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Demographic inference provides insights into the extirpation and ecological dominance of eusocial snapping shrimps

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28 **Abstract**

29

30 Eusocial animals often achieve ecological dominance in the ecosystems where they occur, a
31 process that may be linked to their demography. That is, reproductive division of labor and high
32 reproductive skew in eusocial species is predicted to result in more stable effective population
33 sizes that may make groups more competitive, but also lower effective population sizes that may
34 make groups more susceptible to inbreeding and extinction. We examined the relationship
35 between demography and social organization in one of the few animal lineages where eusociality
36 has evolved recently and repeatedly among close relatives, the *Synalpheus* snapping shrimps.
37 Although eusocial species often dominate the reefs where they occur by outcompeting their non-
38 eusocial relatives for access to sponge hosts, many eusocial species have recently become
39 extirpated across the Caribbean. Coalescent-based historical demographic inference in 12 species
40 found that across nearly 100,000 generations, eusocial species tended to have lower but more
41 stable effective population sizes through time. Our results are consistent with the idea that stable
42 population sizes may enable eusocial shrimps to be more competitively dominant, but they also
43 suggest that recent population declines are likely caused by eusocial shrimps' heightened
44 sensitivity to anthropogenically-driven environmental changes as a result of their low effective
45 population sizes and localized dispersal, rather than to natural cycles of inbreeding and
46 extinction. Thus, although the unique life histories and demography of eusocial shrimps has
47 likely contributed to their persistence and ecological dominance over evolutionary timescales,
48 these social traits may also make them vulnerable to contemporary environmental change.

49

50 **Keywords** – ddRAD; historical demography; effective population size; eusociality; MOMI2;
51 *Synalpheus*

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66 Eusocial species are often the most abundant members of their community (1, 2). Their ability to
67 outcompete conspecifics, expand their niches, and assert their ecological dominance over non-
68 eusocial species—an idea referred to as the ‘social conquest hypothesis’—may be due in part to
69 their ability to cooperate and form complex societies (2, 3). Wilson (4) proposed several
70 population-level qualities of life history and demography that contribute to the ecological success
71 of eusocial ants and their persistence over evolutionary time. Since all of the more than 13,000
72 species of ants are eusocial (5), testing these ideas empirically has been challenging. Moreover,
73 whether these demographic characteristics are shared in other eusocial organisms that exhibit
74 various forms of social complexity and ecological success remains unclear. Although a few
75 studies have examined empirically and comparatively whether social populations and eusocial
76 species have been able to expand their ecological niches (3, 6, 7) and geographic ranges (8)
77 relative to non-social ones, the specific life history and demographic characteristics that allow
78 eusocial species to maintain high population densities that can be sustained for long periods of
79 time remain largely unexplored.

80
81 Social conquest and ecological dominance may be facilitated or hindered by several life history
82 characteristics specific to eusocial species that are known to influence demography and genetic
83 diversity. First, in eusocial species, reproductive division of labor and high reproductive skew
84 may lead to a reduction in effective population size (N_e) (9, 10) because the breeding population
85 (reflected by N_e) is constrained to mainly a single or few reproductive individuals (i.e. queens).
86 In contrast, a much larger portion of the population contributes to breeding in non-eusocial
87 species. Second, reproductives in eusocial species may be buffered from environmental
88 fluctuation by the workers that cooperatively attend them, resulting in more stable N_e over time
89 (11, 12). Similarly, the ability to cooperatively defend and maintain a stable domicile (4) may
90 further buffer the breeding individuals—and indeed the entire group—from environmental
91 fluctuation, similarly resulting in more stable N_e over time. Together, the demographic
92 consequences of these life history characteristics are likely to be lower N_e , but greater population
93 stability over time in eusocial species than non-eusocial species (4). Yet, at the same time, these
94 or other demographic correlates of eusociality can also render some eusocial lineages unstable,
95 resulting in inbreeding, local extinction, and even evolutionary dead-ends. For example, lineages
96 containing social spider species have undergone repeated origins and extinctions, likely due to
97 inbreeding, reduced N_e , and the depletion of genome-wide genetic diversity (13-15). Indeed,
98 instances of inbreeding that generate low genetic diversity and the potential for colony collapse
99 (16)—often in the face of environmental fluctuation—are surprisingly common in other
100 primitively eusocial species like wood-dwelling termites, thrips, spider mites, and naked mole-
101 rats (reviewed in 15). Ultimately, conflicting empirical evidence from insects lead to contrasting
102 predictions about the role of historical demography in social evolution: reproductive division of
103 labor and protection of female reproductives by workers predicts a historical trend of population
104 stability in eusocial species, whereas low N_e , the potential for inbreeding, and reduced genome-
105 wide genetic diversity predicts long-term population instability for eusocial species.

106
107 Testing these contrasting predictions and bridging the gap between these alternative scenarios of
108 the demographic stability of eusociality can be done using coalescent-based methods that infer
109 historical demography. Historical expansions or contractions in population size, as well as
110 population structure and gene flow, leave a measurable signal on the genetic diversity of
111 contemporary populations, which allows for the quantification of the demographic process based

112 on the site frequency spectrum (SFS), a measure of allele frequencies across the genome that can
113 be generated from large-scale sequencing. The effects of demographic processes on the SFS are
114 well studied and have been tested across a range of taxa (17-19). Demographic inference is
115 commonly made using a composite likelihood framework that fits the observed SFS to the
116 expected SFS computed under given demographic histories (17, 20-24). This approach has been
117 used successfully in species ranging from mice (25) to humans (26). Recent studies have also
118 begun modelling comparative demographic processes across multiple taxa simultaneously (20,
119 27-30), including eusocial bees (31) and social spiders (14). These and other studies examine
120 relative patterns of N_e change through time, rather than simply comparing absolute estimates at
121 specific time points (32-41), an approach that would enable us to test alternative demographic
122 scenarios in eusocial lineages. Moreover, the broad use of coalescent-based methods has shown
123 its robustness as a population genetic tool and can accurately select models and estimate
124 parameters using as few as 3-15 individuals and 10,000 – 50,000 single nucleotide
125 polymorphism (SNP) loci (42, 43). Therefore, it is now feasible to use a multi-taxa comparative
126 demographic framework to test long-standing hypotheses underlying how population dynamics
127 influence the ecological consequences of eusociality.

