

LETTER

Ecological generalism facilitates the evolution of sociality in snapping shrimps

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Abstract

Evidence from insects and vertebrates suggests that cooperation may have enabled species to expand their niches, becoming ecological generalists and dominating the ecosystems in which they occur. Consistent with this idea, eusocial species of sponge-dwelling *Synalpheus* shrimps from Belize are ecological generalists with a broader host breadth and higher abundance than non-eusocial species. We evaluate whether sociality promotes ecological generalism (social conquest hypothesis) or whether ecological generalism facilitates the transition to sociality (social transition hypothesis) in 38 *Synalpheus* shrimp species. We find that sociality evolves primarily from host generalists, and almost exclusively so for transitions to eusociality. Additionally, sponge volume is more important for explaining social transitions towards communal breeding than to eusociality, suggesting that different ecological factors may influence the independent evolutionary origins of sociality in *Synalpheus* shrimps. Ultimately, our results are consistent with the social transition hypothesis and the idea that ecological generalism facilitates the transition to sociality.

Keywords

Eusociality, generalist, niche expansion, social conquest, specialist, symbiosis.

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INTRODUCTION

Cooperation, the defining feature of social species characterised by cooperative offspring care, overlapping generations and a reproductive division of labour (Wilson 1975), has been suggested to have enabled many species like ants, termites and even humans to dominate the earth (Wilson 2012). In the most extreme cases, some of these eusocial insects make up more than half of the biomass in the ecosystems in which they occur (Wilson 1975, 2012), yet the mechanisms underlying this ecological dominance by social species (termed the ‘social conquest hypothesis’) (Wilson 2012) remain unknown. Recently, Sun *et al.* (2014) proposed that cooperation in burying beetles allows cooperative, group-living populations to become ecological generalists that thrive in diverse thermal environments by enabling them to both outcompete interspecific competitors for access to resources and to expand their ecological niche. Moreover, comparative work in birds demonstrating that cooperative breeding behaviour has enabled species to expand into and colonise harsh environments (Cornwallis *et al.* 2017), is consistent with the hypothesis that cooperation facilitates the expansion of niche breadth and geographic range size.

An alternative to the idea that sociality facilitates ecological change is that shifts in ecology drive changes in sociality. This scenario is consistent with the long-standing idea that environmental constraints (Emlen 1982; reviewed in Shen *et al.* 2017) or specific environmental features such as patterns of climate variation correlate with and promote cooperation, as has been observed in birds (Jetz & Rubenstein 2011), mammals (Lukas

& Clutton-Brock 2017) and insects (Sheehan *et al.* 2015). Under this scenario, cooperative behaviour is likely to have evolved only after species expanded their ecological range or niche into new environments (Shen *et al.* 2017). Ecological influences on social system may be particularly important for species with specific environmental requirements, such as those that live symbiotically within other organisms (e.g. gall-forming aphids, thrips, acacia ants, sponge-dwelling shrimps) and that rarely leave the safety of these fortress-like domiciles (Rubenstein & Abbot 2017). For example, if becoming a host generalist exposes symbiotic species to greater interspecific competition, then transitioning to being social may enable host generalists to outcompete non-social host specialists for access to resources. Thus, it remains unclear whether sociality is generally a cause or a consequence of ecological dominance, range expansion and niche breadth, particularly for species with specific environmental requirements like those living in symbioses.

The snapping shrimp genus *Synalpheus* not only contains the only known eusocial organisms in the sea, but it is one of the most socially diverse taxa on the planet, ranging from pair-living to communal breeding (group-living) to eusocial species (Hultgren *et al.* 2017). Both eusocial and non-eusocial *Synalpheus* species live symbiotically within sponges, a limiting resource for which species with different social systems compete (Duffy & Macdonald 2010; Hultgren *et al.* 2017). The idea that cooperation has facilitated ecological generalism and niche expansion via greater interspecific competitive ability (Sun *et al.* 2014) is consistent with data from Belize where

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eusocial *Synalpheus* species have a higher relative abundance, occupy a greater proportion of sponges and have a wider sponge host breadth than non-eusocial species (Macdonald *et al.* 2006). Furthermore, community assembly analyses suggest that eusociality enhances competitive ability and drives competitive exclusion of non-eusocial species, and that sponge volume is an important factor in niche use for *Synalpheus* shrimps (Hultgren & Duffy 2012). For example, different species of *Synalpheus* shrimps inhabit both small encrusting sponges that live in the spaces found in dead coral rubble, as well much larger, free-living sponges that grow on healthy reefs (Hultgren *et al.* 2017). Sponges are clearly a limiting resource for both social and non-social *Synalpheus*: typically, > 90% of appropriate sponge species are inhabited by *Synalpheus* at any given site (unpublished data). Furthermore, many individual sponges are occupied by more than one shrimp species; up to five different species of *Synalpheus* can co-occur in a single sponge host, though multiple eusocial species never coexist in the same sponge (Hultgren & Duffy 2012). Despite the apparent ecological dominance of eusocial over non-eusocial species, it remains unclear whether eusociality has enabled shrimp species to become ecological generalists (i.e. sociality promotes niche expansion and ecological generalism consistent with the social conquest hypothesis) (Wilson 2012; Sun *et al.* 2014), or alternatively, whether ecology has fostered the evolution of cooperation (Emlen 1982; Rubenstein & Lovette 2007; Faulkes & Bennett 2013) in this group through the utilisation of more host sponges (i.e. ecological generalism) and facilitated the transition to sociality as habitat becomes saturated (what we refer to as the 'social transition hypothesis').

Here, we explored whether sociality in *Synalpheus* snapping shrimps is a cause or consequence of being an ecological generalist by examining the coevolutionary relationships and transitions among social system and two measures of the ecological niche in shrimp: sponge host breadth and sponge volume (*sensu* Hultgren & Duffy 2012). The *c.* 45 shrimp species in the West Atlantic 'gambarelloides group' (Coutière 1909; Dardeau 1984) exhibit the full range of animal social systems, from the family's ancestral condition of pair-living, to communal breeding groups with approximately equal sex ratios (i.e. multiple mated pairs per sponge), to eusocial colonies with one or multiple queens and a variable number of non-breeding workers (Chak *et al.* 2017; Hultgren *et al.* 2017). Importantly, eusociality has evolved independently multiple times within *Synalpheus* (Duffy *et al.* 2000; Duffy & Macdonald 2010), and eusociality and communal breeding represent distinct social systems that arose independently from pair-living ancestors along alternative evolutionary paths (Chak *et al.* 2017). Moreover, these independently evolved social systems in snapping shrimps – communal breeding and eusociality – are likely to have been selected for by different ecological factors (Chak *et al.* 2017). We used phylogenetic comparative analyses to test the alternative hypotheses that (1) sociality promotes niche expansion and ecological generalism (social conquest hypothesis) vs. (2) ecological generalism facilitates the transition to sociality (social transition hypothesis). By quantifying different axes of the ecological niche – sponge host breadth (the number of sponge species occupied) and

sponge volume (the mean volume of each host sponge species) – we further explored whether different ecological factors may have influenced the independently evolved forms of sociality (i.e. communal breeding vs. eusociality). We examined the coevolutionary transitions among social and sponge ecological states and reconstructed their ancestral states in 38 species of *Synalpheus* shrimps collected across the Caribbean over 27 years. Ultimately, these evolutionary analyses provide critical new evidence for understanding the role of ecology in animal social evolution, and for determining whether sociality is a cause or consequence of being an ecological generalist.

