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Kin structure, ecology and the evolution of social organization in shrimp: a comparative analysis

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Eusocial societies present a Darwinian paradox, yet they have evolved independently in insects, mole-rats and symbiotic shrimp. Historically, eusociality has been thought to arise as a response to ecological challenges, mediated by kin selection, but the role of kin selection has recently been questioned. Here we use phylogenetically independent contrasts to test the association of eusociality with ecological performance and genetic structure (via life history) among 20 species of sponge-dwelling shrimp (*Synalpheus*) in Belize. Consistent with hypotheses that cooperative groups enjoy an advantage in challenging habitats, we show that eusocial species are more abundant, occupy more sponges and have broader host ranges than non-social sister species, and that these patterns are robust to correction for the generally smaller body sizes of eusocial species. In contrast, body size explains less or no variation after accounting for sociality. Despite strong ecological pressures on most sponge-dwellers, however, eusociality arose only in species with non-dispersing larvae, which form family groups subject to kin selection. Thus, superior ability to hold valuable resources may favour eusociality in shrimp but close genetic relatedness is nevertheless key to its origin, as in other eusocial animals.

Keywords: cooperative breeding; ecological constraints; eusociality; life history; phylogeny

1. INTRODUCTION

Eusocial colonies, in which sterile workers help raise offspring of others, present a paradox for evolutionary theory yet they have evolved independently in several lineages of insects (Choe & Crespi 1997), twice in African mole-rats (Jarvis & Bennett 1993), and several times in a single genus of symbiotic shrimp (Duffy 2007). The modern framework for explaining the origins of such cooperation was established by Hamilton (1964) who showed that altruism is favoured when fitness costs to the helper are outweighed by benefits to the recipient weighted by their genetic relatedness. This framework, which integrates ecological challenges and kin structure, has been highly productive in explaining a wide range of behaviours among social animals (Emlen 1991; Bourke & Franks 1995; Crozier & Pamilo 1996; Queller & Strassmann 1998; Strassmann & Queller 2007). Recently, however, the key role of genetic relatedness has been questioned. Wilson (2005) and Wilson & Hölldobler (2005) suggested that ecological pressures alone are sufficient to drive evolution of eusociality, which is favoured by the competitive and defensive superiority of organized groups, and that the kin structure of colonies is more often an epiphenomenon than a cause of eusociality. This argument has proven controversial (Fletcher *et al.* 2006; Foster *et al.* 2006) and has focused renewed attention on how ecology and kin structure interact to foster eusociality.

Two general classes of ecological pressures are believed to select for cooperative social life, both by limiting opportunities for independent breeding and by providing fitness incentives for helping (Emlen 1982). First, in unpredictable or dangerous environments, the chances of successfully raising offspring independently are limited either by predator pressure or harsh environmental conditions. Under such conditions groups are better able to find scattered food, repel enemies, care for young, and thus reduce the risk of brood loss. This scenario has long been a favoured explanation for evolution of eusociality in insects (Wilson 1971; Lin & Michener 1972), and has been termed 'life insurer' eusociality (Queller & Strassmann 1998) in Hymenoptera, in which helpless larvae require extended care and foraging adults are under constant threat from enemies (Queller 1989; Gadagkar 1991). A similar explanation has been offered for sociality in vertebrates threatened by harsh environments with unpredictable food supply. In both naked mole-rats (Faulkes *et al.* 1997) and certain cooperatively breeding bird families (Rubenstein & Lovette 2007), phylogenetically controlled comparative analyses identified significant associations between sociality and unpredictable environmental conditions.

In direct contrast, the second class of ecological drivers of eusociality stems from life in highly favourable environments, where predictably abundant resources support dense populations and attract strong pressure from competitors or other enemies. Among cooperatively breeding birds, the long-standing habitat saturation hypothesis (Selander 1964; Brown 1974; Emlen 1982) holds that in such habitats nest sites are perpetually full, particularly

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in long-lived species (Hatchwell & Komdeur 2000), such that offspring have few opportunities for independent breeding and little option but to live instead as helpers at the nest of parents or other relatives. A global comparative analysis of 182 species of birds supported this hypothesis, confirming that cooperative breeding was significantly associated with sedentary life in warm, invariable climates (Arnold & Owens 1999). A somewhat similar argument has been made for sociality in 'fortress defender' insects, which include certain gall-forming aphids and thrips, and many termites, that live in protected habitats providing both food and shelter (Alexander *et al.* 1991; Crespi 1994; Queller & Strassmann 1998).

Following Hamilton, all of these models of social evolution involve both ecological and genetic elements: environmental challenges offer helpers a chance to enhance their own fitness both directly, via increased survival in the communal territory, and indirectly by increasing production of non-descendent kin. In contrast, Wilson's (2005) and Wilson & Hölldobler's (2005) argument can be considered an extreme version of hypotheses invoking ecological pressures in that it ascribes the fitness advantages of groups solely to superior ecological performance, with little or no role for kin selection. Thus, two fundamental questions arise in explaining how eusociality originates: first, is close genetic relatedness necessary for evolution of cooperative groups? Second, does group living indeed confer ecological advantages in enhancing ability to acquire and defend limited territories or other resources? Despite a long history of research, surprisingly few formal comparative studies have tested the importance of either genetic relatedness (but see Chapman *et al.* 2000; Agnarsson *et al.* 2006; Wenseleers & Ratnieks 2006; Hughes *et al.* 2008) or the hypothesized ecological benefits of social life in groups near the origin of eusociality. This is due in part to the generally ancient origins and phylogenetic conservatism of eusocial life in the major lineages of social insects, which obscure the conditions associated with the origins of eusociality (Crespi 1996).

Tropical sponge-dwelling shrimp (*Synalpheus*) offer a valuable window on the early evolution of eusociality because of their recent radiation (less than 6 Ma, Morrison *et al.* 2004), ecological uniformity, and variation in life history and social organization (Duffy 2007). Unusually among animal taxa, social organization in the single genus *Synalpheus* ranges from heterosexual pairs, to groups with multiple breeders, to eusocial colonies that can contain more than 300 individuals with a single breeding female (the queen), along with sterile workers (Tóth & Bauer 2007) and in some cases morphological castes (Duffy & Macdonald 1999); eusociality has arisen at least three times within the genus (Duffy *et al.* 2000; Duffy 2007). Equally importantly, variation in development mode among species of *Synalpheus* creates variation in group genetic structure: most species of *Synalpheus* produce swimming larvae that exit the sponge and spend time in the plankton, whereas other species produce 'direct-developing', i.e. crawling, larvae (Dobkin 1965; Dobkin 1969) that are sedentary and generally remain in the same sponge with their mother. There is genetic evidence that *Synalpheus* species with crawling larvae have stronger genetic subdivision (Duffy 1993),

and more specifically that eusocial shrimp species live in family groups of full sibs (Duffy 1996*a*; Rubenstein *et al.* 2008). Because crawling larvae are more likely to form kin groups than swimming larvae, classical inclusive fitness theory would predict that direct-developing shrimp species are more likely to evolve eusociality (Hamilton 1964). Thus, variation in social organization and development within *Synalpheus* allows us to test the importance of both kin selection and ecological superiority of groups in the early evolution of eusociality.