128
129 Here, we use a group of socially diverse, sponge-dwelling snapping shrimps in the genus
130 *Synalpheus* to look at the demographic consequences of eusociality and to address whether
131 historical N_e supports a model of demographic stability or instability in eusocial species.
132 *Synalpheus* shrimps in the West Atlantic *gambarelloides* group represent a relatively young
133 lineage that radiated between approximately 5 and 7 Mya (44), yet eusociality has evolved
134 independently at least four times in this group (45) and likely represents an early stage of
135 eusocial evolution because workers are not sterile (46, 47). Species in this clade exhibit a variety
136 of forms of social organization, ranging from pair-living, to communal breeding (multiple mating
137 pairs in the same sponge), to eusociality (one or a few queens and a larger number of non-sterile
138 workers of both sexes) (45-48). Most importantly, there are reports of both ecological dominance
139 and demographic instability in eusocial *Synalpheus* species. The diversity of *Synalpheus* species
140 in Carrie Bow Cay, Belize has been well documented since 1990 and represents the only
141 longitudinal dataset on snapping shrimps currently available. At this reef, the four eusocial
142 shrimp species contributed to >65% of the quantitative samples and eusocial species were 17
143 times as abundant as non-eusocial species (49). Eusocial species also occupied more sponges and
144 had a wider host breadth than their non-eusocial relatives (7). Thus, for more than two decades,
145 eusocial *Synalpheus* outcompeted their non-eusocial relatives and remained the ecologically
146 dominant shrimp species on the reef. However, since 2012, three of the four eusocial species at
147 Carrie Bow Cay have become locally extinct. In addition, two eusocial species in Jamaica have
148 shown population declines associated with an increase of queenless colonies (50), and a eusocial
149 species in Panama has also declined (45). In these same reefs in Jamaica and Panama, pair-living
150 and communal breeding *Synalpheus* species appear to at least be maintaining healthy
151 populations, if not increasing in abundance. Therefore, despite evidence of sustained ecological
152 dominance, eusocial *Synalpheus* shrimps have seen recent population declines over much of their
153 range. These recent population declines could be a snapshot of cyclic population bottlenecks that
154 reflect the long-term demographic instability of eusocial species. However, since the colony
155 organization of eusocial species (i.e., reproductive division of labor and high reproductive skew)
156 (4, 9) also predicts that they could have low but stable population sizes, if eusocial species show
157 a historical trend of population stability, then these recent population declines are more likely to

158 be explained by contemporary environmental change (e.g. increased anthropogenic
159 environmental disturbance).

160
161 To explore the relationship between demography and eusociality, we generated genome-wide
162 SNP data using double digest restriction-site associated DNA sequencing (ddRADseq) and
163 performed demographic inference to compare long-term demographic patterns in four eusocial
164 and eight non-eusocial shrimp species (including five communal breeding and three pair-forming
165 species). We inferred historical N_e by finding which pattern of population size changes over time
166 generated an expected SFS that best matches our observed SFS. Using inferred historical N_e , we
167 then calculated average N_e over multiple timepoints, assuming the same mutation and
168 recombination rates across species (51), and three population stability metrics: (i) the coefficient
169 of variation of N_e across times (CV) to quantify the variation of N_e that is independent of mean
170 N_e , where a smaller value indicates greater population stability; (ii) the ratio of minimum N_e to
171 mean N_e (min/mean N_e), where a larger value indicates a less severe population bottleneck, and
172 thus greater population stability; and (iii) the number of times that two consecutive N_e estimates
173 had less than one order of magnitude difference (no. of <1-order change), where a larger value
174 indicates less drastic changes in N_e , and thus greater population stability. Ultimately, linking
175 demography to social evolution through population genetic approaches (52) not only has the
176 potential to uncover the demographic factors that may have enabled some eusocial species to
177 come to dominate the ecosystems where they occur, but it may also help explain why some
178 eusocial species or lineages go extinct over both evolutionary and ecological timescales.

179

180 **Results**

181 **Genetic diversity and kinship.** For each of the 12 *Synalpheus* species, we sampled 7-8 breeding
182 females (i.e., queens) from different sponges (i.e., colonies) from the same reef whenever
183 possible. Using ddRADseq, we generated >312 million paired-end reads with a median of 2.7
184 million reads per sample. De novo mapping using *Stacks* generated 19,788 – 52,898 SNPs per
185 species (median = 24,307, Table S1 and S2; SRA accession: SAMN14351547 -
186 SAMN14351641). Mean individual observed heterozygosity (H_{obs}) based on all sites or just
187 variant sites did not differ among species exhibiting the three forms of social organization
188 (pMCMC > 0.19, Fig. S1, Table S3, Table S4): the percentage of heterozygous sites across all
189 sites ranged from 0.19 to 0.23% across species, which is similar to that observed in non-social
190 spiders (14) and other non-*Synalpheus* shrimps (53). Moreover, there were low levels of
191 inbreeding in all species: the inbreeding coefficients (F) were positive and ranged from 0.12 to
192 0.54 across species (Fig. S1, Table S3). In contrast to the prediction that eusocial species may be
193 more inbred than non-eusocial species (14), eusocial *Synalpheus* species were significantly more
194 outbred than communal breeding species (pMCMC = 0.032), but only marginally more outbred
195 than non-eusocial (pair-living and communal breeding combined) species (pMCMC = 0.062)
196 (Table S4). Finally, mean average kinship coefficients were negative for all species, meaning
197 that breeding females across sponges were unrelated to each other (Fig. S1, Table S3). However,
198 kinship coefficients were significantly higher in eusocial species than in pair-forming species and
199 non-eusocial species (pMCMC = 0.0003 and 0.02, respectively; Table S4). The relatively higher
200 degree of genetic relatedness among queens over small spatial scales in eusocial versus non-
201 eusocial species is consistent with their different modes of larval dispersal: all eusocial species
202 have crawling larvae that remain in the natal sponge, whereas communal breeding and pair-

