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Reproductive skew drives patterns of sexual dimorphism in sponge-dwelling snapping shrimps

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Sexual dimorphism is typically a result of strong sexual selection on male traits used in male–male competition and subsequent female choice. However, in social species where reproduction is monopolized by one or a few individuals in a group, selection on secondary sexual characteristics may be strong in both sexes. Indeed, sexual dimorphism is reduced in many cooperatively breeding vertebrates and eusocial insects with totipotent workers, presumably because of increased selection on female traits. Here, we examined the relationship between sexual dimorphism and sociality in eight species of *Synalpheus* snapping shrimps that vary in social structure and degree of reproductive skew. In species where reproduction was shared more equitably, most members of both sexes were physiologically capable of breeding. However, in species where reproduction was monopolized by a single individual, a large proportion of females—but not males—were reproductively inactive, suggesting stronger reproductive suppression and conflict among females. Moreover, as skew increased across species, proportional size of the major chela—the primary antagonistic weapon in snapping shrimps—increased among females and sexual dimorphism in major chela size declined. Thus, as reproductive skew increases among *Synalpheus*, female–female competition over reproduction appears to increase, resulting in decreased sexual dimorphism in weapon size.

1. Introduction

Sexual selection often results in sexual dimorphism in which morphological traits related to competition or mate attraction are more pronounced in males [1–3]. This occurs because males can typically increase their reproductive success more by mating multiply than can females [4,5]. The ratio of receptive males to receptive females at any time, the operational sex ratio (OSR) [6], quantifies this intensity of male competition for mates [7]. In polygynous species, the OSR is often male-skewed and positively correlated to the degree of sexual dimorphism in traits related to mating competition, assuming all adults in the population are reproductively active [8]. Interestingly, this assumption is violated in many social animals living in societies with high reproductive skew where most individuals do not reproduce (i.e. helpers or workers).

In cooperatively breeding vertebrates, most helpers are totipotent but not reproductively active. In such systems, both males and females may experience strong intrasexual competition for mates or breeding opportunities, and thus females may have equally high (or even higher) variance in reproductive success than males [8–11]. Ultimately, selection on the same competitive traits used in intrasexual competition for access to mates, resources or social rank can be as strong in females as in males of these social species [9,11,12]. For example, cooperatively breeding birds are generally not sexually dimorphic [13], and sexual dimorphism in plumage and body size is reduced in cooperative African starlings (Sturnidae) compared with their non-cooperative relatives [11]. Similarly, eusocial insects also tend to express low degrees of sexual dimorphism [14], and in

facultatively eusocial species where totipotent (non-sterile) workers can replace the queen (e.g. [15–17]), there may be strong competition among female workers to obtain breeding opportunities. Aggressive interactions between queens and totipotent workers in many Hymenoptera (reviewed in [18]) suggest that eusocial insects exhibit high intrasexual competition among females. For example, in lower termites, neotenic workers of both sexes can replace the royal pair, but only after killing other neotenic [19,20]. Moreover, in the hover wasp *Liostenogaster flavolineata*, whose workers are totipotent, the degree of physical aggression among workers increases with rank [21]. Although sexual dimorphism appears to be reduced in a variety of social species, explicit tests of this hypothesis have been limited to comparisons of social and non-social species (e.g. [11]). A stronger demonstration of how sociality influences the evolution of sexual dimorphism would be to compare related species that vary continuously in their social structures, or their levels of reproductive skew (i.e. number of breeding positions per colony member).

The snapping shrimp genus *Synalpheus* is an ideal group within which to investigate the relationship between reproductive skew and sexual dimorphism because closely related species vary in social structure and show extreme elaboration of weapons used for, among other purposes, obtaining mates. Not only has eusociality evolved independently at least four times [22–24] in the group of approximately 45 West Atlantic (Gambarelloides) species [25], but reproductive skew varies continuously among species with different social structures: (i) *eusocial species* live in colonies with a single or a few ‘queens’ and a few to hundreds of non-breeding workers; (ii) *communal species* live in groups with multiple breeding pairs, typically with equal ratios of adult males and females and (iii) *pair-living species* live in sponges with a single breeding pair per sponge [23,26]. All species within the Gambarelloides groups live obligatorily in sponge canals, and therefore appear to face similar ecological constraints on social living.

In addition to their complex social behaviour, snapping shrimps are also known for their extreme armament elaboration—one of the first pair of walking legs is enlarged to form a snapping claw (major chela) [27], which serves mainly as a weapon and signal in conspecific interactions [28–31]. The larger major chela in males [27,28] is generally considered a sexually selected trait [32] because it mediates male–male competition for access to receptive females in caridean shrimps [33]. Therefore, we expected that larger major chela in females would also be selected for when competition among females is higher.

