

Do sex-changing male snails use mate choice to get a jump on their “size advantage”?

Olivia V. Ambrogio · Jan A. Pechenik

Received: 1 July 2008 / Accepted: 18 June 2009 / Published online: 8 July 2009
© Springer-Verlag 2009

Abstract Individuals of species that change sex from male to female may gain a “size advantage” from that sex change; that is, as males become larger, they become female, thus increasing their fecundity with their size. However, males could also gain an early and different reproductive size advantage by choosing large females as mates. While male preference for large females has been observed in many dioecious species, we know little about male size preference in sex-changing species. In choice experiments, we examined whether males of two congeneric species of marine sex-changing snails, *Crepidula fornicata* and *C. convexa*, chose large females over small ones as partners. We also used choice tests to see whether males of *C. fornicata*, a species whose members form long-term, multi-animal stacks, would choose two females in a stack over a single female. Surprisingly, males of neither species showed a preference for large females, in spite of the documented fecundity advantage associated with large female-size. Males of *C. fornicata* chose slightly, but not significantly, more single females than stacks, suggesting that neither number nor size drives mate choice in these animals. Key factors that may influence this lack of size preference include long association time, the likelihood of sperm competition, and the cost of extended mate search; it may also be that sex-change itself, the very factor that creates female-biased sexual size dimorphism in these species, prevents size preference, as males may gain sufficient reproductive advantage from eventually becoming

large females themselves to offset any benefit of choosing large females.

Introduction

Individuals are expected to choose mates that will improve their reproductive fitness, either directly (e.g. through increased fecundity, reduced parasite load, gifts of food) or indirectly through benefits to offspring (Andersson 1994). While females are often the choosing sex, males of some species can also choose mates to improve their reproductive fitness (see Gwynne 1991; Andersson 1994). Male choosiness is especially likely to occur when males are limited in their opportunities for mates or mating events, where costs of reproduction are high for males, or when species exhibit “role reversal,” with males taking on all or the majority of parental care (Gwynne 1991; Bonduriansky 2001). The most basic requirement for male mate choice, however, is that females vary in fecundity via a selectable trait.

Because in many species female size varies and is positively correlated with fecundity, it is a common and obvious trait for male choice; size preference has been observed in species from fish (Ptacek and Travis 1997; Herdman et al. 2004) to crickets (Bateman and Fleming 2006), and spiders (Bel-Venner et al. 2008). However, certain groups of animals have not been studied in the context of male mate choice in spite of the fact that among them female fecundity also increases with size; these animals are protandrous sequential hermaphrodites, species that change sex from male to female as they grow.

Protandrous sequential hermaphrodites are by the nature of their sex change sexually size dimorphic, with large

Communicated by M. Byrne.

O. V. Ambrogio (✉) · J. A. Pechenik
Department of Biology, Tufts University,
Medford, MA 02155, USA
e-mail: o.ambrogio@gmail.com

females and smaller males. The “size advantage” model for protandrous sex change states that, as with dioecious species that show the same dimorphism, male reproductive success should not be strongly and/or positively affected by size but female fecundity should increase with increasing size (Ghiselin 1969; Warner et al. 1996). In protandrous species, individuals that are initially male gain a size-based reproductive advantage by becoming female as they grow. By choosing large females as mates while they themselves were still male, however, males could also improve their reproductive fitness before changing sex.

In sex-changing species, research and models have primarily examined size and relative size of partners in terms of their influence on the timing of sex change rather than their effects on mate choice (*Crepidula* spp., Coe 1938b; Hoagland 1978; Collin 1995; Warner et al. 1996; protogynous fishes, Muñoz and Warner 2003). It remains to be seen, however, whether sex changers also respond to size differences by actively choosing larger mates.

Crepidula fornicata and *C. convexa* are marine snails whose individuals change sex from male to female (Orton 1909). Female fecundity increases with size and is a variable trait for both species (Hendler and Franz 1971; Li and Pechenik 2007). Both species are suspension feeders, so that individuals need to move only to find and associate with mates. Males, which are smaller and more mobile, are the choosing individuals; they choose their mates by crawling onto the shells of their partners, where they remain for days, months, or years (Coe 1938b). Due to the mechanical requirement of “stacking”—that a male must be able to fit on top of his partner’s shell—males do exhibit a very small relative-size preference, pairing only with animals that are at least marginally ($\geq \sim 1$ mm) larger than they are (see Coe 1938b). It is not known, however, whether males of either species will also exhibit a real size preference when given a choice of pairing with large females rather than small ones. Because individuals of *C. fornicata*, but not *C. convexa*, live in stacks of many individuals for months or years (Coe 1938b), it is possible that *C. fornicata* males make their association choices not on the basis of individual female-size but on the basis of the number of females in a stack. Males of *C. convexa*, whose individuals form short-term associations [fewer than 3 weeks in the lab (Hoagland 1978)] and do not form stacks, may exhibit stronger size preference for mates.