203 living species have swimming larvae that disperse from the natal sponge via the water column (7,
204 45, 54, 55).

205
206 **Demographic inference and stability.** Rather than simply comparing N_e values at specific time
207 points, we examined relative changes in N_e between species to identify broad demographic
208 patterns within groups of species exhibiting different forms of social organization. This approach
209 avoided interpretation of the timing of events and absolute N_e values, both of which can be
210 confounded by potential variations in mutation and recombination rates across species (51).
211 Knowledge of mutation rates and generation times are not well known in *Synalpheus* shrimps
212 and most other social animals (56), and thus, such an analysis could generate uncertainty in
213 absolute N_e estimates. However, in lieu of exact point inferences, the main features of the model
214 (i.e., relative changes, overall size changes, directionality, and broad patterns in demographic
215 history) can be accomplished with confidence through bootstrapping simulated data under the
216 best-model demographic scenario (57). Thus, due to the uncertainty in determining absolute N_e
217 values, reporting on the broad demographic trends and relative changes in N_e is the accepted
218 approach when using coalescent-based modeling to estimate demography from the site frequency
219 spectrum (35-40, 58-61).

220
221 After removing related individuals ($n = 5$ of 96) and drawing one random SNP per locus, we
222 used 11,890 – 26,148 SNPs per species (median = 18,175, Table S1) for demographic inference
223 analysis using *MOMI2*, an efficient and scalable demographic inference software that can handle
224 complex datasets (23, 24). For each species, we ran multiple analyses that varied in the number
225 of times N_e was inferred ($T = 4, 6, \text{ or } 8$ time points) and over different timescales ($G = 60, 80, \text{ or } 100$
226 thousand generations). To examine N_e across species with the same underlying parameters
227 (T and G), we compared the delta AIC (62) across analyses and found that a model that
228 estimated N_e four times across 100,000 generations had the best support across species (Table
229 S4). Estimated values of N_e from this model were generally within the 95% confidence interval
230 of the bootstrap estimates (see Supporting Information: Fig. S2), indicating that the patterns were
231 consistent across 300 different subsets of SNPs. Assuming several generations per year, a time
232 scale of roughly 100,000 generations is likely to span most of the Holocene.

233
234 In general, N_e values were higher and more variable through time in pair-living and communal
235 breeding species, whereas they were lower but more stable through time in eusocial species (Fig.
236 2). There appeared to be a reduction of N_e at 51-75 thousand generations ago for three out of four
237 eusocial species. Similarly, three communal species also showed a reduction of N_e at 26-50
238 thousand generations ago. These shared trends indicate that these species may respond to the
239 same demographic event and gave additional confidence to our estimates. However, since our
240 primary aim was to examine the relative trends of historic N_e among species exhibiting different
241 forms of social organization, in addition to estimating the average population size over multiple
242 timepoints, we also calculated three population stability metrics using inferred historical N_e from
243 the best fit model with the highest log-likelihood. We then used phylogenetic mixed models
244 implemented in *MCMCglmm* (63) to compare these demographic metrics using both a
245 continuous measure of eusociality (eusociality index) and across discrete social categories (64).
246 Importantly, the eusociality index captures the reproductive skew within a group (7, 65, 66),
247 making no *a priori* assumption of social phenotype. Our results confirmed the above patterns
248 statistically in 3 of 4 metrics of population size and stability: as eusociality index increased

249 (hence stronger reproductive skew), mean N_e decreased, CV decreased, and min/mean N_e
250 increased, though no. <1-order change did not change (pMCMC = 0.018, 0.031, 0.025, and 0.63,
251 respectively, Fig. 3; see Supporting Information Table S5). We observed qualitatively similar
252 results using discrete social categories, such that eusocial species had significantly lower mean
253 N_e than non-eusocial species (pMCMC = 0.021), as well as marginally lower CV, higher
254 min/mean N_e , and higher no. of <1-order difference in N_e values than non-eusocial species
255 (pMCMC = 0.055, 0.058, and 0.076, respectively, Fig. 4; see Supporting Information, Table S5).
256 Although the limited number of species in each social category likely contributed to the marginal
257 levels of statistical significance, the results are consistent with those from the analysis using the
258 eusociality index. Finally, analyses using the median demographic metrics across bootstrap
259 estimates showed similar trends, but lacked statistical significance (see Supporting Information,
260 Fig. S3), likely because smaller subsets of SNPs were used in these analyses. Thus, eusocial
261 shrimp species have lower but more stable N_e through time than their non-eusocial relatives.
262