To study the relationship between reproductive skew and sexual dimorphism, we examined sex ratio variation, armament dimorphism and reproductive skew in eight species of communal and eusocial *Synalpheus*. The five eusocial species represent most of the known eusocial species in *Synalpheus*; a few other rare species were only recently described from very small samples, and others have apparently gone locally extinct [34]. The three communal species that we studied represent the primary communal species that can reach large colony size similar to eusocial species. As eusocial *Synalpheus* species have totipotent workers that show reduced reproductive development when the queens are present but compete for dominant breeding positions when queens are removed [35], we hypothesized that as reproductive skew increases (leading to fewer breeding positions per colony member), higher intrasexual competition among females for access to breeding

opportunities would result in stronger selection on weapons in females and ultimately reduced sexual dimorphism. To test this hypothesis, we used both histology and scanning electron microscopy [36,37] to determine the sex and degree of gonadal development of workers. First, we calculated the proportions of mature males and females within colonies to estimate the degree of potential reproductive conflict in each species. Second, we used these data to estimate both the adult sex ratios (ASRs) and OSRs as suggested by Szekely *et al.* [38], as these metrics provide different but complementary information: ASR is more influenced by demographic processes, whereas OSR is more affected by individual mating prospects. Third, we measured sexual dimorphism based on female and male allometries between chela length and body size. Lastly, we calculated the eusociality index [39] for each species as a measure of reproductive skew (*sensu* [23]). We compared these metrics among species of *Synalpheus* to test three key predictions, namely that as reproductive skew increases, (i) reproductive conflict among females would increase, (ii) females would be expected to develop larger weapons and (iii) sexual dimorphism would decrease. Ultimately, this study sheds new light on how patterns of reproductive skew influence the evolution of weapons and sexual dimorphism in social species that cannot be explained by OSR.

2. Material and methods

(a) Histology

We sampled five eusocial *Synalpheus* species (*S. brooksi*, *S. chacei*, *S. duffyi*, *S. elizabethae* and *S. regalis*) and three communal species (*S. dardeauai*, *S. pectiniger* and *S. yano*) from Belize, Florida, Jamaica and Panama between 2003 and 2014. We collected whole sponges using SCUBA, and then removed and identified all shrimps inhabiting each sponge under light microscopy. Individuals of the same species from a single sponge were considered a colony. Ovigerous (i.e. egg-bearing) individuals and those with a brood pouch were considered to be reproductive females (i.e. queens). Individuals with a brood pouch have extended pleura on the abdomen, which indicated a recent release of eggs or larvae, and were found only in communal species; 27 of these females were confirmed to have mature ova by histology. Subsets of non-ovigerous individuals were sexed using histology or scanning electronic microscopy (SEM).

We chose 20 non-ovigerous individuals from four to six colonies from each species for histological examination ($n = 670$ total), excluding visually individuals of the smallest size class (i.e. juveniles). Specimens were preserved in Davidson’s fixative (3 : 3 : 2 : 1 of distilled water, 95% ethanol, 37% formaldehyde and glacial acetic acid), decalcified overnight (in 0.1 g ml^{-1} sodium citrate in 22.5% formic acid), dehydrated, infiltrated and embedded in paraffin using standard protocols [40]. Sagittal sections (3–5 μm) were cut with a rotary microtome and mounted onto glass slides before staining with haematoxylin and eosin. Depending upon an individual’s carapace length (CL), we examined six to 12 sets of three to five continuous sections, each separated by 20–30 μm until at least half of the specimen was sectioned.

Individuals were sexed and classified as immature or mature based on gonadal development. Males were scored for the presence of sperm or testis. Sperm were highly basophilic with the distinct umbrella-shape characteristic of decapod crustaceans and were located in the testis, vas deferens, or in an enlarged sac near the gonad opening (gonopore) at the base of the fifth walking leg. Females were scored for the presence of developing oocytes, young ova or mature ova according to Bell & Lightner

[41]. Mature ova had lipid-filled cytoplasm and were distinctly larger cells than young ova. Thus, individuals were categorized as (i) mature males with sperm and testis, (ii) immature males with only testis, (iii) mature females with mature ova or (iv) immature females with developing oocytes or young ova. Additionally, a few specimens were considered to be hermaphrodites (i.e. intersex) when both a vas deferens and an oviduct were found at the bases of the third and fifth walking legs (coxae of pereopods), respectively [36]. Hereafter, we refer to these individuals as hermaphroditic, rather than intersex (*sensu* [37]), because of histological evidence of sequential hermaphroditism (see the electronic supplemental material).

(b) Scanning electronic microscopy

For sex determination using SEM, we sampled at least 10 non-ovigerous individuals (mean = 17.71; range = 11–24) in the adult size classes per colony for eusocial species and at least four individuals (mean = 4.82; range = 4–7) per colony for communal species (table 1); the lower sample size in communal species was owing to their smaller colony sizes. Ethanol-preserved specimens were dehydrated with hexamethyldisilazane [42] and examined in the Microscopy and Imaging Facility at the American Museum of Natural History, New York. Specimens were scored according to the presence of male gonopores on the bases of the third walking legs and/or female gonopores on the bases of the fifth walking legs [36]. Specimens were considered to be hermaphrodites when both male and females gonopores were present.