Using a field experiment and laboratory choice tests, we studied males’ preference for stacks versus solitary females (*C. fornicata*) and for large females (both species) to determine whether males of either species could acquire an early, choice-based reproductive size advantage while still male.

Methods

Study organisms

Field surveys and experiments with *C. fornicata* were conducted at Lynn Harbor (Nahant, MA) and Narragansett Bay (North Kingston, RI) using snails originating from those sites. For laboratory experiments, *C. fornicata* adults were collected from Lynn Harbor and *C. convexa* adults were collected from Barnstable, MA. Snails were kept in a sea table of flowing seawater at Northeastern University’s Marine Science Center (Nahant, MA), where all experiments were conducted. Since *Crepidula* snails are suspension feeders and the seawater was unfiltered, the animals were able to feed from the water in which they were kept. In order to ensure that they were capable of associating with other adults, for choice experiments we used only males that had been the top animal in either a pair or stack of animals when they were collected. For all experiments, snails within a replicate were never from the same stack or pair of origin; no experimental snails were presented with individuals with which they had been associated when collected. The sex of individual snails was determined by examining the external genitalia: snails were determined to be male if their penis was longer than either of their tentacles and there was no external evidence of a uterine tract; snails were determined to be female if they had a visible uterine tract and no penis (Coe 1938a). “Stacked” females were separated for sexing and then re-associated.

Field experiment—female-size preference in newly recruiting *C. fornicata* juveniles

Crepidula fornicata snails release free-swimming larvae that metamorphose near conspecifics in response to chemical cues from adults (Pechenik and Gee 1993; Li and Pechenik 2007). Mate choice in this species, therefore, may be effected immediately or soon after metamorphosis by juveniles associating with nearby adults. To test this, we placed cement blocks in the intertidal zone in June 2006 with two females—one large (30–33 mm long) and one small (20–23 mm long)—on each block. Each female was placed on a 6-in.-square tile that was attached to the block (one female per tile; two tiles per block). Twice, over 2 months, we observed the number of recruiting juveniles (1) on each tile; (2) within 5 mm of each snail; and (3) associated with each female (i.e. on her shell) to determine whether newly recruited individuals in the field would preferentially approach and/or associate with large females. These experiments were conducted at Nahant, MA ($n = 7$ blocks) and North Kingston, RI ($n = 2$ blocks); because the sample size was low at North Kingston and similar

trends were observed in both locations, we combined results for August for our data analysis. We did not attempt similar experiments with *C. convexa*, however, since they are direct developers whose juveniles do not aggregate (Hoagland 1978).

Choice experiments—general methods

For a clarification of the choice experiments' design, an unusual aspect of *Crepidula* snails behavior must be addressed: unlike most other species whose mate-choice behavior has been better studied, these snails do not move swiftly or frequently, even in "pursuit" of a mate. Previous studies (e.g. Coe 1938a; Ambrogio and Pechenik 2008) and direct observation (visual observations of 20 snails over 2-h periods and time-lapse observations of more than 40 snails over 24- and 48-h periods; Ambrogio, unpublished data) have demonstrated that *Crepidula* males often take days to move and/or to pair with another snail—even one within 10–15 cm of them. While these snails do appear to respond to cues and make mate choices based on them (Coe 1938a; Warner et al. 1996; Ambrogio and Pechenik 2008), they do so on a very different, much slower time scale than those we might expect—and over shorter distances. We designed our choice experiments accordingly; each male and his potential partners were placed in 10-cm glass dishes covered in mesh within tanks of flowing seawater (conditions under which time-lapse observations suggest that males are capable of responding to a combination of pheromonal and tactile cues from potential partners), and their choices were observed and recorded over a period of days or weeks (see specific experiments below) to allow enough time for males to form associations.