Natural history suggests that ecological constraints are a key factor in the evolution of shrimp sociality: host sponges provide both habitat and food, nearly all hosts are occupied in the field (Duffy 1996*b*; Duffy *et al.* 2000), and shrimp defend them fiercely against intruders (Duffy 1996*a*; Duffy *et al.* 2002; Tóth & Duffy 2005), indicating that habitat is valuable and in short supply. These observations appear consistent with both the habitat saturation hypothesis (Selander 1964; Emlen 1982) and the fortress defence model (Crespi 1994; Queller & Strassmann 1998), but they provide only indirect evidence in support of ecological drivers of social evolution. Manipulating host availability or shrimp density in the field to test the habitat saturation hypothesis directly would be ideal, but presents serious logistical challenges. However, if defence against enemies and competitors indeed drives eusociality via colony-level selection, then we should see evidence that eusociality enhances the ability to acquire, defend, and retain limiting host resources relative to less social species. Field data appear consistent with this hypothesis in that eusocial taxa are more abundant than less social taxa on reefs in Belize (Macdonald *et al.* 2006). But two factors complicate this pattern. First, most eusocial species are small-bodied, and because size and abundance are usually inversely correlated in animals, the potential influences of sociality and size are confounded. Second, species within a clade share a phylogenetic history and thus are not independent data points (Felsenstein 1985). Consequently, it is unclear whether patterns in abundance of sponge-dwelling shrimp result from sociality, common ancestry, or small body size. Distinguishing these alternatives requires accounting for shared evolutionary history and variation in body size. Here we use phylogenetically independent contrasts among 20 co-occurring species of *Synalpheus* in Belize to disentangle these factors. We ask three questions: (i) does eusociality confer ecological advantages in ability to obtain and defend host-sponge resources? (ii) Does eusociality depend on close kin structure? (iii) What if any role does body size play in these relationships?

2. MATERIAL AND METHODS

Our analysis is based on sponge-dwelling shrimp specimens collected in the vicinity of Carrie Bow Cay, Belize, between 1990 and 2004 (Macdonald *et al.* 2006). The dataset was restricted to Belize because this is the only site from which we have detailed ecological, morphological and phylogenetic data for the same set of species; the set includes 20 of the more than 35 known species (Macdonald *et al.* 2006; Ríos & Duffy 2007) from the gambarelloides (sponge-dwelling) species group of *Synalpheus* in the West Atlantic, including nearly all of the most common species.

(a) Body mass

Species-typical body masses were estimated for each species by measuring lengths of carapace (CL) and major chela (ChL) for at least four adult females and four of the largest non-ovigerous individuals in a sample for each species (except for *Synalpheus pandionis*, two of each sex). Among non-social species these latter large non-ovigerous individuals are almost certainly adult males, which are morphologically indistinguishable from immature females based on external morphology (Tóth & Bauer 2007). In eusocial species the large, non-ovigerous individuals presumably included both males and non-breeding females, which are identical in size, allometry and frequency (Tóth & Bauer 2007), and in fact are virtually indistinguishable using light microscopy. We then used cross-species correlations between length and dry mass to convert these length measurements to mass. The cross-species correlations were estimated by measuring both lengths and dry masses of body and major chela in 14 male and 28 female shrimp from six species (see the electronic supplementary material, figure S1), and deriving the following equations:

$$\text{body mass} = 0.5986 \times e^{(0.4892 \times \text{CL})}, \quad (r^2 = 0.915)$$

and

$$\text{major chela mass} = 0.3135 \times e^{(0.4268 \times \text{ChL})}, \quad (r^2 = 0.982).$$

Although the number of specimens used for these measurements is modest, the extreme morphological uniformity within and among species in the gambarelloides group of *Synalpheus* (see the electronic supplementary material, figure S1), confirmed by the high r^2 values of these relationships, suggests that the small sample size is unlikely to bias estimates of body mass.

(b) Development mode

To test whether eusociality is associated with close genetic relatedness within colonies, we focused on development mode as a proxy for genetic relatedness among colony members. Over the course of many years collecting in Belize and elsewhere, we opportunistically obtained data on development mode from captive females for 18 species of *Synalpheus*. Development mode was scored as either crawling or swimming based on observations of newly released offspring hatched from captive females in the laboratory; such observations were not available for *Synalpheus brevifrons* or *Synalpheus carpenteri*.

(c) Ecological variables

We calculated three field estimates of ecological performance as proxies for the ability to acquire and defend host-sponge resources. The first two, relative abundance and sponge occupancy, were estimated from samples of rubble-associated sponges collected by divers over the course of 11 years (1994–2004) from among dead coral rubble and branches of live coral (primarily *Porites* sp.) in shallow water (less than 3 m) at a group of patch reefs in the 'Sand Bores', Belize (16°46.655′ N, 88°6.755′ W). The collection consisted of 13 samples from which all *Synalpheus* specimens were sorted and identified, a sample being the collection of rubble-associated sponges made on a single day; this collection produced a total of 2067 shrimp from 18 gambarelloides-group species (Macdonald *et al*. 2006). Relative abundance of a shrimp species was calculated as

the proportion of all shrimp in the collection, i.e. summed across all 13 samples, made up by that species. Sponge occupancy was calculated as the percentage of all individual sponges in the collection that were occupied by the focal shrimp species.

Because these exploratory collections were intended to maximize shrimp diversity, and the cryptic sponges were often not visible prior to collection, we consider the samples unlikely to be strongly biased from natural abundances. Nevertheless, they were not designed specifically to quantify distribution, so we checked the generality of the results by quantifying shrimp and sponge abundance from an additional set of four randomly placed line transects (50×1.5 m) and five quadrats (0.25 m^2) on the outer reef ridge at Carrie Bow Cay (15–20 m).

The third ecological variable we quantified was host range, defined as the total number of sponge species from which a shrimp species has been recorded at least three times in Belize. Host range was estimated from the entire Belizean dataset comprising 623 sampled sponges of 18 species, which produced more than 20 000 shrimp from 27 species in the gambarelloides group (Macdonald *et al*. 2006). Because taxonomy of Caribbean *Synalpheus* is under active revision (Ríos & Duffy 2007; Anker & Toth 2008; Macdonald *et al*. 2009; Hultgren *et al*. in press), we re-examined specimens and host records, particularly for those formerly assigned to *Synalpheus paraneptunus*, which was recently split into six species (Anker & Toth 2008).