(c) Reproductive maturity and sex ratios

We measured CL and major chela length (MCL) from photographs (*sensu* [36]) using IMAGEJ v. 1.48 [43]. We estimated the size at maturity for each sex and species separately as the size of the smallest individuals that had mature gonads (see the electronic supplementary material). Only individuals larger than the size at maturity were considered adults and used in subsequent analyses on proportions of mature males and females, sex ratios, and allometries. Although our delineation of maturation size as the size of the smallest individuals is somewhat arbitrary, a more stringent criterion produced results that were qualitatively similar (see the electronic supplementary material).

As our histological samples represented a subsample of non-ovigerous individuals in each colony (20 individuals out of a maximum colony sizes of 350 and 88 for eusocial and communal species, respectively), we estimated the number of mature males, immature males and non-ovigerous females in non-ovigerous individuals, excluding reproductive females (i.e. those with eggs or extended pleura), based on proportions calculated from the subsample. The total number of mature females included both the observed number of reproductive females and the estimated number of mature non-ovigerous females. Thus, for each colony we calculated (i) the proportion of mature females as the number of mature females to total females, (ii) the proportion of mature males as the number of mature males to total males, (iii) the ASR as the number of males divided by the sum of females and males (mature and immature) and (iv) the OSR as the number of mature males divided by the sum of mature females and mature males. For the proportions of mature females and males, four colonies were excluded from the analysis: two colonies of *S. regalis* that had no females and two colonies of *S. duffyi* in which all colony members were smaller than the maturation size. To estimate potential reproductive conflict, we compared the proportions of mature females and males in communal and eusocial species using generalized linear mixed models with binomial responses, with species and colony included as random factors. *P*-values were obtained from likelihood ratio tests. We further tested for the effect of body size on the difference in the proportion of immature females

between communal and eusocial species (see the electronic supplementary material).

Sex ratios from SEM were calculated from non-hermaphrodites, and ASRs of the entire colony were estimated as they were from histological data. Sex ratios from SEM could not be assessed for *S. duffyi* and *S. pectiniger* because all non-ovigerous individuals were hermaphrodites. As SEM cannot assess the functional sex of an hermaphrodite (see the electronic supplementary material), we performed subsequent analyses based on ASRs from histology. Excluding *S. duffyi* and *S. pectiniger*, for which these calculations were impossible, ASRs calculated from SEM and histology did not differ for any species (all $t < 0.64$, all $p > 0.064$), except for *S. regalis* ($t_{8,91} = 3.37$, $p = 0.0084$; table 1; electronic supplementary material, figure S1). We tested ASRs and OSRs against 0.5 (i.e. a 50:50 sex ratio) in each colony using G-tests of goodness-of-fit with sequential Bonferroni correction, and for each species using repeated G-tests [44]. When sex ratios varied significantly among colonies for a given species, we examined sex ratios for each colony instead of by species.

(d) Social structure

Social structure was estimated using a variation of the eusociality index [38], calculated as $E = 1 - (2 \times Q)/N$, where N is colony size and Q is the number of reproductive females (*sensu* [22,23]). The eusociality index (E) incorporates both a colony's size and its reproductive skew making the simplifying assumption that all breeding individuals contribute equally to offspring production. We determined whether the proportion of mature females, ASR and OSR were each correlated with E using linear regression; we also made similar comparisons based on categories of sociality (communal versus eusocial; see the electronic supplementary material).

(e) Sexual dimorphism

To quantify sexual dimorphism for each species, we first examined the allometry for each sex between the logarithm-transformed CL and MCL using a major-axis regression [45]. We used major-axis regression instead of ordinary least-squares regression because we were interested in the underlying relationship between CL and MCL instead of predicting MCL from CL, and vice versa [46]. To determine if females develop larger weapons with increasing skew, we compared the difference in the allometric slopes of each species by sex and sociality (communal versus eusocial) using ANOVA and performed linear regressions between E and the allometric slopes of females and males.

We quantified sexual dimorphism for each species as the ratio of the male to female allometric slopes of MCL on CL. An allometry ratio equal to 1 means that females and males have the same allometric slope, whereas an allometry ratio of more than 1 means that males have a larger allometric slope than females, and an allometry ratio less than 1 means that females have a larger allometric slope than males. In other words, larger allometric ratios mean that males have a steeper increase in major chela size with CL than females. We used a ratio of slopes instead of the difference because the magnitude of the difference will be affected by the size of the species (range of mean species CL = 2.4–6.4 mm). Additionally, we compared the slopes instead of the intercepts because of a significant interaction between CL and sex in predicting MCL (generalized linear mixed models with species as random factor, $\chi^2_1 = 63.6$, $p < 0.0001$); hence a difference in the intercept cannot accurately quantify sexual dimorphism.