"Stack" choice experiment—*C. fornicata* male preference for single versus paired females

When males join a stack of snails rather than pair with an individual, they join the top of the stack, regardless of whether the individual directly below them is male or female. However, because of the snails' stack formation (closest to the right side of each snail's head, i.e. nearest the genitalia), males can mate with multiple females in a stack—including females that are not directly below them (e.g. Dupont et al. 2006). Thus males of *C. fornicata* may prefer a stack of females to a single female, regardless of her size. In order to test whether males of *C. fornicata* make association choices not on the basis of female size but on the basis of the number of females in a stack, we gave each male in the laboratory a choice of a "stack" of two associated females versus one single female. While this is not a choice males are likely to encounter in the field—in nature females are usually alone or in stacks

composed of many individuals of both sexes as well as those of intermediate sex (Coe 1938b; Collin 1995)—we felt this would be the simplest and most direct means of measuring whether the number of females in a stack has an influence on male preference. A male was placed in a 10-cm-diameter, mesh-covered glass dish in flowing seawater with a choice of a single female or a stack of two females ($n = 14$). All females were approximately the same size (mean shell length of single females was 30.96 mm; top females, 31.21 mm, and bottom females, 35.13 mm), and the difference in shell length between lone females and the top female of a pair—that is, the individual a male would associate with—was not significant (paired t test, $t = 0.2542$, $df = 13$, $p = 0.8033$).

Size-choice experiments—male preference for large females

For both species, we conducted choice tests in the laboratory to determine whether males of either species would choose large females over small females as partners. A male was placed in a 10-cm-diameter, mesh-covered glass dish in flowing seawater with two females, one large and one small (mean shell lengths \pm SD: large = 35.71 ± 3.28 mm, small = 26.69 ± 2.97 mm for *C. fornicata*; large = 13.40 ± 1.29 mm, small = 10.43 ± 1.14 mm for *C. convexa*). According to regression equations for number of offspring released as a function of female shell length (Li and Pechenik 2007), a *C. fornicata* female of the mean "large" shell length would produce approximately 50% more offspring than would a female of the mean "small" shell length. A *C. convexa* female of mean "large" length would produce approximately 60% more offspring than a female of mean "small" length.

Choice experiments were conducted three times for *C. fornicata*, in July and August of 2006 and September of 2007 ($n = 11$, $n = 14$, and $n = 13$) and in April and June of 2007 for *C. convexa* ($n = 15$ and $n = 12$). Males' choice of partner was recorded at several intervals over a period of 6–16 days (*C. fornicata*) or 12–18 days (*C. convexa*), to give males sufficient time to choose a partner. Experiments were run until at least 40% of males had chosen a female and ended after we saw either no difference in the number and types of choices after 6 or more days or after we observed a reduction in the number of males choosing partners.

Data analysis

We analyzed the results of field experiments using paired t tests for each category of association (number of juveniles on a tile, number of juveniles within 5 mm of a female, and number of juveniles associated with a female) (GraphPad

Prism software). Last-day results for choice tests were analyzed using exact binomial tests (<http://home.clara.net/sisa/binomial.htm>). Only replicates in which males chose mates were included in the analyses.

Results

Field experiment—female-size preference in newly recruiting *C. fornicata* juveniles

There were no significant differences in the number of juveniles on large females, near large females, or on tiles of large females compared to small females in either July (two-tailed paired *t* tests: on tiles, $t = 2.650$, $df = 3$, $p = 0.08$; within 5 mm, $t = 1.567$, $df = 3$, $p = 0.22$; on females, $t = 0.00$, $df = 3$, $p = 1.0$) or August (on tiles, $t = 0.1113$, $df = 8$, $p = 0.91$; within 5 mm, $t = 1.414$, $df = 8$, $p = 0.19$; on females, $t = 0.7663$, $df = 8$, $p = 0.47$). The numbers of juveniles (especially on tiles) varied considerably from block to block and from month to month; however, the low number of juveniles (from 0 to 5) that associated with females of either size category was consistent over the course of the experiment (Fig. 1). While the number of juveniles that could fit on a female's shell could depend on the size of the female, (1) Snails that associate in large numbers with another individual will begin to stack, eliminating space issues, and (2) the highest number of juveniles we observed associated with these females (5 juveniles) were still too

few to stack and would fit on the shells of either large or small females.

“Stack” choice experiment—*C. fornicata* male preference for single versus paired females

More *C. fornicata* males paired with single females than with a pair of females; however, this difference in choice was not quite significant (exact binomial test, $n = 10$, $p = 0.054$; Fig. 2).

Size-choice experiments—male preference for large females

Males of neither species showed any consistent or significant preference for either smaller or larger females in the lab, and between 20 and 50% of males did not choose any partner during the course of the experiments (6–18 days). Of those that chose, a larger number of *C. fornicata* males chose large females in July, though this difference was not significant (exact binomial test: $n = 6$, $p = 0.12$), while similar numbers of males chose large and small females in August and September ($n = 9$, $p = 0.25$; $n = 6$, $p = 0.67$; Fig. 3). Of *C. convexa* males, the same or very similar numbers chose large and small females in April (exact binomial test: $n = 8$, $p = 0.64$), and in June ($n = 8$, $p = 0.36$; Fig. 4). During the course of all experiments, several males (2 per species) disassociated from their chosen partner; however, only one male of *C. fornicata* switched partners

