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著者	Satoshi Takeda
journal or publication title	Journal of crustacean biology : a quarterly of the Crustacean Society for the publication of research on any aspect of the biology of crustacea
volume	40
number	2
page range	147-151
year	2020-02-27
URL	http://hdl.handle.net/10097/00131037

doi: 10.1093/jcbiol/ruz097

Journal of Crustacean Biology Advance Access published 27 February 2020

The Crustacean Society

Journal of
Crustacean Biology

Journal of Crustacean Biology 40(2), 147–151, 2020. doi:10.1093/jcbiol/ruz097

Burrowing-site selection by the soldier crab *Mictyris guinotae* Davie, Shih & Chan, 2010 (Decapoda: Brachyura: Mictyridae)

Satoshi Takeda

Marine Biological Station, Tohoku University, Asamushi, Aomori 039-3501, Japan

Correspondence: Satoshi Takeda: e-mail: satoshi.takeda.d5@tohoku.ac.jp

(Received 18 October 2019; accepted 3 December 2019)

ABSTRACT

The soldier crab *Mictyris guinotae* Davie, Shih & Chan, 2010 inhabiting sandy tidal flats in the Ryukyu Is., Japan, are deposit feeders in two regions: its upper habitat where it burrows and the shoreline. The crabs usually migrate between these two regions during the period of emergence at the daytime and night-time low tide. The aim of this study was to determine which kind of sediments are chosen by the crabs when burrowing. Experiments designed to investigate burrowing-site selection revealed that the crabs preferably burrowed in sediment that had been conditioned through feeding by conspecific crabs, but not in sediment that had been conditioned by conspecific crabs walking on its surface. Moreover, the crabs never showed any preference for burrowing in sediment that had been conditioned through feeding by the competitor fiddler crab *Austruca perplexa* (H. Milne Edwards, 1852); both soldier (prey) and fiddler (predator) crabs sympatrically inhabit the tidal flat, but segregate their habitats with a transition area. These results suggest that chemical cues in sediment conditioned through feeding by conspecific soldier crabs affect where crabs burrow.

Key Words: daily migrations, Okinawa, tidal flats

INTRODUCTION

Crabs are an important component of the benthic community on sandy and muddy tidal flats. Most of them, especially crabs of the Superfamily Ocypodoidea, make burrows in the sediment, around which their surface activities are centered; the burrows are used for protection from predators, as refuges from environmental stress (Crane, 1975; Montague, 1980), as a source of water (Crane, 1975; Takeda & Murai, 2003), and as a mating site (Crane, 1975; Christy, 1982; Christy & Wada, 2015). Usually they form colonies consisting of conspecific individuals (e.g., Crane, 1975; Christy &Wada, 2015).

It is known that some crab species inhabiting tidal flats regularly migrate between the upper habitat where they make burrows and the shoreline where they feed (e.g., Christy & Wada, 2015). During the period of emergence at low tide, the crabs go to the shoreline from their upper habitat at the ebb tide and return to their upper habitat at the flood tide as in *Gelasimus vocans* (Linnaeus, 1758) (Nakasone, 1982; Murai *et al*., 1983; Takeda, 2019), *Macrophthalmus japonicas* (De Haan, 1835) (Henmi, 1984, 1989), *Leptuca pugilator* (Bosc, 1802) (Salmon & Hyatt, 1983; Cameron & Forward, 1993), and *Uca cumulanta* Crane, 1943 (Chiussi & Díaz, 2001). Crabs have been described as using two strategies for migrations from the shoreline to their upper habitat: zonal orientation for returning to the colony in the upper habitat, and visual searching for a burrow in the colony (Murakami *et al*., 2018).

The crabs are considered to use both celestial and terrestrial cues for orientation. Celestial cues include the sun and polarized light (Altervogt & von Hargen, 1964; Herrnkind, 1968; Chiussi & Díaz, 2001), whereas terrestrial cues include visual orientational cues such as landscape features (Herrnkind, 1968, 1983; Chiussi & Díaz, 2001) and non-visual orientational cues such as beach slope (y-axis orientation) (Young & Ambrose, 1978; Chiussi & Díaz, 2001) and wind (Herrnkind, 1983).

The soldier crab, *Mictyris guinotae* Davie, Shih & Chan, 2010, is commonly found on muddy sand and sandy tidal flats in estuaries and bays of the Ryukyu Is., Japan. The fiddler crab, *Austruca perplexa* (H. Milne Edwards, 1852), sympatrically inhabits these areas, but the habitats of the soldier (prey) and fiddler (predator) crabs are segregated and separated by a transitional zone (Takeda, 2010).

