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It's the time of the season: seasonal variation in sexually conflicted size-assortative pairing

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Abstract

Size-assortative pairing is common across a wide range of taxa. In many cases, both sexes would benefit from pairing with a mate larger than themselves. As males and females cannot simultaneously be larger than their pair mate, size differences within pairs reflect which sex is able to obtain this benefit. Snapping shrimp can be found in pairs year-round, and both males and females would benefit from pairing with larger individuals. Larger females are more fecund; males, then, are likely to benefit from pairing with larger females primarily in the reproductive season. Larger individuals are more successful competitors and females benefit more from shared burrow defense than males; for females, then, benefits of pairing with larger males are likely to accrue year-round. In this study, we use field data to test whether within-pair size differences in snapping shrimp correspond more to male or female interests, and whether this outcome differs between seasons. We find that size-assortative pairing varies seasonally: although body sizes of paired males and females are highly correlated year-round, the within-pair size difference is greater during the reproductive season than the nonreproductive season. Furthermore, within pairs, females are larger than males during the reproductive season, while pairs are size-matched or male-biased during the nonreproductive season. These changes in within-pair size relationships suggest seasonal differences in which sex has greater control over pair formation, and highlight nonreproductive benefits associated with monogamous pairing. In addition, these results underscore the importance of considering temporal variation in studies of size-assortative pairing.

Significance statement

In many taxa, it is advantageous for both males and females to mate with larger individuals. As both sexes cannot simultaneously mate with larger individuals, size relationships within pairs reflect the outcome of this sexual conflict. In snapping shrimp, pairs cooperate in defending their burrows from invading conspecifics, and larger individuals are better competitors; larger females are also more fecund. Thus, males obtain a reproductive advantage from mating with larger females, while for females, mating with larger males provides social (territorial defense) benefits. Here, we find seasonal differences in within-pair size relationships, such that females are larger than males during the reproductive season, but pairs in the nonreproductive season are size-matched or male-biased. These results suggest seasonal variation in the outcome of conflict over body size within pairs, and highlights the need to consider temporal variation in size-assortative pairing.

Keywords Monogamy · Size-assortative pairing · Sexual conflict · Long-term pairing

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Introduction

Multiple mating can be advantageous to both males and females; nonetheless, monogamous mating systems (both social and genetic) are found across a wide range of vertebrate and invertebrate taxa (Wickler and Seibt 1981; Black 1996; Kvarnemo 2018). When offspring survival requires care from both parents, social monogamy may be beneficial to both sexes (Wittenberger and Tilson 1980; Reichard 2003). Under most hypotheses to account for

social monogamy, however, monogamous pairing is not the optimal outcome for both (or possibly either) males and females (Parker 1983; Kvarnemo 2018; Reichard 2003). Similarly, in many socially monogamous systems, pair mates are similar in size, ornaments, or other characteristics (Jiang et al. 2013; Janicke et al. 2019; Moura et al. 2021). Mutual preferences for similar individuals (e.g., Borghezan et al. 2019) are one possible mechanism leading to assortative pairing, but often assortative pairing results from other mechanisms (Crespi 1989; Harari et al. 1999; Hoefler 2007; Moura and Gonzaga 2017; Ridley 1983) leading to potential conflicts both within and between the sexes over access to preferred mates. For example, if both sexes benefit from pairing with relatively larger individuals, it is not possible for both sexes to achieve this benefit: both sexes cannot simultaneously pair with an individual larger than themselves (Baldauf et al. 2009). Thus, size differences within pairs may also reflect conflict between the sexes in terms of which sex obtains the size of pair mate that provides the largest benefit to them. Patterns of size-assortative pairing can differ between populations or closely related species (Knowlton 1980; McLain and Boromisa 1987), as well as in the same population at different times (Luddecke 2001, Murata and Wada 2002, Moura and Gonzaga 2017; see also review in Moura et al. 2021). Spatial or temporal variation in within-pair size relationships, then, may provide insight into variation in the factors leading to size-assortative pairing. In this study, we explore temporal variation in patterns of size-assortative pairing in the snapping shrimp *Alpheus angulosus,* McClure 2002, a species in which both sexes are likely to benefit from pairing with larger individuals, to determine whether size-assortative pairing better aligns with male or female interests.

Not surprisingly, most hypotheses proposed to explain the evolution of monogamy focus on reproductive benefits (Wittenberger and Tilson 1980; Reichard 2003). However, cooperative behavior between pair mates may lead to other advantages of associating with a pair mate that are only indirectly related to reproduction ("shared duties," Wickler and Seibt 1981), such as shared construction and/or defense of shelters or territories necessary for both survival and reproduction (e.g., Fishelson 1966; Linsenmair 2007; Mathews 2002a; Diniz et al. 2020), advantages associated with improved foraging success and/or defense of resources (Fricke 1986), reducing risk from predators (Swenson 1993), or thermoregulation (Beauchamp 1999). As with reproductive benefits, the degree to which both sexes benefit from cooperative behavior in nonreproductive contexts may vary. For example, cooperative territorial defense may reduce the eviction likelihood of only one sex, suggesting that this cooperative behavior benefits one sex more than the other (Mathews 2002a). Species that remain paired during

the nonreproductive season provide an opportunity to tease apart reproductive and nonreproductive benefits of social monogamy.

