

SEX DIFFERENCES IN PREDATOR EVASION IN THE FIDDLER CRAB
UCA TANGERI (DECAPODA: OCYPODIDAE)

Joana M. Jordão and Rui F. Oliveira

(JMJ, correspondence) ISPA, Unidade de Investigação em Eco-Etologia, R. Jardim do Tabaco, 34, 1149-041 Lisboa, Portugal (jjordao@ispa.pt); (RFO) ISPA, Unidade de Investigação em Eco-Etologia, R. Jardim do Tabaco, 34, 1149-041 Lisboa, Portugal (ruiol@ispa.pt)

A B S T R A C T

The major claw of male fiddler crabs, reaching up to 40% of the individual's total body weight, may impose a cost on males when escaping from predators. To test this hypothesis, 38 males (18 without the major claw) and 19 females were randomly captured and placed, individually, in a straight track. After a five-minute adaptation period, an observer walked toward the crab and triggered its escape reaction. Each crab was subjected to 10 trials with 5-minute intervals between them. The central area of the track was video-recorded with a camera from a height of 1.30 m, pointing to the ground at a 90° angle. Females ran significantly faster than males with claw, but the escape velocity of males without claw did not differ significantly from that of intact males or females. Speed was strongly correlated with air temperature. The distances at which males and females reacted to and hid from approaching humans did not differ. These results are discussed in an ecological and evolutionary perspective.

Fiddler crabs show a pronounced degree of sexual dimorphism (Crane, 1975). Females possess two isomorphic feeding claws, while males have a small claw and a hypertrophied one reaching up to 40% of the individual's total body weight (Rosenberg, 1997). The major claw of the males is used for fighting and threatening (intra-sexual selection) and in a waving display to attract females to the male's burrow for mating (inter-sexual selection) (Crane, 1975).

Males with larger claws have an advantage in male-male competition (Crane, 1967, 1975; Latruffe *et al.*, 1999) and females of several species generally prefer larger males. Female *Uca tangeri* (Eydoux, 1835) visit males with larger claws more often (Latruffe *et al.*, 1999) and, in binary choice tests, spend more time near models of males with larger claws (Oliveira and Custódio, 1998). Hyatt (1977) found a female preference for larger males in *Uca pugilator* (Bosc, 1802) and Christy (1983) also observed that males with larger claws had a mating advantage in the same species. Female *Uca annulipes* (H. Milne Edwards, 1852) mate with males with claws that are larger than the population average (Backwell and Passmore, 1996). In *Uca rapax* (Smith, 1878) there is a significant association between the rate of attracting females and male major claw

length (Greenspan, 1980). However, for *Uca vocans vocans* (Linnaeus, 1758) (see Salmon, 1984) and for *Uca beebei* (Crane, 1941) (see Christy, 1987) no female preference was found for males with larger claws.

So far, a relatively lower food intake rate for males compared to females is the only reported cost for this sexually selected male trait (Weissburg, 1992). Another possible cost could be an impaired ability to escape, due to the claw's weight and form. This is suggested by some empirical observations, although Frix *et al.* (1991) report no differences of escape speeds between males and females of the species *U. pugilator* and *Uca pugnax*. We do not know of any study where direct measures have been taken in *Uca tangeri*. If male escape velocity decreases with increasing relative claw size, then this is likely to be a significant cost because fiddler crabs are severely predated by several seabird species (see Ens *et al.*, 1993; Backwell *et al.*, 1998) and also by rats (von Hagen, 1962; personal observations). This way, claw size (i.e., weight) could be a reliable and honest signal for females to assess male quality, because only males in good condition would be able to grow a large claw without being predated, as long as they would not behave in any other way to reduce their encounter rate with preda-

tors (i.e., they would not behave in ways that offset the cost).

In this study we measured the escape speeds of *U. tangeri* males with the major claw, females, and males without the major claw. We predicted that male *U. tangeri* with claws would have slower escape speed compared to females or to males without claws. We also looked at some characteristics of the response pattern of males and females to the approach of (human) predators.

