*: 171-178.

Karavanich, C., J. Atema, 1998. Individual recognition and memory in lobster dominance. *Anim. Behav. 56*: 1553-1560.

Keller, L. and H.K. Reeve, 1994. Partioning of reproduction in animal societies. *Trends Ecol. Evol. 9:3*:98-102.

Kent, D.S. and J.A. Simpson, 1992. Eusociality in the beetle *Austroplatypus incompertus* (Coleoptera: Curculionidae). *Naturwissenschaften 79*: 86-87.

Knowlton, R.E., 1971. Effects of environmental factors on the larval development of *Alpheus heterochelis* Say and *Palemonetes vulgaris* (Say) (Crustacea Decapoda Caridaea), with ecological notes on larval and adult Alpheidae and Palaemonidae. Ph.D. Thesis. University of North Caroliina, Chapel Hill.

Knowlton R.E., 1980. Sexual selection and dimorphism in two demes of a symbiotic, pair-bonding snapping shrimp. *Evolution. 34*: 161-173

Knowlton R.E., and B.D. Keller, 1982. Symmetric fights as a measure of escalation potential in a symbiotic, territorial snapping shrimp. *Behav. Ecol. Sociobiol. 10*: 289-292.

Knowlton, N. and B.D. Keller, 1986. Larvae which fall far short of their potential: Highly localized recruitment in an alpheid shrimp with extended larval development. *Bull. Mar. Sci. 39*: 213-233.

Koenig, W.D. and F.A. Pitelka. 1981. Ecological factors and kin selection in the

evolution of cooperative breeding in birds. In: *Natural selection and social behavior: Recent research and new theory* (eds. R.D. Alexander and D.W. Tinkle). Chiron Press, New York.

Lin, N. and C.D. Michener, 1972. Evolution of sociality in insects. *Q. Rev. Biol. 47:2*:131-159

Lin, J. and D. Zhang, 2001. Reproduction in a simultaneous hermaphroditic shrimp, *Lysmata wurdemanni*: any two will do. *Marine biology. 139*:1155-1158.

Linsenmaier, K.E., 1987. Kin recognition in subsocial arthropods, in particular in the desert isopod *Hemilepistus reaumuri.* In: *Kin Recognition in Animals.* (eds. D.J.C. Fletcher and C.D. Michener) pp.121-208. John Wiley & Sons Ltd.

MacGinitie GE, and N. MacGinitie, 1949. *Natural history of marine animals*. McGraw Hill, New York.

McClendon, J.F. 1911. On adaptations in structure and habits of some marine animals of Tortugas, Florida. *Papers from the Tortugas Laboratory of the Carnegie Institute of Washington. 3:57*: 62.

Michener, C.D., 1969. Comparative social behavior of bees. *Annu. Rev. Entomol. 14*: 299-342.

Michener, C.D. and D.J. Brothers, 1974. Were workers of eusocial Hymenoptera initially altruistic or oppressed? *Proc. Natl. Acad. Sci. USA 71*: 671-674.

Myles, T.G., 1988. Resource inheritance in social evolution from termites to man. In: *The ecology of social behavior.* (ed. Slobodchikoff, CN.), pp. 379-423. Academic Press, New York.

Myles, T.G. and W.L. Nutting. 1988. Termite eusocial evolution: a re-examination of Bartz's hypothesis and assumptions. *Q. Rev. Biol. 63*: 1-23.

Nakashima, Y., 1987. Reproductive strategies in a partially protandrous shrimp, *Athanas kominatoensis* (Decapoda: Alpheidae): sex change as the best of a bad situation. *J. Ethol. 2*:145-159.

Nolan, B.A. and M. Salmon 1970. The behavior and ecology of snapping shrimp (Crustacea: *Alpheus heterochelis* and *Alpheus normanii*). *Forma et Functio 2*:289-335

Oster, G.F. and E.O. Wilson. 1978. *Caste and ecology in the social insects*. Princeton University Press. Princeton, New Jersey.

Patton, W.K., 1974. Community structure among the animals inhabiting the coral *Pocillopora damicornis* at Heron Island, Australia. In: *Symbiosis in the sea.* (ed. Vernberg, W.B.). Univ. of South Carolina Press, Columbia, S.C.