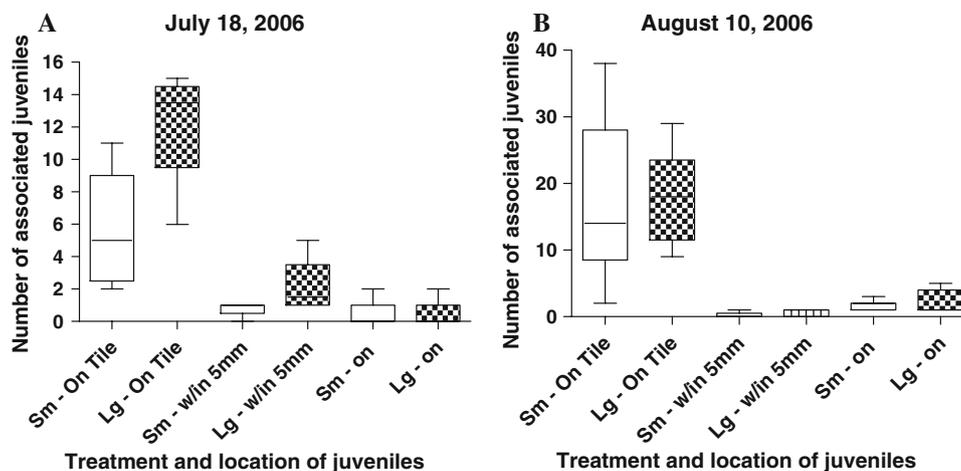


Fig. 1 The average number of *C. fornicata* juveniles associated with or in proximity to either a large female or a small female in the field. Treatment blocks were placed in the field in June (Nahant, MA) or July (North Kingston, RI), 2006. Each treatment block contained two

tiles, one with a large female and one with a small female; we recorded the number of juveniles that were present on each tile, were within 5 mm of each female, or were on each female in **a** July ($n = 4$ treatment block) or **b** August ($n = 9$ treatment block)

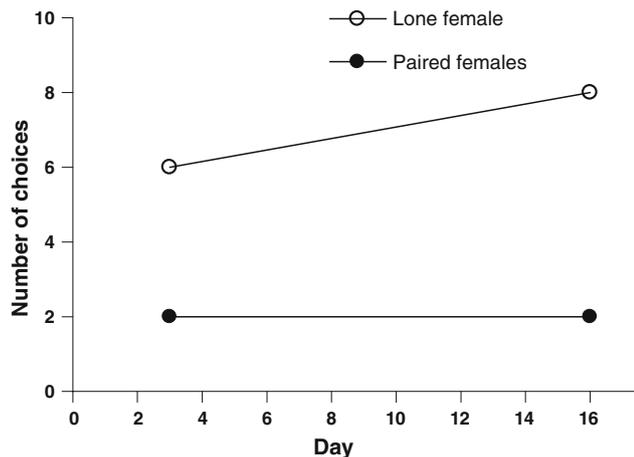


Fig. 2 The number of *C. fornicata* males choosing a single female or a pair of associated females in a laboratory choice experiment. Males were placed in 10-cm-diameter glass dishes in flowing seawater with a single female and a pair of two associated females, and their choice of partner over 16 days was recorded

(from a small to a large female); no males of *C. convexa* changed partners.

Discussion

Males of neither *C. fornicata* nor *C. convexa* preferred large females over small ones as mates in spite of the fact that fecundity increases markedly with female size in both species (Hendler and Franz 1971; Li and Pechenik 2007). It is possible that this lack of preference represents an inability of males to assess female size; however, males of both species are capable of recognizing and exclusively pairing with individuals that are at marginally larger than they are (e.g. Coe 1938b, 1953; Collin 1995), and socially flexible sex change in some *Crepidula* species appears to be influenced by the relative size of surrounding individuals (Warner et al. 1996), suggesting that these snails do have some means of determining the size of potential partners. And other marine gastropods, though not sex changers, have been found to assess mates based on their size [e.g. the gonochoristic periwinkles *Littorina neglecta* (Johnson 1999) and *Littoraria flava* (Cardoso et al. 2007); the simultaneously hermaphroditic sea slug *Roboastra europaea*, Megina and Cervera 2003]. This indifference to female size among male *Crepidula*, then, probably represents a lack of preference rather than an inability of males to make size-related choices, especially as males of both species have shown, in studies with similar sample sizes, a preference for females over males as partners (Ambrogio