Soldier crabs form dense colonies of conspecific individuals on the tidal flats (Yamaguchi, 1976; Takeda & Murai, 2004; Takeda, 2010).

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After the tide recedes, they emerge on the sediment surface or subsurface of their habitat and engage in various activities, mainly feeding (Yamaguchi, 1976; Takeda & Murai, 2004). Feeding occurs in two distant regions: the upper, burrowing habitat with a deep water table and well-drained sediment, and close to the shoreline where the water table is shallow and the sediment is waterlogged (Yamaguchi, 1976; Takeda & Murai, 2004). In the upper habitat, the crabs usually feed beneath the surface of the sediment while creating feeding tunnels running parallel to the sediment surface with a sand roof about 2 cm in height to conceal themselves.

Alternatively, larger soldier crabs, mainly males, emerge from the burrows onto the sediment surface in their upper habitat, move in droves to the shoreline, and feed there while walking. The linear distance between the upper habitat and the shoreline may be up to 15 m (Takeda & Murai, 2004; Takeda, 2010). After feeding near the shoreline around the dead low tide, some of the crabs burrow in the water-logged sediment slightly above the shoreline, and then reside there during the period of submergence (Takeda & Murai, 2004; Takeda, 2005). Others return to their upper habitat during the period of emergence at low tide. During the daytime low tide, the crabs begin burrowing adjacent to their feeding tunnels after arrival at the upper habitat (Takeda, 2005, 2010).

During the night-time low tide, the soldier crabs burrow in areas that are limited in extent in their upper habitat (Takeda & Murai, 2004; Takeda, 2005), when they are unable to use visual cues, unlike daytime (Chiussi & Díaz, 2001). This strongly suggests that soldier crabs can precisely distinguish their upper habitat in some way, without the need for visual cues. It, however, remains unclear how they achieve this.

Megalopae (the final larval stage) of fiddler crabs inhabiting the tidal flat undergo accelerated metamorphosis in the response to chemical cues in sediment that has been conditioned by conspecific adults (O'Connor, 1993, 2005; O'Connor & Gregg, 1998; O'Connor & Judge, 1997, 1999; O'Connor & Van, 2006 for *Minuca pugnax* (Smith, 1870); O'Connor, 1991, 1993 for *L. pugilator*; O'Connor & Judge, 2004 for *Minuca minax* (Le Conte, 1855)). These findings suggest that crabs inhabiting the tidal flat have the ability to distinguish their habitats using chemical cues in sediment conditioned by conspecific individuals.

The aim of this study was to determine whether *M. guinotae* is able to distinguish sediment that had been conditioned by conspecifics. The study examined three kinds of sediment that had been conditioned through walking or feeding by the soldier crab and through feeding by a fiddler crab, *Austruca perplexa*. The possibility that soldier crabs were able to distinguish sediment using chemical cues was investigated by examining differences in the proportions of individuals that initiated burrowing activity on three types of sediment that had been either conditioned or non-conditioned, in addition to the length of time taken to begin burrowing.

MATERIALS AND METHODS

To determine whether the soldier crab distinguishes sediment that had been previously conditioned by conspecific crabs or competitor fiddler crabs when burrowing, the following experiment was carried out for 1.5 h around the daytime dead low tide on the sandy flat at the mouth of the Okukubi River, Okinawa I., Japan (26°27′N, 127°56′E) from 22 to 31 October 2012. A mangrove forest, mainly *Bruguiera gymnorhiza* (L.) Savigny, backs the tidal flat.

Before the experiment, large soldier crabs (carapace length 13.81 ± 0.04 (SE) mm, N = 279) that had been walking on the surface of the sediment were collected on the flat near the shoreline. About 1.5 h before the dead low tide each day, an enclosure (9 cm in height, 60 × 60 cm) made of light-brown acrylic plates was set on the surface of the well-drained sediment with a water table deeper than 20 cm from the sediment surface and devoid of soldier and fiddler crabs (Fig. 1). Any gaps between the bottom margin of the plates and the surface of the sediment were filled with sand, and the sediment surface was flattened. The enclosed area was divided into two subareas (30 × 60 cm) perpendicularly to the shoreline to ensure a balance of y-axis orientation and visual orientation using a mangrove forest as cues for burrowing (Fig. 1). The sediment in one of the two subareas was subsequently covered in a 2–3 mm layer of sediment that had been conditioned by soldier or fiddler crabs (referred to hereafter as the "experimental area"). This collected sediment that had been conditioned by fiddler crabs consisted of pseudofecal pellets after feeding (see Gherardi *et al.*, 2002). The water in these pellets contained a metabolite excreted from the gill chamber, which was used for sorting organic matter in the mouth (Takeda *et al.*, 2004). The collected sediment that had been conditioned by soldier crabs consisted of pseudofecal pellets, which had constructed the roof of feeding tunnels (Takeda & Murai, 2004). Another sample of sediment conditioned by soldier crabs was one consisting of sand that had been walked over by several hundred large soldier crabs while moving to the shoreline from the upper habitat. The sediment in the other subarea was covered in a 2–3mm layer of surface sediment collected from the surrounding area with no crabs (control area).