MATERIALS AND METHODS

Study Site

Fieldwork was conducted in June 1998 and between late May and July 1999 at Quinta do Marlin and Cacela Velha, in the Ria Formosa Natural Park, Algarve, Portugal. The Ria Formosa is approximately 55-km long with a maximum width of 7 km. It consists of a system of mudflats and salt marshes, sheltered by a series of sand barrier islands. Populations of *U. tangeri* are found on almost all the mudflats at Ria Formosa.

Predator Escaping Speed

The study site, Quinta do Mann (Olhão), had an average crab density (1998: 1 burrow/m², Oliveira *et al.*, 2000; 1999: 2.6 burrows/m², unpublished data) lower than other sites in Ria Formosa (e.g., Cacela Velha, 1998: 4 burrows/m², Oliveira *et al.*, 2000; 1999: 12.5 burrows/m², unpublished data), offering large areas without burrows or vegetation for the experimental set-up. Crabs (43 males and 21 females) were captured and placed, isolated, in a straight track for a 5-min adaptation period. Twenty of the males were previously induced to autotomize their major claw by holding them by the claw. They were placed in the track after they appeared to behave normally. The track was 2-m long by 20-cm wide, and the walls were made of smooth wood planks 30-cm high. After the adaptation period, the observer walked toward the crab and triggered its escape reaction. Each crab was subjected to 10 trials with 5-min intervals between them. After the trials, the crabs were weighed using a spring-balance (± 0.25 g) and measured using a Vernier calliper (± 0.01 mm). Major claw length (MCL) and carapace width (CW) were measured. Temperature and wind were recorded using a digital thermometer ($\pm 0.01^\circ\text{C}$) and the Beaufort scale for ecologists (Jones and Reynolds, 1996), respectively. During the trials, the central area of the track was video-recorded with a camera (Sony DCR-TR7000E) at 1.30-m height, pointing to the ground at a 90° angle so that accurate measures could be taken from the recorded video. The total area filmed was approximately 0.42 m². The images were analysed afterwards with an event-recorder (The Observer for Windows v. 3.0, 1997), which permits timing to the nearest 0.04 sec. The path length was measured using the program "ImageTool" (Image-Tool for Windows v. 2.00, 1996) to the nearest 0.001 m. The average and maximum running speed of the 10 trials for each crab were used for statistical analysis.

Predator Reaction and Hiding Distances

Observations took place at Quinta do Mann and Cacela Velha. After choosing a burrow, the observer sat 20 m

away in the direction of the sun and observed the subject through binoculars. After the crab resumed its normal activity for a period of 5 min, the observer would walk in a straight line towards the focal crab. The position of the observer when the crab reacted was marked on the ground. Crabs typically reacted to the approaching observer by running to their burrows, pausing, and finally entering. The position of the observer at the time the subject entered the burrow was marked on the ground. In addition, the position of the focal crab when it first reacted was marked. Afterwards, the distances between the observer and the subject when it first reacted and when it entered the burrow were measured. The distance between the crab and the burrow when it first reacted to the observer was measured for five males and eight females. Subsequently, the subjects were sexed, weighed, and measured.

Statistical Analysis

All statistical analysis was done using the Statistica software package (v. 5.0, 1995). The assumptions of parametric statistics of normality and homogeneity of variance were tested before subsequent analysis.

Escape Speed.—We obtained clear video images of 38 males (18 without the major claw) and 19 females. To check for differences between the groups we did a multiple analysis of covariance (MANCOVA) with average and maximum escape speeds as the dependent variables and temperature as a covariate. We have calculated the partial correlations of both velocities with weight (correcting for temperature in both cases) for all three groups.

Reaction and Hiding Distances.—Our sample consists of a total of 19 males (all with major claw) and 15 females. We have calculated the partial correlations of first-reaction distance and hiding distance with MCL/CW (for males), and weight (for females), controlling for temperature. We have also calculated the partial correlation of first-reaction distance with crab-to-burrow distance controlling for MCL/CW (in males), weight (in females), and temperature (in both males and females).