Snapping shrimp of the genus *Alpheus* are typically found in pairs with correlated body sizes (Nolan and Salmon 1970, Schein 1975, Knowlton 1980, Hughes 1996, Boltaña and Thiel 2001, Mathews 2002b, Costa-Souza et al. 2014; but see Barroso et al. 2019). These pairs are generally assumed to be reproductively monogamous: as is typical of caridean shrimp (Bauer 2004), females do not store sperm, and copulation occurs soon after females molt (Rahman et al. 2003), limiting the opportunity for multiple mating within a reproductive event. In *A. angulosus,* embryos develop over the next 20–21 days, and are released shortly before the female's next molt (approximately once per month, Tracey et al. 2013), at which time females can produce a new clutch of eggs (pers. obs.). Most females collected during the reproductive season (approximately May–October) are carrying embryos (Heuring and Hughes 2019), suggesting that females generally reproduce at each molt through this period. *A. angulosus* males in field-collected pairs are genetic fathers of most eggs currently brooded by his pair mate, suggesting that pairs remain together through multiple reproductive events (Mathews 2007). Pairs may persist because males engage in long-term mate guarding, essentially waiting for their pair mate's next molt rather than searching for another female closer to molt. Nonetheless, pairs do not always persist between reproductive events, and pair stability (i.e., how long particular pairs remain together) may be influenced by environmental factors, including predation risk (Knowlton 1980) and sex ratio (*A. angulosus:* Mathews 2002b). How frequently pairs typically change partners remains unknown, but partner change is not limited to the nonreproductive season (Mathews 2002b).

Larger female snapping shrimp are more fecund (Knowlton 1980; Corey and Reid 1991; Pavanelli et al. 2008, 2010; Costa-Souza et al. 2014); in *A. angulosus*, given the more than two-fold difference in body size among reproductive females and correlated increases in fecundity (Heuring 2016), males would likely benefit from pairing with the largest available females. There are no known reproductive benefits to females for mating with larger males. Larger males are likely to be older, as growth appears indeterminate, but it is not clear that females would gain any advantage from reproducing with older males. The reproductive benefit to males is likely to be greatest in the reproductive season, although males could potentially benefit in the subsequent reproductive season by guarding large females throughout the 6–7 month nonreproductive season.

A. angulosus pairs will jointly defend burrows from intruders of both sexes (Mathews 2002a), and larger individuals are better at winning aggressive interactions in both sexes (*A. angulosus*: Heuring 2016; other *Alpheus*

spp.: Nolan and Salmon 1970, Schein 1977, Hughes 1996, Rahman et al. 2003). Both males and females, then, could potentially benefit from pairing with larger mates for shared territorial defense. However, in *A. angulosus*, females appear to benefit more from shared territorial defense than males: paired females are less likely to be evicted by a female intruder than single females, but paired and single males are equally likely to be evicted by a male intruder (Mathews 2002a). Therefore, females are more likely than males to receive a territorial defense benefit when pairing with larger individuals. As burrows are essential shelter and the primary protection from predators year-round, benefits associated with avoiding eviction are likely to accrue year-round.

While patterns of size-assortative pairing are often interpreted in terms of behavioral mechanisms such as choice and competition, long-term pair fidelity and concomitant growth may also result in strongly correlated pair sizes (Baeza 2008; Baeza et al. 2013). In snapping shrimp, seasonal variation in allometry allows for an indirect test of whether size-assortative pairs result from long-term pair bonds with similar growth. Both male and female snapping shrimp have one greatly enlarged claw—the snapping claw—which produces the snap for which they are named. Claw size is highly correlated with body size and is sexually dimorphic, with males having larger claws for a given body size than females, and this allometry also varies seasonally, most likely due to differential investment in either growth of claw or overall body at each molt (Heuring and Hughes 2019): males have larger claws relative to their body size (i.e., steeper claw x body allometry) in the reproductive season than in the nonreproductive season, while females show the opposite pattern. In other words, males differentially invest in claw size during the reproductive season, while females differentially invest in claw size in the nonreproductive season, resulting in decreased sexual dimorphism in claw size in the nonreproductive season. As a result, if shrimp remain with the same pair mates year-round, pair mates would be predicted to be more similar in claw size during the nonreproductive season than in the reproductive season, as female claw size becomes more similar to male claw size during the nonreproductive season.

In this study, we first tested whether pairs are size-assortative in the field by determining whether male and female body sizes are correlated within pairs, and whether the strength of this correlation differs between the reproductive and nonreproductive seasons. Then, we evaluated whether the difference between male and female size within pairs corresponds to male or female interests. On the one hand, if territorial defense benefits to females drive size-assortative pairing, then within pair sizes will be male-biased (males larger than females—that is, females pairing with males that are larger than themselves, and thus better able to provide assistance in territorial defense). On the other hand,

if reproductive benefits to males drive assortative pairing, then within-pair sizes will be female-biased (females larger than males—that is, males pairing with larger, more fecund females). These outcomes may differ seasonally: while territorial defense benefits to females are likely to accrue year-round, reproductive benefits to males are likely to be greater in the reproductive season. Lastly, if pairs formed during the reproductive season remain intact through the nonreproductive season, the difference in within-pair claw size would be predicted to decrease in the nonreproductive season, given reduced sexual dimorphism in claws during this season.