MATERIAL AND METHODS

Sample collection

We utilised samples collected over 27 years (1988–2014) from nine regions across the Caribbean, including: Chub Cay, Bahamas; various sites on the southern side of Barbados; Carrie Bow Cay, Belize; Jardines de la Reina archipelago, Cuba; various sites on the southern side of Curaçao; Florida Keys, Florida, USA; Discovery Bay, Jamaica; and Bocas del Toro and San Blas, Panama. Sponges were sampled in a similar manner across field expeditions using collection methods described previously (Macdonald *et al.* 2006). Briefly, macroscopic sponges attached to hard substrates or cryptic sponges attached to or infilling between dead coral rubble were collected using SCUBA (5–20 m) or snorkel (< 5 m) from coral reefs and sea grass beds at 1–30 m in depth. Sponges were collected whole and kept submerged in seawater during transportation and until processing at field stations. Sponges were then dissected and all macrofauna were carefully removed from the internal canals of the sponge. Sponge hosts were identified under light microscopy, and live shrimp were collected from each sponge, identified, and preserved in 95% EtOH. Volumes of selected sponges were measured during more recent expeditions (2006–2014) by water displacement (Hultgren & Duffy 2012). Uncertain shrimp specimen identifications were confirmed using COI and 16S sequences and established phylogenies (Hultgren *et al.* 2014).

Our final dataset included 1181 colonies from 38 shrimp species (range = 2–126 colonies/species, mean = 30.28 colonies/species). Species were only included in the dataset if there were at least two colonies in our collection of more than 60 000 shrimps from roughly 4600 colonies collected since 1988. Each shrimp species inhabited 1–9 sponge host species (mean = 2.68). Sponge volume data were available for 697 of the 1181 colonies used in our dataset. Colonies were only included in the dataset if (1) all shrimp within a sponge were identified, (2) they contained at least one ovigerous (i.e. egg-bearing) female, and (3) they contained at least two individuals. Ovigerous females were identified by the presence of eggs in their abdomens, and occasionally by other morphological characteristics such as rounded pleura (i.e. the flaps surrounding the abdominal segments). Individuals without eggs were considered to be a mix of non-reproductive but mature males, non-breeding females and juveniles, all of which are morphologically indistinguishable under ordinary light microscopy (Duffy 2007; Toth & Duffy 2008; Chak *et al.* 2015).

We quantified two variables that describe the ecological niche of snapping shrimps (Hultgren & Duffy 2012) and are likely to influence their social evolution: the total number of sponge host species occupied (sponge host breadth) and the mean sponge host volume for each shrimp species (Table S3). We only included unspecific host identifications in our dataset if they were consistent (i.e. identifiable as the same species) within and across sampling locations. Our measure of host breadth was conservative, as it is likely that shrimp species inhabit more sponge hosts than have been identified in our dataset, representing only nine locations across the Caribbean. However, these variables provide an example of each species' ecological niche breadth (Futuyma & Moreno 1988) and allowed us to classify species as ecological specialists or generalists (see below for details). A phylogenetic least squares regression analysis (PGLS) revealed that mean sponge volume was strongly correlated with other volume measures including minimum sponge volume, maximum sponge volume and each species' range of sponge volumes (Table S1). We categorised each species' social organisation as either being eusocial, communal breeding or pair-living based upon a previous quantitative classification of *Synalpheus* that used a variety of demographic measures (Chak *et al.* 2017; Hultgren *et al.* 2017) and is directly correlated with measures of the eusociality index in this group (Duffy & Macdonald 2010). Where species showed some variability in social system, we categorised them based upon their typical form of social organisation (*sensu* Hultgren *et al.* 2017) (Table S3).

Phylogenetic comparative analysis

To test the two alternative hypotheses relating sociality and ecological generalism in *Synalpheus*, we estimated transition rates between combinations of traits and reconstructed ancestral character states. Our phylogenetic hypothesis was based upon a previously published phylogeny created using three loci (the mitochondrial 16S rRNA locus (16S), the 5' barcoding end of the mitochondrial cytochrome oxidase I gene (COI), and a region of the 18S nuclear large ribosomal subunit (18S)), as well as 33 morphological characters (for details see Hultgren *et al.* 2014; Chak *et al.* 2017). The tree was made ultrametric using non-parametric rate smoothing in the software r8s (Sanderson 2003), with optimal smoothing value determined through cross-validation.

Since our response variable (social system) was categorical with three levels (pair-living, communal breeding, and eusocial), the continuous predictors (sponge host breadth and sponge volume) had to be transformed into categorical variables as well in order to conduct the coevolutionary analyses. Since neither variable was normally distributed nor exhibited natural splits in the data (Table S3), we converted by splitting them at their tertiles: we used the first tertile (33% quantile; 2 sponge hosts) for sponge host number, creating 'specialist' (≤ 2 sponge hosts, $N = 23$) and 'generalist' categories (> 2 sponge hosts, $N = 15$), and the second tertile (66.6% quantile; 385.18 mL) for sponge volume, splitting into 'low sponge volume' (≤ 385.18 mL, $N = 18$) and 'high sponge volume' categories (> 385.18 mL, $N = 14$). We also conducted a sensitivity test of these categorisations using a more stringent definition

of host specialisation (specialist = 1 sponge host; generalist = ≥ 2 sponge hosts; $N_{\text{specialists}} = 14$, $N_{\text{generalists}} = 24$) and host volume (60% quantile, 341.96 mL, $N_{\text{low}} = 19$, $N_{\text{high}} = 13$; a more even cutoff than that could not be used because it would result in quasi-complete separation, with no species being classified as both communal and low volume). Sensitivity analyses gave qualitatively similar results and are presented in the Supporting Information (Figure S1 and Table S2).