(d) Quantifying sociality

We quantified the degree of sociality using the eusociality index of Keller & Perrin (1995) which measures the sum, over a colony, of differences between each individual's contribution to work versus to reproduction. The calculation, assumptions and rationale for using the E index for *Synalpheus* have been described previously (Duffy *et al*. 2000). Briefly, the E index accounts for both reproductive skew and colony size, both of which vary considerably among *Synalpheus* species, and the index can be calculated from data collected over short time spans such as the point estimates available from our collections. In the absence of detailed behavioural data, we made the parsimonious assumption that all individuals in the colony contributed equally to colony work, and that all breeders contributed equally to production of offspring. In this case the Keller and Perrin equation reduces to the proportion of non-breeding individuals in the colony:

$$E = \frac{N - 2 \times \text{Fem}_\text{B}}{N},$$

where N is the total number of individuals and Fem_B the number of breeding (ovigerous) females, in the colony (Fem_B is multiplied by 2 on the assumption that there are an equal number of breeding males and females). Although some of these assumptions are simplistic, we believe that, if anything, they are likely to render our conclusions conservative in that division of labour would result in even higher values of E for the social species we studied. Calculation of the E index built on data from Duffy *et al*. (2000) with addition of data from newer collections. Thus, some species analysed here differ in E-value compared with the previous publication (Duffy *et al*. 2000), the main change being that *Synalpheus brooksi* is now included as a eusocial species (see the electronic supplementary material, table S1).
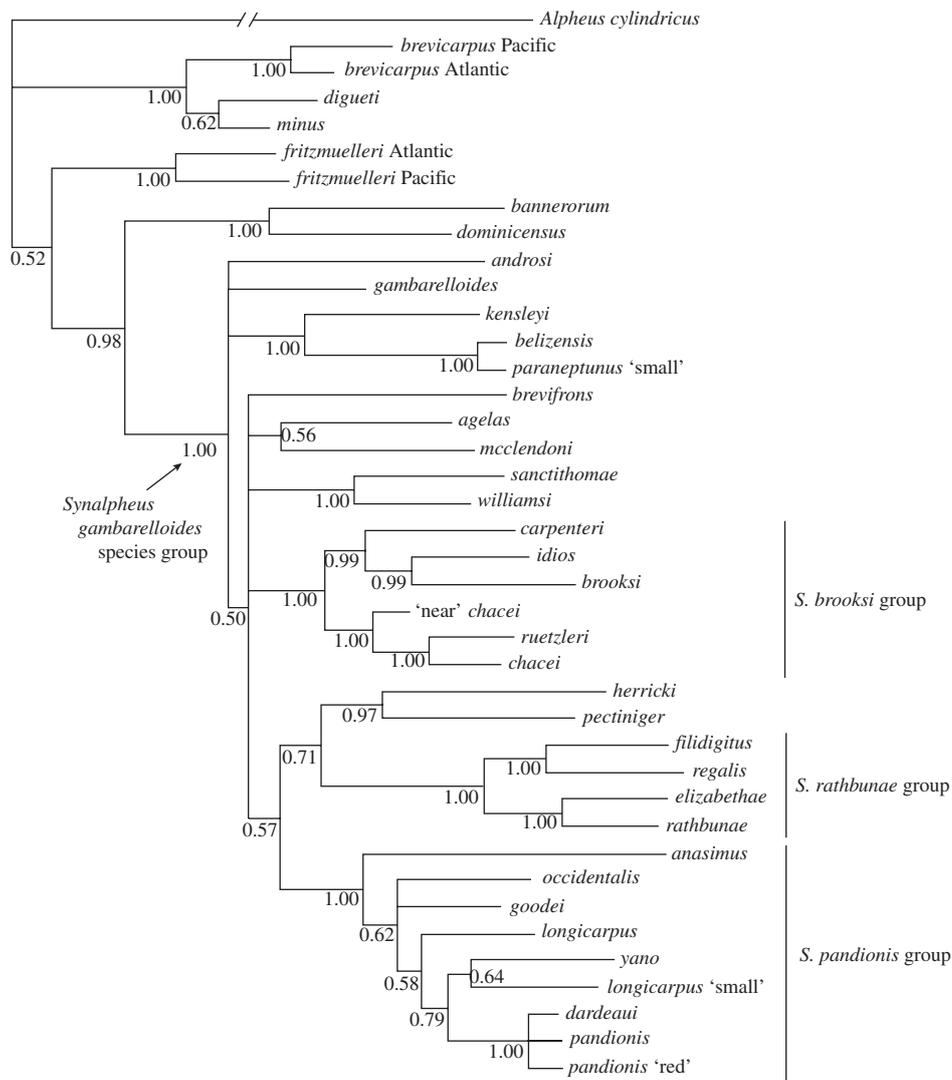
Figure 1. Phylogenetic tree of selected West Atlantic *Synalpheus* species. The tree is a consensus of 24 000 trees from a Bayesian phylogenetic analysis of combined COI, 16S, and morphological characters (data from Morrison *et al*. 2004). Numbers represent Bayesian posterior probabilities for clades with probabilities more than 50%. Clades with probabilities less than 50% are collapsed into polytomies. Synonymies of these species names with those used in previous publications are listed in the electronic supplementary material, table S2.

(e) *Comparative analysis*

Comparative analyses inherently face the possibility that similarity among species reflects the inertia of common ancestry as well as evolutionary adaptation. To factor out effects of common ancestry, we computed phylogenetically independent contrasts (Felsenstein 1985), implemented with the phylogenetic diversity analysis programs (PDAPs) (Midford *et al*. 2005) module in the program MESQUITE (Maddison & Maddison 2006). We based our tests on a new phylogeny (figure 1) obtained from a Bayesian analysis of the dataset used in the most recent examination of *Synalpheus* relationships (Morrison *et al*. 2004). The data included a sequence alignment from Morrison *et al*. (2004) of 1067 genetic characters from portions of the mitochondrial cytochrome c oxidase subunit I and 16S rRNA genes, as well as 66 morphological characters. We analysed the data using MRBAYES v. 3.12 (Ronquist & Huelsenbeck 2003), with a GTR $+\mathrm{I}$ $+\Gamma$ model, the most appropriate according to MODELTEST v. 3.7 (Posada & Crandall 1998), for the molecular data, with parameters independently calculated for the two genes, and the MK model of Lewis (2001) for the morphological data. We ran two simultaneous Markov chain

Monte Carlo searches with four chains each for 25 million generations, and sampled the chain every 1000 generations.

Comparative analyses were performed using pruned phylograms (i.e. with branch lengths proportional to the amount of change along a branch) containing only the 20 Belizean species studied (figure 2). Because Bayesian phylogenetic analyses result in consensus trees, while phylogenetically independent contrasts require strictly bifurcating trees (Felsenstein 1985), we computed contrasts on the pruned versions of the five highest-likelihood trees obtained in the Bayesian analysis.