RESULTS

There were no significant differences in carapace width (*t*-test for independent samples, $P = 0.82$) and weight (*t*-test for independent samples, $P = 0.83$) between males with the major claw and males without the major claw before the claw was removed. After the autotomy of the claw, the weight of these two groups was significantly different (*t*-test for independent samples, $P = 0.02$), but the weight of males without the major claw was not significantly different from that of females (*t*-test for independent samples, $P = 0.65$). This way we can assume that the differences in weight between the males with the major claw and the males without the major claw were attributable to the claw.

Predator Escaping Speed

A multiple analysis of covariance with temperature as a covariate showed significant dif-

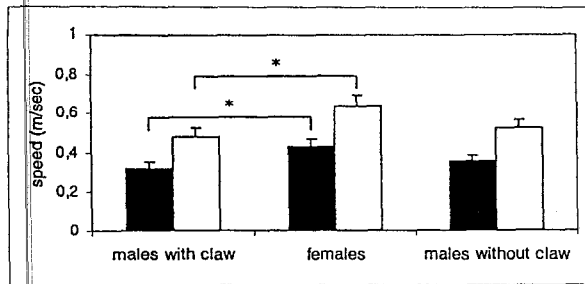


Fig. 1. Average (dark bars) and Maximum (white bars) running speed of males and females. Bars are mean (m/s); T is standard error of mean; * indicates $P < 0.05$.

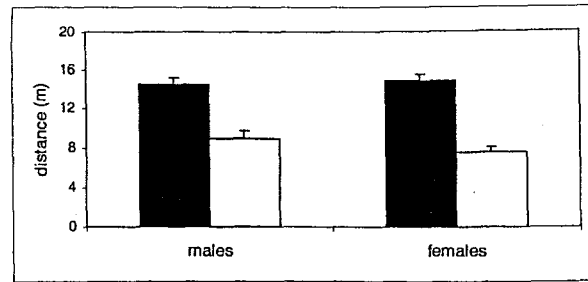


Fig. 2. Reaction (dark bars) and Hiding (white bars) distances for males and females. Bars are mean (m); T is standard error of mean.

ferences between the groups for average running speed ($F_{2,53} = 8.184$, $P = 0.001$) and maximum running speed ($F_{2,53} = 7.559$, $P = 0.001$). *Post-hoc* comparisons (Tukey HSD for unequal n test) showed differences were between males with claw and females (average running speed: $P = 0.01$; maximum running speed: $P = 0.01$). Males without the major claw did not differ significantly from males with the major claw (average running speed: $P = 0.59$; maximum running speed: $P = 0.69$) or females (average running speed: $P = 0.13$; maximum running speed: $P = 0.09$) (Fig. 1).

Partial correlations of both speeds with weight were all non-significant. In males with the major claw, the partial correlations of both average and maximum running speeds with MCL/CW were also non-significant. Temperature had a significant partial correlation with both speeds in all groups (Table 1).

Reaction and Hiding Distances

There was a non-significant trend for males to react sooner to human observers if they were further from the burrow (partial correlation between first-reaction distance and crab-to-burrow distance, controlling for MCL/CW: $r = 0.93$, $P = 0.07$, $n = 5$; partial correlation between first-reaction distance and crab-to-burrow distance, controlling for temperature: $r = 0.94$, $P = 0.07$, $n = 5$). These were not observed in the case of females (partial correlation between first-reaction distance and crab-to-burrow distance, controlling for weight: $r = 0.18$, $P = 0.70$, $n = 8$; partial correlation between first-reaction distance and crab-to-burrow distance, controlling for temperature: $r = 0.24$, $P = 0.60$, $n = 8$). The size of the individuals did not seem to influence their reaction to predators, both in males (par-

tial correlation between first-reaction distance and MCL/CW, controlling for temperature: $r = -0.08$, $P = 0.76$, $n = 19$; partial correlation between hiding distance and MCL/CW, controlling for temperature: $r = 0.08$, $P = 0.762$, $n = 19$) and in females (partial correlation between first-reaction distance and weight, controlling for temperature: $r = -0.11$, $P = 0.71$, $n = 15$; partial correlation between hiding distance and weight, controlling for temperature: $r = 0.49$, $P = 0.08$, $n = 15$) (Fig. 2).