We tested for correlated trait evolution between social system and the ecological variables of interest using a continuous-time Markov model approach to the evolution of discrete traits (Pagel 1994; Pagel & Meade 2006). Prior to fitting the coevolutionary models, we verified that the ecological predictors (sponge host breadth and sponge volume) were not evolutionarily correlated (PGLS of $\log(\text{sponge volume})$ by $\log(\text{sponge number})$: $\beta = 0.12$, $t = 0.64$, $P = 0.53$). Since these variables were not correlated, we assumed that they reflect independent ecological axes and considered the association between these variables and social system in separate coevolutionary models. We tested multiple dependent and independent models of trait evolution (described below) using the reversible-jump MCMC (RJMCMC) approach implemented in BayesTraits (Pagel & Meade 2006). These models estimate transition rates between states of one trait conditioned on the background state of the other trait. Since transition rates represent the rate of change between states in an infinitesimally short time interval, transitions incorporating instantaneous change in both social system and the ecological variable simultaneously were set to zero (Pagel & Meade 2006). We further constrained all of our models to not allow transitions between communal breeding and eusocial states because previous work in *Synalpheus* indicated that communal breeding and eusociality evolved independently from pair-living ancestors (Chak *et al.* 2017). Therefore, models had up to 14 possible transitions estimated through the RJMCMC algorithm, which infers how many different rate parameters are used to define these transitions and the probability of any of the transitions being zero (Pagel & Meade 2006).

To test whether changes in the ecological variables of interest were conditioned on social state (social conquest hypothesis), or if social state transitions were conditioned on ecological variables (social transition hypothesis), we considered seven competing models (Table 1, Figure S2). First, we considered two null models: in the first, all transition rates in the model were constrained to be equal (Null Model 1), and in the second, transitions between social state and sponge state were independent from each other, but could assume different values (Null Model 2). We then tested two models in which transitions between sponge states are facilitated or constrained by the current social state (i.e. social conquest hypothesis) by constraining transitions between social states to be independent of the current sponge state, but allowing transitions between sponge states to be different depending upon their current social state. We then considered three models where sponge state influences transitions between social states (i.e. social transition hypothesis). In all of these models, transitions between sponge states were constrained to be equal across social systems, but transitions between social states were allowed to vary in different ways: in the first, transitions

Table 1 Results from model comparisons

Model*	Description	Sponge host breadth		Sponge volume	
		ln L	BF	ln L	BF
1. Null model 1	All rates equal	-64.87	3.66	-56.79	6.16
2. Null model 2	Transition rates in the same direction between social states are equal across sponge states, and vice-versa	-65.06	4.04	-56.92	6.42
3. Sociality influences sponge transitions	All social state transition rates in same direction equal, and all sponge state transition rates allowed to vary	-67.22	8.36	-56.67	5.92
4. Sponge state influences social transitions	All social state transition rates allowed to vary, and all sponge state transition rates in same direction equal	-63.04	0.00	-53.71	0.00
5. Sponge state influences eusocial transitions	C transition rates in same direction equal, E transition rates allowed to vary, and all sponge state transition rates in same direction equal	-63.66	1.24	-56.13	4.84
6. Sponge state influences communal transitions	E transition rates in same direction equal, C transition rates allowed to vary, and all sponge state transition rates in same direction equal	-65.05	4.02	-55.74	4.06
7. Full model	All social and sponge transition rates allowed to vary	-66.2	6.32	-54.74	2.06

A description of each of the seven models examining transitions rates between social state and either sponge host breadth or sponge volume, as well as their associated marginal ln-likelihood values (ln L) and Bayes Factors (BF, estimated as $2\Delta\ln L$) when compared to the best fitting model (bold). According to this scale, positive evidence toward a model was assumed when $BF > 2$, and strong evidence toward the model when $BF > 6$.

*No models allow transitions between eusociality (E) and communal breeding (C), reflecting their independent evolutionary transitions from pair-living (*sensu* Chak *et al.* 2017).

from/to pair-living to both communal breeding and eusociality were allowed to depend upon sponge state; in the second, we considered models in which only transitions from/to communal breeding or from/to eusociality were conditioned on the ecological variable; in the third, we considered a full model, where both social state and sponge state depend upon and can influence each other.

We ran the seven models to test for the correlated evolution of social system and sponge host breadth and of social system and sponge volume separately. We ran four independent Markov Chains (to verify that they were reaching stationarity at the same likelihood values) for 2 000 000 generations after a 100 000 generation burn-in, sampling every thousandth generation. We used exponential priors for all transition rates with means drawn from a uniform hyperprior (range = 0–10). We then randomly chose one of the four chains per model and used a stepping stone sampler algorithm (250 stones for 5000 iterations each) to estimate the marginal likelihood. We compared the relative performance of models using Bayes Factors (BF), calculated as two times the difference in the log-likelihood of the models. According to this scale, positive evidence toward a model was assumed when $BF > 2$, and strong evidence toward the model when $BF > 6$ (Kass & Raftery 1995). We then calculated the posterior mean of the transition rate parameters in the best model, as well as the proportion of the posterior in which each transition was estimated as zero. Finally, we used BayesTraits to reconstruct the ancestral states of social system and sponge host breadth and sponge volume conditioned on the best model.

RESULTS

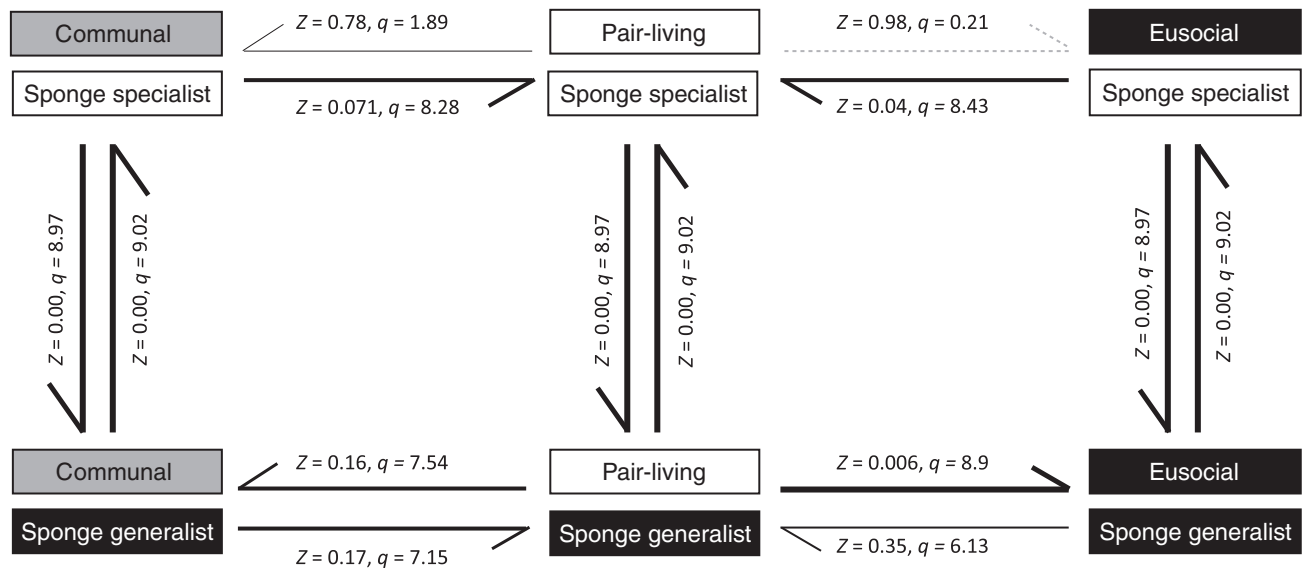
Models reflecting the social transition hypothesis outperformed null models as well as the social conquest hypothesis models for both sponge host breadth and sponge volume (Table 1). In both cases, the model where either sponge host