263 Discussion

264 Cooperation between individuals of the same species leading to the formation of complex
265 societies is thought to have enabled eusocial animals to become ecologically dominant in the
266 areas where they occur, sometimes comprising more than half of the biomass in a given
267 ecosystem (2). The peculiar demographic consequences of eusociality have been suggested to
268 both help and hinder their ecological dominance, although empirical tests of these ideas have
269 largely been lacking. Here, we examined the relationship between demography and eusociality in
270 a socially diverse clade of *Synalpheus* snapping shrimps using historical demographic inference
271 to determine whether eusocial species are more or less demographically stable than their non-
272 eusocial relatives (4). We found that eusocial *Synalpheus* snapping shrimps, across four
273 independently-evolved eusocial lineages, consistently had lower but more stable N_e through time
274 than non-eusocial species. This long-term stability of N_e in eusocial shrimp species supports the
275 idea that reproductive division of labor may enable groups to buffer the breeding individuals
276 (i.e., N_e) against environmental fluctuation or that cooperation may help eusocial species to
277 better defend and maintain their domiciles. Furthermore, Wilson (4) argued that a critical
278 criterion for ecological success was population density that could be sustained for long periods of
279 time. Our results are consistent with this idea, adding to field observations that, for more than
280 two decades, eusocial *Synalpheus* outcompeted their non-eusocial relatives to become the
281 ecologically dominant shrimp species on the reef (7, 49). Although species with low mean N_e
282 may be more susceptible to extinction due to reductions in genetic diversity and high genetic
283 load (67), this does not seem to be the case in eusocial shrimp because eusocial species exhibited
284 less evidence of inbreeding than non-eusocial species. Moreover, we found no evidence of
285 population bottlenecks, cyclical patterns of expansion, or contractions of N_e in eusocial shrimp
286 species, as found in other primitively eusocial animals (15). Instead, eusocial shrimp species
287 appear to be more demographically stable than non-eusocial species, a conclusion that remains
288 robust whether we consider social organization as a categorical or continuous variable. Our results
289 agree with recent ecological models showing primitive eusociality to be generally more
290 successful than solitary nesting in terms of reproduction and extinction probabilities (68). The
291 evolutionary dead-ends observed in social spiders and other primitively eusocial animals may be
292 explained by the advantages of solitary nesting compared to eusociality under very restricted
293 assumptions in simulation studies (68, 69).
294

295 One of the primary motivations for this study was to quantify the demographic consequences of
296 eusociality in snapping shrimps in order to understand the mechanism underlying the ecological
297 dominance of eusocial species on Caribbean reefs. Yet, this study also has more practical
298 implications since eusocial *Synalpheus* species in Belize, Panama, and Jamaica have either gone
299 locally extinct or declined significantly in abundance in recent years, while non-eusocial species
300 have remained stable or increased in abundance over the same timeframe (50). Our findings that
301 eusocial *Synalpheus* species had stable effective population sizes over evolutionary time, and the
302 absence of any evidence of population bottlenecks or cyclical patterns of expansion or
303 contractions of N_e , together suggest that these recent population declines are unprecedented in
304 the last 100,000 generations, spanning most of the Holocene. We propose instead that
305 contemporary population declines may be due to recent environmental changes across the
306 Caribbean, which likely impact eusocial species more strongly because of their lower average N_e
307 and limited ability to disperse. For several decades, direct anthropogenic development and
308 environmental disturbances have negatively impacted coastal and marine ecosystems across the
309 Caribbean (70). A combination of warming sea surface temperatures (71), rising sea level (72),
310 and increased hurricane activity have been affecting the Caribbean, all of which negatively
311 impact benthic communities (73, 74). The global increase in CO_2 has also caused increased
312 acidification, especially in the Caribbean region over the past 25 years, negatively affecting a
313 wide range of biological systems (75). Together, these climate events have had devastating
314 impacts on local ecosystems, including on sponge communities (e.g., 76). Since *Synalpheus* are
315 obligate sponge dwellers, and many are strict host specialists (6), these symbionts may be
316 particularly sensitive to environmental change. Within sponges that host *Synalpheus* shrimps,
317 extreme environmental perturbations are likely driving the global increase in sponge diseases,
318 which has especially affected Mediterranean and Caribbean sponges (77). Increasingly disturbed
319 by anthropogenic pressures, the survival of local snapping shrimp populations is likely
320 dependent on their ability to quickly and efficiently recolonize host sponges. However, the life
321 history of eusocial shrimp species may hamper their ability to recolonize host sponge after a
322 local population crash: eusocial shrimps tend to be host specialists (6) and all eusocial species
323 have crawling larvae that remain in the natal sponge, in contrast to communal breeding and pair-
324 living species that have swimming larvae that can disperse from the natal sponge in the water
325 column (7, 54, 55). Our genetic diversity results support this life history difference: eusocial
326 shrimps have the highest levels of relatedness (Fig. S1) across females from different sponges
327 within a local population (collection site), a pattern seen previously using allozymes (78).
328 Therefore, eusocial species appear to have lower migration and colonization rates than non-
329 eusocial species, hence potentially less gene flow between populations, as shown in an early
330 population genetics study (78). Thus, although eusocial *Synalpheus* species have been
331 ecologically dominant in parts of the Caribbean for at least a few decades (7, 49) and
332 demographically stable for thousands of years, in the face of increased anthropogenic
333 environmental disturbance, eusocial species may be more susceptible to population collapse and
334 extinction than their non-eusocial relatives.

335
336 In conclusion, our analyses are consistent with the idea that eusocial animals tend to be more
337 demographically stable than their non-eusocial relatives; we found a signature of lower and more
338 stable N_e in eusocial shrimps compared to non-eusocial species. In contrast, we found no
339 evidence of cyclic population contractions or extinctions in eusocial species that would indicate
340 population instability. Our results suggest that for at least 100,000 generations spanning

341 thousands of years, eusocial shrimp populations in the Caribbean appear to have been more
342 stable than those of non-eusocial species, suggesting that the recent extirpation of ecologically
343 dominant eusocial species may be driven by anthropogenic changes in combination with their
344 lower N_e and limited dispersal ability. Therefore, the long-term demographic stability in eusocial
345 snapping shrimp is likely one of the key factors in promoting their ecological dominance on
346 tropical reefs, an idea that has been proposed but not tested for eusocial insects that have come to
347 dominate much of the terrestrial world. Yet, the demographic and life history characteristics of
348 eusocial shrimps also render them vulnerable to recent global change. Ultimately, studying
349 changes in demography through time will not only help understand the long-term population
350 dynamics of social organisms, it may also provide critical insights into how social species will
351 cope in the face of increasing climate change and habitat loss.

