Journal of Heredity, 2022, **113**, 552–562
https://doi.org/10.1093/jhered/esac035
Advance access publication 3 August 2022
Original Article

Original Article

Demographic Inference Provides Insights into the Extirpation and Ecological Dominance of Eusocial Snapping Shrimps

Solomon T.C. Chak[1,2,3,*], Stephen E. Harris[1,4,*], Kristin M. Hultgren[5], J. Emmett Duffy[6], Dustin R. Rubenstein[1]

[1]Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY, United States,
[2]Department of Biological Sciences, New Jersey Institute of Technology, Newark, NJ, United States,
[3]Department of Biological Sciences, SUNY College at Old Westbury, Old Westbury, NY, United States,
[4]Biology Department, SUNY Purchase College, Purchase, NY, United States,
[5]Biology Department, Seattle University, Seattle, WA, United States,
[6]Tennenbaum Marine Observatories Network, Smithsonian Institution, Edgewater, MD, United States

[*]These authors contributed equally to this manuscript.
Address correpondence to S.T.C. Chak at the address above, or e-mail: chakt@oldwestbury.edu.
Address correpondence to S.E. Harris at the address above, or e-mail: stephen.harris@purchase.edu.

Corresponding Editor: Jose Lopez

Abstract

Although eusocial animals often achieve ecological dominance in the ecosystems where they occur, many populations are unstable, resulting in local extinction. Both patterns may be linked to the characteristic demography of eusocial species—high reproductive skew and reproductive division of labor support stable effective population sizes that make eusocial groups more competitive in some species, but also lower effective population sizes that increase susceptibility to population collapse in others. Here, we examine the relationship between demography and social organization in *Synalpheus* snapping shrimps, a group in which eusociality has evolved recently and repeatedly. We show using coalescent demographic modeling that eusocial species have had lower but more stable effective population sizes across 100,000 generations. Our results are consistent with the idea that stable population sizes may enable competitive dominance in eusocial shrimps, but they also suggest that recent population declines are likely caused by eusocial shrimps' heightened sensitivity to environmental changes, perhaps as a result of their low effective population sizes and localized dispersal. Thus, although the unique life histories and demography of eusocial shrimps have likely contributed to their persistence and ecological dominance over evolutionary time scales, these social traits may also make them vulnerable to contemporary environmental change.

Key words: crustacean, ddRAD, effective population size, eusociality, historical demography, MOMI2

Eusocial species are often the most abundant members of their community (Wilson 1971, 2012). Their ability to outcompete conspecifics, expand their niches, and assert their ecological dominance over non-eusocial species may be due in part to their ability to cooperate and form complex societies, an idea referred to as the "social conquest hypothesis" (Wilson 2012; Sun *et al*. 2014). Wilson (1987) proposed several population-level qualities of life history and demography that may contribute to the ecological success of eusocial ants and their persistence over evolutionary time. Since all of the more than 13,000 species of ants are eusocial (Holldobler and Wilson 1990), testing these ideas in a comparative framework has been challenging. Moreover, whether these demographic characteristics are shared with other eusocial organisms that exhibit various forms of social complexity and ecological success remains unclear. Although a few comparative studies have examined whether highly social populations and species have been able to expand their ecological niches (Brooks *et al*. 2017; Majer *et al*. 2018) and geographic ranges (Lin *et al*. 2019) relative to nonsocial ones, the specific life history and demographic characteristics that enable eusocial species to sustain their population densities over long periods of time remain largely unexplored.

Social conquest and ecological dominance may be facilitated or hindered by several life history characteristics specific to eusocial species (Wilson 1987). First, eusocial species exhibit a reproductive division of labor in which only a small subset of the population breeds while the rest of the population are workers that do not breed, but instead cooperatively defend and support the colony. Because of this reproductive division of labor within eusocial societies, the number of reproductives in a population may remain relatively stable

Received November 8, 2021; Accepted July 27, 2022

regardless of any fluctuation in the worker population size, resulting both in high reproductive skew and a more stable N_e over time (Wilson 1963; Crozier 1979). Second, the ability to cooperatively defend and maintain a stable domicile (Wilson 1987) may further buffer the breeding individuals—and indeed the entire group—from environmental fluctuation, also resulting in more stable N_e over time.

While eusocial species may exhibit more stable populations than non-eusocial species, their high reproductive skew may also lead to a reduction in effective population size (N_e) (Romiguier *et al.* 2014; Hasselmann *et al.* 2015) because the breeding population (reflected by N_e) is constrained to mainly a single or few reproductive individuals (i.e. queens). Reduced effective population size can lower the efficacy of purifying selection, reduce heterozygosity and allows for the accumulation of deleterious alleles due to drift, and altogether increase the risk of extinction (Kimura 1983; Lynch *et al.* 1995). In addition, inbreeding within social species can further reduce N_e (Charlesworth *et al.* 2003; Charlesworth 2009) and render some lineages unstable, resulting in local extinction and even the extinction of some lineages (i.e. the evolutionary dead-end hypothesis) (Bilde *et al.* 2005; Bilde and Lubin 2011; Settepani *et al.* 2017). For example, lineages of social spiders have undergone repeated origins and extinctions, likely due to biased sex ratios and a lack of premating dispersal, which lead to inbreeding, reduced N_e, and the depletion of genome-wide genetic diversity (Agnarsson *et al.* 2006; Aviles and Purcell 2012; Settepani *et al.* 2017). Indeed, inbreeding that generates low genetic diversity and the potential for colony collapse (Keller and Waller 2002)—often in the face of environmental fluctuation—is surprisingly common in other primitively eusocial species like wood-dwelling termites, thrips, spider mites, and even naked mole rats (reviewed in Aviles and Purcell 2012). Thus, conflicting empirical evidence from insects leads to a paradox in the role that demography plays in social evolution: reproductive division of labor and protection of female reproductives by workers in eusocial species lead to low but stable N_e, whereas reduced N_e in eusocial species may also lead to reduced genome-wide genetic diversity and long-term population instability.

Testing the relative importance of these contrasting demographic influences on population stability in eusocial species can be done using coalescent-based methods that infer historical demography. Historical expansions or contractions in population size, as well as population structure and gene flow, leave a measurable signal on the genetic diversity of contemporary populations, which allows for the quantification of the demographic process based on the site frequency spectrum (SFS), a measure of allele frequencies across the genome that can be generated from large-scale sequencing. The effects of demographic processes on the SFS are well studied and have been tested across a range of taxa (Braverman *et al.* 1995; Bustamante *et al.* 2001; Nielsen 2005). Demographic inference is commonly made using a maximum composite likelihood framework that fits the observed SFS to the expected SFS computed under simulated demographic histories (Bustamante *et al.* 2001; Gutenkunst *et al.* 2009; Lukic and Hey 2012; Kamm *et al.* 2017, 2019; Xue and Hickerson 2017). Recent studies have also begun modeling comparative demographic processes across multiple taxa simultaneously (Xue and Hickerson 2017; Barratt *et al.* 2018; Potter *et al.* 2018; Penalba *et al.* 2019; Rincon-Sandoval *et al.* 2019), including eusocial bees (Lozier 2014) and social spiders (Settepani *et al.* 2017). These and other studies examine relative patterns of N_e change through time, rather than simply comparing absolute estimates at specific time points (Burgarella *et al.* 2015; Crawford *et al.* 2017; Lynch *et al.* 2017; Baeza *et al.* 2019; Fages *et al.* 2019; Hotaling *et al.* 2019; Titus *et al.* 2019; Vendrami *et al.* 2019; Bertola *et al.* 2020; Bolívar-Leguizamón *et al.* 2020), an approach that would enable us to test alternative demographic scenarios in eusocial lineages in a phylogenetically informed context. Moreover, the broad use of coalescent-based methods has shown their robustness as a population genetic tool and can accurately select models and estimate parameters using as few as 3 individuals and 10,000 to 50,000 single-nucleotide polymorphism (SNP) loci (Robinson *et al.* 2014; Nunziata and Weisrock 2018). Therefore, it is now feasible to use a multitaxa comparative demographic framework to test long-standing hypotheses underlying how population dynamics influence the ecological consequences of eusociality.