DISCUSSION

The data presented here show that females run significantly faster than males with the major claw. However, the velocity of males without the major claw does not differ significantly from that of males with the major claw or that of females, assuming values in between these two groups (Fig. 1). In all three groups, speed was strongly correlated with environmental temperature but not with any of the morphometric variables measured (Table 1).

Males with the major claw run significantly slower than females but not, as predicted, because they carry a large claw. We expected that clawless males would run as fast or faster than females and significantly faster than males with claw. There are several possible explanations for these unexpected results.

First, the values we obtained for the running speed of males without the major claw might be underestimates. Even though the crab autotomized the major claw, this process was induced and it may have negatively affected male running speed. Decrease in escape speed in lizards and salamanders after tail autotomy is widely documented (Ballinger *et al.*, 1979; Dowdey and Brodie, 1989; Formanowicz *et al.*, 1990), and Frix *et al.* (1991) also report

Table 1. Partial correlations of average (AvgRS) and maximum (MaxRS) speed with temperature and body weight.

		Temperature	Weight
Males with claw	AvgRS	0.64**	0.05
	MaxRS	0.55**	-0.04
Females	AvgRS	0.67*	0.36
	MaxRS	0.65*	0.06
Males without claw	AvgRS	0.55*	0.08
	MaxRS	0.70*	-0.14

** $P < 0.001$; * $P < 0.05$.

slower speed in fiddler crabs with one of their claws removed, both in males and females.

Second, the prediction that males without the major claw should run faster than males with claw (like females do) is based on the assumption that the body of males and females is basically identical, besides the hypertrophied claw. This may not be the case. The lateral waving species *U. pugilator* and *U. pugnax* (Smith, 1870) (see Crane, 1975) show asymmetry in the ambulatory legs in the case of the males, but not in females (Tazelaar, 1933 in Takeda and Murai, 1993; Miller, 1973). Takeda and Murai (1993) found it also to be the case in *U. annulipes* males, also a lateral waver species (Crane, 1975), and, even though not to the same extent, in *U. tetragonon* (Herbst, 1790), an intermediate waver (Crane, 1975). This asymmetry seems to be correlated to waving pattern display because the vertical wavers (Crane, 1975) tested by Takeda and Murai (1993), that is *U. urvillei* (H. Milne Edwards, 1852), *U. dussumieri* (H. Milne Edwards, 1852), and of *U. vocans*, did not show asymmetry of male ambulatory legs. *Uca tangeri* was not included in the referred study, but male *U. tangeri* are lateral wavers (Crane, 1975), so asymmetry of the ambulatory legs is a plausible possibility, and it may affect running speed.

Third, there may be no difference between males and females in the physical capacity of achieving the same escape speed, and the lower values we obtained for the males with the major claw may reflect a risk-taking behaviour. The risk of an animal being eaten depends on the predation pressure, the ability to escape from the predator, and the ability to defend itself from the predator. All factors considered, the animal makes the decision of how long it can afford to delay the escape (Ydenberg and Dill, 1986). Several studies re-

