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Left–right cheliped asymmetry occurs in a variety of decapod species. Such asymmetries can be present in early development or can arise during sexual differentiation. Male fiddler crabs have a dimorphic enlargement of one of the two chelipeds. This major cheliped has been associated with male reproductive success as a result of female selection or advantage in male–male combat. Because the major cheliped occurs on either the right or the left side, selection pressure could produce populations with right or left cheliped dominance. To ascertain whether populations of dominantly enlarged right- or left-clawed males are present, three fiddler crab species, *Uca longisignalis, U. minax* and *U. pugnax,* from four North American marshes, two on the coast of the Atlantic Ocean, one on the coast of the Chesapeake Bay, and one on the coast of the Gulf of Mexico, were sampled. There were no significant differences in the number of males with right- or left-enlarged chelipeds within all species or marshes sampled. Similarly, when male crabs were grouped arbitrarily into two size classes (major chelipeds <20 mm and ≥20 mm), the number of crabs with right or left major cheliped was similar among the size groups. Mean major propodus size for males was also similar for individuals with either right or left major chelipeds within each of the three species and four marshes. Comparison of morphometric parameters in each population indicated a strong correlation between claw size, carapace width, and carapace length, which was not affected by cheliped laterality. It appears that among these three species of *Uca,* there is no selection for males with cheliped enlargement on either the right or the left side within the geographical range of the species sampled.

Dimorphic cheliped enlargement is characteristic of male fiddler crabs in the genus *Uca*. Unlike the small cheliped that is used for feeding, the major cheliped is used for ritualized combat and courtship waving displays. Although the exact form of these displays is species specific, they occur, in some configuration, in all species of *Uca*. The evolution of the disproportionately large major claw has been attributed to both female choice (Crane, 1975; Hyatt and Salmon, 1978) and reproductive advantage to males with the largest claw (Crane, 1975). Although the major cheliped can occur on either the right or the left side in equal proportion (Crane, 1975; Ahmed, 1976), Green and Schochet (1972) and Barnwell (1982) reported right cheliped enlargement (in >90% of adult males sampled) in *U. vocans* (Linnaeus, 1758) and *U. tetragonon* (Herbst, 1790).

In fiddler crabs, males use the large cheliped in male–male combat and in courtship waving displays (Crane, 1975; Croll and McClintock, 2000). Selection pressure on each of these behaviors could result in left–right dominance in claw asymmetry. At present, the mechanism responsible for right or left cheliped enlargement in male fiddler crabs remains unclear.

Vernberg and Costlow (1966) reported a genetic basis for the handedness of fiddler crabs. In contrast, Yamaguchi (1977) demonstrated that in *U. lacteal,* one of the juvenile male claws must first be autotomized before the mature form of the enlarged cheliped can develop and that the autotomization is random. Although random autotomization may account for equal numbers of enlarged right- and left-clawed individuals, it does not explain the right-handed populations of *U. vocans* and *U. tetragonon* (Green and Schochet, 1972; Barnwell, 1982).

The mating system of fiddler crabs provides at least two opportunities for selection of either right- or left-handed individuals. The first is in ritualized combat, in which males use the enlarged cheliped to ward off intruders, preventing encroachment onto defended mating territory (Crane, 1975; Croll and McClintock, 2000). According to Crane (1975), enlarged cheliped morphology has evolved so that when combative males engage their enlarged claws, there is little chance of damage to either competitor's major claw. The result is a competition based as much on strength and position as on claw size. However, claw interlock, much like shaking hands, requires same-hand engagement. Thus, if combat between opposite-

handed males resulted in differential claw loss, claw damage, or success, selection pressure would favor male fiddler crabs with either all right- or all left-enlarged chelipeds. The second opportunity for selection of handedness is female choice or preference for either right- or left-handed male crabs (Darwin, 1871; Oliveira and Custódio, 1998). Darwin's theory of sexual selection postulates that selection by one sex for a morphological or behavioral character in the opposite sex can lead to dominance or exaggeration of the desired character. Although female selection has not been shown to be acting on handedness in male fiddler crabs, the number of species investigated is limited (Oliveira and Custódio, 1998). Similarly, selection could be acting on morphological differences associated with major cheliped handedness. Although carapace width and depth have been correlated with fiddler crab claw size (Croll, 1995), the relationship between carapace width, carapace length, and major cheliped size as a function of handedness has not been investigated. Understanding these relationships could illuminate selective advantage as a correlate of cheliped handedness.