Here, we use a group of socially diverse, sponge-dwelling snapping shrimps in the genus *Synalpheus* to explore the demographic consequences of eusociality and to address whether historical N_e supports a model of demographic stability or instability in eusocial species. *Synalpheus* shrimps in the West Atlantic *gambarelloides* group represent a relatively young lineage that radiated between approximately 5 and 7 Mya (Morrison *et al.* 2004), yet eusociality has evolved independently at least 4 times within this group from pair-forming ancestors (Hultgren *et al.* 2017). Species in this clade exhibit a variety of forms of social organization, ranging from pair-living, to communal breeding (multiple, unrelated mating pairs in the same sponge with mostly equal or slightly male-biased adult sex ratios), to eusociality (1 or a few queens and a larger number of related, non-reproductive workers of both sexes) (Chak et al. 2015a, 2015b; Chak and Duffy 2017; Hultgren *et al.* 2017). Eusocial shrimps exhibit life history traits and behaviors consistent with the classical definition of eusociality (Michener 1969; Wilson 1971), including overlapping generations, reproductive division of labor, and cooperative care of young (Duffy 1996; Duffy *et al.* 2002). In addition, eusociality in snapping shrimps likely represents an early stage of eusocial evolution because workers are not sterile (Chak et al. 2015a, 2015b). Unlike haplodiploid Hymenoptera, *Synalpheus* shrimps are diploid, similar to termites and mole rats (Duffy 1993, 1996), and eusocial species have extremely large and repetitive genomes likely the result of their demographic histories (Chak et al. 2020, 2021). All eusocial *Synalpheus* species have crawling larvae that remain in the natal sponge, in contrast to all but 1 non-eusocial species that have swimming larvae that can disperse from the natal sponge in the water column (Dobkin 1965, 1967; Duffy and Macdonald 2010; Hultgren *et al.* 2021). Despite strong natal philopatry, there is no genetic evidence of inbreeding in *Synalpheus* (Duffy 2003) and relatedness among individuals in eusocial colonies is high but variable (Rubenstein and Duffy, unpubl data). Although little is known about the mating biology of *Synalpheus* (Hultgren *et al.* 2017), eusocial shrimp appear to avoid inbreeding because of field observation of premating dispersal to nearby vacant sponges (Tóth and Bauer 2007) and their ability to distinguish nestmates from non-nestmates (Duffy 1996; Duffy *et al.* 2002).

There are reports of both ecological dominance and demographic instability in eusocial *Synalpheus* species. The best available data that are consistent with the ecological dominance of eusocial species over non-eusocial species comes from a field collection of rubble-associated sponges between 1990 and 2004 in Carrie Bow Cay, Belize (11 collecting trips and 139 field days across 14 years) (Macdonald *et al.* 2006). This longitudinal dataset looked at sponge occupancy and the relative abundance of 20 *Synalpheus* species (with >2,000 individuals), the full diversity of *Synalpheus* shrimps on this reef. The 4 eusocial shrimp species in Belize initially contributed to >65% of the quantitative samples, and eusocial species were 17 times as abundant as non-eusocial species (Macdonald *et al.* 2006). Phylogenetically controlled comparative analyses showed that eusocial shrimp species in Belize showed several characteristics of ecological dominance over non-eusocial species in the sampled host sponges. Eusocial species 1) had a higher average abundance in sponges, 2) occupied a larger fraction of individual sponges, and 3) had a wider host range of sponge species (Duffy and Macdonald 2010), even after controlling for the effect of body size. Thus, for close to 2 decades, eusocial *Synalpheus* dominated non-eusocial species among rubble-associated sponges in the vicinity of Carrie Bow Cay, Belize.

Despite their ecological success, however, 3 of the 4 eusocial species at Carrie Bow Cay had become locally extinct by 2012 (Duffy *et al.* 2013). In addition, declines have been seen in 2 eusocial species in Jamaica, with an increase in the number of queenless colonies (Duffy *et al.* 2013), and 1 eusocial species in Panama (Hultgren *et al.* 2017). In these same reefs, pair-living and communal breeding *Synalpheus* species appear to at least be maintaining healthy populations, if not increasing in abundance (Duffy *et al.* 2013). Therefore, despite evidence of sustained ecological success, eusocial *Synalpheus* shrimps have seen recent population declines over much of their range at the same time non-eusocial *Synalpheus* species have remained stable or increased in abundance. These recent population declines could be a snapshot of cycles of extinction–recolonization events that reflect the demographic instability of eusocial species, as has been the case in spiders (Agnarsson *et al.* 2006; Aviles and Purcell 2012; Settepani *et al.* 2017). Alternatively, these declines could also be due to recent environmental changes across the Caribbean (Goldenberg *et al.* 2001; Gledhill *et al.* 2008; Klotzbach 2011; Chollett *et al.* 2012; Palanisamy *et al.* 2012; Rioja-Nieto and Álvarez-Filip 2019), including declines in sponge communities (Smith *et al.* 2016). These environmental changes may impact eusocial species more strongly than non-eusocial species because eusocial species have limited dispersal abilities and may be unable to recolonize extirpated populations. Our historical collection of a small number of eusocial and non-eusocial colonies from these localities provides the only opportunity to use genetic data to infer the historical demographies in some of these now locally extinct species.

To explore the relationship between demography and eusociality, we generated genome-wide SNP data using double digest restriction-site-associated DNA sequencing (ddRADseq) and performed demographic inference to compare long-term demographic patterns in 4 eusocial species from each of the 4 independently evolved eusocial lineages and 8 non-eusocial congeners (including 5 communal breeding and 3 pair-forming species). Using inferred historical N_e, we then calculated average N_e over multiple time points, assuming the same mutation and recombination rates across species (Schraiber and Akey 2015), and 3 population stability metrics (see Material and methods). Ultimately, linking demography to social evolution through population genetic approaches (Rubenstein *et al.* 2019) not only has the potential to uncover the demographic factors that may have enabled some eusocial species to come to dominate the ecosystems in which they occur, but it may also help explain why some eusocial species or lineages go extinct over both evolutionary and ecological time scales. Here, we show that eusocial species had lower but more stable effective population sizes across 100,000 generations than non-eusocial species. These results suggest that stable population sizes may enable competitive dominance in eusocial shrimps and likely contribute to their persistence and ecological success over evolutionary time scales, but their low effective population sizes and localized dispersal may also make eusocial species vulnerable to contemporary environmental change.

Materials and methods

Sampling and study species

We sampled 12 species of *Synalpheus* snapping shrimps from 4 sites in the Caribbean (Belize, Barbados, Jamaica, and Panama) between 2004 and 2012 (Table 1, Supplementary Table S1, and Fig. 1). A detailed collection protocol has been reported previously (Macdonald *et al.* 2006). For each species, we sampled 7 to 8 females from the same site with eggs or visible ovarian development to ensure that we were sampling breeding individuals. We sampled females from different sponges whenever possible. Since each sponge represents a single colony for eusocial species, sampling from different sponges ensured that we had a more complete representation at each site. For the demographic inference to be comparable across species, we only used individuals collected within a 5-year period. Due to time constraint, and the fact that several species have gone locally extinct (Duffy *et al.* 2013), we were limited to 12 species and 7 to 8 females from different colonies, enough for confident demographic inference (Robinson *et al.* 2014; Nunziata and Weisrock 2018). Despite this limitation, the sampled species included 3 pair-forming, 5 communal breeding, and 4 eusocial species. The 4 eusocial species included 1 species from each of the lineages that independently evolved eusociality in the genus. Two eusocial species (*S. brooksi* and *S. chacei*) were from Belize where, before the recent population decline, they dominated their habitat over non-eusocial species based on abundance, sponge occupancy, and host ranges (Duffy and Macdonald 2010). Local population extinctions and declines were observed from field surveys for the eusocial species, *S. chacei* from Belize, *S. duffyi* from Jamaica, and *S. rathbunae* from Panama (Duffy *et al.* 2013). Our samples included 8 non-eusocial species that showed stable or increasing populations from the same 3 sites (Duffy *et al.* 2013).

We extracted genomic DNA using several walking legs from alcohol-preserved specimens and followed the protocol in Peterson *et al.* (2012) for ddRADseq (see Supplementary Material). We used *Stacks v2.1* (Rochette *et al.* 2019) to demultiplex and clean raw reads (process_radtags: reads with phred score <10 were discarded) and perform de novo mapping of paired-end reads (denovo_map.pl with the parameters $T = 6$, $m = 3$, $M = 3$, and $n = 2$). We adjusted the minimum proportion of individuals in a population (i.e. a species, since

Table 1. Population genetic statistics for each *Synalpheus* species.