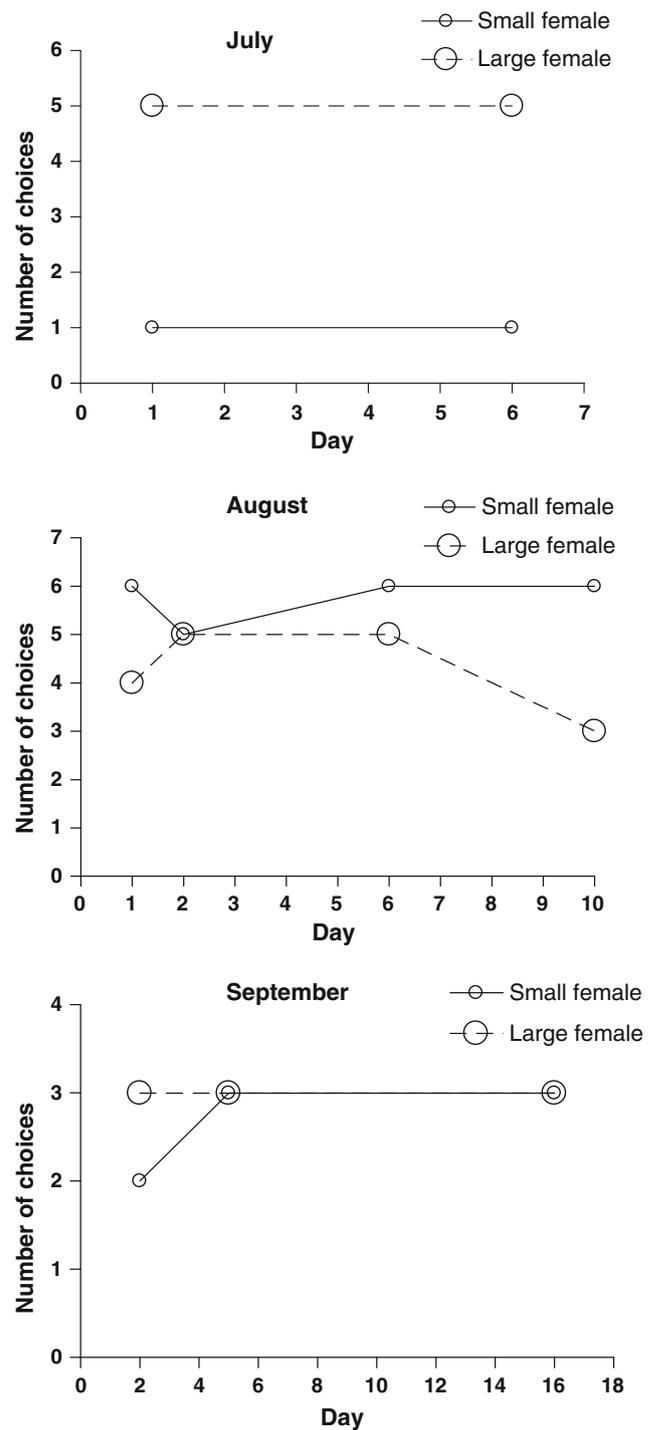


Fig. 3 The number of *C. fornicata* males choosing a large or a small female as a partner in laboratory choice experiments in 2006 in July ($n = 11$) and August ($n = 14$) and in September, 2007 ($n = 13$). Males were placed in 10-cm-diameter glass dishes in flowing seawater with two females, one large and one small, and their choice of partner was recorded over 6–16 days. Different animals were used in each experiment