The present study uses large-scale random sampling to investigate the proportion of right- or left-enlarged chelipeds in male fiddler crabs. Males of three species of *Uca* from four ecologically different regions were sampled to determine the fractions of right- or left-enlarged cheliped configurations.

METHOD

Major cheliped handedness was examined in populations of fiddler crabs by using quadrat sampling during the summer months (June, July, and August) of 1998 and 1999. Four study sites, Dauphin Island, Alabama (30°20.5'N 88°7.5'W), Hunting Island, South Carolina (32°22.5'N 80°27.5'W), Saxis, Virginia (37°55.5'N 75°42.3'W), and Wallops Island, Virginia (37°53.0'N 75°26.5'W), representing four different ecosystems, were selected. *Uca longisignalis* (Salmon and Atsaidés, 1968) was sampled at Dauphin Island, whereas *U. minax* (LeConte, 1855) was sampled at Wallops Island and *U. pugnax* (Smith, 1870) at both Hunting Island and Saxis. A representative sample area was selected in each marsh with an area of approximately 8–9.5 ha. Quadrats (N = 120–140) were established within each area using flags to mark perpendicular transect lines. All quadrats were square and measured 30 m on each side. Sample locations (N = 18–20) per marsh

were selected randomly in each marsh, and collections of crabs were taken at randomly selected quadrat boundary intersections during low tide when fiddler crabs were most active. Quantitative crab collections at all sampling sites were made using a wood box frame (1 m²) with 20-cm-high sides (modified from Teal, 1958; Wolf et al., 1975). Stainless steel skirts extended 12 cm from the bottom of each side. The skirts were designed to penetrate easily into the substratum. At approximately 4 m from the selected site, the box was launched forward and allowed to fall onto the marsh. To prevent subterranean escape of the crabs, the skirts of the box were forced completely into the substratum. All fiddler crabs (carapace width >5 mm) on or below the substrate were captured, measured to the nearest 0.5 mm (carapace width, carapace length, and claw size), counted, identified to species, and released. Carapace width was measured at the greatest distance across the carapace between opposite lateral margins. Similarly, carapace length was measured at the greatest distance along the carapace centerline from anterior to posterior margins. Claw size was determined by measuring the distance between the most proximal portion of the manus and the most distal portion of the pollex.

To determine if handedness was evenly distributed in male fiddler crabs, the number of right- and left-clawed individuals within each sampled marsh were compared to a 1:1 ratio using a chi-square goodness of fit test. Further, to elucidate whether left–right handedness distributions varied between specific size classes within the tested marsh populations, male crabs were arbitrarily divided into two cheliped size classes, <20 mm and ≥20 mm. Contingency table analysis was used to determine if right- and left-clawed individuals occurred in different proportions between the two size groups. Further, to determine if the size of right or left claws varied in the same cheliped size classes, a Student's t-test was used to examine differences in claw size means within each of the two size classes. A Pearson's r correlational analysis, comparing claw handedness and the three selected morphometric characters, claw size, carapace width, and carapace length, was performed to determine if the three characters were associated.

RESULTS

In all the sampled marshes there were no significant ($P > 0.05$) departures from equal numbers of right- or left-enlarged cheliped

TABLE 1.   Pearson's r correlation analysis values comparing male fiddler crabs major cheliped length with carapace width and length to determine the level of covariance. The number of individual fiddler crabs measured is also shown. All crabs were collected during the summer months of 1998 and 1999. The alpha significance level is 0.05, and significant correlations are indicated by (*).