breadth or sponge volume influenced transitions between social systems, both from/to communal breeding and eusociality, was ranked best among the models considered. However, while sponge volume clearly influenced transitions between pair-living and both forms of sociality, the influence of sponge host breadth was more evident on the evolution of eusociality than on communal breeding (BF of 1.24 when comparing the best model to the model where sponge host breadth only influences the evolution of eusociality, vs. BF of 4.02 when compared to the model where sponge host breadth only influences the evolution of communal breeding). Importantly, both for sponge volume and sponge host breadth, the social transition model greatly outperformed the social conquest model (Table 1), indicating little support for the hypothesis that being social facilitates niche expansion.

The transition rates for the best coevolutionary model of sponge host breadth and social system show that while transitions between pair-living and both communal breeding and eusociality occur at approximately similar rates for sponge generalists, these rates were much higher than those among sponge specialists (Fig. 1). This effect was particularly pronounced in the evolution of eusociality among sponge specialists, where transitions from pair-living to eusociality were considered to be zero for almost the entirety of the posterior distribution. In other words, transitions to eusociality occurred almost exclusively in lineages that were already host generalists.

A similar pattern is observed when considering the coevolution of social system and sponge volume, but this time with a more pronounced effect on the evolution of communal breeding than eusociality. Here, we see that transitions between pair-living and sociality are much lower in lineages occupying small sponges than in those occupying large sponges, with transitions to communal breeding being virtually non-existent in the former (Fig. 1). In addition to the influence of sponge volume in gains of sociality, the loss of communal breeding in

(a) Sponge host breadth



(b) Sponge volume

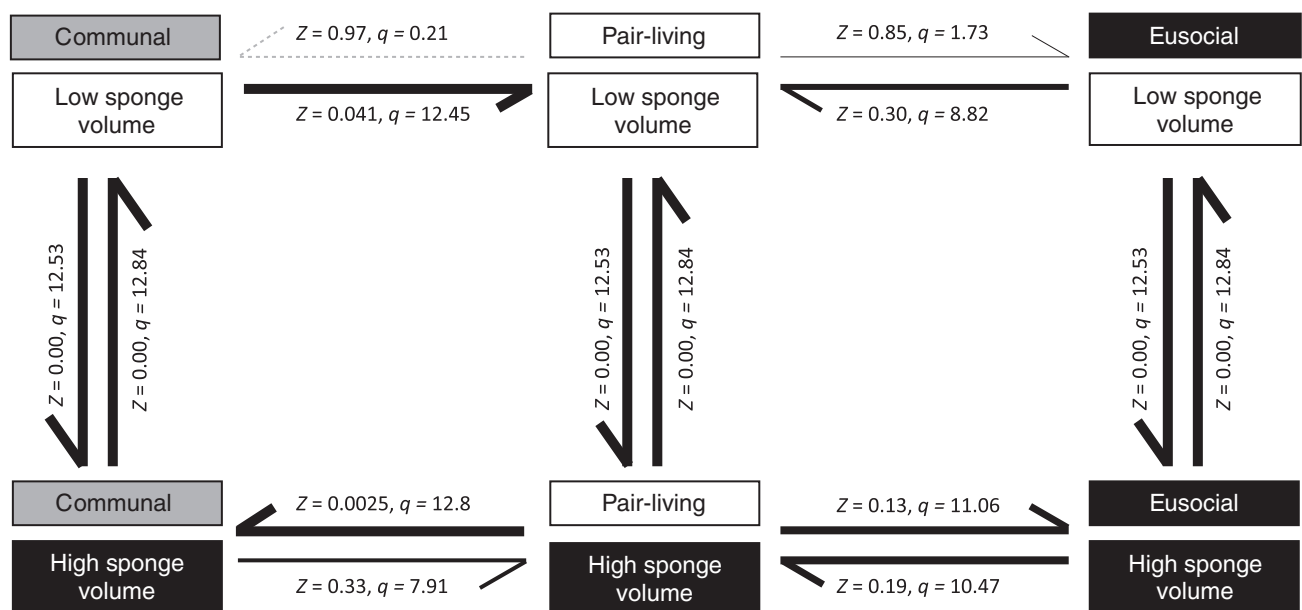


Figure 1 Coevolutionary transition rates for social and sponge states (a: sponge host breadth; b: sponge volume) in snapping shrimps. Z = posterior percentage of times the transitions between two states were classified as zero; q = posterior mean transition rate between two states. Arrow thickness represents the magnitude of the transition rate (q). Dashed arrows indicate that transition rates between two states were < 1.00 .

low volume sponge species is also much higher than in high volume ones, indicating that sociality in general is particularly unstable for species specialised in occupying small sponges.

DISCUSSION

Although environmental factors have long been known to be associated with the evolution of cooperative behaviour (Emlen 1982; Koenig *et al.* 1992; Rubenstein & Lovette 2007), recent work in insects (Sun *et al.* 2014) and birds (Cornwallis *et al.* 2017) has complicated the long-standing view that ecology

drives the evolution of social behaviour (Shen *et al.* 2017). Instead, these new studies demonstrate not only that there is no simple environmental condition or axis that promotes the evolution of sociality, but that cooperation itself may actually enable species to modify or expand their ecological niches (in the case of insects; Sun *et al.* 2014) or geographic ranges (in the case of birds; Cornwallis *et al.* 2017) by allowing them to outcompete other species. Thus, determining the directionality of the relationship between social behaviour and niche breadth remains an important topic of study if we are to understand the role of ecology in shaping sociality and

cooperation more broadly (Dillard & Westneat 2016; Shen *et al.* 2017).