We used multiple regression to test the relative influence of social organization (E index) and body mass on ecological characteristics of *Synalpheus* species; separate regressions, constrained to pass through the origin, were conducted using raw values and phylogenetically independent contrast values. Since body masses were negatively correlated with E (see §3), we also visualized the independent effects of E and body mass as follows. We first regressed contrast values for a response variable (y) against contrasts of body mass (x), then plotted the residuals as the size-corrected estimates of that response variable against contrasts for E.
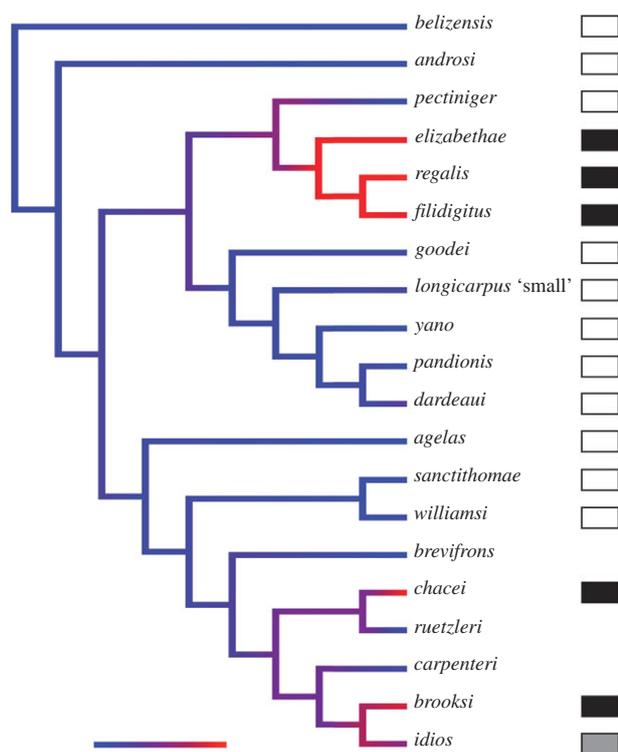
Figure 2. Phylogenetic tree of *Synalpheus* species from Belize. The tree is the highest-likelihood tree from a Bayesian phylogenetic analysis of combined COI, 16S, and morphological characters (data from Morrison *et al.* 2004), pruned to show only those Belizean species used in the comparative analyses. Branch colour indicates social organization, ranging from blue for pair-forming species (eusociality index, $E = 0$) to red for eusocial species ($E \approx 1$). Black rectangles denote species with direct development into crawling, non-dispersing larvae, and open rectangles represent species whose eggs hatch into swimming larvae; the grey rectangle indicates that both types of development have been observed. Synonymies of these species names with those used in previous publications are listed in the electronic supplementary material, table S2.

Similarly, we examined the importance of body mass after correcting for sociality by first regressing contrasts of the response variable (y) against contrasts of E (x), and then plotting the residuals as sociality-corrected contrasts of the response variable against contrasts for body mass. Species mean values are presented in the electronic supplementary material, table S1.

We used Maddison's (1990) concentrated changes test (CCT), implemented in MacClade v. 4, to test whether the phylogenetic association between eusociality and direct development was stronger than expected by chance. In essence, CCT determines whether evolution of two characters is correlated by testing whether changes in one character (eusociality) are significantly concentrated on those branches featuring a second character (direct development). For this analysis we treated eusociality as a binary character since the values of E fell into two relatively discrete groups (see §3). Because we have records of both swimming and crawling larvae from *Synalpheus idios*, we ran separate CCT analyses with *S. idios* larvae coded as swimming or crawling; in both cases we conducted CCT tests on the top five highest-likelihood trees returned by the Bayesian analysis.

3. RESULTS

In both runs of the Bayesian phylogenetic analysis likelihood values converged and reached stationarity within the first 500 trees sampled; we therefore removed the first 500 trees from each run before computing a consensus of the remaining 24 000 sampled trees. The topology of the resultant consensus tree of the COI + 16S + morphological data (figure 1) was similar to the COI + 16S consensus tree of Morrison *et al.* (2004, their Fig. 2C), supporting a monophyletic *Synalpheus* gambarelloides group (posterior probability 100%), and within that clade the monophyly of the *S. brooksi* group, *Synalpheus pandionis* group, and *Synalpheus rathbunae* group. Posterior probabilities of our consensus tree were considerably higher throughout the tree than those of Morrison *et al.* (2004), especially in support of the *S. gambarelloides* group and the *S. rathbunae* group. However, as also found by Morrison *et al.* (2004), many of the deeper interior nodes remained poorly supported.

Although eusociality has evolved repeatedly in *Synalpheus* (Duffy *et al.* 2000; Morrison *et al.* 2004; Didderen *et al.* 2006), our phylogenetically controlled tests using new data for both development mode and social organization showed that eusociality was almost perfectly correlated with direct development, in which eggs hatch as crawling juveniles (figure 2). This association held regardless of whether the apparently variable species *S. idios* was coded as having swimming larvae (Maddison's CCT, $p = 0.005 - 0.006$ for the five trees) or crawling larvae ($p = 0.014 - 0.016$ for the five trees).

One species, *Synalpheus dardeaui*, stood out as exceptionally large, with a body mass 5 and 12 standard deviations larger, for males and females, respectively, than the mean of the other species. When this statistical outlier was removed, eusociality tended to be associated with smaller body mass of both males and females, although this trend was lost after controlling for phylogeny (figure 3).

Phylogenetically controlled comparisons supported substantially higher ecological performance by eusocial groups (figure 4, table 1). Contrasts using the five highest-likelihood Bayesian trees revealed that eusocial shrimp reached much greater average abundances in sponges, occupied a larger fraction of individual sponges, and used a wider range of host species, than their less social sister taxa. These relationships were robust to correction for the smaller body sizes of social species (figure 4), and standardized regression coefficients showed that social organization was a consistently stronger predictor of abundance and niche breadth than was body mass, generally by a factor of two or more; body mass significantly influenced only abundance (table 1). Contrasts performed using the single most parsimonious tree of combined molecular and morphological data from Morrison *et al.* (2004) yielded qualitatively similar results (table 1). Overall, these results imply that greater abundance and niche breadth in eusocial shrimp are primarily direct consequences of social life, rather than macroecological correlates of small body size.