Methods

Shrimp (*Alpheus angulosus*) were collected and measured as in Heuring and Hughes (2019). Briefly, shrimp were collected by hand (May 2014–February 2016) from burrows located among oyster rubble in the intertidal zone at low tide, from three sites around the Charleston Harbor, Charleston County, South Carolina, USA. The primary collection site was at the College of Charleston Marine Lab, located on the southwest side of the harbor (site A, 32.75 N, − 79.90 W); we also collected at a site approximately 1500 m west of site A (site B: 32.75 N, − 79.92 W), and another site across the harbor from site A (site C: 32.77 N, − 79.86 W). In this habitat, *A. angulosus* constructs burrows in soft mud under hard substrate (rocks, oyster rubble, etc.), primarily in the lower intertidal zone, limiting collection to lower low tides (i.e., those that fall below mean lower low water, typically around new and/or full moon). Within the reproductive season (approximately May–October; Heuring and Hughes 2019, see also below), *A. angulosus* females do not appear to reproduce synchronously (Mathews 2002b; Heuring 2016), and egg development at time of collection included recently fertilized, mid-development, and near hatch (Heuring 2016).

Substrate suitable for snapping shrimp burrows is highly abundant; on each collection date, only a small subset of potential substrate can be sampled. We focused our collections in areas where small clumps of hard substrate (oyster rubble, rocks, bricks, etc.) are separated by at least a few centimeters of soft mud (where burrows cannot be constructed), to minimize the likelihood of mistakenly combining animals from different burrows. The small pool of water under each clump of hard substrate was typically too small (generally 30 cm diameter or less) to sustain more than one individual of the same sex, given high levels of potentially lethal same-sex aggression and spacing observed in the lab. Focusing collections on a single habitat type also limits the likelihood that patterns of size-assortative pairing are confounded by differences in habitat structure (see Moura et al. 2021).

To collect shrimp, we gently removed the hard substrate from the mud and sifted through the shallow muddy water (generally less than 15 cm deep) in the depression underneath by hand and/or with a dip net. Shrimp were usually seen before being captured, as they typically swim to the surface and/or edges of the exposed water following the removal of hard substrate. If only one shrimp could be found after digging in the mud under the hard substrate, we considered that individual "single." Some "single" shrimp may have been part of pairs for which we did not find the pair mate, but the frequency of missed individuals is likely to be similar across locations and seasons. When two opposite-sex shrimp were collected from the mud under the same hard substrate, they were considered a pair. Same-sex pairs were rare: of 720 cases in which more than 1 shrimp was collected from under the same hard substrate, 13 were same-sex pairs (11 female, 2 male); these individuals were treated as single in our analyses. Even more rarely (5 of 720 cases total), we would find more than 2 shrimp under the same hard substrate: 2 cases of 3 shrimp, 2 cases of 4 shrimp (both with 2 males and 2 females), and 1 case of 5 shrimp. In these 5 cases, these shrimp were housed together overnight in the lab in a large tank with multiple burrows, and were considered to be paired with the individual they shared a burrow with the next morning; in all cases, shrimp were either alone or in male–female pairs at this time. We did not perform this same overnight test with the few same-sex pairs that were collected, to minimize the risk of same-sex lethal aggression.

All collected shrimp were brought back to the lab for behavioral studies (published elsewhere: Heuring 2016; Heuring and Hughes 2019, 2020). Shrimp were housed individually (if captured as a single) or with their field-captured pair mate in small (15 × 15 × 5 cm) containers with filtered seawater, gravel, and oyster shell or pvc tubing for shelter, and fed flaked fish food every 3 days; containers were cleaned prior to feeding. No animals collected as singles were housed with any other shrimp, and all animals collected in pairs were housed with only their field-captured pair mate. Following behavioral experiments, all shrimp were released at the site of capture in areas we do not typically collect (due to more continuous hard substrate and therefore difficulty in separating shrimp from adjacent burrows), to minimize the likelihood of recapture.

Shrimp body size (body length measured from rostrum to telson) and claw size (length of the claw measured from base of propodus to tip of dactyl) were measured with a ruler to the nearest millimeter within 2 days of capture. (We have found that using a ruler minimizes handling time and autotomization of the snapping claw; for comparison of different measurement techniques, see Heuring and Hughes (2019).) Shrimp with missing or regenerating claws (Pereira et al. 2014) were excluded from analyses of claw size.

As in Heuring and Hughes (2019), the reproductive season was defined as months in which > 50% of field-captured females (averaged across collection dates within each month) were carrying eggs. The nonreproductive season is the remaining months, in all of which 0–20% of captured females were carrying eggs. This operational definition of reproductive periods is thus defined by when the shrimp are observed to be reproducing rather than by calendar months. As has been found in other intertidal crustaceans (e.g., Popp et al. 2020), the beginning and/or end of the reproductive season may vary slightly from year to year, most likely due to local environmental conditions.