We fit allometry ratio as a function of OSR, CL, and either sociality (communal versus eusocial, ANCOVA) or E (multiple regression). We included mean species CL as a covariate in our models to control for body size, as sexual size dimorphism often varies with body size [47]. The proportion of mature females was not used as a predictor because it has the same numerator

Table 1. Proportions of mature females and males, sex ratios (ASR and OSR), proportions of hermaphrodites (herm.) and eusociality index (*E*) in *Synalpheus* spp. from histology and scanning electron microscopy. Values inside brackets are standard errors. ind., individual; prop., proportion.

social system	species	histology					scanning electron microscopy						
		sample size		prop. of mature females	prop. of mature males	ASR	OSR	prop. of herm.	<i>E</i>	sample size		prop. of herm.	
		colony	ind.							colony	ind.		ASR
eusocial	<i>S. brooksi</i>	5	124	0.38 (0.11)	0.96 (0.02)	0.63 (0.04) ^a	0.81 (0.05) ^b	0.00 (0.00)	0.79 (0.06)	3	58	0.55 (0.03)	0.04 (0.02)
	<i>S. chacei</i>	5	91	0.68 (0.09)	0.92 (0.03)	0.70 (0.05) ^a	0.75 (0.06) ^a	0.00 (0.00)	0.90 (0.02)	3	52	0.59 (0.05)	0.10 (0.06)
	<i>S. duffyi</i>	5	49	0.38 (0.31)	0.62 (0.19)	0.50 (0.22) ^b	0.85 (0.08) ^a	0.00 (0.00)	0.89 (0.06)	2	37	n.a.	1.00 (n.a.)
	<i>S. elizabethae</i>	5	117	0.41 (0.09)	0.97 (0.03)	0.54 (0.05) ^c	0.75 (0.04) ^c	0.00 (0.00)	0.96 (0.01)	3	58	0.59 (0.06) ^a	0.19 (0.06)
	<i>S. regalis</i>	6	92	0.26 (0.25)	1.00 (0.00)	0.86 (0.06) ^c	0.99 (0.01) ^c	0.00 (0.00)	0.97 (0.02)	5	96	0.60 (0.05) ^b	0.00 (0.00)
communal	<i>S. dardeauvi</i>	4	31	0.63 (0.05)	0.96 (0.04)	0.48 (0.02)	0.59 (0.04)	0.00 (0.00)	0.34 (0.07)	5	24	0.64 (0.06) ^b	0.00 (0.00)
	<i>S. pectiniger</i>	5	101	0.83 (0.10)	0.97 (0.03)	0.65 (0.07) ^b	0.70 (0.05) ^a	0.15 (0.12)	0.51 (0.08)	1	4	n.a.	1.00 (n.a.)
	<i>S. yano</i>	5	65	0.95 (0.03)	0.97 (0.03)	0.57 (0.04) ^a	0.58 (0.03) ^a	0.00 (0.00)	0.23 (0.04)	3	25	0.61 (0.07) ^a	0.00 (0.00)

^aSex ratio significantly deviated from 50 : 50.^bSex ratio varied significantly among colonies.^cSex ratio varied significantly among colonies, but all colonies were significantly deviated from 50 : 50.

