

# BIASED SEX RATIOS IN FIDDLER CRABS (BRACHYURA, OCYPODIDAE): A REVIEW AND EVALUATION OF THE INFLUENCE OF SAMPLING METHOD, SIZE CLASS, AND SEX-SPECIFIC MORTALITY

BY

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## ABSTRACT

Herein I present a brief review of biased sex ratios in fiddler crabs and examine a limited data set involving a population of *Uca pugilator* (Bosc, 1802) to explore causes of such biases and highlight unresolved questions. Although male-biased sex ratios in *Uca* populations often have been recorded historically, such observations are generally disregarded as sampling error. However, a review of the fiddler crab literature followed by a meta-analysis of published sex ratio data indicated that this trend is significant and widespread, but the causes of male-biased sex ratios and whether they arise at birth or are acquired subsequently remain conjectural. I investigated the influence of sampling method, habitat use, and size class on the sex ratio of Atlantic sand fiddler crabs in a Georgia, U.S.A., salt marsh. Pitfall trapping and excavated-quadrat sampling were used to survey *U. pugilator* across foraging and burrowing habitats. Tethering experiments were conducted to evaluate the influence of differential predation on crab sex ratios. Finally, discarded chelae from salt flats were collected to estimate the size of male crabs consumed in nature. Sex ratio differed significantly among size classes, with the percentage of males increasing with increasing carapace width. Both sampling methods yielded male-biased sex ratios (Pearson chi-square,  $P < 0.001$ ), but females predominated among juvenile crabs (5.0-10.0 mm CW). Females outnumbered males within burrows whereas males dominated in foraging areas (Pearson chi-square,  $P < 0.001$ ). Predation on tethered crabs was low, ranging from 0 to 3.3% ( $N = 145$ ) during 24-hr trials. Taken together, these results suggest that male-biased sex ratios in *U. pugilator* may be derived, owing to differential mortality between the sexes. However, the cause of elevated mortality in females could stem from increased energetic costs associated with reproduction and/or decreased predation on large male crabs resulting from their enlarged major chelae.

## RÉSUMÉ

Je présente ici une brève revue des sex-ratios biaisées chez les crabes violonistes et j'examine un ensemble de données limitées concernant une population de *Uca pugilator* (Bosc, 1802) pour explorer les causes de tels biais et pointer les questions non résolues. Bien que les sex-ratios biaisées

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dans les populations de *Uca* aient souvent été rapportées historiquement, de telles observations sont généralement considérées comme des erreurs d'échantillonnage. Cependant, une revue de la littérature, suivie d'une méta-analyse des données publiées de sex-ratios a indiqué que cette tendance est significative et largement répandue, mais les causes des sex-ratios biaisées en faveur des mâles et le fait qu'elles surviennent à la naissance ou qu'elles soient acquises ultérieurement restent conjonctural. J'ai étudié l'influence de la méthode d'échantillonnage, de l'utilisation de l'habitat et de la classe de taille sur la sex-ratio des crabes violonistes d'un marais salé de Géorgie, USA. Le piégeage et l'échantillonnage par quadrat ont été utilisés pour suivre *U. pugilator* dans ses habitats de fouissage et de terriers. Des expériences de marquage ont été conduites pour évaluer l'influence de la prédation différentielle sur les sex-ratios des crabes. Finalement, les pinces abandonnées ont été collectées pour estimer la taille des crabes mâles consommés dans la nature. La sex-ratio diffère significativement parmi les classes de taille, le pourcentage des mâles augmentant avec l'augmentation de la largeur de la carapace. Les deux types d'échantillonnage ont révélé des sex-ratios biaisées en faveur des mâles (Pearson chi-square,  $P < 0,001$ ), mais les femelles prédominaient parmi les crabes juvéniles (5,0-10,0 mm CW). Les femelles surpassaient les mâles en nombre à l'intérieur des terriers tandis que les mâles dominaient dans les zones de fouissage (Pearson chi-square,  $P < 0,001$ ). La prédation sur les mâles marqués était basse, allant de 0 à 3,3% ( $N = 145$ ) sur des tests de 24 heures. L'ensemble des résultats suggèrent que les sex-ratios biaisées en faveur des mâles chez *U. pugilator* peuvent être modifiées, à cause d'une mortalité différente dans les deux sexes. Cependant, la cause de la mortalité élevée chez les femelles pourrait provenir des coûts énergétiques accrus liés à la reproduction, et/ou à la prédation réduite sur les grands crabes mâles grâce à leur grande pince.

## INTRODUCTION

### Biased sex ratios in fiddler crabs

All species of *Uca* exhibit extreme sexual dimorphism. Female crabs are equipped with two smaller feeding chelae, whereas adult males possess one feeding chela and one enlarged "major cheliped" (see reviews by Crane, 1975; and Montague, 1980a). The major cheliped may constitute up to 48% of an adult male's body mass and is considered a classic example of sexual selection (Darwin, 1871; Christy & Salmon, 1984). Adult males use the major claw in courtship displays, territorial disputes, and acoustical signaling (Crane, 1975; Christy & Salmon, 1984). However, the claw is dysfunctional for foraging, and males may spend more time foraging relative to females (Valiela et al., 1974; Weissburg, 1992, 1993). Considering that crabs away from burrows are more susceptible to predation, some researchers have suggested that the increased foraging time, prolonged courtship rituals, and conspicuous morphology of male crabs make them more vulnerable to predators (Valiela et al., 1974; Montague, 1980a; Christy & Salmon, 1984; Koga et al., 2001). Moreover, male crabs often confront disturbance with a threat posture, further increasing their predation risk (Crane, 1975; Christy, 1982).

However, a review of the fiddler crab literature reveals that many populations of *Uca* from several continents exhibit adult sex ratios biased in favor of males

(table I). In studies of fiddler crabs from temperate and tropical estuaries, male-to-female ratios significantly exceeding unity have been documented in at least 14 species (table I). Males may be four times more abundant than females in some species (Emmerson, 1994). Generally, natural selection favors a sex ratio of 1 : 1 parental expenditure on offspring (Fisher, 1930; MacArthur, 1965; May, 1983). Although deviant sex ratios are common in marine Crustacea, owing to sequential hermaphroditism, sex-specific habitat use, and differential growth rates (Wenner, 1972), the trend in *Uca* is notable in its widespread and consistent bias toward males. Male fiddler crabs are both territorial and promiscuous, conditions that should favor female-biased sex ratios (Fisher, 1930). Montague (1980a) suggested male biases in fiddler crab populations were a sampling artifact resulting from a focus on surface sampling and a failure to incorporate differential habitat use. Ovigerous females spend prolonged periods underground and, when on the surface, often forage closer to water sources, creating spatial separation from foraging males (Montague, 1980a; Macia et al., 2001). However, subsequent studies have continued to record male-biased sex ratios, even with sampling designs that incorporate excavation of burrows as well as temporal and spatial variability (Frith & Brunenmeister, 1980; Bertness & Miller, 1984; Emmerson, 1994; Croll & McClintock, 2000; table I), suggesting this trend has ecological significance (Spivak et al., 1991).