In total, across the nearly 2-year study period, we collected 1680 shrimp in 56 collections on 54 days (on 2 days in the reproductive season, we collected at 2 of the sites; in total, there were 42 collections across 11 months in the reproductive season, and 14 collections across 6 months in the nonreproductive season). Collection attempts with fewer than 5 shrimps (typically on days when tides did not allow access to appropriate habitat) were excluded from these totals and subsequent analysis. Note that the apparently higher collection effort for reproductive seasons is driven by 2 months (June 2014 and July 2015; see Fig. 1A) when more shrimp were needed for behavioral studies; excluding these 2 months, the number of collections per month for both reproductive and nonreproductive seasons ranged from 1–4, and depended primarily on the number of days with sufficiently low tides. Most of these collections occurred at our primary site (site A: $n = 31$ days in the reproductive season; $n = 11$ days in the nonreproductive season; site B: $n = 8$ days in the reproductive season; $n = 2$ in the nonreproductive season; site C: $n = 3$ days in the reproductive season; $n = 1$ day in the nonreproductive season).

Seasonal variation in pairing

We tested for seasonal variation in pairing (expressed as number of paired individuals collected per total individuals at each collection) using a generalized linear mixed model (Gaussian distribution and identity link function) with collection date and site as random effects and season (reproductive or nonreproductive) as a fixed effect. Because differences in the likelihood of being paired could be driven by seasonal variation in sex ratio, we also used binomial generalized linear models to determine whether adult sex ratio (expressed as number of males per total individuals; Wilson and Hardy 2002) varies seasonally, in two comparisons: first, we compared adult sex ratio across seasons for all shrimp collected ($n = 42$ collections in reproductive season and $n = 14$ collections in nonreproductive season); second, we compared adult sex ratio only among shrimp that were not collected in a pair ($n = 36$ collections in reproductive season and $n = 14$ in nonreproductive season) because a high
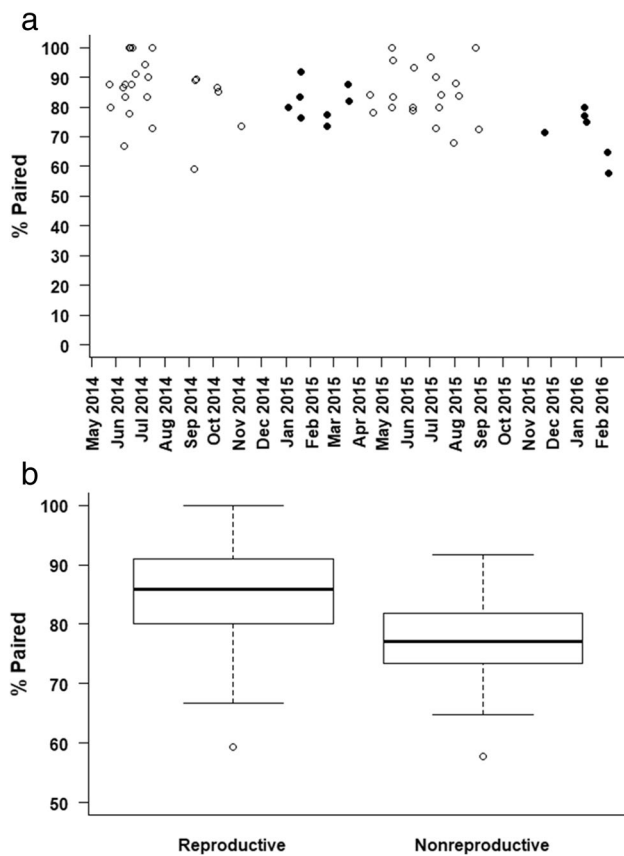
Fig. 1 Seasonal variation in pairing in *A. angulosus*: percent shrimp collected in pairs. **A** Percent shrimp in pairs across collection dates (open circles = reproductive season, *n* = 42; filled circles = nonreproductive season, *n* = 14). Note that reproductive and nonreproductive seasons are operationally defined by the percentage of shrimp reproducing, and so the timing of these seasons may vary slightly between years. **B** Percent shrimp collected in pairs is greater in the reproductive than nonreproductive season

percentage of paired shrimp in the first analysis may obscure a sex ratio bias among unpaired shrimp.

Seasonal variation in size-assortative pairing: correlated sizes

To determine whether body sizes of paired males and females are correlated in both the reproductive and nonreproductive seasons, and whether this relationship differs seasonally, we first used Pearson partial correlations to control for collection date within season (reproductive season *n* = 485 pairs, nonreproductive season *n* = 195 pairs). We then compared the partial correlation coefficients from the reproductive and nonreproductive seasons using Fisher's *z* test, which calculates significance based on *Z*-transformed correlation coefficients (cocor; Diedenhofen and Musch 2015).