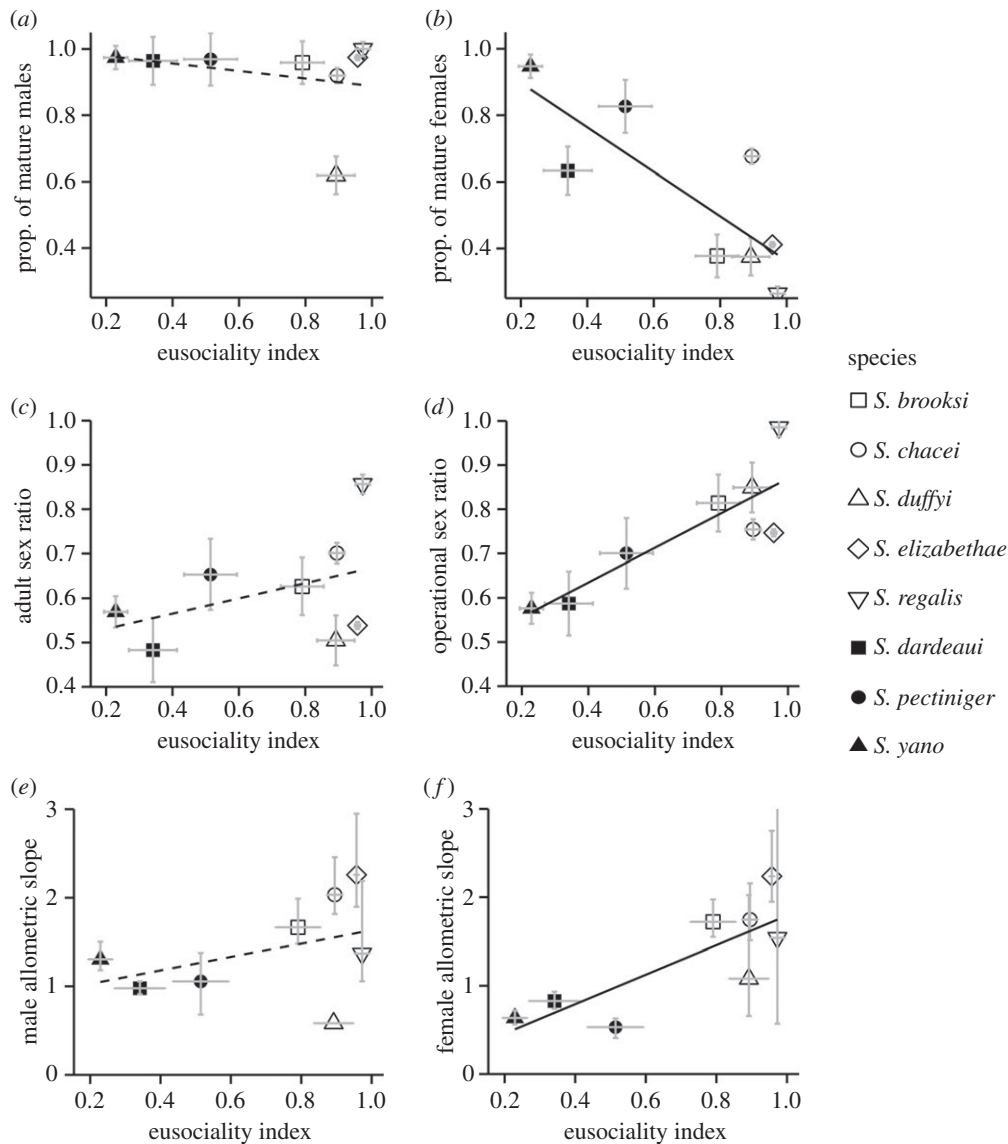


Figure 1. Relationships between eusociality index (E) and (a) proportion of mature males, (b) proportion of mature females, (c) ASR, (d) OSR, (e) male allometric slope and (f) female allometric slope in *Synalpheus*. Grey error bars indicate standard errors. Open and closed symbols represent eusocial and communal species, respectively. Solid and dashed lines indicate significant (at $p < 0.05$) and non-significant regressions, respectively.

as OSR. Importantly, to control for shared evolutionary histories, we calculated phylogenetic contrasts [48] for all variables using the R package *ape* [49] and repeated the regression analysis. A phylogenetic tree of the eight species was extracted from a Bayesian consensus tree consisting of 1958 bp from three genes (16S, COI and EF2) [50]. We also performed a linear regression of allometry ratio and OSR. All analyses were performed with R v. 3.0.1 [51].

3. Results

(a) Reproductive maturity and sex ratios

Proportions of mature females and males, ASRs, OSRs and E for each species are shown in table 1. Significantly more males were reproductively mature than females in both communal and eusocial species (communal: $\chi^2_1 = 17.44$, $p < 0.0001$; eusocial $\chi^2_1 = 210.25$, $p < 0.0001$; electronic supplementary material, figure S2a). The proportions of reproductively mature males in eusocial and communal species did not differ ($\chi^2_1 = 0.33$, $p = 0.57$; electronic supplementary material, figure S2a), but eusocial species had a lower proportion of mature females than did communal species ($\chi^2_1 = 4.52$, $p = 0.033$; electronic supplementary material, figure S2a). This is consistent with

the finding for *S. elizabethae* [35], that female—but not male—workers in eusocial species were reproductively suppressed.

In most species, nearly all males were mature and the proportion of mature males did not vary with E ($F_{1,6} = 0.47$, $p = 0.52$, adj. $r^2 = -0.083$, figure 1a). By contrast, the proportion of mature females was strongly negatively correlated with E ($F_{1,6} = 11.18$, $p = 0.016$, adj. $r^2 = 0.59$, figure 1b), such that species exhibiting high reproductive skew had lower proportions of mature females. ASRs of most species from both histology and SEM averaged near 50:50 or slightly male-skewed, but many species showed high variability among colonies (table 1; electronic supplementary material, figure S3). Although ASR was not significantly related to E ($F_{1,6} = 1.243$, $p = 0.31$, adj. $r^2 = 0.034$, figure 1c), OSR increased strongly with E ($F_{1,6} = 15.93$, $p = 0.0072$, adj. $r^2 = 0.68$, figure 1d), becoming more male-biased as skew increased (see also table 1; electronic supplementary material, figure S1).