To explore male-biased sex ratios in fiddler crab populations more quantitatively, I performed a mixed model meta-analysis (Gurevitch & Hedges, 2001) on the data presented in table I ( $N = 25$  studies). Relevant papers were obtained through general and cited reference searches using the Institute for Scientific Information's Web of Science<sup>®</sup> computer database and through the references listed therein. Observed sex ratios reported from field studies were compared against the expected numbers of each sex under a theoretically postulated 1 : 1 sex ratio with an identical sample size. The natural logarithm of the odds ratio was used to measure effect size and its variance was estimated as the sum of the reciprocal sample sizes from each sex (observed and expected) (Fleiss, 1994). The cumulative effect size ( $\pm 95\%$  CI) was calculated as  $0.369 \pm 0.190$ , indicating a significant, overall bias in favor of males ( $P < 0.01$ ; table I). Although this result is limited by the number of studies included in the analysis, it does suggest that, at least among published field studies, reported sex ratios in fiddler crabs deviate significantly from the expected 1 : 1 ratio.

Factors that may contribute to sex ratio biases in fiddler crabs include (i) differential growth rates, (ii) differential production of gametes, and (iii) differential mortality between the sexes. With respect to growth rates, breeding females may forgo foraging and even delay somatic growth in favor of egg production, resulting in an under-representation of females among larger size classes (Colby

TABLE I

Mixed effects meta-analysis model comparing observed and expected sex ratios in various species and subspecies of fiddler crabs (genus *Uca*). Listed are the percentage of male crabs relative to the total number examined, the male-to-female ratio (M : F), the sample size (N), and the effect size<sup>†</sup>. Data were obtained directly from listed references or estimated from figures therein. Meta-analysis indicated a significant, overall bias in favor of males ( $P < 0.01$ , cumulative effect size  $\pm 95\%$  confidence interval =  $0.369 \pm 0.190$ ). Meta-analysis methods follow from Fleiss (1994) and Gurevitch & Hedges (2001)

Species	Locality	Sampling method	Male (%)	M : F	N	Effect size $\ln(o)^{\dagger}$	Reference
<i>Uca annulipes</i> (H. Milne Edwards, 1852)	Inhaca Island, Mozambique	Excavated quadrats	65	1.86*	5952	0.619	1
<i>Uca beebei</i> Crane, 1941	Republic of Panama	Surface sampling	49	0.97	697	-0.032	2
<i>Uca beebei</i>	Republic of Panama	Visual estimates	36	0.57*	1256	-0.559	3
<i>Uca burgersi</i> Holthuis, 1967	Barbuda Island, Caribbean	Excavated quadrats	67	2.02*	535	0.704	4
<i>Uca chlorophthalmus</i> (H. Milne Edwards, 1837)	Mgazana estuary, Transkei	Hand digging	65	1.87*	4022	0.626	5
<i>Uca cumulanta</i> Crane, 1943	Turpialito, Venezuela	Partial excavation	54	1.16	657	0.149	6
<i>Uca forcipita</i> (Adams & White, 1848)	Phuket Island, Thailand	Excavated quadrats	55	1.20	66	0.182	7
<i>Uca lactea annulipes</i> (H. Milne Edwards, 1837)	Phuket Island, Thailand	Excavated quadrats	69	2.19*	577	0.783	7
<i>Uca lactea annulipes</i>	Mgazana estuary, Transkei	Hand digging	82	4.51*	2517	1.506	5
<i>Uca latimanus</i> (Rathbun, 1893)	Republic of Panama	Visual estimates	72	2.57*	528	0.943	3
<i>Uca longisignalis</i> (Salmon & Atsáides, 1968)	Dauphin Island, Alabama, U.S.A.	Excavated quadrats	62	1.66 <sup>‡</sup>			8
<i>Uca longisignalis</i>	Louisiana, U.S.A.	Surface sampling	57	1.33*	796	0.2884	9
<i>Uca minax</i> (LeConte, 1855)	Saxis, Virginia, U.S.A.	Excavated quadrats	55	1.24 <sup>‡</sup>			8
<i>Uca musica tersichores</i> Crane, 1941	Republic of Panama	Visual estimates	51	1.05	718	0.0502	3
<i>Uca panacea</i> (Novak & Salmon, 1974)	Mustang Island, Texas, U.S.A.	Excavated quadrats	63	1.73*	371	0.547	10
<i>Uca pugilator</i> (Bosc, 1802)	Shackleford, North Carolina, U.S.A.	Excavated quadrats	39	0.64*	6953	-0.448	11
<i>Uca pugilator</i>	Shackleford, North Carolina, U.S.A.	Pitfall traps	39	0.65*	4993	-0.437	12
<i>Uca pugilator</i>	Chapaquoi, Massachusetts, U.S.A.	Visual estimates		<1			13

TABLE I  
(Continued)