Synalpheus species	Social organization	Collection country	Sample size	H_{obs} (all sites)	H_{obs} (variant sites)	Inbreeding coefficient (F_{IS})	Mean kinship coefficient
agelas	Pair	Jamaica	8	0.22	0.44	0.29	−2.05
bousfieldi	Pair	Belize	8	0.20	0.50	0.32	−2.74
longicarpus small	Pair	Belize	8	0.22	0.60	0.12	−1.70
carpenteri	Communal	Jamaica	8	0.23	0.45	0.30	−1.46
dardeaui	Communal	Belize	9	0.23	0.34	0.26	−0.53
herricki	Communal	Belize	8	0.22	0.67	0.14	−0.90
idios	Communal	Jamaica	7	0.18	0.19	0.54	−0.71
yano	Communal	Barbados	8	0.20	0.28	0.45	−0.93
brooksi	Eusocial	Barbados	8	0.19	0.38	0.13	−0.14
chacei	Eusocial	Panama	8	0.20	0.31	0.16	−0.22
duffyi	Eusocial	Panama	8	0.22	0.45	0.21	−1.19
rathbunae	Eusocial	Panama	8	0.26	0.45	0.14	−0.26

Mean individual observed heterozygosity (H_{obs}) is the percentage of heterozygous sites across all sites or variant sites only. Pair: pair-living, communal: communal breeding. Kinship coefficients with negative values indicate unrelated relationships.

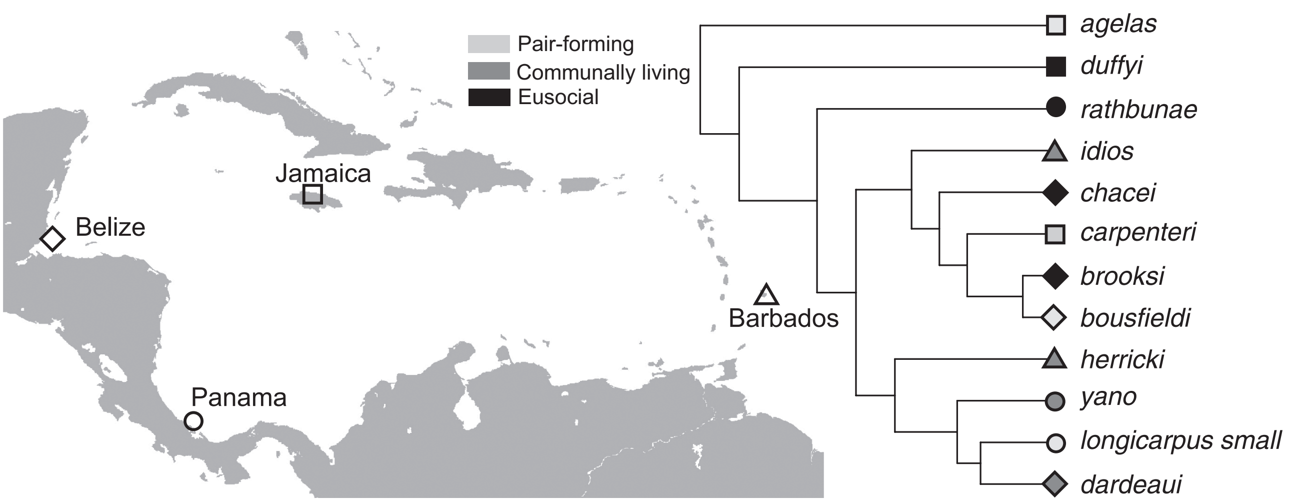

Fig. 1. Collection sites and evolutionary relationships among 12 sponge-dwelling snapping shrimps in the genus *Synalpheus* used for comparative demographic inference. Each shape corresponds to a different sampling locality. The color of each shape corresponds to the form of social organization (white: pair-living, gray: communal breeding, and black: eusocial). The map is modified from Wikimedia Commons under CC BY-SA 3.0.

all samples of each were collected from 1 population) required to process a locus for that population (r) to be 0.5 to 0.875 in *populations* in the *Stacks* pipeline to obtain around 20,000 SNPs per species (range = 19,778 to 52,898). We calculated mean individual and site missingness using *VCFtools* v0.1.16 (Danecek *et al.* 2011).

Genetic diversity and kinship

We calculated several statistics to summarize the genetic diversity at the individual level, and to quantify the levels of inbreeding and kinship among females, each from different sponges within the same collection site. First, we estimated observed heterozygosity (H_{obs}) for each sample from *populations* in the *Stacks* pipeline and took the mean H_{obs} for each species. We also calculated H_{obs} based on variant sites only. We calculated the averaged inbreeding coefficient (F) across individuals for each species using *VCFtools* v0.1.16 (Danecek *et al.* 2011). An individual is fully inbred when $F = 1$ and fully outbred when $F = 0$ (Wright 1922). Finally, we used *King* v2.1.6 (Manichaikul *et al.* 2010) to calculate the genome-wide relatedness between each female within a species. We took the mean kinship coefficient between pairs of individuals (1 female per sponge) for each species. For each genetic statistic (mean H_{obs}, F, and mean kinship coefficient), we performed phylogenetic mixed model regressions using the R package *MCMCglmm* v2.29 (Hadfield 2010) to test whether they differed according to the form of social organization (pair-forming vs. communal breeding vs. eusocial) or eusociality (eusocial vs. non-eusocial), while controlling for phylogenetic non-independence between species (see Supplementary Material). We used a Bayesian consensus tree of *Synalpheus* species, constructed with 16S, 18S, and COI sequence data (Chak *et al.* 2017).

Demographic inference

We examined changes in N_e through time by generating confidence intervals around the main features of the model (i.e. relative changes, overall size changes, directionality, and broad patterns in demographic history) through bootstrapping simulated data under the best-model demographic scenario (Gattepaille *et al.* 2013).

Within species, for pairs of individuals that were closer than third-degree-related (>25%, based on kinship coefficients >0.089), we randomly removed 1 individual using *VCFtools* v0.1.16 (Danecek *et al.* 2011). In total, we removed 2 individuals from *S. rathbunae* and 1 individual each from *S. agelas*, *S. carpenteri*, and *S. chacei.* We then extracted 1 random SNP per locus using the script *vcfparser.py* (Silva *et al.* 2018) to generate a vcf file for demographic inference analysis using *MOMI2* v2.1.16 (Kamm *et al.* 2017, 2019), a model-based method that infers demographic parameters by fitting the expected SFS under a set of user-defined parameters to that of the observed data. We used 11,890 to 26,148 SNPs per species (median = 18,175, Supplementary Table S1) for demographic inference. Initial N_e was set at 1e + 6 and maximum N_e at 1e + 21 for all species (see Supplementary Material). We ran 300 random starts to find the model with the highest log-likelihood. We further ran 300 bootstraps, each with 50 random starts to find the model with the highest log-likelihood support.

For comparative purposes, we inferred N_e from T fixed time ranges across G generations for all species. Preliminary analyses showed that estimating N_e at fixed time ranges (e.g. 1 to 20, 21 to 40, 41 to 60, and 61 to 80 thousand generations) gave better model support than estimating N_e at fixed times (e.g. 20, 40, 60, and 80 thousand generations) (Supplementary Fig. S1). To find the best specification of model parameters T (number of time ranges) and G (maximum number of generations), we ran 7 models that differed in T (4, 6, and 8) and G (60, 80, and 100 thousand). We did not estimate N_e changes that were less than 10,000 generations apart because our preliminary analysis showed that the order of magnitude that we can estimate change among the 12 species was about 10,000 generations (see Supplementary Material). For each species, we compared the support for each parameter set using delta AIC (Akaike 1998). The model with delta AIC = 0 had the best support and models with delta AIC < 3 were considered to be equally supported best models.

The model that estimated N_e 4 times across 100,000 generations (i.e. $T = 4$ and $G = 100{,}000$) was most frequently supported across species under the criteria of delta AIC < 3 (Supplementary Table S2). Estimated values of N_e from this model were generally within the 95% confidence interval of the bootstrap estimates (Supplementary Fig. S2), indicating that the patterns were consistent across 300 different subsets of SNPs. Assuming several generations per year, a time scale of roughly 100,000 generations is likely to span most of the Holocene. We ran additional analyses to show that our results remained robust even after removing 2 species that may have less power due to potentially high ancestral effective population sizes (see Supplementary Material). We also conducted a sensitivity analysis by estimating N_e 6, 9, and 10 times across 100,000 generations (despite having lower likelihood scores in these models) to test whether the number of N_e estimates may affect the patterns observed in the comparative analysis below (see Supplementary Material).

Model-free demographic inference methods explore an unrestricted parameter space but require a large number of SNPs (Liu and Fu 2015). We performed a model-free analysis using *Stairway Plot 2* (Liu and Fu 2015, 2020), though with a much smaller subset of 6 species where the number of SNPs was adequate for this analysis, to test whether the results are consistent with those observed in the comparative analysis below (see Supplementary Material).