Body size and claw size are highly correlated and this allometry varies seasonally (Heuring and Hughes 2019); for this reason, we also tested whether the correlation between paired male and female claw sizes also differs seasonally, as would be predicted if shrimp remain with the same pair mate year-round (reproductive season *n* = 413 pairs, nonreproductive season *n* = 164 pairs).

Seasonal variation in size-assortative pairing: within-pair size relationships

To determine whether the size relationship within pairs (i.e., which sex is larger and to what degree) differs between seasons, we first calculated within-pair relative body size (for each pair: male size minus female size) and compared these values between reproductive and nonreproductive seasons using general linear mixed models with collection month and site as random effects and season (reproductive and nonreproductive) as a fixed effect. We opted to use the difference in size rather than the ratio of male/female size because the analysis of ratios can be misleading if the relationship between numerator and denominator does not pass through the origin, as is the case here (Curran-Everett 2013). In addition, we tested whether the size difference within pairs for each season differed from 0, using one-sample *t*-tests.

Seasonal variation in claw allometry (Heuring and Hughes 2019) predicts that pairs remaining together from the reproductive to the nonreproductive season will be more similar in claw size in the nonreproductive season. For this reason, we repeated the above analyses on within pair differences in claw size (again: male size – female size). All statistical analyses were performed using R 4.0.3 (R Core Team 2020). We evaluated assumptions through examination of residuals, and model fit by AIC scores.

Results

Seasonal variation in pairing

Most shrimp were found in male–female pairs in both seasons (median > 75% for both seasons, Fig. 1a). Nonetheless, significantly more shrimp were found paired in the reproductive season than nonreproductive season. The models including either collection date or year and site as random factors were overfitted; we subsequently removed these variables to test for an effect of season (reproductive season *n* = 42 collections, nonreproductive season *n* = 14 collections; *t*-test: *t* = 2.784, df = 54, *p* = 0.007; Fig. 1b). Note that this result should be treated with caution, as the small number of collection dates precludes directly testing for temporal effects within season.

Sex ratios did not differ between seasons. The best fitting model included only season as a fixed effect (for all shrimp collected: binomial GLM: $z = -0.066$, $\chi^2 = 0.0043$, df = 54, $p = 0.947$; for unpaired shrimp only: $z = -0.442$, $\chi^2 = 0.195$, df = 54, $p = 0.659$). Including all shrimp, 49% were male in both seasons. Among shrimp collected while single, 43% were male in the reproductive season, and 46% in the non-reproductive seasons (44% overall).

Seasonal variation in size-assortative pairing: correlated sizes

Male and female body lengths within pairs are highly correlated overall (both seasons combined, Pearson correlation: $r_{680} = 0.707$, $p < 0.001$). Within the reproductive season, partial correlations revealed a significant correlation between male and female body length (Pearson partial correlation: $r_{483} = 0.767$, $p < 0.001$), and no effect of collection date ($r_{483} = 0.023$, $p = 0.610$). Within the nonreproductive season, we found the same: male and female body length were significantly correlated (Pearson partial correlation: $r_{193} = 0.596$, $p < 0.001$), with no effect of collection date ($r_{193} = -0.034$, $p = 0.640$, Fig. 2a). Although pairs are assortative by body size year-round, the correlation between body sizes is significantly stronger during the reproductive season than during the nonreproductive season (Fisher's $z = 3.823$, $p < 0.001$).

Male and female claw lengths are similarly correlated overall (both seasons combined, Pearson correlation: $r_{576} = 0.658$, $p < 0.001$). Within the reproductive season, male and female claw lengths are significantly correlated within pairs (Pearson partial correlation: $r_{411} = 0.657$, $p < 0.001$), but partial correlations revealed no significant effect of collection date ($r_{411} = 0.013$, $p = 0.796$). Similarly, within the nonreproductive season, male and female claw lengths are significantly correlated within pairs (Pearson partial correlation: $r_{162} = 0.628$, $p < 0.001$), but partial correlations revealed no significant effect of collection date ($r_{162} = -0.104$, $p = 0.186$, Fig. 2b). In contrast with body size, however, the correlations between male and female claw length did not differ between seasons (Fisher's $z = 0.540$, $p = 0.589$).