Pearse, A.S. 1932. Inhabitants of certain sponges at Dry Tortugas. *Papers of the Tortugas Laboratory of the Carnegie Institute of Washington 27*:117-124.

Perrin N, and L. Lehmann. 2001. Is sociality driven by the costs of dispersal or the benefits of philopatry? A role for kin discrimination-mechanisms. *Am. Nat. 158*:471-483.

Pusey, A.E. and M. Wolf. 1996. Inbreeding avoidance in animals. *Trends Ecol. Evol. 11*:201-206.

Queller, D.C., 1989. The evolution of eusociality: Reproductive head starts of workers. *Proc. Natl. Acad. Sci. USA* 86:3224-3226.

Queller, D.C. and J.E. Strassman. 1998. Kin selection and social insects: Social insects provide the most surprising predictions and satisfying tests of kin selection. *BioScience 48:3*:165-175.

Ratnieks, F.L.W. 1988. Reproductive harmony via mutual policing by workers in eusocial Hymenoptera. *Am. Nat. 132*:217236.

Reed, J.K., R.H. Gore, L.E. Scotto, and K.A. Wilson. 1982. Community composition, areal and trophic relationships of decapods associated with shallow- and deep-water *Oculina varicosa* coral reefs. *Bull. Mar. Sci. 32*:761-786.

Reeve, H.K., D.F. Westneat, W.A. Noon, P.W. Sherman and C.F. Aquadro, 1990. DNA "fingerprinting" reveals high levels of inbreeding in colonies of the eusocial naked mole-rat. *Proc. Nat. Acad. Sci. USA 87*:2496-2500.

Reeve, H.K. and P.W. Sherman, 1991. Intracolonial aggression and nepotism by the breeding female naked mole-rat In: *The biology of the naked mole-rat*. (eds. Sherman, P.W., J.U.M. Jarvis, and R.D. Alexander) pp. 337-357. Princeton University Press, Princeton, N.J.

Reiswig, H.M., 1973. Population dynamics of three Jamaican Demospongiae. *Bull. Mar. Sci. 23*:191-226.

Ríos, R. and J.E. Duffy. 1999. *Synalpheus williamsi* (Decapoda: Alpheidae), a new sponge-dwelling shrimp from the Caribbean. *Proc. Biol. Soc. Wash.* 112: 541-552.

Robinson, G.E., 1992. Regulation of division of labor in insect societies. *Annu. Rev. Entomol*. 37:637-665

Ruetzler, K., 1976. Ecology of Tunisian commercial sponges. *Tethys* 7:249-264.

Rufino, M.M. and D.A. Jones, 2001. Binary individual recognition in *Lysmata debelius. J. Crust. Biol.* 21:388-392

Schein, H., 1975. Aspects of the aggressive and sexual behaviour of *Alpheus heterochaelis* Say. *Mar. Behav. Physiol*. 3:83-96

Schein, H., 1977. The role of snapping in *Alpheus heterochaelis* Say, 1818, the big-clawed snapping shrimp. *Crustaceana* 33:182-188.

Schultz, S., Wuppermann, K., Schmitz, B., 1998. Behavioural interactions of snapping shrimp (*Alpheus heterochaelis*) with conspecifics and sympatric crabs (*Eurypanopeus depressus*). *Zoology Analysis of Complex Systems Suppl*. I. 101:85.

Seger, J., 1991., Cooperation and conflict in social insects. In: *Behavioural ecology. An evolutionary approach*. 3rd edition. (Krebs, J.R. and N.B. Davies, Eds.) Blackwell, Oxford.

Selander, R.K., 1964. Speciation in wrens of the genus *Campylorhynchus. Univ. Calif. Pubs. Zool*. 74:1-224

Shellman-Reeve, J.S. 2001. Genetic relatedness and partner preference in a monogamous, wood-dwelling termite. *Anim. Behav.* 61:869-876.

Sherman, P.W., E.A. Lacey, H.K. Reeve, and L. Keller. 1995. The eusociality continuum. *Behavioral Ecol*., 6:102-108.

Shultz, J.W. and J.C. Regier, 2000. Phylogenetic analysis of arthropods using two nuclear protein-encoding genes supports a crustacean + hexapod clade. *Proc. R. Soc. Lond., Ser.* B: 267:1011-1019.

Snelgrove, P.V.R., and J.B. Lewis. 1989. Response of a coral-associated crustacean community to eutrophication. *Mar. Biol*. 101:249-257.