Phylogenetic comparative analysis

Due to the uncertainty in determining absolute N_e values, we reported on broad demographic trends and relative changes in N_e (Burgarella *et al.* 2015; Crawford *et al.* 2017; Lynch *et al.* 2017; Baeza *et al.* 2019; Fages *et al.* 2019; Hotaling *et al.* 2019; Titus *et al.* 2019; Vendrami *et al.* 2019; Bertola *et al.* 2020; Bolivar-Leguizamon *et al.* 2020). From the best fit model with the highest log-likelihood, we used the N_e values estimated across 10,000 to 100,000 generations for each species. We calculated the average N_e across time (mean N_e), as well as 3 population stability metrics for comparative analyses: 1) the coefficient of variation of N_e across times (CV) to quantify the variation of N_e that is independent of mean N_e, where a smaller value indicates greater population stability; 2) the ratio of minimum N_e to mean N_e (min/mean N_e), where a larger value indicates a less severe population bottleneck, and thus greater population stability; and 3) the number of times that 2 consecutive N_e estimates had less than 1 order of magnitude difference (no. of <1-order change), where a larger value indicates less drastic changes in N_e, and thus greater population stability. We did not include the N_e estimate at time 0 (i.e. the most recent N_e) in our analysis because this estimate was strongly correlated with the initial N_e that we specified in *MOMI2* (data not shown). Further, demographic inference based on ddRAD may not adequately reflect recent population changes (Lozier 2014) unless the sample size per population was very large (>30) (Nunziata and Weisrock 2018; Marandel *et al.* 2020). We used the Shapiro–Wilk's test to check for normality, ultimately log-transforming mean N_e, CV, and min/mean N_e.

We performed phylogenetic mixed model regressions using *MCMCglmm* (Hadfield 2010) as described in Supplementary Material. Briefly, we tested whether the 4 metrics of population size and stability differed according to the form of social organization (pair-forming vs. communal breeding vs. eusocial) or eusociality (eusocial vs. non-eusocial), while controlling for phylogenetic non-independence between species and treating collection site as a random factor. We performed the same analyses using the demographic metrics calculated from the median of 300 bootstraps N_e estimates. We also performed a similar analysis using the eusociality index, which captures the degree of reproductive skew within a group and has been used to measure the level of eusociality in *Synalpheus* and other invertebrates (Keller and Perrin 1995; Duffy and Macdonald 2010). This index makes no a priori assumption of social phenotype, avoiding misclassification of a species' social organization and better capturing the continuum of social diversity among species (Sherman *et al.* 1995). The eusociality index was calculated as $E = 1 - ((2 \times \text{NOF})/\text{CS})$, where CS is the colony size and hence the total number of individuals in a sponge and NOF is the number of ovigerous females in a sponge based on data from Chak *et al.* (2017). Therefore, species with high values of the eusociality index have greater reproductive skew.

Results

Genetic diversity and kinship

We generated >312 million paired-end reads with a median of 2.7 million reads per sample (i.e. 7 to 8 breeding females for each of 12 *Synalpheus* species). De novo mapping using *Stacks* generated 19,788 to 52,898 SNPs per species (median = 24,307, Supplementary Tables S1 and S3; SRA accession: SAMN14351547 to SAMN14351641). Mean H_{obs} based on all sites or just variant sites did not differ among species exhibiting the 3 forms of social organization (pMCMC > 0.19, Supplementary Fig. S3, Supplementary Tables S4 and S5): the percentage of heterozygous sites across all sites ranged from 0.19% to 0.23% across species, which is similar to that observed in nonsocial spiders (Settepani *et al.* 2017) and other non-*Synalpheus* shrimps (Yuan *et al.* 2018). Moreover, there were low levels of inbreeding in all species: the inbreeding coefficients (F) were positive and ranged from 0.12 to 0.54 across species (Supplementary Fig. S3, Table 1). Although some social species are highly inbred due to a lack of premating dispersal (Bilde and Lubin 2011), eusocial *Synalpheus* species were instead significantly more outbred than communal breeding species (pMCMC = 0.032), but only marginally more outbred than non-eusocial (pair-living and communal breeding combined) species (pMCMC = 0.062) (Supplementary Table S4). Finally, mean average kinship coefficients were negative for all species, meaning that breeding females across sponges were unrelated to each other (Supplementary Fig. S3, Table 1). However, kinship coefficients were significantly higher in eusocial species than in pair-forming species and non-eusocial species (pMCMC = 0.0003 and 0.02, respectively; Supplementary Table S4).

Demographic inference and stability

We found that N_e values were generally higher and more variable through time in pair-living and communal breeding species, whereas N_e values were lower but more stable through time in eusocial species (Fig. 2). The relative trends of historic N_e were calculated using 3 population stability metrics using inferred historical N_e from the best fit model with the highest log-likelihood. We then used phylogenetic mixed models implemented in *MCMCglmm* (Hadfield 2010) to compare these demographic metrics using both a continuous measure of eusociality (eusociality index) and across discrete social categories (Chak *et al.* 2017). Importantly, the eusociality index captures the reproductive skew within a group (Keller and Perrin 1995; Sherman *et al.* 1995; Duffy and Macdonald 2010), making no a priori assumption of social phenotype. Our results confirmed the above patterns in 3 of 4 metrics of population size and stability: as the eusociality index increased (hence stronger reproductive skew), mean N_e decreased, CV decreased, and min/mean N_e increased, though no. <1-order changes did not vary (pMCMC = 0.018, 0.031, 0.025, and 0.63, respectively, Fig. 3; Supplementary Table S5). We observed qualitatively similar results using discrete social categories, though the limited number of species in each social category likely contributed to the marginal levels of statistical significance. Specifically, eusocial species had significantly lower mean N_e than non-eusocial species (pMCMC = 0.021), as well as marginally lower CV, higher min/mean N_e, and higher no. of <1-order difference in N_e values than non-eusocial species (pMCMC = 0.055, 0.058, and 0.076, respectively, Fig. 4; Supplementary Table S5). Analyses using the median demographic metrics across bootstrap estimates showed similar trends, but lacked statistical significance (Supplementary Fig. S4), likely because much smaller subsets of SNPs were used in these analyses. Analyses based on models with more than 4 N_e estimates (6, 8, and 10 estimates) resulted in the same, though nonsignificant, trends between demographic metrics and eusociality index (Supplementary Fig. S8). While these models had lower likelihood support than the models with 4 N_e estimates, their results suggest that the pattern observed is not limited to models with 4 N_e estimates. Finally, we also found the same, though nonsignificant, trends when calculating continuous N_e in *Stairway Plot 2* using the 6 *Synalpheus* species with large enough SNP datasets (Supplementary Figs. S9 and S10). Together, our results suggest that eusocial shrimp species have lower but more stable N_e through time than their non-eusocial relatives.

Discussion

Cooperation among individuals of the same species leading to the formation of complex societies is thought to have enabled eusocial animals to become ecologically dominant in the areas where they occur, sometimes comprising more than half of the biomass in a given terrestrial ecosystem (Wilson

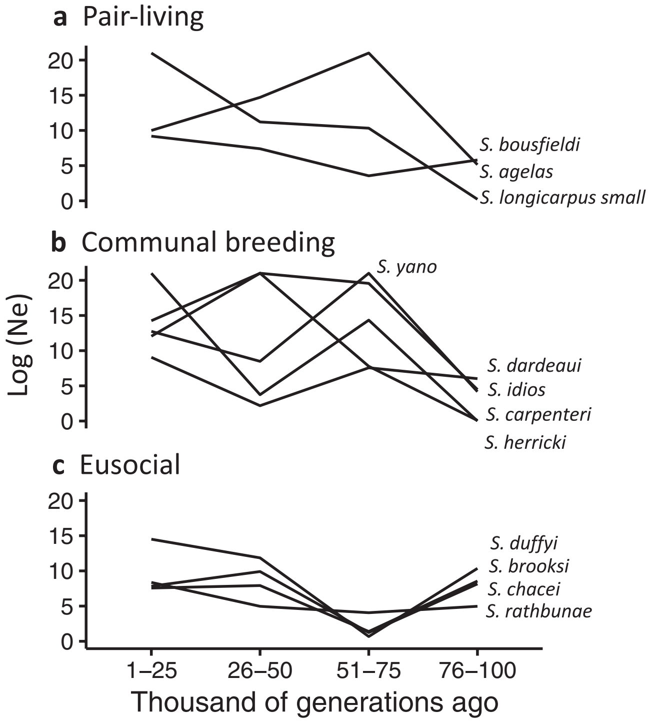

Fig. 2. Best model estimates of N_e across 100,000 generations in 12 *Synalpheus* species exhibiting different forms of social organization (a: pair-living, b: communal breeding, c: eusocial). Each line represents N_e for a species, with species label on the right. Bootstrap estimates are shown in Supplementary Fig. S2.