Species	Locality	Sampling method	Male (%)	M:F	N	Effect size $\ln(o)^{\dagger}$	Reference
<i>Uca pugnax</i> (Smith, 1870)	Woods Hole, Massachusetts, U.S.A.	Hand digging	68	2.17*	415	0.774	14
<i>Uca pugnax</i>	Great Sippewissett, Massachusetts, U.S.A.	n/a	57	1.33*	713	0.285	15
<i>Uca pugnax</i>	Sapelo Island, Georgia, U.S.A.	Excavated quadrats	53	1.13*	7503	0.116	16
<i>Uca pugnax</i>	Smith Cove, Rhode Island, U.S.A.	Excavated quadrats	52	1.07	141	0.071	17
<i>Uca pugnax</i>	Sapelo Island, Georgia, U.S.A.	Excavated quadrats	63	1.70*	989	0.532	18
<i>Uca pugnax</i>	Hunting Island, South Carolina, U.S.A.	Excavated quadrats	65	1.87 <sup>‡</sup>			8
<i>Uca pugnax</i>	Wallops Island, Virginia, U.S.A.	Excavated quadrats	69	2.26 <sup>‡</sup>			8
<i>Uca rapax</i> (Smith, 1870)	Venezuela	Partial excavation	61	1.54*	1552	0.432	6
<i>Uca rapax</i>	Matanzas Inlet, Florida, U.S.A.	Resin casts	44	0.79*	565	-0.238	19
<i>Uca rapax</i>	Florida, U.S.A.	Excavated quadrats	59	1.46*	408	0.377	20
<i>Uca spinicarpa</i> (Rathbun, 1901)	Louisiana, U.S.A.	Hand digging	56	1.25*	756	0.223	9
<i>Uca tangeri</i> (Eydoux, 1835)	Rio Formosa, Portugal	Visual estimates	54	1.18*	3072	0.164	21
<i>Uca tangeri</i>	Mira estuary, Portugal	Visual estimates	55	1.22	263	0.206	21
<i>Uca tangeri</i>	Rio Formosa, Portugal	Emergence traps	60	1.50*	1000s	0.406	22
<i>Uca tetragonon</i> (Herbst, 1790)	Surin Island, Thailand	Excavated quadrats	48	0.93	251	-0.072	23
<i>Uca uruguayensis</i> Nobili, 1901	Mar Chiquita Lagoon, Argentina	Excavated quadrats	63	1.68*	1310	0.521	24
<i>Uca uruguayensis</i>	Arroyo San Clemente, Argentina	Excavated quadrats	70	2.33*	41	0.882	25
<i>Uca urvillei</i> (H. Milne Edwards, 1852)	Phuket Island, Thailand	Excavated quadrats	70	2.35*	134	0.854	7
<i>Uca urvillei</i>	Mgazana Estuary, Transkei	Hand digging	75	2.96*	1419	1.086	5
<i>Uca virens</i> (Salmon & Atsideds, 1968)	Mustang Island, Texas, U.S.A.	Excavated quadrats	52	1.08			10
<i>Uca vocans</i> (Linnaeus, 1758)	Phuket Island, Thailand	Excavated quadrats	66	1.95	56	0.666	7
<i>Uca vocans hesperiae</i> (Crane, 1975)	Mgazana Estuary, Transkei	Hand digging	66	1.94*	999	0.662	5

<sup>†</sup>Natural logarithm of the sample odds ratio (Fleiss, 1994).\*Significant deviation from the expected 1 : 1 ratio ( $G$  test,  $P < 0.05$ ).<sup>‡</sup>Significance of bias could not be evaluated due to data format.

<sup>1</sup>Macia et al., 2001; <sup>2</sup>Koga et al., 2001; <sup>3</sup>Zucker, 1978; <sup>4</sup>Gibbs, 1974; <sup>5</sup>Emmerson, 1994; <sup>6</sup>Ahmed, 1976; <sup>7</sup>Frith & Brunenmeister, 1980; <sup>8</sup>Croll & McClintock, 2000; <sup>9</sup>Mouton & Felder, 1995; <sup>10</sup>Powers, 1975; <sup>11</sup>Colby & Fonseca, 1984; <sup>12</sup>Salmon & Hyatt, 1983; <sup>13</sup>Knopf, 1966; <sup>14</sup>Pearse, 1914; <sup>15</sup>Valiela et al., 1974; <sup>16</sup>Wolf et al., 1975; <sup>17</sup>Bertness & Miller, 1984; <sup>18</sup>Shanholtzer, 1973; <sup>19</sup>Genoni, 1991; <sup>20</sup>Genoni, 1985; <sup>21</sup>Oliveira et al., 2000; <sup>22</sup>Wolfrath, 1993; <sup>23</sup>Frith & Frith, 1977; <sup>24</sup>Spivak et al., 1991; <sup>25</sup>Iribarne & Martinez, 1999.

& Fonseca, 1984; Sukumaran & Neelakantan, 1997). However, this should result in an over-representation of females at intermediate size classes: a phenomenon that is rarely observed. Alternatively, biased sex ratios may be intrinsic, resulting from a greater production of male offspring. Unfortunately, juvenile crabs are often excluded from studies of fiddler crabs owing to their small size and incomplete sexual dimorphism. This issue may be addressed indirectly by collecting and rearing juvenile crabs until dimorphic characteristics are evident. Yamaguchi (1977) reared over 13,000 juvenile *U. lactea* (De Haan, 1835) to cheliped differentiation and reported approximately equal numbers of males and females, suggesting that differential gamete production also is unlikely to explain male-biased sex ratios.

Differential mortality may also cause deviations in adult sex ratios (e.g., Leigh, 1970; Spieth, 1974). Field and laboratory studies with crustacean zooplankton have demonstrated that predation can cause biased adult sex ratios if there are significant physical or behavioral differences between male and female prey (Maly, 1970; Hairston et al., 1983; Blais & Maly, 1993). Recent studies on fiddler crabs suggest that male and female crabs experience differential vulnerabilities to natural predators. Bildstein et al. (1989) found that captive ibises were four times more likely to consume females or males with their major chela removed than intact males. Ibises also rejected male crabs in burrows twice as often as female crabs. In a number of instances, male crabs were observed to clamp down on the ibises' bill with their major claw, frequently causing the rapid release of the crab (Bildstein et al., 1989). Male crabs incur a greater handling time by avian predators, as the major claw is removed and discarded prior to consuming the remainder of the crab, whereas female or juvenile crabs may be swallowed whole (Wolf et al., 1975; Iribarne & Martinez, 1999). The size and sex of crabs consumed by predators, as well as the individual foraging strategies of predators, most likely vary as a function of age and species in birds. For example, while ibises, plovers, and house crows feed predominantly on female and juvenile fiddler crabs, adult whimbrels, ruddy turnstones, and grackles consume a greater proportion of males (Altevogt, 1955; Christy & Salmon, 1984; Backwell et al., 1998; Iribarne & Martinez, 1999; Koga et al., 2001). Thus, rather than focusing on individual species or groups of predators (e.g., Aves), there is a need to evaluate the net effect of a community of predators, integrated across time and space, on the sex ratios of fiddler crab populations.