By explicitly testing whether sociality (both eusociality and communal breeding) in *Synalpheus* shrimps promotes ecological generalism (social conquest hypothesis) (Wilson 2012; Sun *et al.* 2014), or whether ecological generalism facilitates the transition to sociality (social transition hypothesis), we were able to explore the directionality of the relationship between social behaviour and ecology. Our comparative results presented here are consistent with the social transition hypothesis and the idea that ecological generalism facilitates the transition to sociality. We show that transitions to sociality – both communal breeding and eusociality – occur primarily from host generalists, and almost exclusively so for transitions to eusociality. Sponge volume is also important in explaining social transitions, with sociality evolving primarily from pair-living species occupying large sponges. However, sponge volume was more important for explaining social transitions to communal breeding, relative to transitions to eusociality. Thus, different aspects of the sponge niche (host breadth vs. host size) had differential effects on transitions to communal vs. eusocial living, consistent with the idea that different ecological factors likely underlie the independent evolutionary origins of sociality observed in *Synalpheus* shrimps (Chak *et al.* 2017).

The idea that environmental constraints promote social evolution in general, and group-living in particular, is well established (Emlen 1982; Koenig *et al.* 1992; Shen *et al.* 2017). Our results are consistent with this ecological constraints framework because in *Synalpheus*, inhabiting a narrow range of sponge species, or inhabiting small sponge hosts, constrains the evolution of eusociality and communal breeding respectively. However, narrow host breadths constrain the evolution of eusociality more than the evolution of communal breeding, perhaps because a narrow host breadth limits eusocial species' ability to compete for access to sponges. Although being a host generalist may expose symbiotic species like sponge-dwelling shrimps to greater interspecific competition, it also may promote the evolution of cooperation as a way to improve competitive ability. Consistent with this idea, previous work in *Synalpheus* shrimps from reefs in Belize showed that eusocial species are ecological generalists that have a higher relative abundance, occupy a greater percentage of sponges, and have a broader host breadth than communal breeding and pair-living species (Macdonald *et al.* 2006). Eusocial *Synalpheus* species are also less likely to co-occur with closely related congeners, and never co-occur in a sponge with other eusocial species (Hultgren & Duffy 2012).

We also found that sponge volume – specifically, small sponge hosts – appears to constrain the evolution of sociality in *Synalpheus*, likely because small sponges support fewer individuals (Hultgren & Duffy 2010). Intriguingly, sponge volume was more important for predicting transitions to communal breeding rather than transitions to eusociality, although both eusocial and communal species live in large groups. It is possible that communal species are more likely to be constrained by sponge size limits than eusocial species because their colonies are comprised of unrelated pairs that may compete with one another in some cases (Hultgren *et al.* 2017).

That is, eusocial colonies may be able to exist at higher densities than communal groups, and sponge volume may thus be more limiting to the evolution of communal living. In fact, some *Synalpheus* species exhibit both pair-living and communal breeding (Chak *et al.* 2017; Hultgren *et al.* 2017). This social plasticity is likely driven by sponge size, with small sponges supporting one conspecific pair and larger sponges supporting multiple conspecific pairs. Because eusocial colonies are comprised of related individuals known for cooperating with one another (Duffy 1996; Rubenstein *et al.* 2008), sponge size (and its effects on shrimp density) is likely to be less constraining to the adoption of eusociality than to communal breeding.

We also examined alternative variables (life history traits) that could mediate the relationship between sociality and ecological generalism. For example, body size of obligate mutualists or parasites often matches their host's size (Johnson *et al.* 2005). Host specialisation or generalism could be driven by the number of host species with appropriate inner canal sizes, relative to shrimp body size (Hultgren & Duffy 2010, 2012). If smaller shrimp species could use a greater breadth of sponge hosts (e.g. utilising sponge hosts with both large and small canals), and body size was also related to transitions to sociality – perhaps by causing these species to be at a competitive disadvantage – then body size may mediate the positive relationship between generalism and sociality. In support of this idea, eusocial species in *Synalpheus* have relatively smaller body sizes than pair-living species (Duffy & Macdonald 2010), putting them at a disadvantage when competing with larger pair-living shrimps (Hultgren & Duffy 2012). However, data from Belize suggest that the strong relationship between social behaviour and host breadth was robust to corrections for body size. That is, sociality was a consistently stronger predictor of sponge host breadth and abundance than body mass (Duffy & Macdonald 2010), suggesting that body size does not drive shrimp-host associations. Additionally, most shrimp species only inhabit a subset of size-matched hosts (Hultgren & Duffy 2010, 2012), and sponges may modify their canal sizes as they grow to accommodate their shrimp inhabitants (Hultgren & Duffy 2010). Finally, canal size does not necessarily increase with larger volume sponges (Hultgren & Duffy 2012), suggesting that body size cannot account for the relationship we see between sponge volume and sociality. Together, this evidence suggests that body size does not explain the pattern we see between ecological generalism and sociality.

Much previous work has shown the importance of kin selection for the evolution of eusociality in snapping shrimps (Duffy & Macdonald 2010; Chak *et al.* 2017) and other taxa (Jarvis *et al.* 1994; Hughes *et al.* 2008; Bourke 2014; Kapheim *et al.* 2015). Although kin selection likely influenced sociality in eusocial species, which form tightly structured, closely related communities, it is unlikely that kin selection promoted the evolution of communal breeding in *Synalpheus* since communal colonies are comprised of unrelated pairs (Duffy & Macdonald 2010). This demographic distinction is further supported by work suggesting that eusociality and communal living each evolved along independent evolutionary trajectories from pair-living shrimp species (Chak *et al.* 2017). These differences in evolutionary trajectories in *Synalpheus* could be

related to differences in larval dispersal, which has been suggested to be a pre-adaptation to eusociality in this group (Duffy & Macdonald 2010; Hultgren *et al.* 2017). That is, both communal breeding and pair-living species produce swimming, presumably dispersing larvae, a strategy that likely contributes both to low relatedness among communal colony members (Hultgren *et al.* 2017) and a host generalist strategy because shrimp will have greater opportunities to settle on a variety of host species (Poisot *et al.* 2011). In contrast, eusocial species exhibit direct larval development (brooding) with most individuals remaining in their natal sponge and forming kin-based communities (Duffy & Macdonald 2010). Among eusocial species, individuals that do disperse to found new colonies (Hultgren *et al.* 2014) are limited by the distance they can crawl or swim, which would likely promote host specialisation (LaJeunesse *et al.* 2010).