The nine quantitative samples from the outer reef ridge produced 123 shrimp from 11 species in 22 individual sponges. These included one eusocial shrimp species (*Synalpheus chacei*) that comprised 80 per cent of total
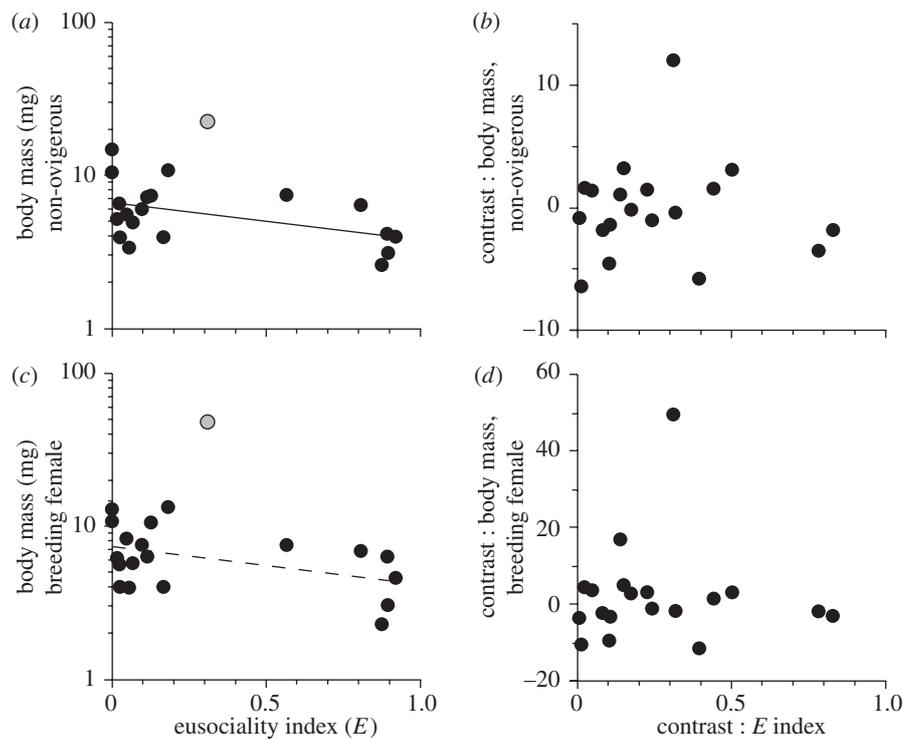
Figure 3. Relationships between body size and social organization among Belizean species of *Synalpheus*, shown separately for (*a,b*) non-ovigerous individuals (males and non-breeding females) and (*c,d*) breeding females. Social organization is quantified by the eusociality index (*E*) of Keller & Perrin (1995). (*a,c*) Raw values; (*b,d*) phylogenetically independent contrasts. In (*a,c*), regression statistics were calculated for all species ((*a*) $p = 0.094$; $r^2 = 0.148$; (*c*) $p = 0.174$; $r^2 = 0.100$) and for all species excluding the outlier *S. dardeaui* ((*a*) $p = 0.042$; $r^2 = 0.222$; (*c*) $p = 0.056$; $r^2 = 0.199$); regression lines exclude *S. dardeaui* (grey symbol). Regressions on contrasts were not significant ((*b*) $p = 0.967$, $r^2 = 0$; (*d*) $p = 0.981$, $r^2 = 0$). Regressions significant at $p < 0.05$ (solid lines) and $0.05 < p < 0.10$ (dashed lines) are indicated.

individuals collected and occupied seven sponges; in contrast, the 10 non-eusocial species collectively comprised only 20 per cent of individuals and occupied an average of 1.5 sponges each. The dominance and greater sponge occupancy by social species in this dataset is quite similar to that of the larger collection from the shallow-water rubble dataset and suggests that patterns in the latter are not strongly biased.

4. DISCUSSION

Our comparative analysis confirms that eusociality in shrimp is associated with superior ecological performance, but also that eusociality evolved only in lineages with life history that enables formation of family groups and kin selection. These results, together with natural history, suggest that a unique constellation of ecological and life history factors can explain the distribution of eusociality in shrimp. First, as argued previously (Duffy 2003), ecology set the stage for cooperative group formation in that all sponge-dwelling shrimp occupy valuable host resources that provide both food and shelter, and there is strong competition for these resources. Snapping shrimp, moreover, possess an effective weapon to defend the resource, the large snapping claw. These characteristics are shared with fortress-defender insects, and have been argued as sufficient conditions for evolution of eusociality because they aggregate kin and select for cooperation, which confers superior ability to hold and defend the valuable nest resource (Crespi 1994). Consistent with the latter

hypothesis, social shrimp species are more abundant, on average, than less social species on Belizean reefs (Macdonald *et al.* 2006). But as in any correlative analysis, cause and effect are difficult to distinguish. Because social shrimp species are also small-bodied and several are close phylogenetic relatives, the significance of the association between eusociality and abundance could not be judged rigorously before. Here we have controlled for both phylogenetic relationships and body size and show that eusociality in sponge-dwelling shrimp remains strongly associated with greater abundance, greater occupancy of limiting habitat (individual sponges), and greater niche breadth (host range). In contrast, after controlling for social level, body size significantly affected only abundance, implying that superior ecological performance is primarily a consequence of eusociality rather than of small body size.