port changes and temporary variation in behaviours and escape tactics that conform to this cost-benefit analysis. For example, when predation pressure is higher, female *U. beebei* reduce their mate sampling activity, and males wave less and build fewer mud pillars (Koga *et al.*, 1998). Gravid female lizards, *Lacerta vivipara* (Jacquin, 1787), are burdened by the weight of the clutch and have slower running speed. They remain motionless, allow human predators to approach closer, and rely on crypsis more than males and non-gravid females do (Bawens and Thoen, 1981). In another lizard, *Psammotromus algirus* (Linneus, 1758), old males are very brightly colored and conspicuous. They do not allow humans to approach as close as dull young males do, and they have longer flight distances. Also, among old males, the ones mate-guarding a female, and thus with increased costs of fleeing, allow closer approaches than the ones who are alone (Martin and López, 1999). In the particular case of *U. tangeri*, males have to spend more time in feeding activities than females (Faria, 1994) due to having only one useful claw for feeding. Also, males have to compete with each other for mates by waving to wandering females (Backwell *et al.*, 1999). Not hiding away in the burrow is, therefore, more beneficial for males than females (i.e., the costs of fleeing are higher in males). In addition, the enlarged claw is a powerful weapon used in defence, and it may confer protection from predators (i.e., the costs of staying are smaller in males). In a study of forager escaping tactics, Formanowicz and Brodie (1988) reported that only males of *U. panacea* chose to stay beside a food item and defend themselves, and Bildstein *et al.* (1989) demonstrated higher handling costs of males for the predators, the cost associated with the major claw. Additional evidence of risk-taking behaviour by male fiddler crabs is presented by Frix *et al.* (1991); male and female *U. pugnax* and *U. pugilator*, when approached by a simulated avian predator, retreat to their burrows and, initially, descend similar distances. After the burrow has been probed with a bill, however, females descended significantly further than males. Escape speed was also measured in this latter study, and no differences were found between males and females in these two species. However, each crab was subjected to only one trial and the

variable used was the time it took the subject to run along the experimental track, considering the path to be a straight line. Also, time was measured with a stopwatch (K. L. Bildstein, personal communication), which may not be as accurate as using an event recorder.

In this context it is somehow surprising that there are no differences between males and females in reaction and hiding distances because, as discussed above, we would expect that human observers could approach to males closer than to females. However, Altevogt (1959) and von Hagen (1962) do not mention any sex differences in reaction distances for the European population of *U. tangeri*, either. The value reported by Altevogt (1959) (10 to 15 m) is similar to ours, but the value reported by von Hagen (1962), 25 m in the same circumstances and up to 30 m if the observer is walking towards the Sun, is much higher. The hiding distances are more in accord to our results: 6 or 7 m or 9 m if the observer is walking or running, respectively, with the back towards the Sun. This discrepancy in values is probably due to different approach speed by the observers. The distance to the burrow seems to be an important factor in reaction distance, as expected (Ydenberg and Dill, 1986), but our sample is too small to permit clear references.

There was no correlation between speed, body weight, and relative claw size (MCL/CW). The higher the MCL/CW, the bigger and heavier the claw in relation to the crab, because claw weight is highly correlated to its length (J. N. Jordão and R. F. Oliveira, unpublished data). According to the honest signal hypothesis, males with larger claws can pay the energetic cost of escaping, so no correlation was expected. Some mechanisms must have evolved to cope with claw weight. Frix *et al.* (1991) also found no correlation between speed and crab size, but, on the opposite hand, Ens *et al.* (1993) mention that larger crabs of *U. tangeri* run faster.

The strong correlation between temperature and speed that we obtained for all three groups is an indicator that our data is trustworthy. The levels of activity of ectothermic animals are well known to be strongly temperature dependent (e.g., Bennett, 1980; Hertz *et al.*, 1982). There have been several reports relating fiddler crab waving display and temperature. On cold days, significantly fewer male *U. tangeri*

wave than on warm days, and the wave is slower and has more interruptions (von Hagen, 1962). Also, spontaneous waving, in the absence of females, increases from 0.7 waves in 10 sec at 17°C, to 4.7 waves in 10 sec at 44°C (von Hagen, 1962). Moreover, Doherty (1982) reported that waving frequency and wave duration decreased with environmental temperature for *U. minax* and *U. pugnax*.

In summary, the evidence presented here does not support our prediction that claw size and weight are costly because they reduce predator evasion ability. However, our results do not imply that the claw is not a costly ornament, and thus an honest signal of male quality. Other potential costs (e.g., energetic costs) of the enlarged claw, and of the waving display in which it is used, need to be considered.