I investigated the influence of size class, habitat use, and sampling method on sex ratio in a population of *Uca pugilator* (Bosc, 1802). For each sampling method and habitat type, the relationship between sex ratio and crab size was determined, with particular emphasis on comparing juvenile and adult crabs. To assess the relative strength of sex-specific predation in the field, I conducted tethering experiments with male and female crabs, exposing them to a spectrum

of different predators. Finally, the relative vulnerabilities of male fiddler crabs of different sizes were evaluated by comparing living males in the population with those consumed in tethering experiments and with those consumed in nature.

## MATERIALS AND METHODS

### Study site and species

Studies were conducted on the southwestern shore of Sapelo Island (31°N 81°W), a barrier island off the coast of Georgia. Study sites were situated within *Spartina*-dominated marsh areas around Dean Creek, near the University of Georgia Marine Institute. Detailed descriptions of the abiotic and biotic characteristics of the marsh may be found elsewhere (e.g., Pomeroy & Wiegert, 1981).

The Atlantic sand fiddler crab, *Uca pugilator*, is commonly found on sandy substrates in the high marsh and salt flats of estuarine systems from Cape Cod, Massachusetts, to Corpus Christi, Texas (Crane, 1975; Montague, 1980a). Crabs form burrows in lightly vegetated or exposed regions of the upper intertidal zone. During low tide crabs leave their burrows and forage closer to the water, sometimes forming large herds or "droves" thought to reduce predation risk (Montague, 1980a; Christy, 1982; Christy & Salmon, 1984). Between March and September, adult males compete for breeding burrows preferred by females in a resource-defense polygynous mating system (Christy & Salmon, 1984). Males mate with up to three females, each of which will spend from 3 to 17 days underground while their eggs develop (Christy, 1982).

### Field surveys

Atlantic sand fiddler crabs in Dean Creek Marsh were sampled during the month of October, 2001. Dates well beyond the species' reproductive season helped to minimize the confounding effects of courtship and breeding activity on sampling accuracy. Although the sampling period was relatively short, examination of a large number (> 500) fiddler crabs provided a time-integrated "snapshot" to examine instantaneous patterns of crab sex ratio. To evaluate the effects of sampling bias on crab sex ratio, two different sampling methods were used: pitfall traps and excavated quadrats. For the former, a 4 m by 0.3 m drift fence made of aluminum screening (1 mm mesh size) was placed between an area supporting a high density of *U. pugilator* burrows and a nearby, yet spatially distinct foraging area. The fence was pushed firmly into the substrate with wooden stakes. Three 9.5 l steel buckets, placed at each end and at the center of the fence, served as pitfall traps. Each bucket was bisected by the fence, allowing crabs to fall in from either side. A small amount of water and sand were placed in the bottom of each bucket to reduce

agonism and water stress among the crabs. Pitfall traps were checked twice daily at 10:00 hrs and 17:00 hrs and any crabs were removed and returned to the laboratory for inspection.

For quadrat sampling, I established five 50 m transects running between the crabs' burrows and the corresponding foraging area. Five points along each transect were selected at random for sampling. At each point, a 19 l bucket (615 cm<sup>2</sup>) with the bottom removed was pressed quickly and firmly into the sand. Sediment within the quadrat area was excavated to a depth of at least 0.3 m and sorted either by hand or with a 2 mm sieve. Adult crabs were returned to the laboratory and measured (carapace width [CW]) to the nearest 0.1 mm with Vernier callipers. Crabs were sexed by the presence or absence of an enlarged chela (major claw) and verified by examination of the abdomen shape. The size (propodus length [PL]) of each major claw as well as its position (left or right) were also recorded. For crabs  $\leq 8.0$  mm in CW, for which abdominal shape is a less reliable predictor of sex, 25% of all "females" (individuals without a major chela) were further inspected using a stereo-dissecting scope to tease open the abdomen and count the number of pleopods. This inspection served to cross-validate the accuracy of sex determination through external characteristics (i.e., major chela and abdominal shape).

### Predation experiments

To evaluate the relative predation intensity on *U. pugilator*, individual crabs were secured to 0.5 m monofilament (8 lb test) tethers by tying the line around the crab and securing it to the carapace with a drop of super glue (Ross cyanoacrylate cement). Tethers were attached to numbered washers and secured with 18 cm metal spikes pushed completely into the sand, adapted from previous studies of relative predation levels on brachyuran crabs (e.g., Heck & Thoman, 1981). Although tethering prevents crabs from fleeing if predators approach, they frequently continue to forage and dig burrows (Wilson et al., 1990). Adult male and female crabs were selected at random and tethered at one of two sites: an "upper" site composed predominantly of sand and infrequently inundated during high tides, and a "lower", mud substrate site, which flooded during most high tides and supported sympatric populations of *U. pugilator* and *U. pugnax* (Smith, 1870) (fig. 1). The upper site was included to expose crabs to terrestrial predators such as birds and mammals whereas the lower site catered to predatory crabs (e.g., *Callinectes* and *Eurytium*) and fishes. Crabs were always placed a minimum of 2 m apart to prevent tether entanglement and were censused daily at 09:00 hrs and 16:00 hrs. During each census, crabs remaining alive were counted while any discarded remains of consumed crabs were removed.





Fig. 1. Field sites for tethering experiments on Sapelo Island, Georgia, U.S.A. A, upper site: infrequently inundated during high tides; B, lower site: flooded during most high tides.

#### Natural predation of fiddler crabs

Many researchers have noted that when predators consume adult male fiddler crabs, they rarely ( $< 1\%$ ) consume the major chela (Crane, 1975; Bildstein et al., 1989; Zwarts & Blomert, 1990; Iribarne & Martinez, 1999; but see Lee & Kneib, 1994). Crane (1975) noted that the ground was "littered with inedible claws". Moreover, despite aggressive use of the major claw in territorial disputes between males, the appendage is infrequently lost in such encounters (Crane, 1975; Ricketts et al., 1985). Thus, it was assumed that non-molted major claws found on salt flats were the consequence of successful or attempted predation. Isolated major chelae were collected from three salt flats near Dean Creek Marsh. Claws were collected, measured, and inspected morphologically to ensure that they belonged to *U. pugilator*. At two sites, all claws were cleared from a designated area and the appearance of new claws was monitored over a five-day period. Carapace width of the "dead" crabs was back-calculated using the equation relating male chela size to carapace width generated from field sampling. The estimated size frequency of

crabs consumed in nature was then compared with the size of male crabs in the sample population and those consumed in tethering experiments.