352

353 **Materials and Methods**

354 **Sampling and study species.** We sampled 12 species of *Synalpheus* snapping shrimps from four
355 sites in the Caribbean (Belize, Barbados, Jamaica, and Panama) between 2004 and 2012 (Fig. 1).
356 A detailed collection protocol has been reported previously (49). For each species, we sampled
357 7-8 females, enough for confident demographic inference (42, 43), with eggs or visible ovarian
358 development to ensure that we were sampling breeding individuals. We sampled females from
359 different sponges whenever possible. For eusocial species, each sponge represented a colony.
360 Thus, sampling from different sponges ensured that we had a more complete representation of
361 the population at each site. All individuals were collected within a 5-year sampling period
362 (Supporting Information: Table S1).

363

364 Our sampled species included three pair-forming, five communal breeding, and four eusocial
365 species. The four eusocial species included one species from each of the lineages that
366 independently evolved eusociality in the genus *Synalpheus*. Two eusocial species (*S. brooksi* and
367 *S. chacei*) were from Belize where, before the recent population decline, they dominated their
368 habitat over non-eusocial species based on abundance, sponge occupancy, and host ranges (7).
369 Local population declines were observed from field surveys for *S. chacei* from Belize, *S. duffyi*
370 from Jamaica, and *S. rathbunae* from Panama (50). For a meaningful comparison of historical
371 demographics, we included non-eusocial species that showed stable or increasing populations
372 from the same three sites (50).

373

374 **Double digest restriction-site associated DNA sequencing.** We extracted genomic DNA using
375 several walking legs from alcohol-preserved specimens using Qiagen DNAeasy Tissue Kits.
376 Extracted DNA was quantified using a Qubit 3.0 Fluorometer with the dsDNA HS assay
377 (ThermoFisher Scientific) and visualized on 2% agarose gels. We followed the protocol in
378 Peterson et al. (2012) using the restriction enzymes EcoRI and MspI. We used the recommended
379 size selection criterion (338bp – 414bp) based on the estimated genome sizes of each species,
380 which ranged from approximately 6.49 to 20.74 pg (where 1 pg = 978 Mbp) (79). Briefly, we
381 digested 1,000 ng of genomic DNA with EcoRI and MspI (New England Biolabs) and cleaned
382 the digested DNA using Agencourt AMPure XP beads (Beckman Coulter Life Sciences). We
383 ligated the double-digested DNA with barcoded adaptors that were 5-fold in excess to prevent
384 the formation of chimeras. We pooled and bead-cleaned barcoded samples before size selection
385 using a Pippin Prep and a dye-free 2% Agarose gel cassette with internal standards (CDF2010,
386 Sage Science). We performed a 10-cycle PCR using a Phusion PCR Kit according to the

387 manufacturer's protocol (New England Biolabs) with multiplexed primers and adjusted PCR
388 products to 10 μ M for sequencing on either an Illumina HiSeq2500 (125 bp paired-end, New
389 York Genome Center) or an Illumina HiSeq 3000 (150 bp paired-end, Center for Genome
390 Research and Biocomputing at Oregon State University).

391
392 We used *Stacks* v2.1 (80) to demultiplex and clean raw reads (*process_radtags: reads with phred*
393 *score <10 were discarded*) and perform *de novo* mapping of paired-end reads (*denovo_map.pl*
394 with the parameters T = 6, m = 3, M = 3, and n = 2). We adjusted the parameter *r* (0.5 – 0.875) in
395 *populations* in the *Stacks* pipeline to obtain around 20,000 SNPs per species (19,778 – 52,898).

396
397 **Genetic diversity and kinship.** We calculated several statistics to summarize the genetic
398 diversity at the individual level, and to quantify the levels of inbreeding and kinship among
399 females, each from different sponges within the same collection site. First, we estimated
400 observed heterozygosity (H_{obs}) for each sample from *populations* in the *Stacks* pipeline, which is
401 essentially the number of heterozygous sites divided by the total number of fixed and variant
402 sites for each sample, and took the mean H_{obs} for each species. We also calculated H_{obs} based on
403 variant sites only. We calculated the averaged inbreeding coefficient (F) across individuals for
404 each species using *VCFtools* v0.1.16 (81). F measures the probability that two alleles at a given
405 locus are identical by descent. An individual is fully inbred when F = 1 and fully outbred when F
406 = 0 (82). Finally, we used *King* v2.1.6 (83) to calculate the genome-wide relatedness between
407 each female within a species. We took the mean kinship coefficient between pairs of individuals
408 (one female per sponge) for each species. For each genetic statistic (mean H_{obs} , F, and mean
409 kinship coefficient), we performed phylogenetic mixed model regressions using the R package
410 *MCMCglmm* v2.29 (63) to test whether they differed according to the form of social organization
411 (pair-forming vs. communal breeding vs. eusocial) or eusociality (eusocial vs. non-eusocial),
412 while controlling for phylogenetic non-independence between species. We used a Bayesian
413 consensus tree of *Synalpheus* species, constructed with 16S, 18S, and COI sequence data (64).
414 We used weakly informative priors (variance parameters, V = 1, degree of belief, nu = 0.002),
415 but more or less informative priors yielded the same results (nu = 0.02 or 0.0002). We
416 ran 2,000,000 Markov Chain Monte Carlo (MCMC) iterations with 50,000 iterations of burn-in
417 and a thinning interval of 250. Pairwise differences between categories of sociality or eusociality
418 were tested by comparing the difference in posterior distributions of each category (e.g., eusocial
419 – communal breeding) and calculating a pMCMC value as twice the probability that the posterior
420 distribution of the difference is above or below zero (63).