Since our study finds that eusocial species tend to be host generalists rather than specialists, the previously documented differences in dispersal mode between eusocial and non-eusocial species could have resulted from changes in host use, which in turn facilitated changes in social behaviour. Specifically, ecological generalism might actually facilitate changes towards limited dispersal, since individuals are able to use most of the local sponges, thereby creating conditions for kin selection within colonies. In contrast, species that specialise on only a few widely distributed host sponges might benefit from pelagic dispersal, which would allow them to move further from their natal sponge and prevent aggregation of kin groups. Furthermore, this change in colonisation pattern of generalists might lead to local habitat saturation, as unoccupied hosts could be more quickly recolonised from any neighbouring sponge even if it does not happen to be of the same sponge species. Habitat saturation may in turn reinforce the kin-selected benefits of reduced dispersal and promote family-living, as it does in other social taxa (Emlen 1982). Thus, changes in local vs. global competition for ecological resources might favour the evolution of delayed dispersal resulting in the formation of kin groups and the evolution of eusociality.

Transitions to eusociality are relatively common within snapping shrimps in comparison to the number of transitions estimated in other taxonomic groups. In fact, eusociality is estimated to have evolved four times within the *c.* 45 shrimp species in the West Atlantic 'gambarelloides group' (Duffy & Macdonald 2010; Chak *et al.* 2017). This is a proportionally large number when compared to the estimated two transitions to eusociality within corbiculate bees, a group of ~ 1000 species (Cardinal & Danforth 2011) and 12 transitions estimated within all insects (Wilson & Hölldobler 2005). In addition, eusociality within *Synalpheus* appears to be relatively stable, with only one estimated reversal to pair-living (Fig. 2) (Hultgren & Brandt 2015). The rarity and instability of eusociality observed in other taxa, and particularly in primitively eusocial species (Wilson & Hölldobler 2005; Fu *et al.* 2014), can be attributed to its high extinction risk (Fu *et al.* 2014), which is driven primarily by reduced genetic diversity due to inbreeding (Agnarsson *et al.* 2006; Settepani *et al.* 2017). It is possible that eusociality is more common and more stable in snapping shrimps relative to the eusocial insects because of the intense competition that shrimps experience over host sponges. In

fact, snapping shrimps exhibit many of the features known to promote the evolution of eusociality (Duffy 2007; Chak *et al.* 2017) such as an environment that favours cooperation due to ecological constraints (Fu *et al.* 2014), short-term reproductive advantages (Agnarsson *et al.* 2006) and limited dispersal abilities (Avilés & Purcell 2012). These life history traits not only may predispose the evolution of eusociality, but also prevent it from reversals (Fu *et al.* 2014).

Finally, our results are important to consider in the light of other recent studies relating social evolution to ecology. The patterns presented here may differ from recent work in burying beetles (Sun *et al.* 2014) and birds (Cornwallis *et al.* 2017) that both support the social conquest hypothesis because of differences in study design. That is, Sun *et al.*'s (2014) study empirically examined the reproductive success of several populations of burying beetles along an environmental gradient (temperature). In contrast, our study was comparative in nature, focusing upon species-level traits, and did not directly measure fitness. Although both our study and the work by Cornwallis *et al.* (2017) share a comparative design, the latter study measured how cooperation impacted shifts in the climatic niche. In contrast, we explicitly measured niche expansion/contraction, which is considerably different from the niche shifts considered in birds and is more analogous to range shifts (Cornwallis *et al.* 2017). Moreover, we defined the ecological niche more narrowly because shrimp are symbiotic, obligate sponge-dwellers. This narrow definition is common in studies examining ecological generalism and specialisation among symbiotic organisms (Schemske 1982). In contrast, the niche in birds was defined by a principal component analysis of environmental variables and therefore represents a broader representation of a species' niche (Cornwallis *et al.* 2017). Together, the results from all of these and other studies suggest that there is no simple explanation for the ecological causes or consequences of sociality, and that researchers should continue to explore these questions both empirically and comparatively.

In conclusion, our results are consistent with the social transition hypothesis arguing that ecological generalism promotes the transition to sociality in snapping shrimps. Transitions to both eusociality and communal breeding occur either exclusively or more frequently from host generalists than from host specialists. These results contrast with the predictions of the social conquest hypothesis (Wilson 2012), as well as with experimental support for that hypothesis from burying beetles (Sun *et al.* 2014) and comparative work in birds (Cornwallis *et al.* 2017). Instead, our analyses suggest that cooperation within group-living animals is facilitated by, rather than a product of, their ecological niche (Emlen 1982). More specifically, broader ecological niches in snapping shrimps appear to evolve before cooperation and facilitate the transition to sociality, particularly eusociality. Although our power within this study is limited by a relatively small sample size of 38 species and only five transitions to or from eusociality, the model results all overwhelmingly support the social transition hypothesis. The broader relevancy of the social transition hypothesis needs to be tested further in taxonomic groups exhibiting a range of social systems such as bees, wasps (Johnson *et al.* 2013) and spiders (Agnarsson *et al.* 2007), all of which are more speciose lineages than *Synalpheus* but have fewer social transitions.