## RESULTS

A total of 544 individuals of *Uca pugilator* were sexed and measured. The overall sex ratio was biased in favor of males (305 males and 239 females,  $\chi^2 = 8.01$ ,  $df = 1$ ,  $P = 0.005$ ). However, crab size (CW) interacted significantly with sex ratio, with a greater proportion of juvenile females (5.0-10.0 mm), an approximately equivalent proportion of each sex in intermediate size classes (10.1-15.0 mm), and a greater proportion of males among adults (15.1-20.5 mm) (fig. 2).

### Pitfall traps

Two hundred and twenty one crabs were removed from pitfall traps. Crabs ranged in size from 7.5 to 18.3 mm with a mean ( $\pm 1$  SE) of  $14.7 \pm 0.14$  (fig. 3). The majority of crabs were adults ( $N = 107$ ) or intermediate size classes ( $N = 108$ ); few juvenile crabs ( $N = 6$ ) or large adult ( $> 18.0$  mm) crabs were recovered. Male crabs significantly outnumbered females (126 males and 95 females;  $\chi^2 = 4.35$ ,  $df = 1$ ,  $P = 0.037$ ).

### Quadrat excavations

Twenty-five excavated quadrats yielded 323 crabs: 179 males and 144 females. The average density ( $\pm 1$  SE) of *U. pugilator* measured  $164.4 \pm 16.3 \text{ m}^{-2}$ . Carapace width ranged between 5.5 and 20.5 mm with a mean size ( $\pm 1$  SE) of  $13.4 \pm 0.19$  (fig. 3). Juvenile females were more than twice as prevalent as juvenile males whereas males and females occurred in equal proportions in intermediate

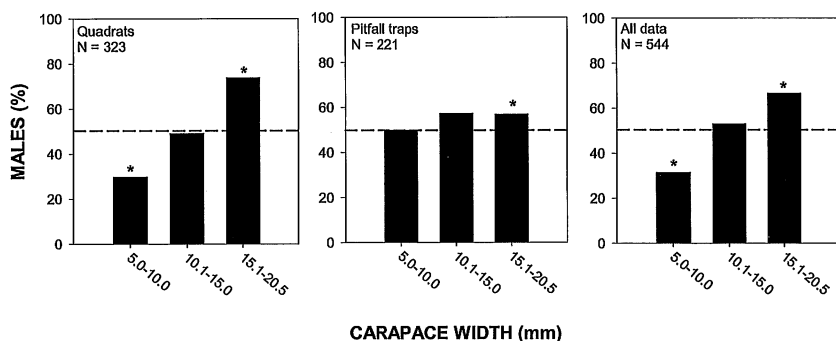


Fig. 2. *Uca pugilator* (Bosc, 1802) sex ratio (percentage male) as a function of carapace width. Dashed line denotes the expected 50 : 50 male-to-female ratio. Asterisks (\*) indicate significant deviation from an even sex ratio (Pearson chi-square,  $P < 0.05$ ).

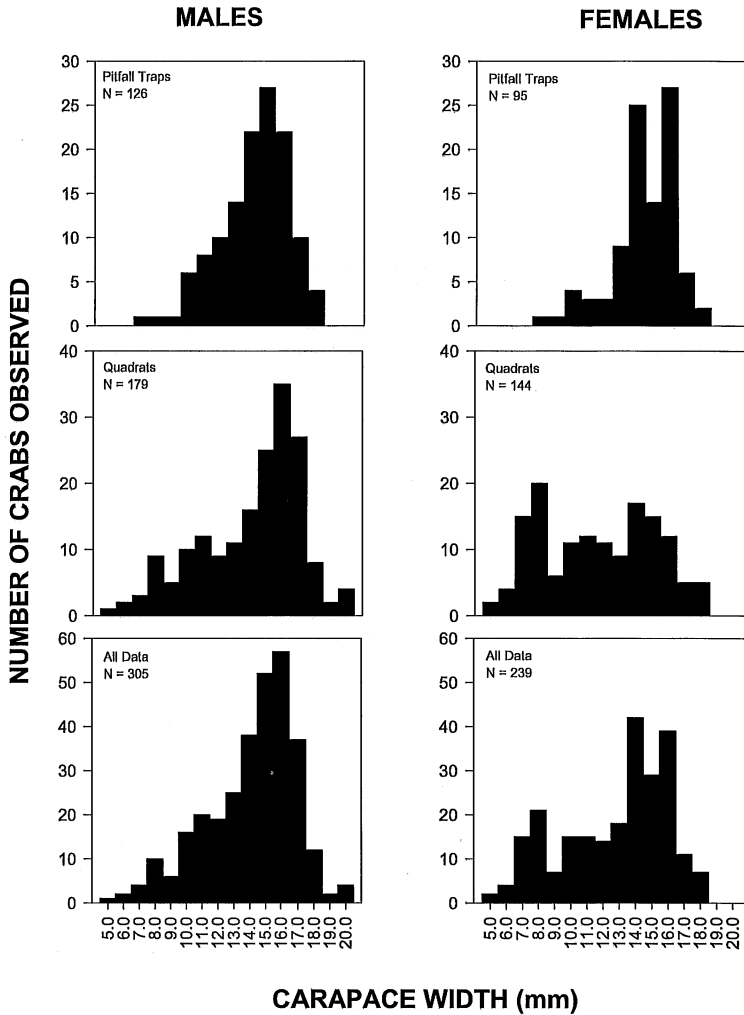


Fig. 3. Size distributions of male and female *Uca pugilator* (Bosc, 1802) separated by sampling method.

size classes and adult males greatly outnumbered adult females (fig. 2;  $\chi^2 = 38.14$ ,  $df = 2$ ,  $P < 0.0001$ ). In exposed foraging areas, males were seven times more abundant than females; within burrows however, females outnumbered males by 30% ( $\chi^2 = 58.02$ ,  $df = 1$ ,  $P < 0.0001$ ). Crabs in "droves" or herds on foraging grounds were significantly larger than those in burrows or those captured in pitfall traps, regardless of sex (fig. 4; 2-way ANOVA,  $F_{[1,319,0.05]} = 105.66$ ,  $P < 0.0001$ ).