421
422 **Demographic inference.** For pairs of individuals that were closer than 3rd-degree-related (>
423 25%, based on kinship coefficients > 0.089), we randomly removed one individual using
424 *VCFtools* v0.1.16 (81). We removed two individuals from *S. rathbunae* and one individual each
425 from *S. agelas*, *S. carpenteri*, and *S. chacei*. We then extracted one random SNP per locus using
426 the script *vcfparser.py* (84) to generate a vcf file for demographic inference analysis using
427 *MOMI2* v2.1.16 (23, 24). For comparative purposes, we chose to infer N_e from T fixed time
428 ranges across G generations for all species. Initial N_e was set at 1e+6 and maximum N_e at 1e+21
429 for all species. The value of initial N_e was based on the mean N_e across species from single N_e
430 models (See Supporting Information). The value of maximum N_e was based on running multiple
431 models with different parameter values and finding the value that yielded the highest log-
432 likelihood across species (See Supporting Information). We ran 300 random starts to find the

433 model with the highest log-likelihood. We further ran 300 bootstraps, each with 50 random starts
434 to find the model with the highest log-likelihood support. Preliminary analyses showed that
435 estimating N_e at fixed time ranges (e.g., 1-20, 21-40, 41-60, and 61-80 thousand generations)
436 gave better model support than estimating N_e at fixed times (e.g., 20, 40, 60, and 80 thousand
437 generations) (see Supporting Information: Fig. S4).

438
439 To find the best specification of model parameters T (number of time ranges) and G (maximum
440 number of generations), we ran seven models that differed in T (4, 6, and 8) and G (60, 80, and
441 100 thousand). We did not estimate N_e changes that were less than 10,000 generations apart
442 because our preliminary analysis showed that the order of magnitude that we can estimate
443 change among the 12 species was about 10,000 generations (See Supporting Information). For
444 each species, we compared the support for each parameter set using delta AIC (62). The model
445 with delta AIC = 0 had the best support and models with delta AIC < 3 were considered to be
446 equally-supported best models. We chose the model with the parameter set that was most
447 frequently supported across species under the criteria of delta AIC < 3 (Table S5).

448
449 **Phylogenetic comparative analysis.** From the best fit model with the highest log-likelihood, we
450 used the N_e values estimated across 10,000 – 100,000 generations for each species. We
451 calculated mean N_e across time (mean N_e), as well as three population stability metrics for
452 comparative analyses: (i) the coefficient of variation of N_e based on the log-normal distribution
453 (CV); (ii) the ratio of minimum N_e to mean N_e (min/mean N_e); and (iii) the number of times
454 where two consecutive N_e estimates had less than one order of magnitude difference (no. of <1-
455 order change). We did not include the N_e estimate at time 0 (i.e. the most recent N_e) in our
456 analysis because this estimate was strongly correlated with the initial N_e that we specified in
457 *MOMI2* (data not shown). Further, demographic inference based on ddRAD may not reflect
458 recent population changes (31) unless sample size per population was very large (> 30) (42, 85).
459 We used the Shapiro-Wilk's test to check for normality, ultimately log-transforming mean N_e ,
460 CV, and min/mean N_e .

461
462 We performed phylogenetic mixed model regressions using *MCMCglmm* (63) as described
463 above. Briefly, we tested whether the four metrics of population size and stability differed
464 according to the form of social organization (pair-forming vs. communal breeding vs. eusocial)
465 or eusociality (eusocial vs. non-eusocial), while controlling for phylogenetic non-independence
466 between species and treating collection site as a random factor. We performed the same analyses
467 using the demographic metrics calculated from the median of 300 bootstraps N_e estimates. We
468 also performed a similar analysis using the eusociality index ($E = 1 - ((2 \times \text{NOF}) / \text{CS})$) where
469 CS, colony size, is the total number of individuals in a sponge and NOF is the number of
470 ovigerous females in a sponge based on data from (64), which captures the degree of
471 reproductive skew within a group and has been used to measure the level of eusociality in
472 *Synalpheus* and other invertebrates (7, 65).

473
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479

480 **Author Contributions.** D.R.R and S.E.H. designed the study. S.T.C.C. and S.E.H. performed
481 the experiment, conducted analyses, and drafted the manuscript. All authors collected specimens
482 and revised the manuscript.

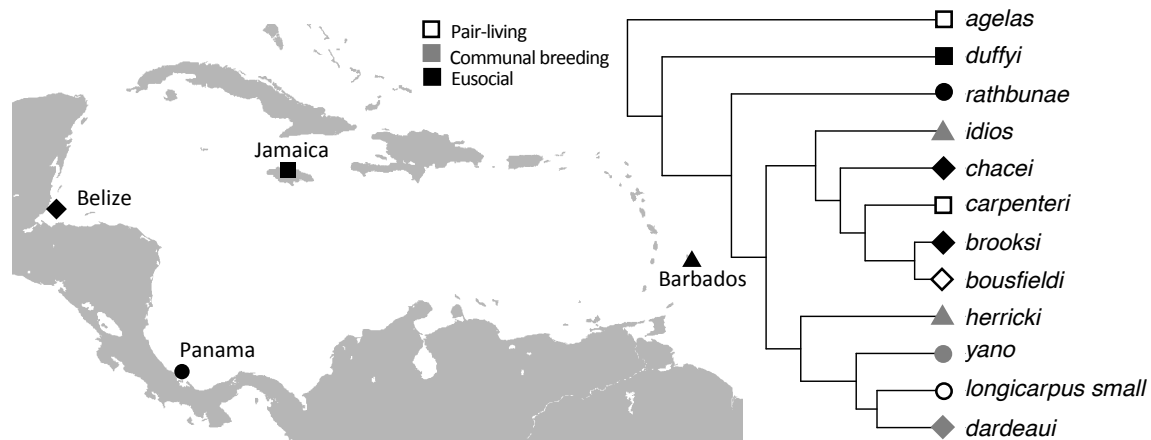
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484 The authors declare no conflict of interest.