(b) Sexual dimorphism

We quantified sexual dimorphism for each species by the allometry of CL and MCL (electronic supplementary material, figure S4). Overall, allometric slopes did not differ

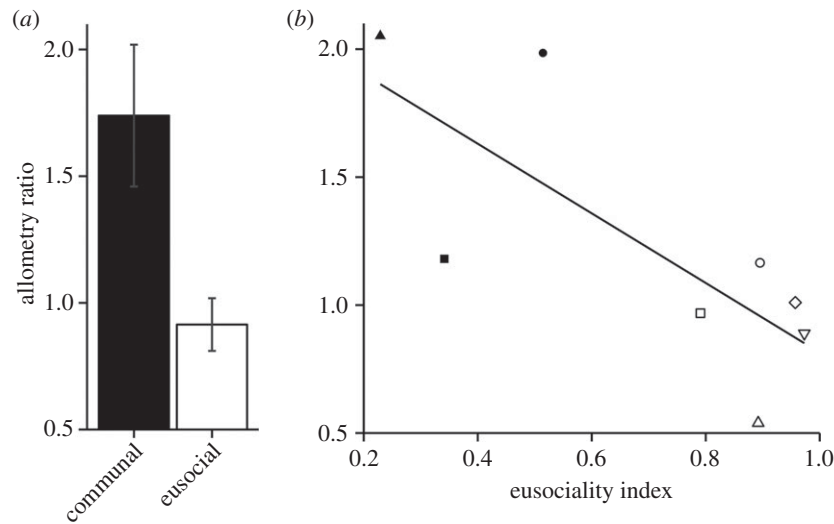


Figure 2. Relationships between allometry ratio and (a) sociality and (b) eusociality index. White and black bars represent communal and eusocial species, respectively. Open and closed symbols represent eusocial and communal species, respectively; see figure 1 for more detail on symbols used in (b).

Table 2. Results of multiple regressions estimating the effects of (a) sociality or (b) eusociality index, CL and OSR on allometry ratio using raw data and (c) phylogenetic contrasts in *Synalpheus*.

data type	predictor variable	<i>F</i>	d.f.	<i>p</i>	adj. <i>r</i> ²	β	<i>t</i> ₁	<i>p</i>
(a) raw data	overall model	13.22	3, 4	0.015	0.84			
	sociality	17.45	1, 4	0.014		−1.20	−4.18	0.014
	CL	11.18	1, 4	0.029		−0.36	−3.34	0.029
	OSR	2.10	1, 4	0.22		−1.51	−1.45	0.22
(b) raw data	overall model	7.56	3, 4	0.04	0.74			
	eusociality index	9.11	1, 4	0.034		−2.40	−3.02	0.039
	CL	7.30	1, 4	0.054		−0.40	−2.70	0.054
	OSR	0.44	1, 4	0.54		−0.94	−0.67	0.54
(c) contrasts	overall model	23.03	3, 3	0.013	0.92			
	eusociality index	40.30	1, 3	0.0079		−3.10	−6.35	0.0079
	CL	42.34	1, 3	0.0074		−0.44	−6.50	0.0074
	OSR	1.09	1, 3	0.37		−0.76	−1.05	0.37

between the sexes ($F_{1,1} = 0.25$, $p = 0.62$), but eusocial species had steeper allometry, i.e. larger major chela for a given body size (CL) than communal species ($F_{1,1} = 9.47$, $p = 0.0088$). The allometric slopes of male chelae were mostly positive or isometric, whereas the allometric slopes of female chelae were negative for communal species but positive for eusocial species (electronic supplementary material, figures S4 and S5). Moreover, allometric slopes increased with *E* in females ($F_{6,1} = 10.95$, $p = 0.016$, adj. $r^2 = 0.58$, figure 1f) but not in males ($F_{6,1} = 1.15$, $p = 0.32$, adj. $r^2 = 0.022$, figure 1e). Thus, in eusocial species with high reproductive skew, large females had proportionally larger chelae, whereas in communal species with lower skew, large females had proportionally smaller chelae.

Allometry ratio (i.e. the degree of sexual dimorphism in chela allometry) was significantly higher in communal species than eusocial species (table 2 and figure 2a) and decreased with *E* (figure 2b). Moreover, multiple regression showed that allometry ratio was significantly related to *E* and mean CL, but not to OSR, both using raw data (table 2

and figure 3) and phylogenetically independent contrasts (table 2; electronic supplementary material, figure S6). Critically, the allometry ratio decreased as *E* increased (i.e. greater skew), as CL increased (i.e. body size), but not as OSR increased, both using raw data (table 2 and figure 3) and phylogenetically independent contrasts (table 2; electronic supplementary material, figure S6). Finally, raw values of allometry ratio were not significantly correlated with OSR ($F_{1,6} = 4.92$, $p = 0.068$, adj. $r^2 = 0.36$, figure 3d).