Individuals of *U. pugilator*  $\leq 8.0$  mm were sexed reliably using chelal and subabdominal structures. There were no instances in which sex was ambiguous, and male *U. pugilator* with enlarged chelae were observed at carapace widths

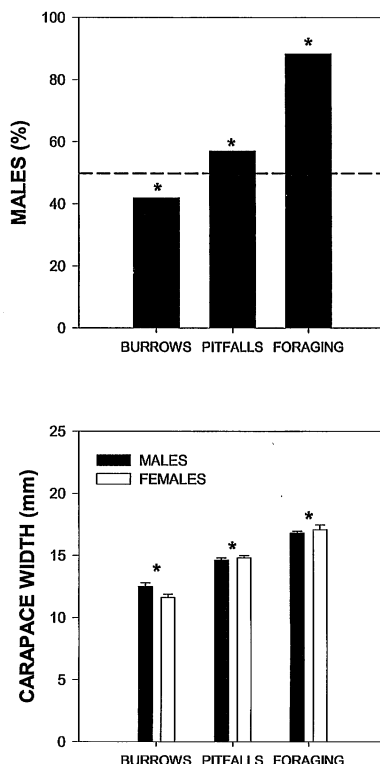


Fig. 4. Sex ratios (percentage males) and mean sizes ( $\pm 1$  SE) of male and female *Uca pugilator* (Bosc, 1802) by habitat and sampling type. In the upper figure, dashed line denotes the expected 50:50 male-to-female ratio while asterisks (\*) indicate significant deviation from a sex ratio of unity (Pearson chi-square,  $P < 0.05$ ). In the lower figure, asterisks denote significant overall differences of mean crab size by habitat type (2-way ANOVA,  $P < 0.05$ ).

as small as 5.5 mm. To further verify this method, 349 juvenile (2.5-10.0 mm) *U. pugnax* were also inspected. One hundred and twenty-eight males and 123 females between 4.0 and 10.0 mm were recorded. For crabs with a carapace width between 2.5 and 4.0 mm, abdominal structures were more difficult to observe and possibly subject to error (Ahmed, 1976). Seventy-one "females" and 21 males were observed within this size range. Although enlarged chelae were observed in males with carapace widths of 2.7 mm, it is not known if all males developed the major chela at the same rate. Yamaguchi (1977) reported that pleopods developed in *U. lactea* by 3.0 mm CW but chelae dimorphism was not reliable until 5.0 mm CW.

#### Chelae of living crabs

A combined total of 305 male crabs were examined and measured. Propodus length ranged from 3.4 to 29.4 mm with a mean ( $\pm 1$  SE) of  $18.1 \pm 0.34$ . Of these,

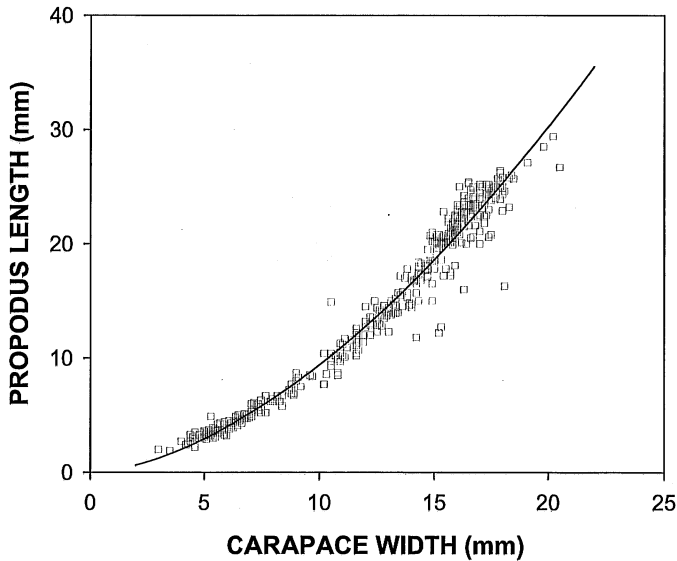


Fig. 5. Relationship between carapace width and propodus length of major chelae among living male *Uca pugilator* (Bosc, 1802).  $PL = 0.193CW^{1.687}$ ,  $R^2 = 0.967$ ,  $P < 0.0001$ ,  $N = 299$ .

12 (3.9%) exhibited missing or obviously regenerating major chelae, presumably a result of failed predation. Six (1.9%) had malformed or damaged major chelae, including polydactyly, abnormal curvature of the pollex, and missing dactyli. Excluding these individuals, a power function provided the best description of the relationship between carapace width and propodus length ( $R^2 = 0.967$ ,  $P < 0.0001$ ; fig. 5). Overall, the proportion of right "handed" (right chela = major claw) crabs significantly exceeded the proportion of left-handed individuals ( $\chi^2 = 3.99$ ,  $df = 1$ ,  $P = 0.046$ ), but this relationship varied with size class. Among adults, right-handed crabs were twice as prevalent as left-handed individuals whereas the proportions of each group were nearly equivalent in juvenile and intermediate size classes (fig. 6).

Three (1.3%) female crabs possessed a "major" claw, a phenomenon rarely reported in the literature. While relatively small compared to those of males, these chelae could be as much as  $1.75\times$  the size of the minor chela. One (0.4%) female crab was missing a chela, a significantly lower frequency than that observed among males ( $G = 8.65$ ,  $P < 0.005$ ).

#### Recovered chelae

One hundred and twenty major chelae, ranging in size from 8.4 to 27.2 mm, were recovered from three salt flats dominated by *U. pugilator*. At the two sites for which density data were recorded, chela densities were  $0.24$  and  $0.31\text{ m}^{-2}$ . Following removal of chelae from these sites, the reappearance rate was low,

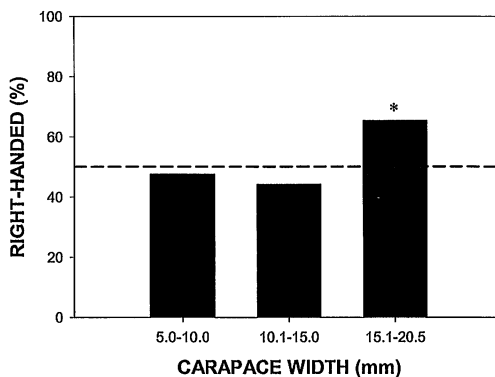


Fig. 6. Right-handedness (percentage of living male *Uca pugilator* (Bosc, 1802) with major chela on right side) by carapace width. Juvenile crabs correspond to size range 5.0-10.0 mm, intermediate sized-crabs to 10.1-15.0 mm, and adult crabs to 15.1-20.5 mm. The dashed line denotes the expected 50 : 50 left-to-right handedness ratio.  $N = 305$ .

measuring  $0.03$  to  $0.04 \text{ m}^{-2} \text{ day}^{-1}$ . The average propodus length of recovered chelae from all sites were similar (1-way ANOVA;  $F_{[2,117,0.05]} = 0.45$ ,  $df = 2$ ,  $P = 0.452$ ) and the data were pooled for comparison with chelae from living crabs. Average propodus length among recovered chelae was significantly larger than that of living males (1-way ANOVA;  $F_{[1,403,0.05]} = 34.31$ ,  $P < 0.0001$ ) owing to the lack of small-sized chelae among recovered claws. Carapace width was estimated for each of the recovered chelae using the power function relating to carapace width and propodus length in living crabs. With the exception of small size classes, the size distribution of “dead” crabs calculated from the recovered claws corresponds closely with the size distribution of living male crabs (fig. 7). Among the recovered chelae, however, left-handed claws were more abundant, and chela status (living or recovered) interacted significantly with handedness (left or right) ( $\chi^2 = 5.04$ ,  $df = 1$ ,  $P = 0.025$ ;  $N = 397$ ).