While these results are consistent with an advantage of eusociality under ecological pressures, the ecological explanation remains incomplete. This is because all sponge-dwelling shrimp species appear to meet the sufficient conditions proposed for fortress defence eusociality (Crespi 1994), yet only a subset of these species exhibit eusociality. Our results indicate that the critical factor distinguishing the eusocial species of *Synalpheus* is the production of non-dispersing larvae that allow accumulation of close relatives, and therefore the operation of kin selection. Building on more complete data on development mode and social organization than previously available, and controlling for phylogeny,
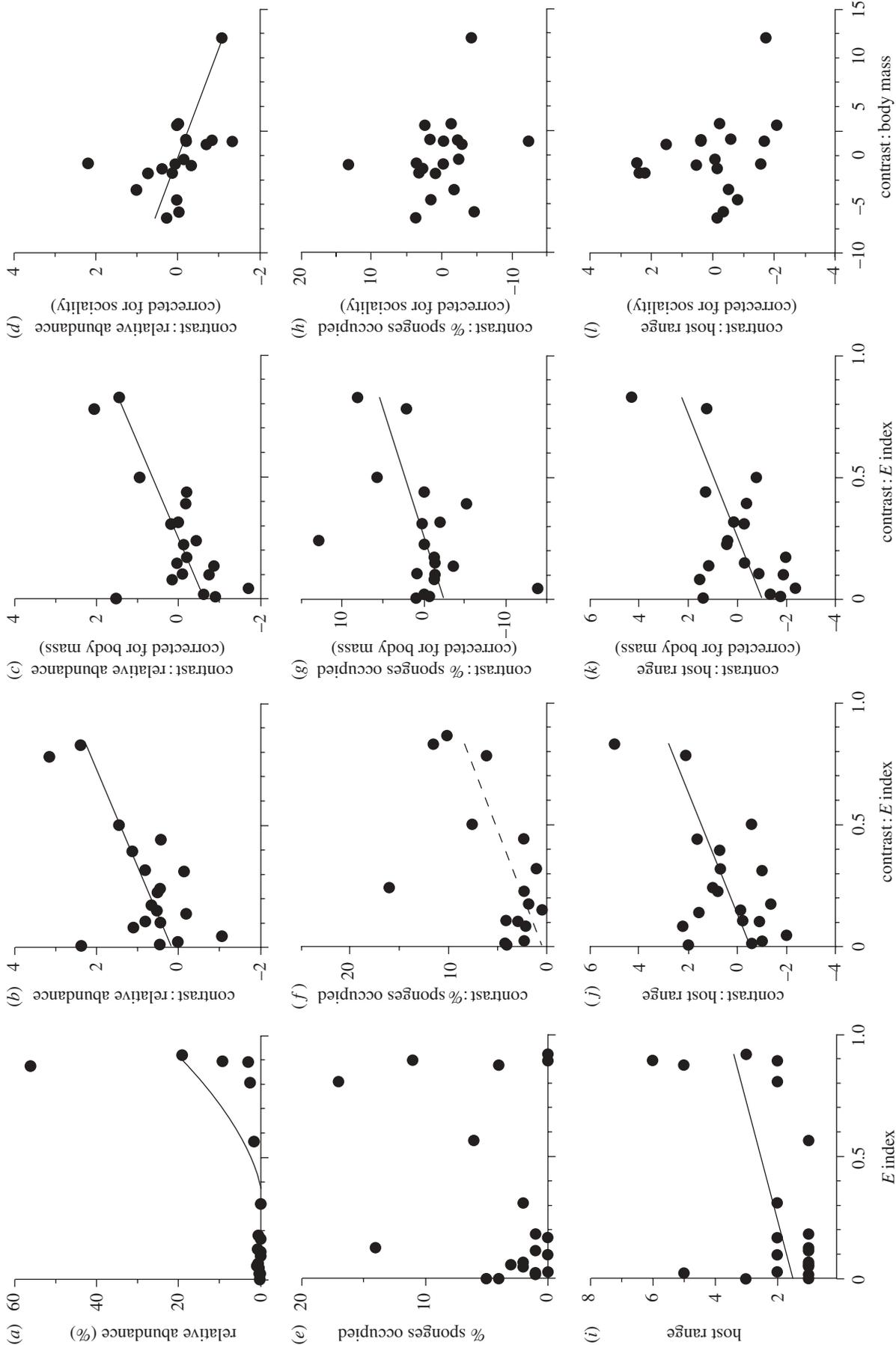
Figure 4. Relationships between ecological dominance, social organization and body size among Belizean species of *Synalpheus*. (*a,e,i*) raw data; (*b,f,j*) phylogenetically independent contrasts based on Bayesian analysis; in (*c,g,k*), contrasts use values of the eusociality index (*E*) corrected for body size; in (*d,h,l*), contrasts use values of body size corrected for *E* (see §2). All plotted contrasts used the highest-likelihood tree from the Bayesian analysis; summaries of statistics from the top five trees are shown in table 1. Solid lines or curves show regressions significant at $p < 0.05$, and the dashed line indicates $0.05 < p < 0.10$.

Table 1. Results of multiple regressions estimating the effects of social organization (*E* index) and body mass on ecological parameters in Belizean *Synalpheus*. Separate regressions are computed for raw data and for phylogenetically independent contrasts using each of the five highest-likelihood trees from the Bayesian analysis (figure 1); *p* and r^2 entries show the median and range (in parentheses) of values for the five Bayesian trees. β is the standardized regression coefficient. Contrasts based on the single most parsimonious tree obtained by Morrison *et al.* (2004) are shown for comparison. r^2 values for relationships with negative slopes are shown as negative.

response variable	*E* index		body mass		r^2
	p	β	*p*	β	
raw data					
abundance	<0.0001	0.83	0.338	0.15	0.74
ocupancy	<0.0001	0.73	0.895	0.02	0.61
host range	<0.0001	0.97	0.055	0.46	0.70
contrasts based on Bayesian trees (top 5)					
abundance	<0.0001	0.65 (0.63−0.68)	0.041 (0.031−0.046)	−0.35 (0.34−0.37)	0.70 (0.70−0.72)
ocupancy	0.006 (0.004−0.006)	0.44 (0.43−0.46)	0.254 (0.182−0.288)	−0.23 (0.23−0.27)	0.40 (0.40−0.44)
host range	0.006 (0.005−0.007)	0.44 (0.42−0.46)	0.306 (0.229−0.400)	−0.22 (0.18−0.25)	0.41 (0.38−0.41)
contrasts based on maximum parsimony tree (Morrison et al. 2004):					
abundance	0.011	0.47	0.425	−0.18	0.43
ocupancy	0.018	0.44	0.660	−0.11	0.36
host range	0.028	0.39	0.811	−0.06	0.30

we found an almost perfect association of non-dispersing larval development and eusociality among sponge-dwelling shrimp in Belize.

The relative importance of ecological pressures and kin selection in the evolution of eusociality has generated recent controversy (Wilson 2005; Wilson & Hölldobler 2005; Fletcher *et al.* 2006). Although most eusocial and cooperatively breeding animals live in family groups, Wilson (2005) and Wilson & Hölldobler (2005) argued that this is a consequence, rather than a cause, of social group formation, which they suggested is driven primarily by the ecological superiority of organized groups. Against this hypothesis, Hughes *et al.* (2008) showed that monogamy—which maximizes relatedness of offspring—was ancestral in all eight Hymenopteran lineages that evolved eusociality. An important role for kin structure is also supported by the association of sociality with inbreeding in certain thrips (Chapman *et al.* 2000) and spiders (Agnarsson *et al.* 2006). Sponge-dwelling shrimp provide an independent test of the role of kin structure in the origin of eusociality. As far as is known all alpheids are monogamous (Knowlton 1980; Rahman *et al.* 2003; Mathews 2007), but in most species the planktonically dispersing larvae, which are typical of decapod crustaceans, prevent accumulation of kin groups. *Synalpheus*, however, is unusual among alpheids in that the single genus contains species that produce swimming larvae, as well as species whose eggs hatch directly into crawling juveniles. Our finding that eusociality occurs only in shrimp species with non-dispersing larvae parallels the pattern in Hymenoptera (Hughes *et al.* 2008) and supports the hypothesis that eusociality requires conditions that foster kin selection. Indeed because the shrimp species we studied are otherwise similar in sharing the sponge-dwelling habit, are closely related, and many are similar in body size, we regard the tight association between crawling larvae and eusociality as especially strong support for the necessity of close kin structure in the origin of eusocial colonies.