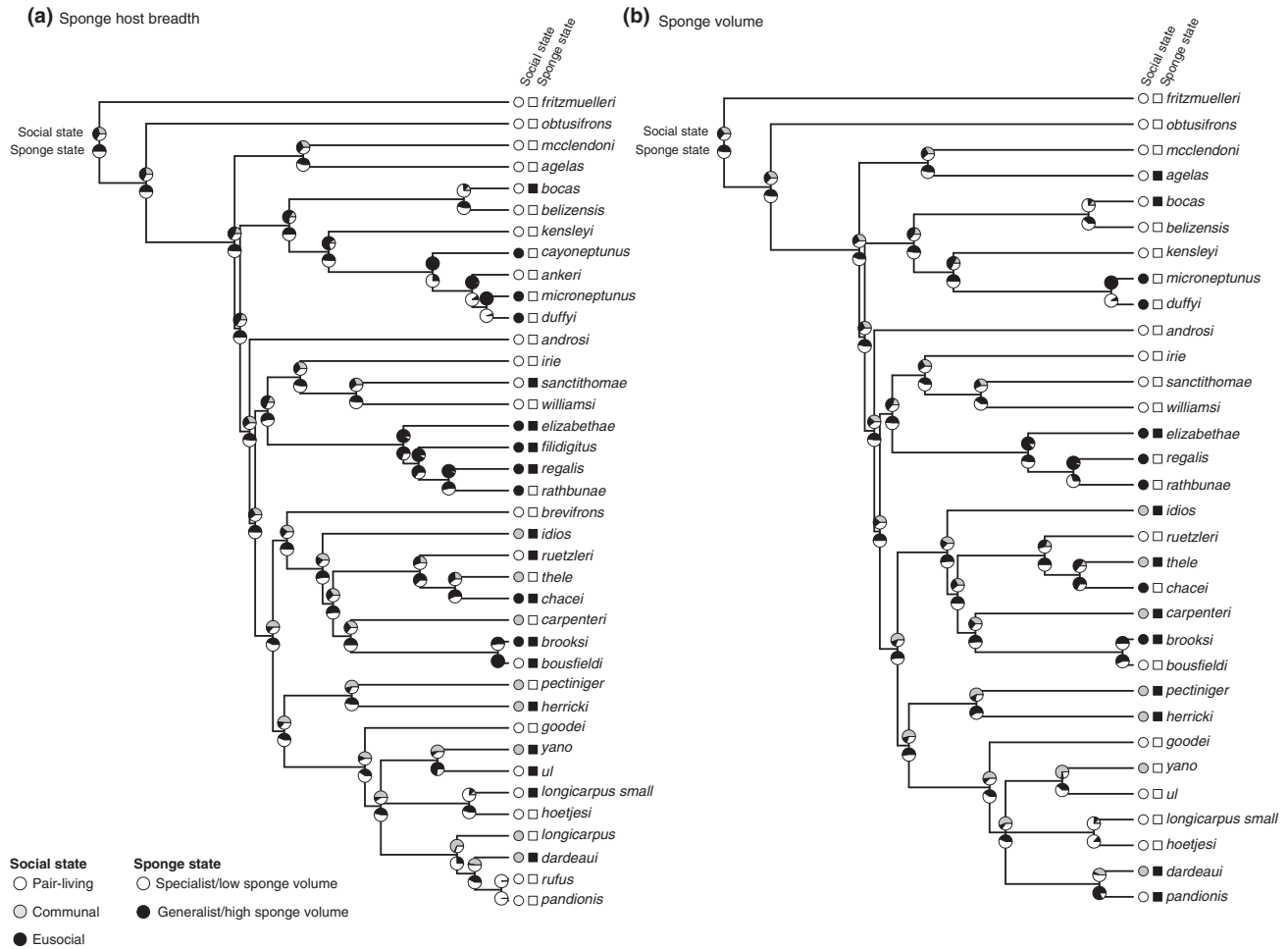


Figure 2 Ancestral state reconstructions for social and sponge states (a: sponge host breadth; b: sponge volume) in snapping shrimps. Reconstruction of social state and sponge host breadth showed four origins of eusociality and one reversal from eusociality to pair-living (Fig. 1), consistent with previous work in this system (Duffy & Macdonald 2010; Hultgren & Duffy 2011; Hultgren & Brandt 2015; Chak *et al.* 2017). However, the origins of pair-living, communal breeding, sponge host breadth and sponge volume were less clear, suggesting that many evolutionary transitions in social and sponge state occurred recently. Pie charts at nodes represent the posterior probabilities of being in each sponge state (top pie chart) and each social state (bottom pie chart). Circles at tips indicate the current social and sponge states for each species.

Clearly, additional empirical work is also needed to fully identify all of the possible mechanisms behind the ecological causes and consequences of sociality. In addition to sponge host breadth being important, particularly for eusocial species, we found that sponge host size was also relevant. However, this ecological variable – which represented an independent axis of the ecological niche from host breadth – was more important in explaining the transition to communal breeding than to eusociality. Ultimately, our study highlights the importance of testing for directionality underlying commonly observed correlations between ecology and social behaviour, and illustrates how sociality may be a consequence – rather than a cause – of ecological dominance in some groups of animals.

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AUTHOR CONTRIBUTIONS

KCB and DRR designed the study, all authors collected the data, KCB and RM analysed the data, KCB and DRR wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