Soest, R.W.M. van. 1978. Marine sponges from Curacao and other Caribbean localities. Part I. Keratosa. *Stud. Fauna Curacao Caribb. Isl*. 56(179):1-94.

Soest, R.W.M. van. 1980. Marine sponges from Curacao and other Caribbean localities. Part II. Haplosclerida. *Stud. Fauna Curacao Caribb. Isl*. 62(191):1-173.

Soest, R.W.M. van. 1984. Marine sponges from Curacao and other Caribbean localities. Part III. Poecilosclerida. *Stud. Fauna Curacao Caribb. Isl*. 66(199):1-167.

Spanier, E., J.S. Cobb, and M.-J. James, 1993. Why are there no reports of eusocial marine crustaceans? *Oikos*. 67:573-576.

Starr, C.K. 1985. Enabling mechanisms in the origin of eusociality in the Hymenoptera – the sting's the thing. *Annals Entomol. Soc. Amer.* 78:836-840.

Stern, D.L. and W.A. Foster, 1996. The evolution of soldiers in aphids. *Biol. Rev*. 77:27-79.

Strassmann, J.E. and D.C. Queller, 1989. Ecological determinants of social evolution. In: *The genetics of social evolution.* (ed. Breed M.D. and R.E. Page) Westview, Boulder, Colorado, pp 81-101.

Strathmann, R.R., 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. *Annu. Rev. Ecol. Syst*. 16:339-361.

Suzuki, H., 1970. Taxonomic review of four alpheid shrimp belonging to the genus *Athanas*, with reference to their sexual phenomena. *Science Reports of the Yokohama National University, Section II. Biological and Geological Sciences* 17:1-38..

Thiel, M., 1997. Reproductive biology of an epibenthic amphipod (*Dyopedos monacanthus*) with extended parental care. *J. Mar. Biol. Ass. U.K.* 77:1059-1072.

Thiel, M., 1999. Host-use and population demographics of the ascidian-dwelling amphipod *Leucothoe spinicarpa*: indication for extended parental care and advanced social behaviour. *J. Nat. Hist*. 33:193-206.

Thiel, M., S. Sampson, and L. Watling. 1997. Extended parental care in two endobenthic amphipods. *J. Nat. Hist*. 31:713-725.

Thomas, J.D., 1997. Systematics, ecology and phylogeny of the Anamixidae (Crustacea:Amphipoda). *Records Austr. Musuem.* 49:35-98

Thorne, B.L., 1997. Evolution of eusociality in termites. *Annu. Rev. Ecol. Syst*.

J. E. Duffy: Eusociality in sponge-dwelling shrimp

28:27-54.Wcislo, W.T. 1997. Are behavioral classifications blinders to natural variation? In: *Social behavior in insects and arachnids* (eds. Choe, J. and B.J. Crespi), pp 8-13. Cambridge Univ. Press, Cambridge, UK.

Wcislo, W.T. and B.N. Danforth., 1997. Secondarily solitary: the evolutionary loss of social behavior. *Trends Ecol. Evol.* 12:468-474.

Weir, B.S. and C.C. Cockerham, 1984. Estimating F-statistics for the analysis of population structure. *Evolution*, 38:1358-1370.

Wenzel JW, Pickering J (1991) Cooperative foraging, productivity, and the central limit theorem. *Proc. Nat. Acad. Sci. USA* 88:36-38.

West-Eberhard, M.J., 1981. Intragroup selection and the evolution of insect societies. In: *Natural selection and social behavior. Recent research and new theory*. (Alexander, R.D. and D.W. Tinkle, Eds.) Chiron Press, NY.

Wiedenmayer, F., 1977. *Shallow-water sponges of the western Bahamas.* Birkhäuser Verlag, Basel and Stuttgart.

Wilson, E.O., 1971. *The Insect Societies*. Belknap Press of Harvard University, Cambridge, MA.

Wilson, E.O., 1975. *Sociobiology*. Belknap, Cambridge, Massachusetts

Wilson, E.O., 1985. The sociogenesis of insect colonies. *Science*. 228:1489-1495.

Wilson, E.O., 1990. *Success and Dominance in Ecosystems: the Case of the Social Insects*. Ecology Inst, Oldendorf/Luhe, Germany.