	Right claw		Left claw	
	Carapace width	Carapace length	Carapace width	Carapace length
Dauphin Island (*Uca longisignalis*)	0.955* (n = 273)	0.930* (n = 273)	0.954* (n = 229)	0.925* (n = 229)
Hunting Island (*U. pugnax*)	0.929* (n = 239)	0.907* (n = 239)	0.908* (n = 235)	0.897* (n = 235)
Saxis (*U. minax*)	0.903* (n = 32)	0.900* (n = 32)	0.811* (n = 35)	0.812* (n = 35)
Wallops Island (*U. pugnax*)	0.961* (n = 326)	0.949* (n = 326)	0.941* (n = 305)	0.924* (n = 305)

males (R or L, respectively) (Dauphin Island: R = 273, L = 229; Hunting Island: R = 239, L = 235; Saxis: R = 32, L = 35; Wallops Island: R = 326, L = 305). Similarly, when male fiddler crabs were divided into two size categories, <20 mm and ≥20 mm, there were no significant ($P > 0.05$) differences in the numbers of males with right or left major chelipeds within either size group [Dauphin Island: (<20 mm) R = 222, L = 176, (≥20 mm) R = 50, L = 54; Hunting Island: (<20 mm) R = 212, L = 212, (≥20 mm) R = 27, L = 23; Saxis: (<20 mm) R = 2, L = 8, (≥20 mm) R = 30, L = 28; Wallops Island: (<20 mm) R = 257, L = 242, (≥20 mm) R = 69, L = 62]. When major chelipeds were compared by size and handedness, there were no significant ($P > 0.05$) differences in the mean cheliped size among right- or left-handed groups in any of the four sampled marshes (Dauphin Island: R = 12.9 mm, L = 13.8 mm; Hunting Island: R = 12.3 mm, L = 11.6 mm; Saxis: R = 28.4 mm, L = 32.2 mm; Wallops Island: R = 14.0 mm, L = 13.9 mm). Correlation analysis between major cheliped size and carapace width, as well as between major cheliped size and carapace length, indicated significant ($P < 0.05$) associations in both right- and left-handed groups (Table 1). Further, when major cheliped size,

carapace width, and carapace length were compared, both right- and left-handed groups had similar ($P < 0.05$) associations (Table 2).

DISCUSSION

Although a small number of *Uca* species exhibit right-handed dominance associated with the major cheliped (Green and Schochet, 1972; Barnwell, 1982), most fiddler crabs are thought to be randomly right or left clawed (Crane, 1975). However, verification of random major cheliped handedness, using large-scale random sampling, has not been completed. The present study supports the random pattern.

The three species examined in this study, *U. longisignalis, U. minax,* and *U. pugnax,* are members of more recently evolved fiddler crab subgenera (Crane, 1975). All three species are assumed to be heteroclawed, with an approximate right- to left-enlarged claw ratio of 1:1 (Crane, 1975). However, large-scale random collections to determine claw laterality have not been undertaken previously for any of these three species. The need for a large sample size is underscored by the present study. Some 1-m² sample plots with 50–100 male fiddler crabs contained left- and right-handed

TABLE 2.   Regression analysis r values of male fiddler crab major claw length, carapace width, and carapace length. The adjusted squared multiple r is indicated as well as the number of crabs measured. All crabs were collected during the summer months of 1998 and 1999. The alpha significance level is 0.05, and significant correlations are indicated by (*).

	Right claw	Left claw
Dauphin Island (*Uca longisignalis*)	0.912* (n = 273)	0.910* (n = 229)
Hunting Island (*U. pugnax*)	0.863* (n = 239)	0.834* (n = 235)
Saxis (*U. minax*)	0.815* (n = 32)	0.660* (n = 35)
Wallops Island (*U. pugnax*)	0.927* (n = 326)	0.884* (n = 305)

males in equal proportions, whereas in other plots males with left- or right-enlarged claws occurred in dominant (>90%) proportions. However, when samples within each marsh were combined, there were no significant differences in the number of right- or left-handed adult males.