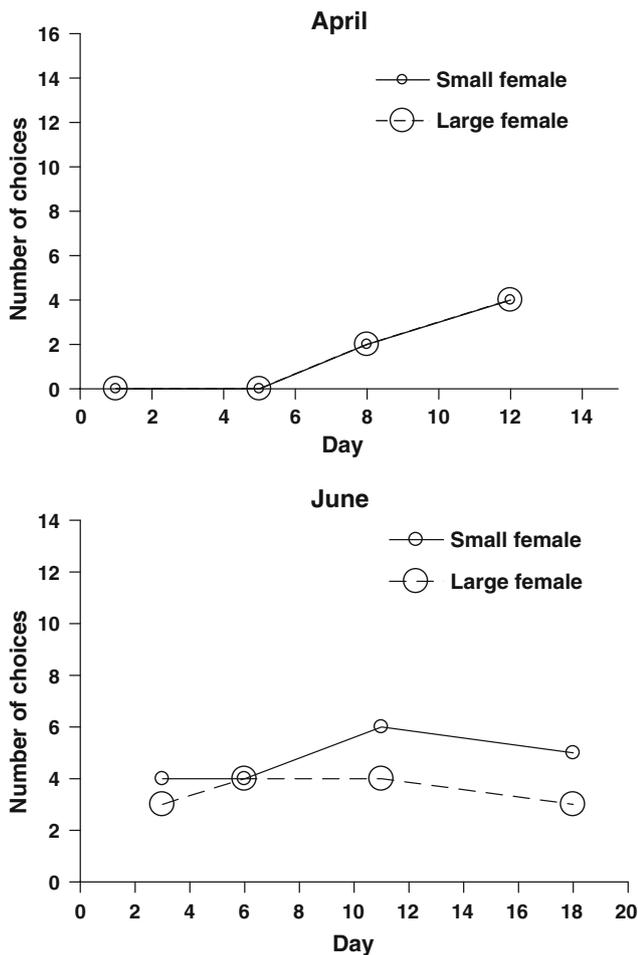


Fig. 4 The number of *C. convexa* males choosing a large or a small female as a partner in laboratory choice experiments in April ($n = 15$) and June ($n = 12$), 2007. Males were placed in 10-cm-diameter glass dishes in flowing seawater with two females, one large and one small, and their choice of partner was recorded over 12–18 days. Different animals were used in each experiment

and Pechenik 2008), and in choice tests males of *C. convexa* paired exclusively with conspecific rather than heterospecific females (Ambrogio, unpublished data). While distinguishing size may depend on the ability to sense tactile rather than chemical cues, time-lapse observations suggest that *C. convexa* and *C. fornicata* males may also use touch in identifying potential mates (Ambrogio, unpublished data).

Because male mate-choice is a less common—or less commonly studied—phenomenon than female mate choice (Andersson 1994), the reasons behind greater or lesser degrees of male mate preference are not yet well explored. Our study has demonstrated that males will not always exhibit expected mate preferences in spite of what appear to be gains they could acquire from these choices. Below we address an element that has been shown to influence male mate preference in other species and describe several

key factors in *C. fornicata* and *C. convexa* whose costs could act to reduce the reproductive advantage of size preference or whose benefits could override the usefulness of such a preference.

Size-assortative mating, where large males pair with large females and small males with small females, has been observed in several species with male mate choice, including snakes (Shine 2003), periwinkle snails (Cardoso et al. 2007; Johnson 1999), and guppies (Basolo 2004). This factor, however, seems unlikely to influence mate choice in *Crepidula* snails, as physical competition, which is often a cause of size-assortative mating (Rahman et al. 2002; Hoeffler 2007; Bel-Venner et al. 2008), does not occur in these species (personal observation; see also Coe 1938a; Hoagland 1978). Also, solitary *Crepidula* males do not vary extensively in size and usually change sex when they are relatively small [approximately 15 mm, *C. fornicata*; approximately 9 mm, *C. convexa* (Coe 1938a, b)]. A large, lone male of *C. fornicata* is more likely to begin to change sex than to demonstrate stronger size preferences.

The possibility that *C. fornicata* males prefer multiple females to single females of any size was not supported by our research. Instead, males paired more often, though not quite significantly more often, with single females than with two-female stacks—a surprising result, given that a male in a stack should be able to fertilize the eggs from both females. This may be due to the extreme rarity of such female-only stacks in nature. All of the two-female stacks used in the choice experiment were artificially created by removing upper, male- or transition-phase animals from existing stacks; although male–female pairs were abundant in the field, we found no female–female pairs nor any larger stack that was composed exclusively of females. It is possible that males failed to recognize the stacks because they had never encountered ones with a similar composition in nature. Regardless of the cause, however, the number of available females does not appear to be driving mate choice in these snails any more than size does.

Among these *Crepidula* species, a factor that may complicate size preference is sperm competition. Multiple paternity is common in *C. fornicata*, as has been found from both allozyme analysis of larvae (Gaffney and McGee 1992) and from recent paternity analyses using microsatellite loci, where 14 out of 18 females (78%) produced broods with multiple paternity (Dupont et al. 2006). If a male is unlikely to sire all or even most of the offspring in a brood, the reproductive advantage of choosing a larger female would be reduced, and factors other than size, such as the number of male competitors present, could influence male choice. If so, considering that males of both species are likely to mate with several females during the course of the breeding season, males may not always show a preference for large females. However, while the likelihood of

sperm competition may influence males' choosiness in ways that will complicate size preferences, the current data on sperm competition (e.g. Dupont et al. 2006; Proestou et al. 2008) are not complete enough to determine whether it could offset such preferences. Also, in many species with pre- and post-copulatory male competition, males still demonstrate a preference for large females over small ones, as in garter snakes (Shine et al. 2006), pond turtles (Poschadel et al. 2006), Soay sheep (Preston et al. 2005), and fiddler crabs (Reading and Backwell 2007), and in some cases males exhibit a stronger degree of size preference in situations with high male–male competition (Bel-Venner et al. 2008). More research must be done with *C. fornicata* on the influence of mating position and number of competitors on sperm competition—as well as the comparative amounts of sperm competition in large versus small females—and in *C. convexa* on the presence and likelihood of sperm competition before we can assess the importance of this factor on mate choice.