REFERENCES

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

- Agnarsson, I., Maddison, W.P. & Avilés, L. (2007). The phylogeny of the social *Anelosimus* spiders (Araneae: Theridiidae) inferred from six molecular loci and morphology. *Mol. Phylogenet. Evol.*, 43, 833–851.
- Avilés, L. & Purcell, J. (2012). The evolution of inbred social systems in spiders and other organisms. *Adv. Study Beh.*, 44, 99–133.
- Bourke, A.F.G. (2014). Hamilton's rule and the causes of social evolution. *Philos. Trans. R. Soc. B. Biol. Sci.*, 369, 10.
- Cardinal, S. & Danforth, B.N. (2011). The antiquity and evolutionary history of social behavior in bees. *PLoS ONE*, 6, e21086.
- Chak, S.T.C., Rubenstein, D.R. & Duffy, J.E. (2015). Social control of reproduction and breeding monopolization in the eusocial snapping shrimp *Synalpheus elizabethae*. *Am. Nat.*, 186, 660–668.
- Chak, S.T.C., Duffy, J.E., Hultgren, K.M. & Rubenstein, D.R. (2017). Evolutionary transitions towards eusociality in snapping shrimps. *Nat. Ecol. Evol.*, 1, 0096.
- Cornwallis, C.K., Botero, C.A., Rubenstein, D.R., Downing, P.A., West, S.A. & Griffin, A.S. (2017). Cooperation facilitates the colonisation of harsh environments. *Nat. Ecol. Evol.*, 1, 0057.
- Coutière, H. (1909). The American species of snapping shrimps of the genus *Synalpheus*. *Proc. U. S. Nat. Mus.*, 36, 1–93.
- Dardeau, M. (1984). *Synalpheus* shrimps (Crustacea: Decapoda: Alpheidae). I. The Gambarelloides group, with a description of a new species. *Mem. Hourglass Cruises*, 1–125.
- Dillard, J.R. & Westneat, D.F. (2016). Disentangling the correlated evolution of monogamy and cooperation. *Trends Ecol. Evol.*, 31, 503–513.
- Duffy, J.E. (1996). Eusociality in a coral-reef shrimp. *Nature*, 381, 512.
- 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 Duffy, J.E. & Thiel, M.). Oxford University Press, New York, pp. 387–409.
- Duffy, J.E. & Macdonald, K.S. (2010). Kin structure, ecology and the evolution of social organization in shrimp: a comparative analysis. *Proc. R. Soc. B-Biol. Sci.*, 277, 575–584.
- Duffy, J.E., Morrison, C.L. & Rios, R. (2000). Multiple origins of eusociality among sponge-dwelling shrimps (*Synalpheus*). *Evol.*, 54, 503–516.
- Emlen, S.T. (1982). The evolution of helping. I. An ecological constraints model. *Am. Nat.*, 119, 29–39.
- Faulkes, C.G. & Bennett, N.C. (2013). Plasticity and constraints on social evolution in African mole-rats: ultimate and proximate factors. *Philos. Trans. R. Soc. B. Biol. Sci.*, 368, 20120347.
- Fu, F., Kocher, S.D. & Nowak, M.A. (2014). The risk-return trade-off between solitary and eusocial reproduction. *Ecol. Lett.*, 18, 74–84.
- Futuyma, D.J. & Moreno, G. (1988). The evolution of ecological specialization. *Annu. Rev. Ecol. Syst.*, 19, 207–233.
- 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.
- Hultgren, K.M. & Brandt, A. (2015). Taxonomy and phylogenetics of the *Synalpheus paranepuntus*-species-complex (Decapoda: Alpheidae), with a description of two new species. *J. Crustacean Biol.*, 35, 547–558.
- Hultgren, K.M. & Duffy, J.E. (2010). Sponge host characteristics shape the community structure of their shrimp associates. *Mar. Ecol. Prog. Ser.*, 407, 1–12.
- Hultgren, K.M. & Duffy, J.E. (2011). Multi-locus phylogeny of sponge-dwelling snapping shrimp (Caridea: Alpheidae: *Synalpheus*) supports morphology-based species concepts. *J. Crustacean Biol.*, 31, 352–360.
- Hultgren, K.M. & Duffy, J.E. (2012). Phylogenetic community ecology and the role of social dominance in sponge-dwelling shrimp. *Ecol. Lett.*, 15, 704–713.
- Hultgren, K.M., Hurt, C. & Anker, A. (2014). Phylogenetic relationships within the snapping shrimp genus *Synalpheus* (Decapoda: Alpheidae). *Mol. Phylogenet. Evol.*, 77, 116–125.
- Hultgren, K.M., Duffy, J.E. & Rubenstein, D.R. (2017). Sociality in snapping shrimps. In: *Comparative Social Evolution* (eds Rubenstein, D.R. & Abbot, P.). Cambridge University Press, Cambridge, UK, pp. 224–249.
- Jarvis, J.U.M., O'Riain, M.J., Bennett, N.C. & Sherman, P.W. (1994). Mammalian eusociality – a family affair. *Trends Ecol. Evol.*, 9, 47–51.
- Jetz, W. & Rubenstein, D.R. (2011). Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Curr. Biol.*, 21, 72–78.
- Johnson, K.P., Bush, S.E. & Clayton, D.H. (2005). Correlated evolution of host and parasite body size: tests of Harrison's Rule using birds and lice. *Evol.*, 59, 1744–1753.
- Johnson, B.R., Borowiec, M.L., Chiu, J.C., Lee, E.K., Atallah, J. & Ward, P.S. (2013). Phylogenomics resolves evolutionary relationships among ants, bees, and wasps. *Curr. Biol.*, 23, 2058–2062.
- Kapheim, K.M., Nonacs, P., Smith, A.R., Wayne, R.K. & Wcislo, W.T. (2015). Kinship, parental manipulation and evolutionary origins of eusociality. *Proc. R. Soc. B-Biol. Sci.*, 282, 20142886.
- Kass, R.E. & Raftery, A.E. (1995). Bayes factors. *J. Am. Stat. Assoc.*, 90, 773–795.
- Koenig, W.D., Pitelka, F.A., Carmen, W.J., Mumme, R.L. & Stanback, M.T. (1992). The evolution of delayed dispersal in cooperative breeders. *Q. Rev. Biol.*, 67, 111–150.
- LaJeunesse, T.C., Pettay, D.T., Sampayo, E.M., Phongsuwan, N., Brown, B., Obura, D.O. et al. (2010). Long-standing environmental conditions, geographic isolation and host–symbiont specificity influence the relative ecological dominance and genetic diversification of coral endosymbionts in the genus *Symbiodinium*. *J. Biogeogr.*, 37, 785–800.
- Lukas, D. & Clutton-Brock, T. (2017). Climate and the distribution of cooperative breeding in mammals. *Roy. Soc. Open Sci.*, 4, 160897.
- Macdonald, K.S., Rios, 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.
- Pagel, M. (1994). Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc. R. Soc. B-Biol. Sci.*, 255, 37–45.
- Pagel, M. & Meade, A. (2006). Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *Am. Nat.*, 167, 808–825.
- Poisot, T., Bever, J.D., Nemri, A., Thrall, P.H. & Hochberg, M.E. (2011). A conceptual framework for the evolution of ecological specialisation. *Ecol. Lett.*, 14, 841–851.
- Rubenstein, D.R. & Abbot, P. (2017). Social synthesis: opportunities for comparative social evolution. In: *Comparative Social Evolution* (eds Rubenstein, D.R. & Abbot, P.). Cambridge University Press, Cambridge, pp. 427–452.
- Rubenstein, D.R. & Lovette, I.J. (2007). Temporal environmental variability drives the evolution of cooperative breeding in birds. *Curr. Biol.*, 17, 1414–1419.
- 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. Resour.*, 8, 890–894.
- Sanderson, M.J. (2003). r8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. *Bioinformatics*, 19, 301–302.
- Schemske, D.W. (1982). Ecological correlates of a neotropical mutualism: ant assemblages at *Costus* extrafloral nectaries. *Ecology*, 63, 932–941.
- Settepani, V., Schou, M.F., Greve, M., Grinsted, L., Bechsgaard, J. & Bilde, T. (2017). Evolution of sociality in spiders leads to depleted genomic diversity at both population and species level. *Mol. Ecol.*, 26, 4197–4210.
- Sheehan, M.J., Botero, C.A., Hendry, T.A., Sedio, B.E., Jandt, J.M., Weiner, S. et al. (2015). Different axes of environmental variation explain the presence vs. extent of cooperative nest founding associations in *Polistes* paper wasps. *Ecol. Lett.*, 18, 1057–1067.
- Shen, S.F., Emlen, S.T., Koenig, W.D. & Rubenstein, D.R. (2017). The ecology of cooperative breeding behaviour. *Ecol. Lett.*, 20, 708–720.
- Sun, S.-J., Rubenstein, D.R., Chen, B.-F., Chan, S.-F., Liu, J.-N., Liu, M. et al. (2014). Climate-mediated cooperation promotes niche expansion in burying beetles. *eLife*, 3, e02440.

- Toth, E. & Duffy, J.E. (2008). Influence of sociality on allometric growth and morphological differentiation in sponge-dwelling alpheid shrimp. *Biol. J. Linn. Soc.*, 94, 527–540.
- Wilson, E.O. (1975). *Sociobiology: The New Synthesis*. Belknap Press of Harvard University Press, Cambridge.
- Wilson, E.O. (2012). *The Social Conquest of Earth*. WW Norton & Company, New York and London.
- Wilson, E.O. & Hölldobler, B. (2005). Eusociality: origin and consequences. *Proc. Natl Acad. Sci. USA*, 102, 13367–13371.

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