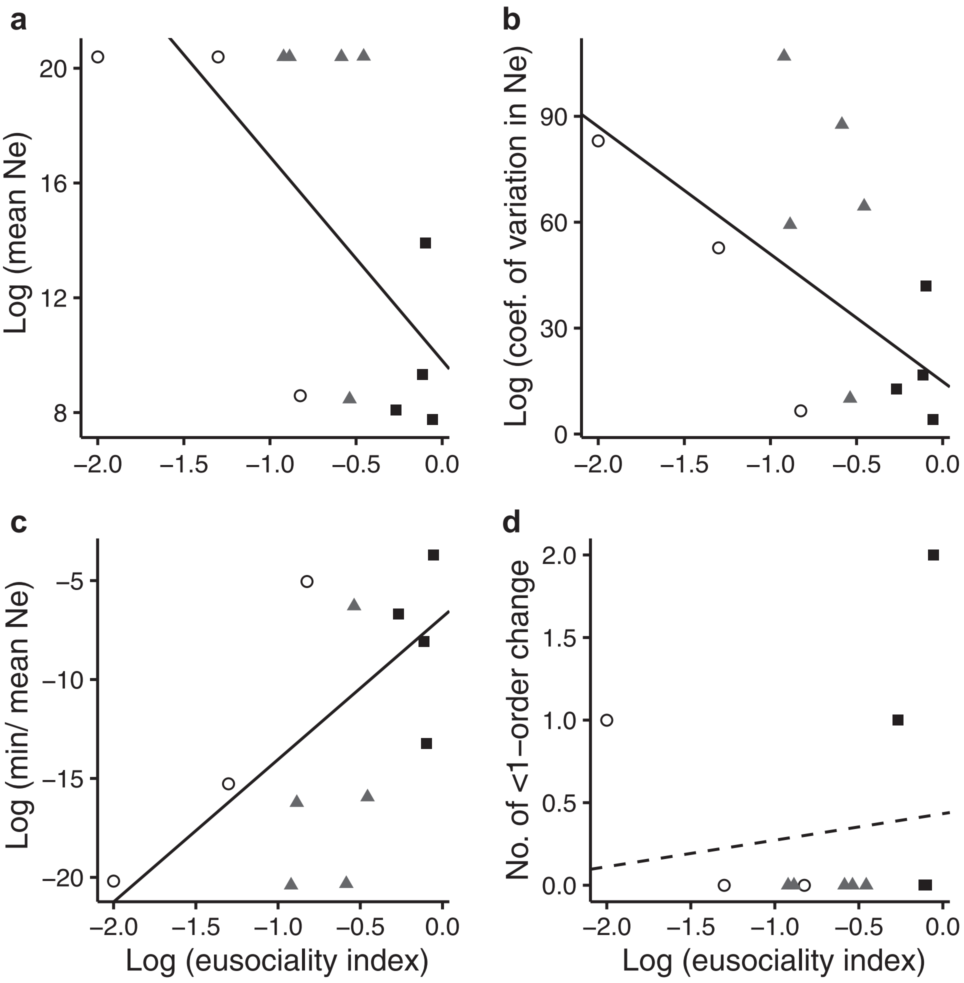

Fig. 3. Relationships between the eusociality index and metrics of population size and stability in 12 *Synalpheus* species: (a) mean effective population size (N_e) across time, (b) coefficient of variation in N_e, (c) min/mean N_e, and (d) no. of <1-order change in N_e. Symbols represent raw values: open circles = pair-forming species, gray triangles = communal breeding species, dark squares = eusocial species. Solid and dashed lines represent significant and nonsignificant regression slopes predicted using Bayesian phylogenetic mixed models, respectively. Eusocial species have higher reproductive skew and higher values of the eusociality index than non-eusocial species.

2012). Although the peculiar demographic characteristics of eusocial societies such as low effective population size have been suggested to both help and hinder their ecological success, empirical tests of these ideas have largely been lacking. Using historical demographic inference to determine whether eusocial species are more or less demographically stable than their non-eusocial relatives (Wilson 1987), we examined the relationship between demography and eusociality in a socially diverse clade of *Synalpheus* snapping shrimps where eusocial species are known to be ecologically dominant over non-eusocial species in their sponge hosts (Macdonald *et al.* 2006; Duffy and Macdonald 2010). We found that eusocial *Synalpheus* snapping shrimps, across 4 independently evolved eusocial lineages, consistently had lower but more stable N_e through time than non-eusocial species. Although our analysis cannot infer recent changes in N_e and N_e change at short evolutionary time scales (e.g. Bechsgaard *et al.* 2019), the observed long-term population stability in eusocial shrimp species supports the idea that cooperation may help eusocial species to better defend and maintain their domiciles. Furthermore, Wilson (1987) argued that a critical criterion for ecological success was population density that could be sustained for long periods of time. Our results are consistent with this idea, adding to field observations demonstrating that, for close to 2 decades, eusocial *Synalpheus* were more ecologically dominant than their non-eusocial relatives in terms of relative abundance, sponge occupancy, and host breadth in rubble-associated sponges in a Belizean reef (Macdonald *et al.* 2006; Duffy and Macdonald 2010).

The lower N_e in eusocial shrimp species is consistent with results from Romiguier *et al.* (2014), who found evidence supporting reduced N_e in eusocial insects, including low genetic polymorphisms and high nonsynonymous/synonymous (d*N*/d*S*) ratios that are more in line with vertebrates than other insects. In *Synalpheus*, mitochondrial genomes also show increased synonymous substitution rates and high d*N*/d*S* ratios (Chak *et al.* 2020). Therefore, our results are similar to those in eusocial insects showing that reproductive division of labor and high reproductive skew can lead to lower N_e in eusocial species (Romiguier *et al.* 2014; Hasselmann *et al.* 2015). Although species with low mean N_e may be more susceptible to extinction due to reductions in genetic diversity and high genetic load (Newman and Pilson 1997), this does

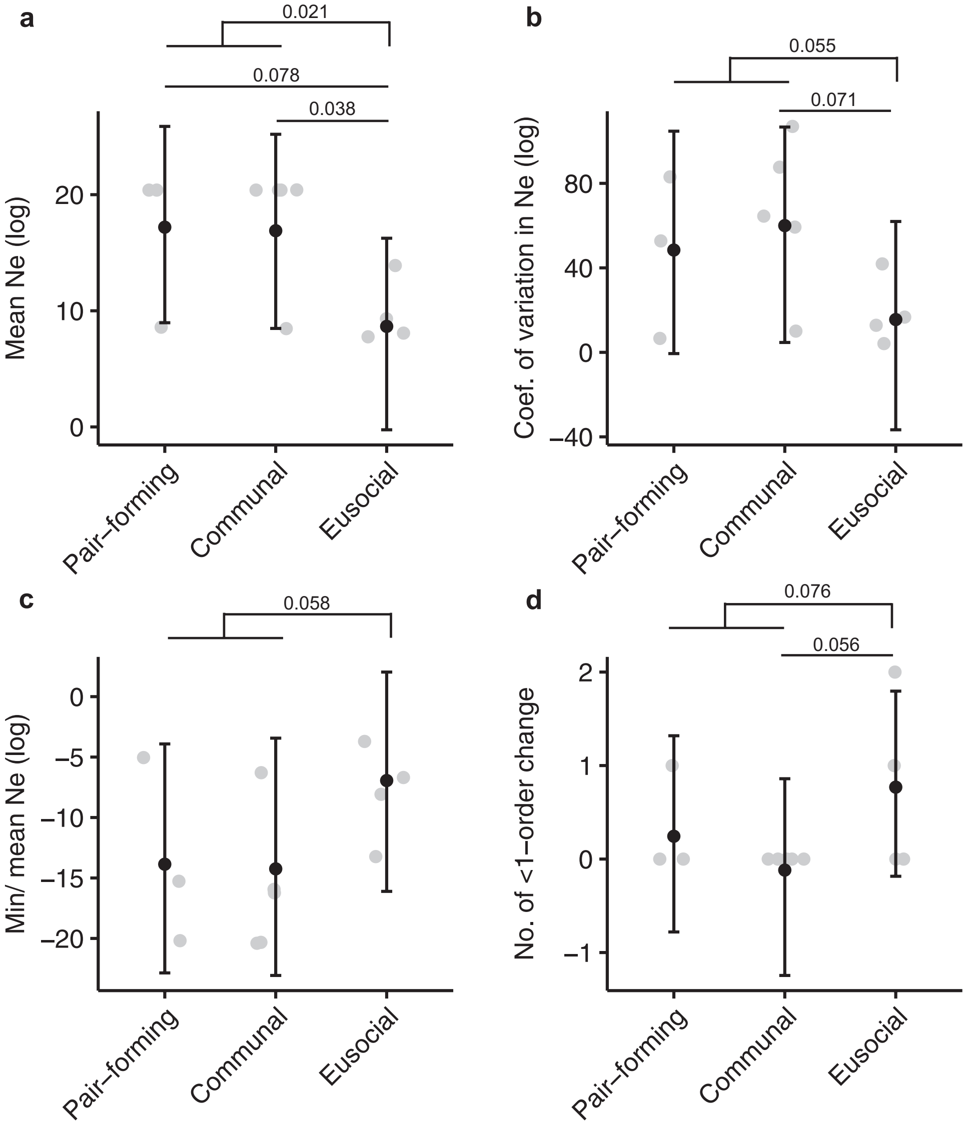

Fig. 4. Metrics of population size and stability across 12 *Synalpheus* shrimp species exhibiting different forms of social organization. Eusocial species have lower mean effective population size (N_e) across time (a), but more stable values of N_e across generation time as indicated by lower CV (b), higher min/mean N_e (c), and higher no. <1-order change (d). Gray dots are raw values, black dots are posterior mean predicted using Bayesian phylogenetic mixed model, bars are the 95% posterior distributions, and the numbers show pMCMC values, which are twice the probability that the posterior distribution of the difference is above or below zero.