We also found that eusocial shrimp are relatively small-bodied. Since this trend disappeared after controlling for phylogeny, the most parsimonious conclusion is that eusociality evolved in species that were already small-bodied, rather than vice versa. This pattern might also support a role for kin structure, via life history, in favouring eusociality: in many marine invertebrate groups, small body size is associated with development via non-planktonic ('brooding') larvae (Strathmann 1985). Thus, the association of eusociality with small body size in *Synalpheus* may result because small-bodied species more commonly have restricted larval dispersal, fostering kin group formation and cooperation among relatives.

In summary, natural history suggests that shrimp eusociality originated in stable, physically benign environments with strong competitor pressure as in many cooperatively breeding birds (Arnold & Owens 1999) and fortress-defender insects (Crespi 1994; Queller & Strassmann 1998). Phylogenetically independent contrasts confirm that eusocial shrimp species enjoy strong ecological advantages in greater local abundance, occupation of a larger fraction of limiting habitat, and use of a wider range of resources (hosts) compared with non-social relatives, consistent with the hypothesis that eusociality confers a competitive advantage in such saturated habitats (Wilson & Hölldobler 2005). Presumably this advantage is related to the cooperative nest defence previously demonstrated in social shrimp (Tóth & Duffy 2005). Yet, while these ecological pressures appear common to most or all species of sponge-dwelling shrimp, our comparative analysis also shows that eusociality evolved only in lineages with reduced dispersal, confirming that factors promoting close genetic relatedness and the opportunity for kin selection were essential

to evolution of eusociality in shrimp as they were in insects (Hughes *et al*. 2008). Thus, data for shrimp support Hamilton's (1964) recognition that both ecological pressures and close kinship are key to the solution of the eusociality paradox.

REFERENCES

Agnarsson, I., Aviles, L., Coddington, J. A. & Maddison, W. P. 2006 Sociality in Theridiid spiders: repeated origins of an evolutionary dead end. *Evolution* **60**, 2342–2351.

Alexander, R. D., Noonan, K. M. & Crespi, B. J. 1991 The evolution of eusociality. In *The biology of the naked mole-rat* (eds P. W. Sherman, J. U. M. Jarvis & R. D. Alexander), pp. 3–44. Princeton, NJ: Princeton University Press.

Anker, A. & Toth, E. 2008 A preliminary revision of the *Synalpheus paraneptunus* Coutiere, 1909 species complex (Crustacea: Decapoda: Alpheidae). *Zootaxa* **1915**, 1–28.

Arnold, K. E. & Owens, I. P. F. 1999 Cooperative breeding in birds: the role of ecology. *Behav. Ecol.* **10**, 465–471. (doi:10.1093/beheco/10.5.465)

Bourke, A. F. G. & Franks, N. R. 1995 *Social evolution in ants*. Princeton, NJ: Princeton University Press.

Brown, J. L. 1974 Alternate routes to sociality in jays—with a theory for the evolution of altruism and communal breeding. *Am. Zool.* **14**, 63–80.

Chapman, T. W., Crespi, B. J., Kranz, B. D. & Schwarz, M. P. 2000 High relatedness and inbreeding at the origin of eusociality in gall-inducing thrips. *Proc. Natl Acad. Sci. USA* **97**, 1648–1650. (doi:10.1073/pnas.020510097)

Choe, J. & Crespi, B. J. 1997 *The evolution of social behavior in insects and arachnids*. Cambridge, UK: Cambridge University Press.

Crespi, B. J. 1994 Three conditions for the evolution of eusociality—are they sufficient? *Insectes Sociaux* **41**, 395–400. (doi:10.1007/BF01240642)

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* (ed. E. P. Martins), pp. 253–287. Oxford, UK: Oxford University Press.

Crozier, R. H. & Pamilo, P. 1996 *Evolution of social insect colonies. Sex allocation and kin selection*. Oxford, UK: Oxford University Press.

Didderen, K., Fransen, C. H. J. M. & DeVoogd, N. J. 2006 Observations on sponge-dwelling colonies of *Synalpheus* (Decapoda, Alpheidae) of Sulawesi, Indonesia. *Crustaceana* **79**, 961–975. (doi:10.1163/1568540067788 15937)

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. 1993 Genetic population-structure in two tropical sponge-dwelling shrimps that differ in dispersal potential. *Mar. Biol.* **116**, 459–470. (doi:10.1007/BF00350063)

Duffy, J. E. 1996a Eusociality in a coral-reef shrimp. *Nature* **381**, 512–514. (doi:10.1038/381512a0)

Duffy, J. E. 1996b *Synalpheus regalis*, new species, a sponge-dwelling shrimp from the Belize Barrier Reef with comments on host specificity in *Synalpheus*. *J. Crustacean Biol.* **16**, 564–573. (doi:10.2307/1548748)

Duffy, J. E. 2003 The ecology and evolution of eusociality in sponge-dwelling shrimp. In *Genes, behaviors, and evolution in social insects* (eds T. Kikuchi, S. Higashi & N. Azuma), pp. 217–252. Sapporo, Japan: University of Hokkaido Press.

Duffy, J. E. 2007 Ecology and evolution of eusociality in sponge-dwelling shrimp. In *Evolutionary ecology of social and sexual systems: crustaceans as model organisms* (eds J. E. Duffy & M. Thiel), pp. 387–409. New York, NY: Oxford University Press.

Duffy, J. E. & Macdonald, K. S. 1999 Colony structure of the social snapping shrimp *Synalpheus filidigitus* in Belize. *J. Crustacean Biol.* **19**, 283–292. (doi:10.2307/1549235)

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

Duffy, J. E., Morrison, C. L. & Macdonald, K. S. 2002 Colony defense and behavioral differentiation in the eusocial shrimp *Synalpheus regalis*. *Behav. Ecol. Sociobiol.* **51**, 488–495. (doi:10.1007/s00265-002-0455-5)

Emlen, S. T. 1982 The evolution of helping. I. An ecological constraints model. *Am. Nat.* **119**, 29–39. (doi:10.1086/283888)

Emlen, S. T. 1991 Evolution of cooperative breeding in birds and mammals. In *Behavioural ecology. An evolutionary approach* (eds J. R. Krebs & N. B. Davies), 3rd edn. pp. 301–335. Oxford, UK: Blackwell.