#### Tethering experiments

Few tethered crabs of either sex were eaten, regardless of tidal position (upper versus lower site). In 24-hr trials, predators consumed 2.4% ( $N = 60$  individual trials) of females and 0% ( $N = 91$  individual trials) of males tethered at the upper site. At the lower site, 1.9% ( $N = 101$  individual trials) of females and 1.9% ( $N = 108$  individual trials) of males were eaten after 24 hours. In all predation events, a small piece of glued carapace remained tethered as evidence the crab had been eaten. Most tethered crabs foraged, dug burrows, and interacted with “free” crabs, and many survived on tethers for up to 100 hours, at which point the experiment was terminated.

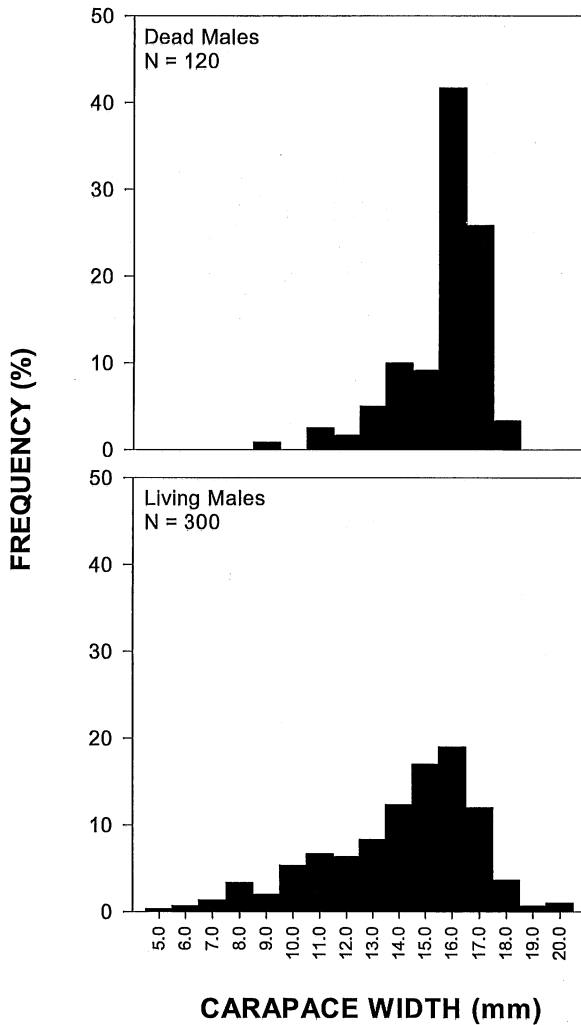


Fig. 7. Size frequency distribution of carapace width between living and "consumed" *Uca pugilator* (Bosc, 1802). Carapace width of dead crabs ( $N = 120$ ) estimated from the power function between PL and CW obtained from measurements of living crabs ( $N = 299$ ).

#### DISCUSSION

##### Biased sex ratios in Atlantic sand fiddler crabs

These results suggest that both habitat use and size class significantly influence the sex ratio in *Uca pugilator*. Although female crabs outnumbered males among juveniles, they declined in proportion with increasing size classes. Among adults, males were more than twice as abundant as females. Crabs foraging on salt flats were predominantly male and significantly larger than those removed from spatially disparate burrowing areas, which were mostly female. This sex-dependent

use of habitat is unlikely to result from reproductive behavior, as October is beyond the species' breeding season and no ovigerous females were observed, but may be a consequence of behavioral or physiological differences between the sexes. With two feeding chelae, females can forage more efficiently than male crabs, thus spending less time away from refuge (Valiela et al., 1974). Alternatively, males could out-compete females for access to prime foraging areas (Weissburg, 1992, 1993). Croll & McClintock (2000) reported similar aggregations of large males in three fiddler crab species and concluded that the behavior was a function of reproductive behavior. However, the observation of this tendency in male *U. pugilator* outside of the species' reproductive season suggests that, at least in this species, other factors are also involved.

The mating system of *Uca pugilator* has been described as resource-defense polygyny (Christy & Salmon, 1984), which ought to favor a female-biased sex ratio as males are territorial and promiscuous. By including juvenile crabs in this survey and using subabdominal structures to verify sex, I found that the primary sex ratio does favor females. However, with increasing carapace width the sex ratio showed an increasing bias in favor of males, suggesting that the deviant sex ratio among adults is acquired (Shanholtzer, 1973). It is unlikely that females simply fail to grow as large as males, as no significant differences between the average sizes of each sex across habitat types were noted. Male crabs may experience lower intensities of predation once their major chela becomes sufficiently large to either (i) deter predators owing to increased handling time (e.g., Bildstein et al., 1989) or (ii) offer males a "second chance" by autotomizing after the crab is captured by a predator (e.g., Lee & Kneib, 1994). Male crabs exhibited a significantly higher frequency of missing and regenerating chelae than female crabs (3.9% v. 0.4%). Assuming claws are lost due to attempted predation (e.g., Crane, 1975) and that males are equally or less susceptible to predators (e.g., Bildstein et al., 1989), these second chances may become important when integrated over time.

#### Predation and food limitation in fiddler crabs

One of the most surprising findings was the extremely low predation rate on tethered fiddler crabs. Studies involving numerous species of crabs tethered over 24-hr periods report predation rates between 10 and 70%, depending on the year, habitat, and location (e.g., Wilson et al., 1990; Heck & Wilson, 1987). Crabs in unvegetated areas, as in the current experiment, generally experience even higher predation (Heck & Thoman, 1981). Previous tethering experiments with fiddler crabs on Sapelo Island have recorded average 24-hr loss rates of 50% (L. Eby, unpubl. data). In the current study, less than 3% of the *U. pugilator* tethered on salt flats and mud flats were consumed during 24-hr trials. Many crabs persisted for 100 hours.