not seem to be the case in eusocial snapping shrimps, at least in the period where we can confidently infer effective population sizes. In eusocial species, the reproductive division of labor and cooperative defense may buffer the breeding individuals from environmental fluctuation, hence stabilizing N_e; this could alleviate the detrimental effects of having low N_e in eusocial species and reduce the risk of extinction. Also, eusocial *Synalpheus* species may exhibit premating dispersal (Tóth and Bauer 2007) and inbreeding avoidance (Duffy 1996; Duffy *et al.* 2002), hence do not appear to suffer from inbreeding like some social species that lack premating dispersal (Bilde and Lubin 2011; Aviles and Purcell 2012). Furthermore, our demographic inference assumed constant mutation rates across species, but recent analyses based on mitochondrial genes in 8 *Synalpheus* species found that eusocial species have lower synonymous substitution rates (Chak *et al.* 2020). Although the pattern in mitochondrial genes may not reflect those in the nuclear genome, assuming a lower mutation rate for eusocial species would further reduce the N_e estimates for eusocial species, hence exaggerating instead of contradicting the pattern of lower N_e in eusocial species observed here.

Moreover, we found no evidence of population bottlenecks, cyclical patterns of expansion, or contractions of N_e in eusocial shrimp species, as found in other primitively eusocial animals (Aviles and Purcell 2012). Instead, eusocial shrimp species appear to be more demographically stable than non-eusocial species, a conclusion that remains robust whether we consider social organization as a categorical or continuous variable. Our results agree with recent ecological models showing that primitively eusocial species have higher reproduction and lower extinction probabilities than solitary nesters (Field and Toyoizumi 2020).

Although eusocial *Synalpheus* are the ecologically dominant shrimp species among their sponge hosts (Macdonald *et al.* 2006; Duffy and Macdonald 2010), eusocial species in Belize, Panama, and Jamaica have either gone locally extinct or declined significantly in abundance in recent years, while non-eusocial species have remained stable or increased in abundance over the same timeframe (Duffy *et al.* 2013). Our findings that eusocial *Synalpheus* species had stable effective population sizes over evolutionary time, as well as the absence of any evidence of population bottlenecks or cyclical patterns of expansion or contractions of N_e, together suggest that these recent, widespread population declines are unprecedented in the last 100,000 generations, spanning most of the Holocene. The contemporary population declines could instead be due to recent environmental changes across the Caribbean including warming sea surface temperatures (Chollett *et al.* 2012), ocean acidification (Gledhill *et al.* 2008), rising sea levels (Palanisamy *et al.* 2012), increased hurricane activity (Goldenberg *et al.* 2001; Klotzbach 2011), and declines in sponge communities (Smith *et al.* 2016). These changes may impact eusocial species more strongly than non-eusocial species because of their limited ability to disperse. Although our sampling did not allow us to infer about recent demographic changes, our results are consistent with other evidence that eusocial species likely disperse less than non-eusocial species because they have the highest levels of relatedness (Supplementary Fig. S3) across females from different sponges within a local population (collection site). This pattern was also seen previously using allozymes (Duffy 1993) and is strongly supported by life history observations that all eusocial species have crawling larvae that remain in the natal sponge, whereas non-eusocial species have swimming larvae that can disperse from the natal sponge in the water column (Dobkin 1965, 1967; Duffy and Macdonald 2010). Hence, eusocial shrimp species may be less able to disperse and recolonize host sponges after recent population crashes than non-eusocial species. Thus, although eusocial *Synalpheus* species have been ecologically dominant in parts of the Caribbean for decades (Macdonald *et al.* 2006; Duffy and Macdonald 2010) and demographically stable for thousands of years, they appear more susceptible to population collapse and extinction in the face of increased rates of anthropogenic-driven environmental disturbance.

In conclusion, our results suggest that for at least 100,000 generations, spanning thousands of years, eusocial shrimp populations in the Caribbean have been more stable than those of non-eusocial species. This is supported by a signature of lower and more stable N_e in eusocial shrimps compared with non-eusocial species, and no evidence of cyclic population contractions or extinctions in eusocial species that would indicate population instability. Therefore, the long-term demographic stability in eusocial snapping shrimp is likely one of the key factors in promoting their ecological dominance among the community of sponge-dwelling shrimps, an idea that has been proposed but not tested for eusocial insects that have come to dominate much of the terrestrial world. The recent extirpation of ecologically dominant eusocial species at several Caribbean sites presents a sharp contrast to this long-term history, and may be driven by anthropogenic changes in combination with their lower N_e and limited dispersal ability. Thus, the same demographic and life history characteristics of eusocial shrimps that make them successful over evolutionary time scales also render them vulnerable to recent global change. Ultimately, studying changes in demography through time will not only help us to understand the long-term population dynamics of social organisms, it may also provide critical insights into how social species will cope in the face of increasing climate change and habitat loss.

Supplementary material

Supplementary material is available at *Journal of Heredity* online.

Funding

S.T.C.C. was supported by the Simons Foundation via the Life Sciences Research Foundation. S.E.H. was supported by the Frontiers of Science Fellowship at Columbia University. D.R.R. was supported by the US National Science Foundation (IOS-1121435, IOS-1257530, IOS-1439985). This work made use of the high-performance computing resources from Columbia University.

Conflict of interest statement

None declared.

Data availability

Supporting data are available from the Supporting Information. Sequence reads were deposited in NCBI's Sequence Read Archive (accession numbers: SAMN14351547 to SAMN14351641). Additional data is available in Figshare (https://doi.org/10.6084/m9.figshare.15205701.v1).

Authors' contributions

DRR and SEH designed the study. STCC and SEH performed the experiment, conducted analyses, and drafted the manuscript. All authors collected specimens and revised the manuscript.

References

Agnarsson I, Avilés L, Coddington JA, Maddison WP, Funk D. Sociality in Theridiid spiders: repeated origins of an evolutionary dead end. *Evolution*. 2006;60(11):2342–2351.

Akaike H. Information theory and an extension of the maximum likelihood principle. In: Parzen E, Tanabe K, Kitagawa G, editors. *Selected papers of Hirotugu Akaike*. Springer, New York NY; 1998. pp. 199–213.

Aviles L, Purcell J. The evolution of inbred social systems in spiders and other organisms: from short-term gains to long-term evolutionary dead ends? *Adv Study Behav*. 2012;44:99–143.

Baeza JA, Umaña-Castro R, Mejia-Ortiz LM. Historical demography of the Caribbean spiny lobster *Panulirus argus* (Latreille, 1804) (Decapoda: Achelata: Palinuridae) in the Florida Keys, USA inferred using single nucleotide polymorphisms (SNPs). *J Crustac Biol*. 2019;39(4):378–385.

Barratt CD, Bwong BA, Jehle R, Liedtke HC, Nagel P, Onstein RE, Portik DM, Streicher JW, Loader SP. Vanishing refuge? Testing the forest refuge hypothesis in coastal East Africa using genome-wide sequence data for seven amphibians. *Mol Ecol*. 2018;27(21):4289–4308.

Bechsgaard J, Schou MF, Vanthournout B, Hendrickx F, Knudsen B, Settepani V, Schierup MH, Bilde T. Evidence for faster X chromosome evolution in spiders. *Mol Biol Evol*. 2019;36(6):1281–1293.

Bertola LD, Boehm JT, Putman NF, Xue AT, Robinson JD, Harris S, Baldwin CC, Overcast I, Hickerson MJ. Asymmetrical gene flow in five co-distributed syngnathids explained by ocean currents and rafting propensity. *Proc R Soc B Biol Sci*. 2020;287(1926):20200657.