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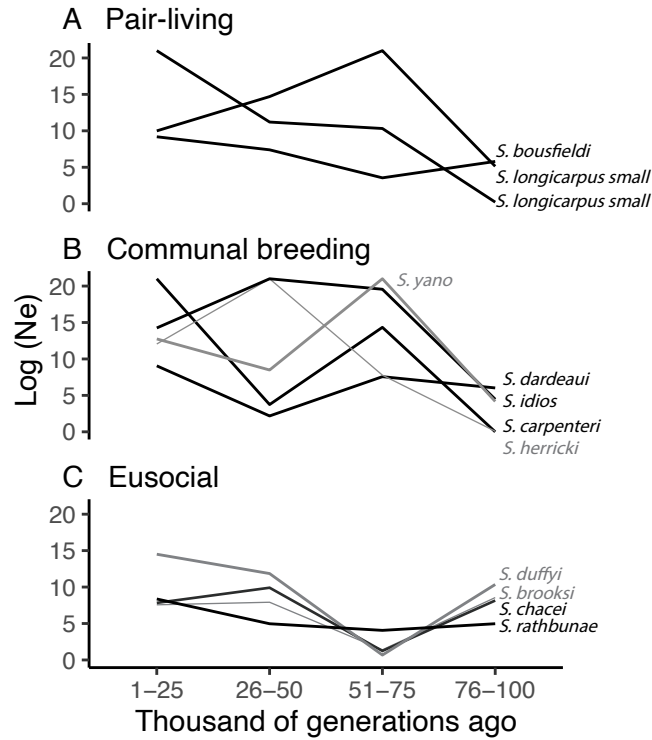
486 **Data Availability.** Supporting data is available from the Supporting Information. Sequence
487 reads were deposited in NCBI's Sequence Read Archive (Accession numbers: SAMN14351547
488 - SAMN14351641). Additional data is available in Dryad.

489



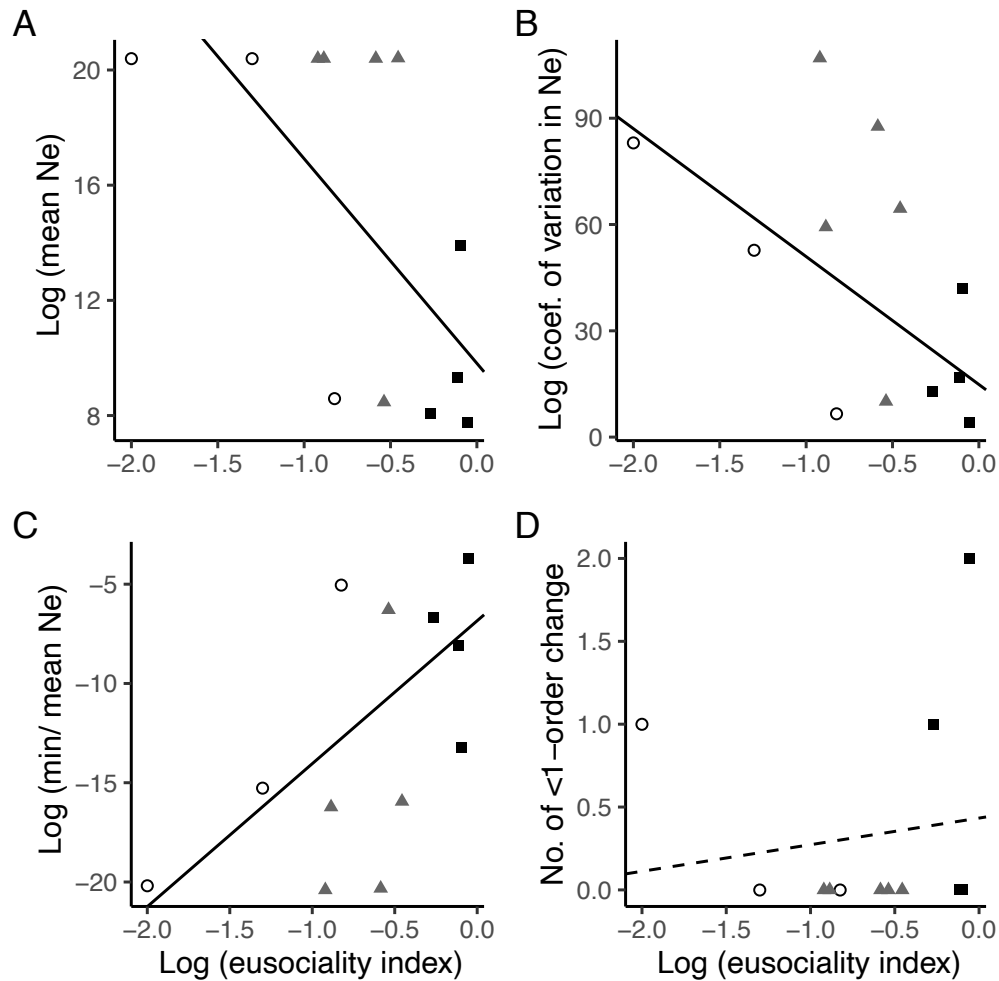
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Fig. 1. Collection sites and evolutionary relationships among 12 sponge-dwelling snapping shrimps in the genus *Synalpheus* used for comparative demographic inference. Each shape corresponds to a different sampling locality. The color of each shape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