ACKNOWLEDGEMENTS

This study was funded by Fundação para a Ciência e Tecnologia (grant PRAXIS XXI/BD/19835/99) and Instituto para a Conservação da Natureza. We thank: Ria Formosa Natural Park, Portugal, and especially its former Director Professor Luis Fonseca, for permission to work in their protected area and for logistic support; Ana Curto and Fiona Burford for help in the field; João P. Martins and three anonymous reviewers for helpful comments; colleagues at ISPA, Lisboa, also provided diverse support at all stages of the study.

LITERATURE CITED

- Altevogt, R. 1959. Ökologische und ethologische Studien an Europas einziger Winkerkrabbe *Uca tangeri* Eydoux.—Zeitschrift für Morphologie und Ökologie der Tiere 48: 123–146.
- Backwell, P. R. Y., M. D. Jennions, J. H. Christy, and N. I. Passmore. 1999. Female choice in the synchronously waving fiddler crab *Uca annulipes*.—Ethology 105: 415–421.
- , P. D. O'Hara, and J. H. Christy. 1998. Prey availability and selective foraging in shorebirds.—Animal Behaviour 55: 1659–1667.
- , and N. I. Passmore. 1996. Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, *Uca annulipes*.—Behavioral Ecology and Sociobiology 38: 407–416.
- Ballinger, R. E., F. W. Nietfeldt, and F. F. Krupa. 1979. An experimental analysis of the role of the tail in attaining high running speed in *Cnemidophorus sexlineatus* (Reptilia: Squamata: Lacertilia).—Herpetologica 35: 114–116.
- Bauwens, D., and C. Thoen. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*.—Journal of Animal Ecology 50: 733–743.
- Bennett, A. F. 1980. The thermal dependence of lizard behaviour.—Animal Behaviour 28: 752–762.
- Bildstein, K. L., S. G. McDowell, and I. L. Brisbin. 1989. Consequences of sexual dimorphism in sand fiddler crabs, *Uca pugilator*: differential vulnerability to avian predation.—Animal Behaviour 37: 133–139.