Bilde T, Lubin Y. Group living in spiders: cooperative breeding and coloniality. In: Herberstein ME, editor. *Spider behaviour: flexibility and versatility*. Cambridge (UK): Cambridge University Press; 2011. pp. 275–306.

Bilde T, Lubin Y, Smith D, Schneider JM, Maklakov AA. The transition to social inbred mating systems in spiders: role of inbreeding tolerance in a subsocial predecessor. *Evolution*. 2005;59(1):160–174.

Bolívar-Leguizamón SD, Silveira LF, Derryberry EP, Brumfield RT, Bravo GA. Phylogeography of the Variable Antshrike (*Thamnophilus caerulescens*), a South American passerine distributed along multiple environmental gradients. *Mol Phylogenet Evol*. 2020;148:106810.

Braverman JM, Hudson RR, Kaplan NL, Langley CH, Stephan W. The hitchhiking effect on the site frequency spectrum of DNA polymorphisms. *Genetics*. 1995;140(2):783–796.

Brooks KC, Maia R, Duffy JE, Hultgren KM, Rubenstein DR. Ecological generalism facilitates the evolution of sociality in snapping shrimps. *Ecol Lett*. 2017;20(12):1516–1525.

Burgarella C, Gayral P, Ballenghien M, Bernard A, David P, Jarne P, Correa A, Hurtrez-Bousses S, Escobar J, Galtier N, et al. Molecular evolution of freshwater snails with contrasting mating systems. *Mol Biol Evol*. 2015;32(9):2403–2416.

Bustamante CD, Wakeley J, Sawyer S, Hartl DL. Directional selection and the site-frequency spectrum. *Genetics*. 2001;159(4):1779–1788.

Chak STC, Baeza JA, Barden P. Eusociality shapes convergent patterns of molecular evolution across mitochondrial genomes of snapping shrimps. *Mol Biol Evol*. 2020;38(1):1372–1383.

Chak STC, Duffy JE. Crustacean social evolution. In: Roitberg B (ed) *Reference module in life sciences*. Elsevier; 2017.

Chak STC, Duffy JE, Hultgren KM, Rubenstein DR. Evolutionary transitions towards eusociality in snapping shrimps. *Nat Ecol Evol*. 2017;1(4):1–7.

Chak STC, Duffy JE, Rubenstein DR. Reproductive skew drives patterns of sexual dimorphism in sponge-dwelling snapping shrimps. *Proc R Soc B Biol Sci*. 2015a;282(1809):20150342.

Chak STC, Harris SE, Hultgren KM, Jeffery NW, Rubenstein DR. Eusociality in snapping shrimps is associated with larger genomes and an accumulation of transposable elements. *Proc Natl Acad Sci USA*. 2021;118(24):e2025051118.

Chak STC, Rubenstein DR, Duffy JE. Social control of reproduction and breeding monopolization in the eusocial snapping shrimp *Synalpheus elizabethae*. *Am Nat*. 2015b;186(5):660–668.

Charlesworth B. Effective population size and patterns of molecular evolution and variation. *Nat Rev Genet*. 2009;10(3):195–205.

Charlesworth B, Charlesworth D, Barton NH. The effects of genetic and geographic structure on neutral variation. *Annu Rev Ecol Evol Syst*. 2003;34(1):99–125.

Chollett I, Müller-Karger FE, Heron SF, Skirving W, Mumby PJ. Seasonal and spatial heterogeneity of recent sea surface temperature trends in the Caribbean Sea and southeast Gulf of Mexico. *Mar Pollut Bull*. 2012;64(5):956–965.

Crawford JE, Alves JM, Palmer WJ, Day JP, Sylla M, Ramasamy R, Surendran SN, Black WCT, Pain A, Jiggins FM. Population genomics reveals that an anthropophilic population of *Aedes aegypti* mosquitoes in West Africa recently gave rise to American and Asian populations of this major disease vector. *BMC Biol*. 2017;15(1):16.

Crozier R.H. Genetics of sociality. In: Hermann, HR, (ed). *Social Insects*, Vol 1. Academic Press: New York NY. 1979. pp. 223–286.

Danecek P, Auton A, Abecasis G, Albers CA, Banks E, Depristo MA, Handsaker RE, Lunter G, Marth GT, Sherry ST, et al. The variant call format and VCFtools. *Bioinformatics*. 2011;27(15):2156–2158.

Dobkin S. The first post-embryonic stage of *Synalpheus brooksi* Coutière. *Bull Mar Sci*. 1965;15(2):450–462.

Dobkin S. *Abbreviated larval development in caridean shrimps and its significance in the artificial culture of these animals*. FAO Fisheries Reports. 1967. 57:935–945.

Duffy JE. Genetic population structure in two tropical sponge-dwelling shrimps that differ in dispersal potential. *Mar Biol*. 1993;116(3):459–470.

Duffy JE. Eusociality in a coral-reef shrimp. *Nature*. 1996;381(6582):512–514.

Duffy JE. The ecology and evolution of eusociality in sponge-dwelling shrimp. In: Kikuchi T, Azuma N, Higashi S, editors. *Genes, behavior, and evolution in social insects*. Hokkaido (Japan): University of Hokkaido Press; 2003. pp. 1–38.

Duffy JE, Macdonald KS. Kin structure, ecology and the evolution of social organization in shrimp: a comparative analysis. *Proc Biol Sci*. 2010;277(1681):575–584.

Duffy JE, Macdonald Iii KS, Hultgren KM, Chak STC, Rubenstein DR. Decline and local extinction of Caribbean eusocial shrimp. *PLoS One*. 2013;8(2):e54637.

Duffy JE, Morrison CL, Macdonald KS. Colony defense and behavioral differentiation in the eusocial shrimp *Synalpheus regalis*. *Behav Ecol Sociobiol*. 2002;51(5):488–495.

Fages A, Hanghøj K, Khan N, Gaunitz C, Seguin-Orlando A, Leonardi M, Mccrory Constantz C, Gamba C, Al-Rasheid KAS, Albizuri S, et al. Tracking five millennia of horse management with extensive ancient genome time series. *Cell*. 2019;177(6):1419–1435.e31.

Field J, Toyoizumi H. The evolution of eusociality: no risk-return tradeoff but the ecology matters. *Ecol Lett*. 2020;23(3):518–526.

Gattepaille LM, Jakobsson M, Blum MG. Inferring population size changes with sequence and SNP data: lessons from human bottlenecks. *Heredity (Edinb)*. 2013;110(5):409–419.

Gledhill DK, Wanninkhof R, Millero FJ, Eakin M. Ocean acidification of the Greater Caribbean Region 1996–2006. *J Geophys Res Oceans*. 2008;113(C10):1–11.

Goldenberg SB, Landsea CW, Mestas-Nuñez AM, Gray WM. The recent increase in Atlantic hurricane activity: causes and implications. *Science*. 2001;293(5529):474–479.

Gutenkunst RN, Hernandez RD, Williamson SH, Bustamante CD. Inferring the joint demographic history of multiple populations from multidimensional SNP frequency data. *PLoS Genet*. 2009;5(10):e1000695.

Hadfield JD. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J Stat Softw*. 2010;33(2):1–22.

Hasselmann M, Ferretti L, Zayed A. Beyond fruit-flies: population genomic advances in non-*Drosophila* arthropods. *Brief Funct Genomics*. 2015;14(6):424–431.

Holldobler B, Wilson EO. *The ants*. Cambridge (MA): Harvard University Press; 1990.

Hotaling S, Shain DH, Lang SA, Bagley RK, Tronstad LM, Weisrock DW, Kelley JL. Long-distance dispersal, ice sheet dynamics and mountaintop isolation underlie the genetic structure of glacier ice worms. *Proc Biol Sci*. 2019;286(1905):20190983.

Hultgren KM, Chak STC, Bjelajac J, Macdonald KS. Correlated evolution of larval development, egg size and genome size across two genera of snapping shrimp. *J Evol Biol*. 2021;34(11):1827–1839.

Hultgren KM, Duffy JE, Rubenstein DR. Sociality in shrimps. In: Rubenstein DR, Abbot P, editors. *Comparative social evolution*. Cambridge (UK): Cambridge University Press; 2017. pp. 224–249.

Kamm J, Terhorst J, Durbin R, Song YS. Efficiently inferring the demographic history of many populations with allele count data. *J Am Stat Assoc*. 2019; 115(531): 1472–1487. doi:10.1080/01621459.2019.1635482.1-16

Kamm JA, Terhorst J, Song YS. Efficient computation of the joint sample frequency spectra for multiple populations. *J Comput Graph Stat*. 2017;26(1):182–194.