The most likely factor in explaining the low level of predation observed is seasonal variation. Predation events are probably episodic and seasonally variable, particularly for locally important avian predators such as white ibis (Bildstein et al., 1989). De Boer & Longamane (1996) found that bird density in estuarine systems increased by twenty-fold between winter and summer. Mud crabs (*Eurytium limosum* (Say, 1818)), which are locally abundant and were expected to impact crabs at the lower site substantially, may have been negatively influenced by temperature (Kneib & Weeks, 1990) or neap tides. In addition, blue crab (*Callinectes sapidus* Rathbun, 1896) populations, often an important predator in Atlantic estuaries, have been declining in recent years (R. Kneib, pers. comm.). Other predators, such as raccoons (Teal, 1958), frequented the area as their tracks were found each morning around the tethered crabs, but elected not to take advantage of the resource.

Alternatively, predation may not be an important determinant of fiddler crab sex ratios. Considering the enormous size of many fiddler crab populations ( $10^6$ - $10^9$  per marsh) relative to most predators (even a community of predators), the degree to which predation limits fiddler crab abundance remains an open question. Based on nutrient enhancement studies in the field and laboratory, Montague (1980b) suggested that fiddler crab populations are limited by food resources, not by predators. Similarly, Christy & Salmon (1984) observed that *U. pugilator* populations were probably limited by food availability. Genoni (1985) determined that increasing the food supply in experimental plots caused an increase in the density, recruitment, and organic content of *U. rapax* (Smith, 1870). Treatments in which predators were excluded showed no additional effect. However, predatory crabs were not removed from enclosures, clouding interpretations regarding the effects of predators.

#### Recovery of crab chelae

Further evidence for low predation rates on male crabs during this study may be inferred from the low re-appearance rate of discarded major chelae after individual salt flats were cleared ( $< 0.05 \text{ m}^{-2} \text{ day}^{-1}$ ). Many bird predators remove and discard a male crab's major chela before consuming the animal (Bildstein et al., 1989; Iribarne & Martinez, 1999). In laboratory trials, captive birds refuse to eat the major chelipeds of males owing to their low digestibility (Zwarts & Blomert, 1990). I found that the average back-calculated carapace width of dead crabs was significantly larger than that of living males. Several hypotheses can be offered to explain this trend: first, crabs with a carapace width of 16 mm or greater support a formidable major claw (PL > 20 mm), which predators might remove before eating the crab. Smaller crabs with less developed major chelae might be consumed whole, leaving no record of their predation. Second, the pattern may be

a consequence of differential habitat use: large males are competitively dominant and may exclude smaller crabs from prime foraging areas, leaving large chelae over-represented. Finally, this pattern may be the simple result of aging: larger, older crabs are more likely to senesce and die, particularly if predation is not a major cause of mortality among crabs (see above). Further use of recovered chelae as an indicator of predation will be hindered until a better understanding of the predominant sources of fiddler crab mortality are available.

It is unlikely that the recovered claws represent molts or claws lost from living crabs, as a significant interaction between handedness (right versus left) and claw origin (recovered versus living) was observed, with most living crabs exhibiting right-handedness and most recovered claws exhibiting left-handedness. However, right-handedness among living crabs was only dominant among the largest size class, suggesting that left-handed adult males were dying more frequently than right-handed individuals. This pattern may result from asymmetries on the part of predators, as found for foraging strategies of certain birds (Koga et al., 2001). Most predatory brachyurans, for example, are equipped with a crusher chela on their right side, presumably to handle asymmetric prey such as gastropods (Lee, 1995). Among fiddler crabs, many species exhibit either a 1 : 1 ratio of right- to left-handed males or a bias in favor of right-handedness (Yamaguchi & Henmi, 2001).

#### General comments on sex ratios in *Uca*

DeRivera & Vehrencamp (2001) hypothesized that female gametic investment (indicated by clutch size) and asynchrony among receptive females (indicated by tidal height occupied) should be positively correlated with the degree of male-bias in an *Uca* species' sex ratio. Using the data presented in their paper, I found no relationships between these factors and the percentage of males in the populations included in table I. This is hardly surprising, however, given (i) the high level of sex ratio variation within a species and (ii) the confounding effects of post-recruitment mortality. Breeding synchrony, gametic investment, and other aspects of a species' mating system may control the primary sex ratio, but predation and other sources of differential mortality will interact to determine the adult sex ratio. Thus, while juvenile *U. pugilator* exhibited a female bias corresponding to the species' relatively low clutch size, polygyny, and high degree of synchrony (supratidal zone), male crabs were over-represented among adults. Similar shifts in sex ratio with size class have been reported by Shanholtzer (1973) and Spivak et al. (1991), emphasizing the importance of distinguishing between primary and adult sex ratios.

A review of recorded sex ratios in fiddler crabs illustrates that, in many species and populations, the percentage of males significantly exceeds that of females

(table I). However, it also reveals that sex ratio is strongly influenced by species, year, habitat use, and location. Although I recorded a significant male-bias in the sex ratio of *U. pugilator* from Sapelo Island over a brief period of study, independent of sampling method, several previous studies have noted a greater proportion of females in sand fiddler crab populations (Knopf, 1966; Salmon & Hyatt, 1983; Colby & Fonseca, 1984). Local factors such as food supply and predation pressure are probably important determinants of adult sex ratio at the population level. In addition to spatial variability, the effects of temporal variation at short (tidal and lunar cycles), intermediate (seasonal), and long (interannual) time scales on sex ratios can be substantial and warrant further investigation (D. Pope, unpubl. data; Emmerson, 1994). Challenges and suggestions for the continued study of fiddler crab sex ratios include (i) increased attention to the distinction between intrinsic (primary) and derived (adult) biases in the percentage of males in a population, (ii) a greater emphasis on rearing immature crabs or using molecular techniques to verify primary sex ratios, and (iii) determination of the relative importance of predation and food limitation in sex-specific mortality rates. Although results of both the literature review and empirical study suggest male-biased sex ratios are acquired through post-recruitment processes, elucidation of the mechanism responsible will require a long-term, multifactor experiment that manipulates both predation pressure and food availability.

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