- Christy, J. H. 1983. Female choice in the resource-defense mating system of the sand fiddler crab, *Uca pugilator*.—*Behavioral Ecology and Sociobiology* 12: 169–180.
- . 1987. Female choice and the breeding behavior of the fiddler crab *Uca beebei*.—*Journal of Crustacean Biology* 7: 624–635.
- Crane, J. 1967. Combat and its ritualization in fiddler crabs (Ocypodidae) with special reference to *Uca rapax*.—*Zoologica (New York)* 52: 49–76.
- . 1975. *Fiddler Crabs of the World*. Princeton University Press, New Jersey. 736 pp.
- Doherty, J. A. 1982. Stereotypy and the effects of temperature on some spatio-temporal subcomponents of the "courtship wave" in the fiddler crabs *Uca minax* (Le Conte) and *Uca pugnax* (Smith) (Brachyura, Ocypodidae).—*Animal Behaviour* 30: 352–363.
- Dowdey, T. G., and E. D. Brodie, Jr. 1989. Antipredator strategies of salananders: individual and geographical variation in responses of *Eurycea bislineata* to snakes.—*Animal Behaviour* 38: 707–711.
- Ens, B. J., M. Klaassen, and L. Zwarts. 1993. Flocking and feeding in the fiddler crab (*Uca tangeri*): prey availability as risk-taking behaviour.—*Netherlands Journal of Sea Research* 31: 477–494.
- Faria, M. N. 1994. Estudo Técnico n.º 1: Aspectos do comportamento das bocas-de-cavalete *Uca tangeri* EIDOUX (Ocypodidae, Brachyura) no Parque Natural da Ria Formosa. PNRF, Algarve.
- Formanowicz, D. R., Jr., and E. D. Brodie, Jr. 1988. Predation risk and forager escape tactics.—*Animal Behaviour* 36: 1836–1838.
- , ———, and P. J. Bradley. 1990. Behavioural compensation for tail loss in the ground skink, *Scincella lateralis*.—*Animal Behaviour* 40: 782–784.
- Frix, M. S., M. E. Hostetler, and K. L. Bildstein. 1991. Intra- and interspecies differences in responses of Atlantic sand (*Uca pugilator*) and Atlantic marsh (*U. pugnax*) fiddler crabs to simulated avian predators.—*Journal of Crustacean Biology* 11: 523–529.
- Greenspan, B. N. 1980. Male size and reproductive success in the communal courtship system of the fiddler crab *Uca rapax*.—*Animal Behaviour* 28: 387–392.
- Hertz, P. E., R. B. Huey, and E. Nevo. 1982. Fight versus flight: body temperature influences defensive responses of lizards.—*Animal Behaviour* 30: 676–679.
- Hyatt, G. W. 1977. Field studies of size-dependent changes in waving display and other behavior in the fiddler crab, *Uca pugilator* (Brachyura, Ocypodidae).—*Marine Behavior and Physiology* 4: 283–292.
- Jones, J. C., and J. D. Reynolds. 1996. Environmental variables. Pp. 281–316 in W. J. Sutherland, ed. *Ecological Census Techniques: A Handbook*. Cambridge University Press, Cambridge.
- Koga, T., P. R. Y. Backwell, M. D. Jennions, and J. H. Christy. 1998. Elevated predation risk changes mating behaviour and courtship in a fiddler crab.—*Proceedings of the Royal Society of London B* 265: 1385–1390.
- Latruffe, C., P. K. McGregor, and R. F. Oliveira. 1999. Visual signalling and sexual selection in male fiddler crabs *Uca tangeri*.—*Marine Ecology Progress Series* 189: 233–240.
- Martín, J., and P. López. 1999. Nuptial coloration and mate guarding affect escape decisions of male lizards *Psammotromus algirus*.—*Ethology* 105: 439–447.
- Miller, D. C. 1973. Growth in *Uca*, 1. Ontogeny of asymmetry in *Uca pugilator* (Bosc) (Decapoda, Ocypodidae).—*Crustaceana* 24: 119–131.
- Oliveira, R. F., and M. R. Custódio. 1998. Claw size, waving display and female choice in the European fiddler crab, *Uca tangeri*.—*Ethology, Ecology & Evolution* 10: 241–251.
- , J. L. Machado, J. N. Jordão, F. L. Burford, C. Latruffe, and P. K. McGregor. 2000. Human exploitation of male fiddler crab claws: behavioural consequences and implications for conservation.—*Animal Conservation* 3: 1–5.
- Rosenberg, M. S. 1997. Evolution of shape differences between the major and minor chelipeds of *Uca pugnax* (Decapoda: Ocypodidae).—*Journal of Crustacean Biology* 17: 52–59.
- Salmon, N. 1984. The courtship, aggression and mating system of a "primitive" fiddler crab (*Uca vocans*: Ocypodidae).—*Transactions of the Zoological Society of London* 37: 1–50.
- Takeda, S., and M. Murai. 1993. Asymmetry in male fiddler crabs is related to the basic pattern of claw-waving display.—*Biological Bulletin* 184: 203–208.
- von Hagen, H. 1962. Freilandstudien zur Sexual und Fortpflanzungsbiologie von *Uca tangeri* in Andalusien.—*Zeitschrift für Morphologie und Ökologie der Tiere* 51: 611–725.
- Weissburg, M. 1992. Functional analysis of fiddler crab foraging: sex-specific mechanics and constraints in *Uca pugnax* (Smith).—*Journal of Experimental Marine Biology and Ecology* 156: 105–124.
- Ydenberg, R. C., and L. N. Dill. 1986. The economics of fleeing from predators. Pp. 229–249 in J. S. Rosenblatt, C. Beer, M.-C. Busnel, and P. J. B. Slater, eds. *Advances in the Study of Behavior*. Vol. 16. Academic Press, Orlando.

RECEIVED: 5 July 2000.

ACCEPTED: 16 April 2001.