Keller L, Perrin N. Quantifying the level of eusociality. *Proc R Soc B Biol Sci*. 1995;260(1359):311–315.

Keller LF, Waller DM. Inbreeding effects in wild populations. *Trends Ecol Evol*. 2002;17(5):230–241.

Kimura M. *The neutral theory of molecular evolution*. Cambridge, UK: Cambridge University Press; 1983.

Klotzbach PJ. The influence of El Niño-Southern Oscillation and the Atlantic Multidecadal Oscillation on Caribbean tropical cyclone activity. *J Clim*. 2011;24(3):721–731.

Lin Y-H, Chan S-F, Rubenstein DR, Liu M, Shen S-F. Resolving the paradox of environmental quality and sociality: the ecological causes and consequences of cooperative breeding in two lineages of birds. *Am Nat*. 2019;194(2):207–216.

Liu X, Fu Y-X. Exploring population size changes using SNP frequency spectra. *Nat Genet*. 2015;47(5):555–559.

Liu X, Fu Y-X. Stairway Plot 2: demographic history inference with folded SNP frequency spectra. *Genome Biol*. 2020;21(1):1–9.

Lozier JD. Revisiting comparisons of genetic diversity in stable and declining species: assessing genome-wide polymorphism in North American bumble bees using RAD sequencing. *Mol Ecol*. 2014;23(4):788–801.

Lukic S, Hey J. Demographic inference using spectral methods on SNP data, with an analysis of the human out-of-Africa expansion. *Genetics*. 2012;192(2):619–639.

Lynch M, Conery J, Burger R. Mutation accumulation and the extinction of small populations. *Am Nat*. 1995;146(4):489–518.

Lynch M, Gutenkunst R, Ackerman M, Spitze K, Ye Z, Maruki T, Jia Z. Population genomics of *Daphnia pulex*. *Genetics*. 2017;206(1):315–332.

Macdonald KS, Ríos R, Duffy JE. Biodiversity, host specificity, and dominance by eusocial species among sponge-dwelling alpheid shrimp on the Belize Barrier Reef. *Divers Distrib*. 2006;12(2):165–178.

Majer M, Holm C, Lubin Y, Bilde T. Cooperative foraging expands dietary niche but does not offset intra-group competition for resources in social spiders. *Sci Rep*. 2018;8(1) :1–13.

Manichaikul A, Mychaleckyj JC, Rich SS, Daly K, Sale M, Chen W-M. Robust relationship inference in genome-wide association studies. *Bioinformatics*. 2010;26(22):2867–2873.

Marandel F, Charrier G, Lamy JB, Le Cam S, Lorance P, Trenkel VM. Estimating effective population size using RADseq: effects of SNP selection and sample size. *Ecol Evol*. 2020;10(4):1929–1937.

Michener CD. Comparative social behavior of bees. *Annu Rev Entomol*. 1969;14(1):299–342.

Morrison CL, Ríos R, Duffy JE. Phylogenetic evidence for an ancient rapid radiation of Caribbean sponge-dwelling snapping shrimps (*Synalpheus*). *Mol Phylogenet Evol*. 2004;30(3):563–581.

Newman D, Pilson D. Increased probability of extinction due to decreased genetic effective population size: experimental populations of *Clarkia pulchella*. *Evolution*. 1997;51(2):354–362.

Nielsen R. Molecular signatures of natural selection. *Annu Rev Genet*. 2005;39(1):197–218.

Nunziata SO, Weisrock DW. Estimation of contemporary effective population size and population declines using RAD sequence data. *Heredity (Edinb)*. 2018;120(3):196–207.

Palanisamy H, Becker M, Meyssignac B, Henry O, Cazenave A. Regional sea level change and variability in the Caribbean Sea since 1950. *J Geod Sci*. 2012;2(2):125–133.

Penalba JV, Joseph L, Moritz C. Current geography masks dynamic history of gene flow during speciation in northern Australian birds. *Mol Ecol*. 2019;28(3):630–643.

Peterson BK, Weber JN, Kay EH, Fisher HS, Hoekstra HE. 2012. Double digest RADseq: an inexpensive method for De Novo SNP discovery and genotyping in model and non-model species. *PloS One*, 7(5):e37135.

Potter S, Xue AT, Bragg JG, Rosauer DF, Roycroft EJ, Moritz C. Pleistocene climatic changes drive diversification across a tropical savanna. *Mol Ecol*. 2018;27(2):520–532.

Rincon-Sandoval M, Betancur RR, Maldonado-Ocampo JA. Comparative phylogeography of trans-Andean freshwater fishes based on genome-wide nuclear and mitochondrial markers. *Mol Ecol*. 2019;28(5):1096–1115.

Rioja-Nieto R, Álvarez-Filip L. Coral reef systems of the Mexican Caribbean: status, recent trends and conservation. *Mar Pollut Bull*. 2019;140:616–625.

Robinson JD, Coffman AJ, Hickerson MJ, Gutenkunst RN. Sampling strategies for frequency spectrum-based population genomic inference. *BMC Evol Biol*. 2014;14(1):1–16.

Rochette NC, Rivera-Colón AG, Catchen JM. Stacks 2: analytical methods for paired-end sequencing improve RADseq-based population genomics. *Molecular Ecology*. 2019; 28(21):4737–4754.

Romiguier J, Lourenco J, Gayral P, Faivre N, Weinert LA, Ravel S, Ballenghien M, Cahais V, Bernard A, Loire E, et al. Population genomics of eusocial insects: the costs of a vertebrate-like effective population size. *J Evol Biol*. 2014;27(3):593–603.

Rubenstein DR, Agren JA, Carbone L, Elde NC, Hoekstra HE, Kapheim KM, Keller L, Moreau CS, Toth AL, Yeaman S, et al. Coevolution of genome architecture and social behavior. *Trends Ecol Evol*. 2019;34(9):844–855.

Schraiber JG, Akey JM. Methods and models for unravelling human evolutionary history. *Nat Rev Genet*. 2015;16(12):727–740.

Settepani V, Schou MF, Greve M, Grinsted L, Bechsgaard J, Bilde T. Evolution of sociality in spiders leads to depleted genomic diversity at both population and species levels. *Mol Ecol*. 2017;26(16):4197–4210.

Sherman PW, Lacey EA, Reeve HK, Keller L. The eusociality continuum. *Behav Ecol*. 1995;6(1):102–108.

Silva DN, Várzea V, Paulo OS, Batista D. Population genomic footprints of host adaptation, introgression and recombination in coffee leaf rust. *Mol Plant Pathol*. 2018;19(7):1742–1753.

Smith TB, Gyory J, Brandt ME, Miller WJ, Jossart J, Nemeth RS. Caribbean mesophotic coral ecosystems are unlikely climate change refugia. *Glob Change Biol*. 2016;22(8):2756–2765.

Sun S-J, Rubenstein DR, Chen B-F, Chan S-F, Liu J-N, Liu M, Hwang W, Yang P-S, Shen S-F. Climate-mediated cooperation promotes niche expansion in burying beetles. *eLife*. 2014;3:e02440.

Titus BM, Blischak PD, Daly M. Genomic signatures of sympatric speciation with historical and contemporary gene flow in a tropical anthozoan (Hexacorallia: Actiniaria). *Mol Ecol*. 2019;28(15):3572–3586.

Tóth E, Bauer RT. Gonopore sexing technique allows determination of sex ratios and helper composition in eusocial shrimps. *Mar Biol*. 2007;151(5):1875–1886.

Vendrami DLJ, De Noia M, Telesca L, Handal W, Charrier G, Boudry P, Eberhart-Phillips L, Hoffman JI. RAD sequencing sheds new light on the genetic structure and local adaptation of European scallops and resolves their demographic histories. *Sci Rep*. 2019;9(1):1–13.

Wilson EO. Social modifications related to rareness in ant species. *Evolution*. 1963;17(2):249–253.

Wilson EO. *The insect societies*. Cambridge (MA): Belknap Press of Harvard University Press; 1971.

Wilson EO. Causes of ecological success: the case of the ants. *J Anim Ecol*. 1987;56(1):1–9.

Wilson EO. *The social conquest of earth*. New York (NY): Liveright Publishing; 2012.

Wright S. Coefficients of inbreeding and relationship. *Am Nat*. 1922;56(645):330–338.

Xue AT, Hickerson MJ. multi-dice: r package for comparative population genomic inference under hierarchical co-demographic models of independent single-population size changes. *Mol Ecol Resour*. 2017;17(6):e212–e224.

Yuan J, Zhang X, Liu C, Yu Y, Wei J, Li F, Xiang J. Genomic resources and comparative analyses of two economical penaeid shrimp species, *Marsupenaeus japonicus* and *Penaeus monodon*. *Mar Genomics*. 2018;39:22–25.