Seasonal variation in size-assortative pairing: within-pair size relationships

Body length difference within pairs (male length – female length) differed between seasons (Fig. 3a), with pairs collected during the reproductive season having relatively larger females (i.e., females larger than males) than in the nonreproductive season (GLMM: $F_{(1,15.18)} = 23.891$, $p < 0.001$; Fig. 3b). This pattern is maintained if the difference between sexes is standardized by male size (i.e., (male – female)/
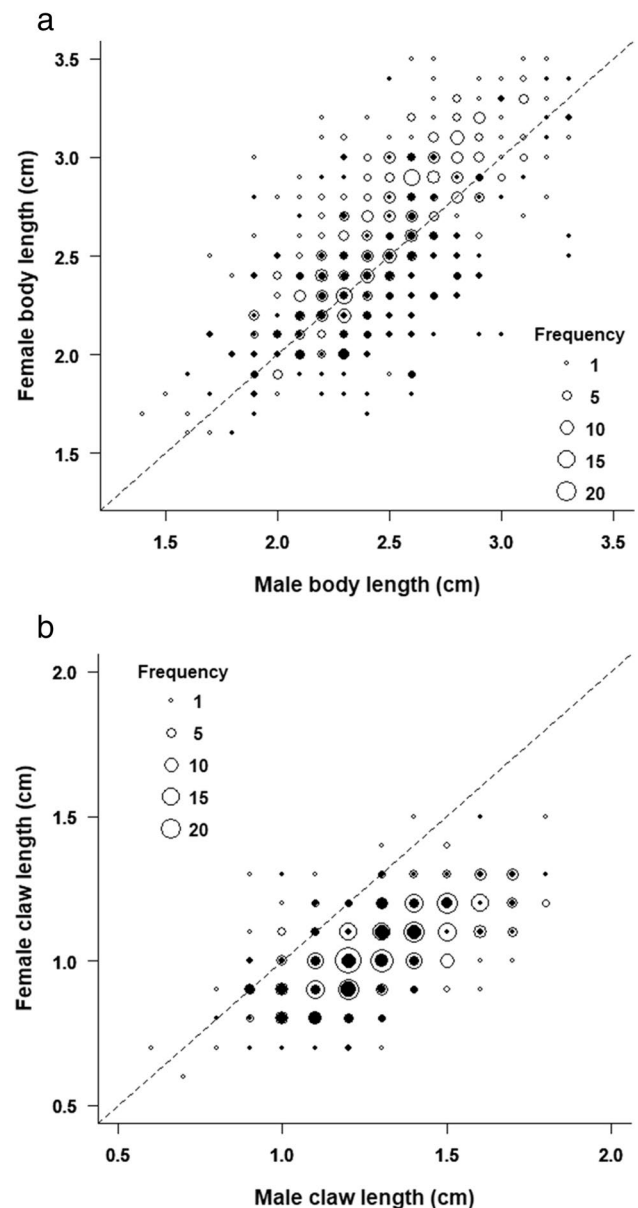

Fig. 2 Assortative pairing by body size (**A**) and claw size (**B**) in the reproductive (open circles) and nonreproductive (filled circles) seasons. Dashed line = 1:1. Body sizes are highly correlated in both reproductive and nonreproductive seasons; the correlation is stronger in the reproductive season. Claw sizes are also highly correlated in both seasons, with no difference between seasons

male). In the reproductive season, females were larger than males (mean difference (male – female body size) = –0.16, one-sample t-test (null = 0): $t_{484} = -13.84$, $p < 0.001$). In contrast, in the nonreproductive season, males tended to be larger than females, although by a much smaller degree (mean difference (male – female body size) = 0.05, one-sample t-test (null = 0): $t_{194} = 2.40$, $p < 0.018$).

Claw length (male length – female length) within pairs, on the other hand, did not differ by season (GLMM:
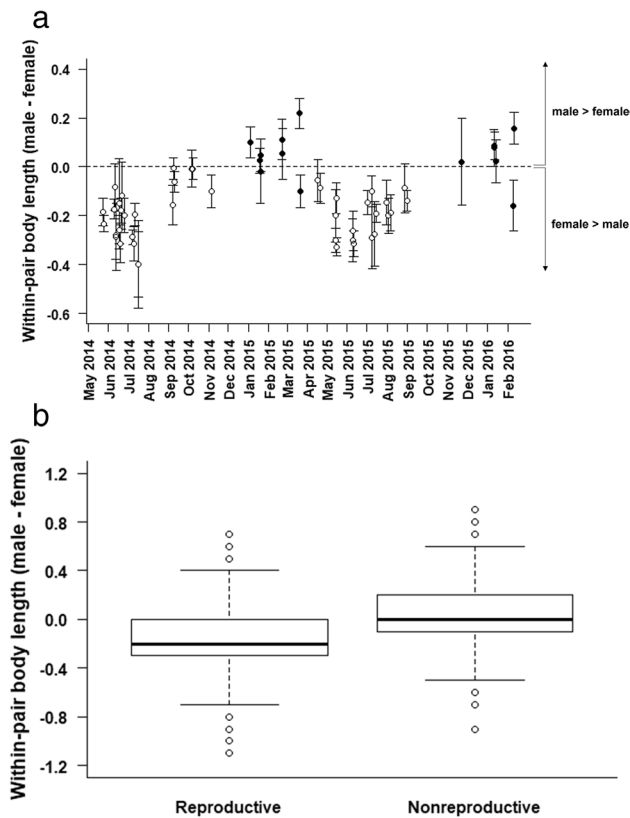
Fig. 3 Seasonal variation in within-pair relative body size (male size–female size). **A** Within-pair relative body size across months (mean ± SE; open circles = reproductive season, $n = 42$ collections; filled circles = nonreproductive season, $n = 14$ collections); **B** relative within-pair body size (male–female) is greater in nonreproductive season than in the reproductive season. In the reproductive season, within-pair size differences are less than 0 (males smaller than females); in the nonreproductive season, within-pair size differences are greater than or equal to 0. Box plot as in Fig. 1

$F_{(1,14.383)} = 0.545$, $p = 0.472$). The mean difference in claw size (male – female) was significantly greater than zero in both seasons: reproductive season: mean = 0.26, one-sample t-test: $t_{412} = 32.17$, $p < 0.001$; nonreproductive season: mean = 0.24, one-sample t-test: $t_{163} = 20.04$, $p < 0.001$). Year-round, males have claws that are approximately 18% larger than the female with which they are paired (mean for nonreproductive season = 18.3%, reproductive season = 18.2%; median for both seasons = 20%; Fig. 2b).