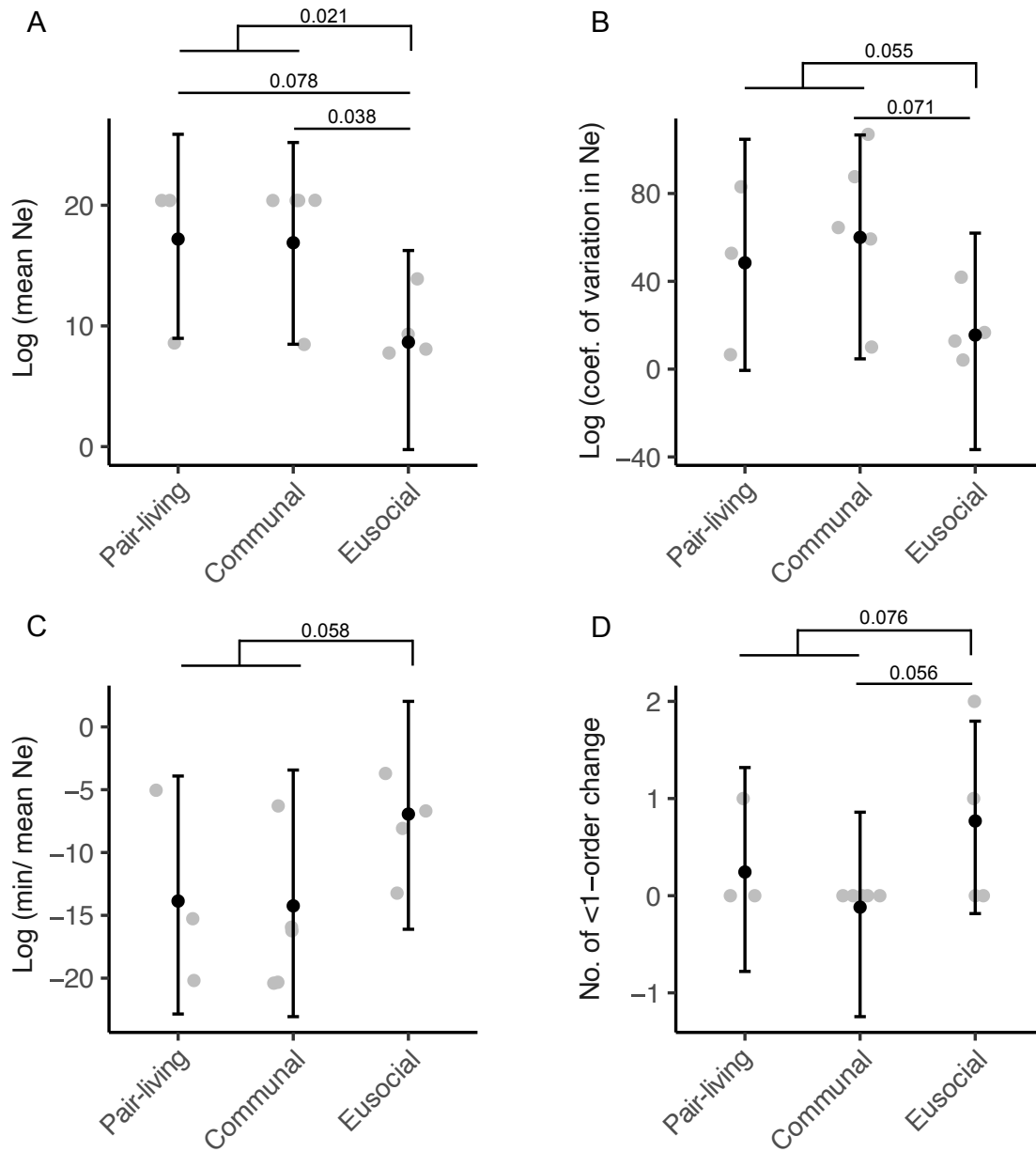
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Fig. 2. Best model estimates of N_e across 100,000 generations in 12 *Synalpheus* species exhibiting different forms of social organization (A: pair-living, B: communal breeding, C: eusocial). Each line represents N_e for a species, with species label on the right. Some lines were shown as grey or thin grey lines for clarity. Bootstrap estimates are shown in Fig S2.



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505

506 **Fig. 3.** Relationships between the eusociality index and metrics of population size and stability in
507 12 *Synalpheus* species: (A) mean N_e across time, (B) coefficient of variation in N_e , (C) min/mean
508 N_e and (D) No. of <1-order change in N_e . Symbols represent raw values: open circles = pair-
509 forming species, grey triangles = communal breeding species, dark squares = eusocial species.
510 Solid and dashed lines represent significant and non-significant regression slopes predicted using
511 Bayesian phylogenetic mixed models, respectively.



512
513

514 **Fig. 4.** Metrics of population size and stability across 12 *Synalpheus* shrimps exhibiting different
515 forms of social organization. Eusocial species have lower mean N_e across time (A), but more
516 stable values of N_e across generation time as indicated by lower CV (B), higher min/mean N_e
517 (C), and higher no. <1-order change (D). Grey dots are raw values, black dots are posterior mean
518 predicted using Bayesian phylogenetic mixed model, bars are the 95% posterior distributions,
519 and pMCMC values are twice the probability that the posterior distribution of the difference is
520 above or below zero.

521

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