4. Discussion

Selection on traits used for access to mates, resources or social rank may be similarly strong in both sexes in social vertebrates and insects with totipotent workers because intra-sexual competition is similarly strong in females and males [9,11,12]. Here, we show that patterns of sexual dimorphism in secondary sexual characteristics do not just differ between social and non-social species (*sensu* [11]), but instead vary

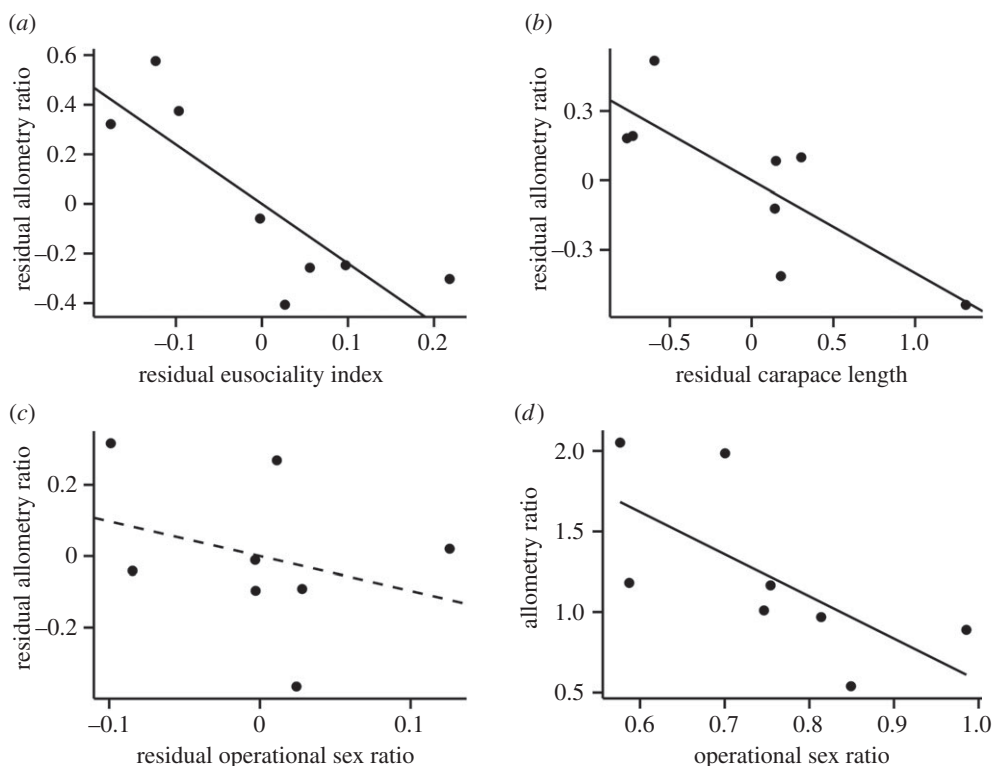


Figure 3. Relationships between allometry ratio, eusociality index (E), OSR and CL. Axes show (a) partial residuals controlling for OSR and CL, (b) partial residuals controlling for E and OSR, (c) partial residuals controlling for E and CL, and (d) regression of raw allometry ratio and OSR. Solid and dashed lines indicate significant (at $p < 0.05$) and non-significant regressions, respectively. In (a,b), the degree of sexual dimorphism in chela allometry (i.e. allometry ratio) decreased as reproductive skew (i.e. E) and CL increased. In (c,d), sexual dimorphism decreased with OSR but not after controlling for E and CL.

continuously among closely related social species that differ in their degree of reproductive skew. In agreement with our predictions, as reproductive skew increased (indicated by increasing E) across sponge-dwelling snapping shrimps, (i) potential reproductive conflict among females increased because fewer females were able to reach reproductive maturity, (ii) females—but not males—had larger competitive weapons (i.e. the snapping chela), and importantly (iii) sexual dimorphism of the snapping chela decreased. Moreover, sexual dimorphism in *Synalpheus* was well predicted by the degree of reproductive skew, but not by OSR.

The difference between ASR and OSR reflects mating prospects of individuals driven by underlying physiology or proximate mating opportunity [38]. In *Synalpheus*, sociality and the presence of reproductive suppression in species with high reproductive skew (suggested here and experimentally demonstrated in [35]) dramatically affected the transition from ASR to OSR. Both SEM and histological analysis indicated that the ASRs of eusocial and communal species were similar, indicating that *Synalpheus* species with very different social structures may have similar demographic structures [38]. OSR deviated only slightly from ASR (and a 50:50 sex ratio) in low-skew species; however, OSR deviated considerably from ASR, being heavily male-biased, in high-skew species. The higher OSRs in high-skew species were owing to sex-specific reproductive suppression in females, hence the prevalence of mature female workers—but not male workers—decreased. Although the positive relationship between OSR and E may seem circular, it is not: high values of E are the result of high queen to workers ratios (i.e. reproductive skew) regardless of the sexes and maturation status of the workers. Thus, the calculation of E is independent of OSR or the proportion of mature females or males in a colony.