Discussion

In the snapping shrimp *Alpheus angulosus*, we find that size-assortative pairing varies seasonally, corresponding to differences between the reproductive and nonreproductive periods. While body sizes of paired males and females are correlated in both seasons, this correlation is stronger in the

reproductive season. Furthermore, within pairs, females are larger than males in the reproductive season, while pairs are more similar in size or male-biased in the nonreproductive season. Such seasonal variation in size-assortative pairing—here measured as changes in both the correlation between male and female sizes across the population and within-pair size differences—has rarely been reported (but see Murata and Wada 2002; Moura and Gonzaga 2017), and when potential seasonal (or other temporal) variation is not considered, such variation could obscure or confound patterns of within-pair characteristics (Moura et al. 2021). Moreover, as both social and environmental factors leading to size-assortative pairing can vary temporally, seasonal variation in size-assortative pairing may offer insight into the processes involved.

In snapping shrimp, both fecundity (Knowlton 1980; Corey and Reid 1991; Pavanelli et al. 2008, 2010; Costa-Souza et al. 2014) and territorial defense ability (Nolan and Salmon 1970; Schein 1977; Hughes 1996; Rahman et al. 2003; Heuring 2016) increase with size; thus, larger (i.e., older) individuals are likely to be more successful than smaller individuals, and pairs of larger individuals are likely to be more successful than pairs of smaller individuals. Moreover, both males and females are likely to benefit from pairing with individuals larger than themselves: males obtain a reproductive (i.e., fecundity) benefit from pairing with larger females, while females (more so than males) are likely to benefit from the greater competitive ability of larger mates in cooperative territorial defense. Both sexes cannot simultaneously pair with individuals larger than themselves, however. Our results suggest that males "win" this conflict during the reproductive season, with the interests of females having greater influence on size relationships within pairs during the nonreproductive season.

Seasonal variation in size-assortative pairing could result from a number of different mechanisms. In some symbiotic crustaceans, long-term pair fidelity and concomitant growth results in strongly correlated pair sizes (Baeza 2008, Baeza et al. 2013, but see Knowlton 1980), but as correlated pair sizes can result from many other mechanisms than long-term pair fidelity (Borghezan et al. 2019; Harari et al. 1999; Hoefler 2007; Moura and Gonzaga 2017; Moura et al. 2021), conclusions with regard to pair fidelity (or lack thereof) cannot be drawn from size-assortative pairing alone. Indeed, even with long-term pair fidelity, sex differences in seasonal growth patterns could result in seasonal variation in size-assortative pairing. In snapping shrimp, both males and females show seasonal differences in claw allometry, suggesting differential investment in growth at molts—that is, investment more in growth of claw or growth of overall body size—during the reproductive and nonreproductive seasons (Heuring and Hughes 2019). Males have larger claws relative to their body size (steeper allometric slope)

in the reproductive season than in the nonreproductive season; females show precisely the opposite seasonal pattern (Heuring and Hughes 2019). If males (more so than females) invest in growth of overall body size during the nonreproductive season, then pairs which are female-biased in body size during the reproductive season would become more similar in body size or male-biased during the nonreproductive season, even without any changes in pair fidelity or pair formation behavior. At the same time, however, these differences in claw allometry—steeper allometric slope for females and shallower allometric slope for males in the nonreproductive season—predict that claw size difference within pairs should decrease in the nonreproductive season, if pairs remain with the same partners year-round. We find no seasonal change in within-pair claw size differences here, suggesting that pairs collected in the nonreproductive season are unlikely to be long-term pairs maintained from the reproductive season, at least as can be detected with this indirect measure. While direct observation of pair fidelity in the field is challenging given the habitat, current lab studies are directly exploring environmental influences on pair fidelity.

In arthropods, size-assortative pairing may often be the result of male choice for larger, more fecund females, combined with a large male advantage in male-male competition (Ridley 1983; Crespi 1989). These conditions are met in *A. angulosus*: at the high end of the size range of animals in this study, larger females are more fecund and larger males are more successful in male-male competitions (Heuring 2016); assuming these size advantages are maintained across the full range of adult shrimp, larger males would generally be expected to successfully compete for larger, more fecund females. Furthermore, in choice tests, male *A. angulosus* prefer larger females (Heuring and Hughes 2020), suggesting that male mate preferences play an important role in maintaining size-assortative pairing. Monogamy driven by benefits to males may be common in taxa where males benefit via mate guarding while females do not derive reproductive benefits from pairing (Seibt and Wickler 1979). However, male preferences for larger females did not differ between the reproductive and nonreproductive season (Heuring and Hughes 2020); changes in male preferences, then, cannot account for the changes in size-assortative pairing observed here. While males prefer larger females year-round, they apparently are able to fulfill this preference only during the reproductive season, when the benefits to them are greatest.