Another factor that might reduce size preference in these species is the time required to engage in mate searching, which may outweigh the value of being choosy. Increased costs associated with searching or mate discrimination, due to breeding-time constraints or limited numbers of potential mates, can lead to instances of reduced pickiness in species such as fiddler crabs (Backwell and Passmore 1996), tungara frogs (Lynch et al. 2005), gobies (Borg et al. 2006), garter snakes (Shine et al. 2006), and bushcrickets (Lehmann 2007). Search time, in slow-moving species like *C. fornicata* and *C. convexa*, may serve as its own time constraint on mate choice, making it more worthwhile to pair with whichever female is most easily accessible.

Additionally, other reproductive benefits may influence size preference. In *C. fornicata*, in which mating associations are maintained for months or years (Coe 1938b; Hoagland 1978), the initial size of the female a male chooses might only be pertinent for the first hatch she produces with that male: as the pair remains associated the female will grow, and the size of her broods will grow as well. In this case, males that chose females regardless of their size would still, eventually, be partnered with a large female. For *C. convexa*, whose males pair with a female for generally less than a month (Hoagland 1978) and presumably mate with multiple females during a breeding season, partners may be sufficiently abundant to make choosiness unnecessary.

Finally, it may be that the very system that should make large females desirable is at the same time what offsets the value of size preference. Sex change itself, though it has led to female-biased sexual size dimorphism, will also eventually improve males' reproductive success—whether they choose large females or not. “Eventually” is not immediately, but that may not present a difficulty for these

long-lived snails. Males in our choice experiments took days and sometimes weeks to choose any female as a partner, if they paired at all, demonstrating a lack of haste that is perhaps understandable in species that live several years, often remain paired for weeks or more at a time, and have long breeding seasons (April–October). If males of these slow-moving, slow-to-pair species will eventually become large, fecund females regardless, the early reproductive advantage of selecting large female partners may not be worth the effort of selection.

We have discovered a surprising lack of female-size preference among males of *C. fornicata* and *C. convexa* and have suggested several important factors that could affect the lack of size preference that we observed. In *Crepidula* spp. the benefits of long-term association, promiscuity, and sex-change size advantage may work in combination with the potential costs of choosing large females (e.g. increased sperm competition, increased search time) to offset the value of size preference.

The effects of such factors on male mate preference in these and other species remain to be examined; our work demonstrates that influences other than female fecundity can clearly operate to lead to unpredicted absences of size preference.

References

- Ambrogio OV, Pechenik JA (2008) When is a male not a male? Sex recognition and choice in two sex-changing species. *Behav Ecol Sociobiol* 62:1779–1786. doi:10.1007/s00265-008-0606-4
- Andersson M (1994) *Sexual selection*. Princeton University Press, Princeton
- Backwell PRY, Passmore NI (1996) Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, *Uca annulipes*. *Behav Ecol Sociobiol* 38:407–416
- Basolo AL (2004) Variation between and within the sexes in body size preferences. *Anim Behav* 68:75–82
- Bateman PW, Fleming PA (2006) Males are selective too: mating, but not courtship, with sequential females influences choosiness in male field crickets (*Gryllus bimaculatus*). *Behav Ecol Sociobiol* 59:577–581
- Bel-Venner MC, Dray S, Allaine D, Menu F, Venner S (2008) Unexpected male choosiness for mates in a spider. *Proc R Soc Lond B Biol Sci* 275:77–82
- Bonduriansky R (2001) The evolution of male mate choice in insects: a synthesis of ideas and evidence. *Biol Rev* 76:305–339
- Borg AA, Forsgren E, Amundsen T (2006) Seasonal change in female choice for male size in the two-spotted goby. *Anim Behav* 72:763–771
- Cardoso RS, Costa DS, Loureiro VF (2007) Mating behaviour of the marine snail *Littoraria flava* (Mollusca: Caenogastropoda) on a boulder shore of south-east Brazil. *J Mar Biol Assoc UK* 87:947–952
- Coe W (1938a) Conditions influencing the change of sex in mollusks of the genus *Crepidula*. *J Exp Biol* 122:5–19