Classical sexual selection theory predicts that when only males compete for mates, sexual dimorphism should increase with OSR because as OSR increases (i.e. more reproductively mature males than females), males would evolve larger secondary sexual traits to compete more effectively for females [6,7]. In contrast to this prediction, we found that sexual dimorphism in fighting chelae (as depicted by allometry ratios) actually decreased with OSR. However, after controlling for the effect of E and mean species body size, OSR no longer predicted sexual dimorphism. Although OSR did not drive the overall pattern of sexual dimorphism in *Synalpheus*, low-skew species did exhibit sexual dimorphism: males of communal *Synalpheus* species had proportionally larger major chelae than females. This is expected because in communal species, males have easy access to female neighbours, and as males of caridean shrimps can mate multiple times within a molt-cycle [52,53], they may have a higher variance in reproductive success (and be under stronger sexual selection) than females.

Why do *Synalpheus* species depart from the prediction that male-biased OSR should select for stronger sexual dimorphism? Similar to cooperatively breeding vertebrates and facultatively eusocial insects with totipotent workers, reduced sexual dimorphism may be driven by increased selection on females to compete with other females for reproductive opportunities and/or access to mates [10,11,54]. We have shown elsewhere that in the eusocial *S. elizabethae*, queens can suppress reproduction in female—but not male—workers [35]. The prevalence of immature female workers in high-skew *Synalpheus* species found in this study is consistent with the hypothesis that the sex-specific reproductive suppression demonstrated in *S. elizabethae* is also operating in these other species. The immature workers in these species are reproductively primed for becoming

replacement queens [35], hence, the potential for reproductive conflict among females is high. As most males are reproductively capable but the queen typically mates with a single one [55], competition among males and the variance of male reproductive success may remain high in eusocial *Synalpheus* species. Although it is unclear how often a worker could inherit a colony in eusocial shrimps, worker inheritance occurs in eusocial species like termites [18,54,56] and naked mole-rats [57]. Although species with multiple breeding females per colony (e.g. *S. brooksi* and *S. elizabethae*) are predicted to exhibit stronger intraspecific reproductive competition among females than species with a single breeder per colony [58], reproductive skew (i.e. E) incorporates the degree of breeding by multiple reproducers into the ratio of the number of queens to colony size. Therefore, we expect female–female competition to increase linearly with reproductive skew. In support of this idea, we have shown that (i) female allometric slopes were higher as reproductive skew increased and (ii) female *Synalpheus* had larger chelae in species with higher skew. This is strikingly similar to African starlings, in which females in cooperatively breeding species were more ornamented than non-cooperative species [11]. Finally, we have shown that sexual dimorphism decreased (i.e. became more monomorphic) with increasing skew.

The pattern we observed in sexual dimorphism of the major chela also reflects other aspects of social behaviour in *Synalpheus*. The trend of relatively larger chelae in eusocial species (although only significant in females) suggests that eusocial species may be better competitors against rivals of the same size in conventional (non-sexual) competition, irrespective of their ability to cooperatively defend [30]; this is consistent with community-level data showing that eusocial species were more abundant than non-social species on Belizean coral reefs [23]. Larger weapons in eusocial species may be adaptive for colony defence as in many social insects where selection acts on traits used to defend valuable resources that colonies control [59]. Therefore, chela size may be driven by both natural and sexual/social selection. Moreover, females in communal species had smaller major chelae at a given size (negative allometry) than males, while the pattern is reversed in eusocial species. This could reflect differential resource

allocation, such that females in communal species allocate more resources to reproduction [60], whereas females in eusocial species allocate more resources to weaponry.

Although social vertebrates and invertebrates differ greatly in their ecology, life history and genetic systems, social systems with strong reproductive skew appear to have a similar effect of reducing the degree of sexual dimorphism in weapons used in intrasexual competition in both kinds of animals. We have shown that species of snapping shrimps with high reproductive skew are sexually monomorphic in the snapping chela, despite having highly male-skewed OSRs. This is likely a result of selection in eusocial species for larger antagonistic weaponry in females used in intrasexual competition for breeding opportunities, as supported by the rarity of reproductively mature females in highly skewed species [61]. Thus, this study not only supports the recent refocus on social competition among females in altruistic societies [10,54,61,62], but also demonstrates consistent differences in patterns of sexual dimorphism among social species with different forms of altruistic societies, not just between social and non-social species.

Data Accessibility. Data available from table 1 and the Dryad Digital Repository: 10.5061/dryad.h360q.

Authors' Contributions. S.T.C.C. carried out the experiment and histology work, carried out the statistical analyses, participated in the design of the study and drafted the manuscript; S.T.C.C., J.E.D. and D.R.R. conceived of the study, designed the study, coordinated the study and helped draft the manuscript. All authors gave final approval for publication.

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