Size-assortative pairing shifts from being female-biased in the reproductive season, as would be more advantageous to males, to size-matched or male-biased pairs in the nonreproductive season, as would be more advantageous to females, given greater competitive ability of larger males in territorial defense (Hughes 1996). Furthermore, although male and female sizes remain correlated in the nonreproductive season, this correlation is weaker than in

the reproductive season. What mechanisms underlie these changes in size-assortative pairing—that is, how do these male-biased or size-matched pairs form, and why is the correlation between male and female size not as strong as in the reproductive season? While pair preferences do not change, sampling of potential pair mates (measured as the number of switches between choice options in mate choice trials) does vary seasonally: when the choice options were the focal animal's pair mate and a size-matched novel individual, females (but not males) engaged in more of this sampling behavior in the nonreproductive season than in the reproductive season (Heuring and Hughes 2020). While females do not show a preference for the larger of two novel males in either season (Heuring and Hughes 2020), this increased sampling behavior in the nonreproductive season when choosing between their current mate and a size-matched male raises the question of whether they express a preference relative to their current pair mate, based on size or some other variable. If so, females may actively explore other pair mate options during the nonreproductive season (rather than doing so between mating events during the reproductive season), leading to male-biased or similar-sized pairs forming at this time. Increased mate switching may also account for the weaker correlation between male and female sizes in the nonreproductive season. For females, seasonal differences in sampling behavior may occur because sampling during the reproductive season may be too costly due to higher locomotor costs and/or impaired escape ability resulting from carrying eggs on their pleopods (swimmerets). Females, in other words, may need to trade off benefits of searching for new mates vs. risks associated with reduced locomotor capacity.

Female aggressive behavior may also play a role in seasonal variation in size-assortative pairing. Interactions leading to pair formation begin with aggression, with aggressive behaviors decreasing if pair formation is successful (Nolan and Salmon 1970). Females are generally far more aggressive than males (Hughes et al. 2014), and potentially lethal aggression can occur when opposite-sex individuals do not pair (Hughes, unpub. data). Thus, while males prefer to pair with larger females (Heuring and Hughes 2020), interacting with larger females may also pose a significantly greater risk. The fecundity benefits of pairing with larger females may outweigh this risk in the reproductive season but are unlikely to do so in the nonreproductive season. Furthermore, the risk of interacting with larger females is likely to be greatest during the nonreproductive season, as the sexual dimorphism in claw size is minimized at that time (Heuring and Hughes 2019). It is not clear why females are generally more aggressive than males and differentially invest in growth of larger weaponry in the nonreproductive season, although ensuring pairing with competitively competent

males is one possibility, resulting in a sexual arms race in armaments (Parker 1983).

To summarize, as predicted by the hypothesis that size-assortative pairing is driven by benefits to males, female *A. angulosus* tend to be larger than males within pairs—but only during the reproductive season—and the correlation between the body sizes of paired males and females was stronger during the reproductive season as compared to the nonreproductive season. Fewer shrimp were collected in pairs during nonreproductive season, even though the sex ratio in the population did not change; as females would benefit from shared territorial defense year-round, this decline in pairing suggests that reproductive benefits to males underlie the high degree of pairing in the reproductive season. Thus, advantages to males (i.e., mate guarding larger, more fecund females between sequential reproductive events) appear to drive both high rates of pairing and assortative pairing—measured as both within-pair size relationships and population-wide correlation between male and female size—during the reproductive season. In the nonreproductive season, however, within-pair size relationships shift such that females are paired with similar-sized or larger males, as would benefit females in cooperative territorial defense, and while the correlation between male and female size remains, it is weaker than in the reproductive season. Neither seasonal differences in growth nor changes in pair preferences can account for these seasonal differences in assortative pairing. High female aggression may be too costly to males in the nonreproductive season; changes in female mate sampling behavior may also favor changes in pairs at this time.

Persistent monogamous pairing has been documented across an array of taxa, including other crustaceans, birds, fish, and mammals (Black 1996), and size-assortative pairing is similarly widespread (Janicke et al. 2019, Moura et al. 2021). Temporal variation in size-assortative pairing, however, is rarely considered, especially with regard to changes between reproductive and nonreproductive periods. Focusing solely on male–female associations during the reproductive season neglects the fact that many—perhaps most—mating systems are also social systems. Even when our primary objective is the exploration of the reproductive consequences of behaviors such as pair choice and fidelity, studying the role of these behaviors for a subset of the time in which they are expressed yields an incomplete understanding of their function and evolution.

Author contribution WLH measured the shrimp and performed the statistical analyses. Authors collaborated equally on conception, generating hypotheses, and writing.

Data availability Data have been archived at https://doi.org/10.6084/m9.figshare.20377113.

Code availability Code has been archived at https://doi.org/10.6084/m9.figshare.20377125.

Declarations

Ethics approval NA.

Conflict of interest The author declare no competing interests.

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