- Coe W (1938b) Influence of association on the sexual phases of gastropods having protandric consecutive sexuality. *Biol Bull* 75:274–285
- Coe WR (1953) Influences of association, isolation, and nutrition on the sexuality of snails of the genus *Crepidula*. *J Exp Zool* 122:5–19
- Collin R (1995) Sex, size, and position: a test of models predicting size at sex change in the protandrous gastropod *Crepidula fornicata*. *Am Nat* 146:815–831
- Dupont L, Richard J, Paulet YM, Thouzeau G, Viard F (2006) Gregariousness and protandry promote reproductive insurance in the invasive gastropod *Crepidula fornicata*: evidence from assignment of larval paternity. *Mol Ecol* 15:3009–3021
- Gaffney PM, McGee B (1992) Multiple paternity in *Crepidula fornicata* (Linnaeus). *Veliger* 35:12–15
- Ghiselin M (1969) The evolution of hermaphroditism among animals. *Q Rev Biol* 44:189–208
- Gwynne DT (1991) Sexual competition among females—what causes courtship-role reversal? *Trends Ecol Evol* 6:118–121
- Hendler G, Franz DR (1971) Population dynamics and life-history of *Crepidula convexa* Say (Gastropoda-Prosobranchia) in Delaware Bay. *Biol Bull* 141:514
- Herdman EJE, Kelly CD, Godin JGJ (2004) Male mate choice in the guppy (*Poecilia reticulata*): Do males prefer larger females as mates? *Ethology* 110:97–111
- Hoagland KE (1978) Protandry and the evolution of environmentally mediated sex change: a study of the Mollusca. *Malacologia* 17:365–391
- Hoefler CD (2007) Male mate choice and size-assortative pairing in a jumping spider, *Phidippus clarus*. *Anim Behav* 73:943–954
- Johnson L (1999) Size assortative mating in the marine snail *Littorina neglecta*. *J Exp Mar Biol Ecol* 79:1131–1132
- Lehmann GUC (2007) Density-dependent plasticity of sequential mate choice in a bushcricket (Orthoptera: Tettigoniidae). *Aust J Zool* 55:123–130
- Li W, Pechenik JA (2007) Effect of inbreeding on reproduction and juvenile performance in two marine gastropods with contrasting reproductive patterns. *Mar Ecol Prog Ser* 346:219–234
- Lynch KS, Rand AS, Ryan MJ, Wilczynski W (2005) Plasticity in female mate choice associated with changing reproductive states. *Anim Behav* 69:689–699
- Megina C, Cervera JL (2003) Diet, prey selection and cannibalism in the hunter opisthobranch *Robostra europaea*. *J Mar Biol Assoc UK* 83:489–495
- Muñoz R, Warner R (2003) A new version of the size-advantage hypothesis for sex change: incorporating sperm competition and size-fecundity skew. *Am Nat* 161:749–761
- Orton J (1909) On the occurrence of protandric hermaphroditism in the mollusc *Crepidula fornicata*. *Proc Roy Soc London* 81:468–484
- Pechenik JA, Gee CC (1993) Onset of metamorphic competence in larvae of the gastropod *Crepidula fornicata* (L.), judged by a natural and an artificial cue. *J Exp Mar Biol Ecol* 167:59–72
- Poschadel JR, Meyer-Lucht Y, Plath M (2006) Response to chemical cues from conspecifics reflects male mating preference for large females and avoidance of large competitors in the European pond turtle, *Emys orbicularis*. *Behaviour* 143:569–587
- Preston BT, Stevenson IR, Pemberton JM, Coltman DW, Wilson K (2005) Male mate choice influences female promiscuity in Soay sheep. *Proc R Soc Lond B Biol Sci* 272:365–373
- Proestou D, Goldsmith M, Twombly S (2008) Patterns of male reproductive success in *Crepidula fornicata* provides new insight for sex allocation and optimal sex change. *Biol Bull* 214:194–202
- Ptacek MB, Travis J (1997) Mate choice in the sailfin molly, *Poecilia latipinna*. *Evol Int J org Evol* 51:1217–1231
- Rahman N, Dunham DW, Govind CK (2002) Size-assortative pairing in the big-clawed snapping shrimp, *Alpheus heterochelis*. *Behaviour* 139:1443–1468
- Reading KL, Backwell PRY (2007) Can beggars be choosers? Male mate choice in a fiddler crab. *Anim Behav* 74:867–872
- Shine R, Philips B, Wayne H, LeMaster M, Mason R (2003) The lexicon of love: what cues cause size-assortative courtship by male garter snakes? *Behav Ecol Sociobiol* 53:243–237
- Shine R, Webb JK, Lane A, Mason RT (2006) Flexible mate choice: a male snake's preference for larger females is modified by the sizes of females encountered. *Anim Behav* 71:203–209
- Warner R, Fitch D, Standish J (1996) Social control of sex change in the shelf limpet *Crepidula norrisiarum*: size-specific responses to local group composition. *J Exp Mar Biol Ecol* 204:155–167