Faulkes, C. G., Bennett, N. C., Bruford, M. W., O'Brien, H. P., Aguilar, G. H. & Jarvis, J. U. M. 1997 Ecological constraints drive social evolution in the African mole-rats. *Proc. R. Soc. Lond. B* **264**, 1619–1627. (doi:10.1098/rspb.1997.0226)

Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15. (doi:10.1086/284325)

Fletcher, J. A., Zwick, M., Doebeli, M. & Wilson, D. S. 2006 What's wrong with inclusive fitness? *Trends Ecol. Evol.* **21**, 597–598. (doi:10.1016/j.tree.2006.08.008)

Foster, K. R., Wenseleers, T. & Ratnieks, F. L. W. 2006 Kin selection is the key to altruism. *Trends Ecol. Evol.* **21**, 57–60. (doi:10.1016/j.tree.2005.11.020)

Gadagkar, R. 1991 Demographic predisposition to the evolution of eusociality—a hierachy of models. *Proc. Natl Acad. Sci. USA* **88**, 10 993–10 997. (doi:10.1073/pnas.88.24.10993)

Hamilton, W. D. 1964 The genetical evolution of social behaviour. *J. Theor. Biol.* **7**, 1–52. (doi:10.1016/0022-5193(64)90038-4)

Hatchwell, B. J. & Komdeur, J. 2000 Ecological constraints, life history traits and the evolution of cooperative breeding. *Anim. Behav.* **59**, 1079–1086. (doi:10.1006/anbe.2000.1394)

Hughes, W. O. H., Oldroyd, B. P., Beekman, M. & Ratnieks, F. L. W. 2008 Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science* **320**, 1213–1216. (doi:10.1126/science.1156108)

Hultgren, K. M., MacDonald, K. S. & Duffy, J. E. In press. Sponge-dwelling snapping shrimp of Curaçao, with descriptions of three new species. *Zootaxa*.

Jarvis, J. U. M. & Bennett, N. C. 1993 Eusociality has evolved independently in 2 genera of bathyergid mole-rats—but occurs in no other subterranean mammal. *Behav. Ecol. Sociobiol.* **33**, 253–260. (doi:10.1007/BF02027122)

Keller, L. & Perrin, N. 1995 Quantifying the level of eusociality. *Proc. R. Soc. Lond. B* **260**, 311–315. (doi:10.1098/rspb.1995.0097)

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

Lewis, P. O. 2001 A likelihood approach to estimating phylogeny from discrete morphological character data. *Syst. Biol.* **50**, 913–925. (doi:10.1080/10635150 1753462876)

Lin, N. & Michener, C. D. 1972 Evolution of sociality in insects. *Q. Rev. Biol.* **47**. (doi:10.1086/407216)

Macdonald, K. S., Ríos, R. & Duffy, J. E. 2006 Biodiversity, host specificity, and dominance by eusocial species among sponge-dwelling alpheid shrimp on the Belize Barrier Reef. *Divers. Distrib.* **12**, 165–178. (doi:10.1111/j.1366-9516.2005.00213.x)

Macdonald, K. S., Hultgren, K. M. & Duffy, J. E. 2009 Sponge-dwelling snapping shrimp of Discovery Bay, Jamaica, with descriptions of four new species. *Zootaxa* **2199**, 1–57.

Maddison, W. P. 1990 A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* **44**, 539–557. (doi:10.2307/2409434)

Maddison, W. P. & Maddison, D. R. 2006 Mesquite: a modular system for evolutionary analysis. Version 1.1. http://mesquiteproject.org.

Mathews, L. M. 2007 Evidence for high rates of in-pair paternity in the socially monogamous snapping shrimp *Alpheus angulosus*. *Aquat. Biol.* **1**, 55–62.

Midford, P. E., Garland, T. J. & Maddison, W. P. 2005 PDAP Package of Mesquite. Version 1.07.

Morrison, C. L., Rios, R. & Duffy, J. E. 2004 Phylogenetic evidence for an ancient rapid radiation of Caribbean sponge-dwelling snapping shrimps (*Synalpheus*). *Mol. Phylogenet. Evol.* **30**, 563–581. (doi:10.1016/S1055-7903(03)00252-5)

Posada, D. & Crandall, K. A. 1998 Modeltest: testing the model of DNA substitution. *Bioinformatics* **14**, 817–818. (doi:10.1093/bioinformatics/14.9.817)

Queller, D. C. 1989 The evolution of eusociality: reproductive head starts of workers. *Proc. Natl Acad. Sci. USA* **86**, 3224–3226. (doi:10.1073/pnas.86.9.3224)

Queller, D. C. & Strassmann, J. E. 1998 Kin selection and social insects. *Bioscience* **48**, 165–175. (doi:10.2307/1313262)

Rahman, N., Dunham, D. W. & Govind, C. K. 2003 Social monogamy in the big-clawed snapping shrimp. *Alpheus heterochelis*. *Ethology* **109**, 457–473. (doi:10.1046/j.1439-0310.2003.00885.x)

Ríos, R. & Duffy, J. E. 2007 A review of the sponge-dwelling snapping shrimp from Carrie Bow Cay, Belize, with description of *Zuzalpheus*, new genus, and six new species (Crustacea: Decapoda: Alpheidae). *Zootaxa* **1602**, 1–89.

Ronquist, F. & Huelsenbeck, J. P. 2003 MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**, 1572–1574. (doi:10.1093/bioinformatics/btg180)

Rubenstein, D. R. & Lovette, I. J. 2007 Temporal environmental variability drives the evolution of cooperative breeding in birds. *Curr. Biol.* **17**, 1414–1419. (doi:10.1016/j.cub.2007.07.032)

Rubenstein, D. R., McCleery, B. V. & Duffy, J. E. 2008 Microsatellite development suggests evidence of polyploidy in the social sponge-dwelling snapping shrimp *Zuzalpheus brooksi*. *Mol. Ecol. Resources* **8**, 890–894. (doi:10.1111/j.1755-0998.2008.02100.x)

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

Strassmann, J. E. & Queller, D. C. 2007 Insect societies as divided organisms: the complexities of purpose and cross-purpose. *Proc. Natl Acad. Sci. USA* **104**, 8619–8626. (doi:10.1073/pnas.0701285104)

Strathmann, R. R. 1985 Feeding and nonfeeding larval development and life-history evolution in marine-invertebrates. *Annu. Rev. Ecol. Syst.* **16**, 339–361. (doi:10.1146/annurev.es.16.110185.002011)

Tóth, E. & Bauer, R. T. 2007 Gonopore sexing technique allows determination of sex ratios and helper composition in eusocial shrimps. *Mar. Biol.* **151**, 1875–1886. (doi:10.1007/s00227-007-0618-z)

Tóth, E. & Duffy, J. E. 2005 Coordinated group response to nest intruders in social shrimp. *Biol. Lett.* **1**, 49–52. (doi:10.1098/rsbl.2004.0237)

Wenseleers, T. & Ratnieks, F. L. W. 2006 Comparative analysis of worker reproduction and policing in eusocial hymenoptera supports relatedness theory. *Am. Nat.* **168**, E163–E179. (doi:10.1086/508619)

Wilson, E. O. 1971 *The insect societies*. Cambridge, MA: Harvard University Press.

Wilson, E. O. 2005 Kin selection as the key to altruism: its rise and fall. *Soc. Res.* **72**, 159–166.

Wilson, E. O. & Hölldobler, B. 2005 Eusociality: origin and consequences. *Proc. Natl Acad. Sci. USA* **102**, 13 367–13 371. (doi:10.1073/pnas.0505858102)