In the four sampled marshes, mortality selection does not appear to be acting on male fiddler crabs with respect to major claw handedness. Even when male crabs were divided into size groups, there was no apparent differential survival. Thus, it appears that the 1:1 right–left claw configuration present in smaller, and therefore younger, male crabs persists as they grow.

When cheliped length was considered in relation to cheliped laterality, there was no significant difference in the mean size of right- or left-handed male claws. The absence of a significant size difference between right- and left-handed male claws adds credence to the premise that there is no selection for male cheliped laterality. Analogously, claw size was strongly correlated with both carapace length and width in all the sampled marshes and species regardless of claw laterality. Therefore, it appears that these morphological characters grow in proportionality with the major claw regardless of the lateral position of the major cheliped.

LITERATURE CITED

AHMED, M. 1976. A study of the normal and abberrant sexual types of the Venezuelan fiddler crabs *Uca cumulanta* and *U. rapax*. Bull. Mar. Sci. 26:499–505.

BARNWELL, F. H. 1982. The prevalence of male right-handedness in the Indo-West Pacific fiddler crabs *Uca Vocans* (Linnaeus) and *U. tetragonon* (Herbst) (Decapoda: Ocypodidae). J. Crustac. Biol. 2:70–83.

CRANE, J. 1975. Fiddler crabs of the world, (Ocypodidae: genus *Uca*). Princeton Univ. Press, Princeton, NJ.

CROLL, G. 1995. Population structure, feeding behavior, substratum selection, and predation of *Uca pugnax* and *Uca pugilator* in the marshes of Hunting Island, South Carolina. M.S. thesis, Bloomsburg Univ. of Pennsylvania, Bloomsburg, PA.

———, AND J. B. MCCLINTOCK. 2000. An evaluation of lekking behavior in the fiddler crab *Uca* spp. J. Exp. Mar. Biol. Ecol. 254:109–121.

DARWIN, C. 1871. The descent of man, and selection in relation to sex. John Murray, London.

GREEN, J. P., AND J. SCHOCHET. 1972. Chela type of *Uca vocans*. Am. Zool. 12:714–715.

HYATT, G. W., AND M. SALMON. 1978. Combat in the fiddler crabs *Uca pugilator* and *U. pugnax:* a quantitative analysis. Behaviour 65:182–211.

LeCONTE, J. 1855. On a new species of *Gelasimus*. Proc. Acad. Nat. Sci. Phila. 7:402–402.

OLIVEIRA, R. F., AND M. R. CUSTÓDIO. 1998. Claw size, waving display and female choice in the European fiddler crab, *Uca tangeri*. Ethol. Ecol. Evol. 10:241–251.

SALMON, M., AND S. ATSAIDÉS. 1968. Behavioral, morphological, and ecological evidence for two new species of the fiddler crabs (Genus *Uca*) from the Gulf Coast of the United States. Proc. Biol. Soc. Wash. 81:275–290.

SMITH, S. I. 1870. Notes on American crustacea. No. 1. Ocypodoidea. Trans. Connecticut Acad. Arts Sci. 2:113–176.

TEAL, J. M. 1958. The distribution of fiddler crabs in Georgia salt marshes. Ecology 39:185–193.

VERNBERG, J. F., AND J. D. COSTLOW. 1966. Handedness in fiddler crabs (Genus *Uca*). Crustaceana 11:61–64.

WOLF, P. I., S. F. SHANHOLTZER, AND R. J. REIMOLD. 1975. Population estimates for Uca pugnax (Smith 1870) on the Duplin Estuary Marsh, Georgia, U.S.A. (Decapoda Brachyura, Ocypodidae). Crustacea 29:79–91.

YAMAGUCHI, T. 1977. Studies on the handedness of the fiddler crab, *Uca lactea*. Biol. Bull. 152:424–436.

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