A round cork plate (10 cm diameter) was then placed on the sediment in the center of the enclosed area (Fig. 1), and a soldier crab of known carapace length was placed on the cork plate and covered with a conical opaque vessel (6 cm diameter). After carefully removing the vessel, the length of time taken for the soldier crab to begin digging a burrow in the sediment after leaving the cork plate was recorded; burrowing was defined as the burial in the sediment of the entire body of a crab. Also recorded was the walking course and position where crab had dug a burrow within the experimental area, the control area, and the area intermediate between the two. The soldier crab was then removed from the sediment, and the remaining depression was filled with conditioned or non-conditioned sand, and flattened. Another soldier crab was subsequently placed on the cork plate for the next observation. The experiment was carried out a maximum of ten times in each fenced enclosure. The enclosure was set up 11 times for

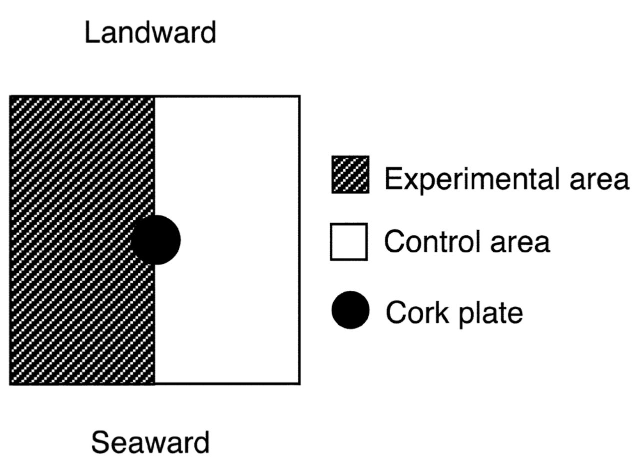

Figure 1. Diagram of experimental area. The area fenced by the enclosure (9 cm height, 60 × 60 cm) was divided into two subareas (30 × 60 cm). The sediment in one of the two subareas was covered with sediment that had been conditioned through feeding by fiddler crabs *Austruca perplexa*, or through walking or feeding soldier crabs *Mictyris guinotae* (experimental area), and that in other subareas was covered with sediment that had been collected from the surrounding area without crabs (control area). A round cork plate (10 cm diameter) was placed on the sediment in the center of the enclosed area.

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sediment that had been conditioned by fiddler crabs and through walking by soldier crabs, respectively, and nine times for sediment that had been conditioned through feeding by soldier crabs.

Repeated-measures analysis of variance (ANOVA) was used to examine the significance of differences in the length of time taken for soldier crabs to begin burrowing into the sediment, as well as the carapace length of soldier crabs among the conditioned and non-conditioned areas in the three experiments designed to investigate sediment selection. When a significant difference was recognized, the Tukey-Cramer test was used to determine the significance of differences between each pair of any of the factors.

Using the actual number of individuals encountered, Chi-square test was conducted to examine differences in the proportions of individuals that burrowed in the conditioned and non-conditioned areas in the experiment designed to investigate sediment selection.

RESULTS

The behavior of 279 soldier crabs that were tested was divided into five categories: burrowing 1) in the control area, 2) in the experimental area, 3) at the border between the control and experimental areas after walking on either of the two areas, and 4) in the control area and 5) experimental area after walking on both areas (Table 1). The proportions of individuals that burrowed in the control and experimental areas, excluding those that burrowed at the border, did not differ between crabs that walked on either of the two areas in each experiment (Fig. 2). Moreover, the proportion did not differ among the three experiments (Chi-square test: $\chi^2 = 0.701$, $P = 0.7043$).

The proportion of individuals that burrowed in the control area and the experimental area did not differ between crabs that walked on both areas in the experiments using sediment conditioned by fiddler crabs and walked on by soldier crabs, but differed significantly in the experiment using sediment that had been conditioned through feeding by soldier crabs (Fig. 3). In the enclosed area containing sediment that had been conditioned through feeding by soldier crabs, the proportion of individuals that burrowed in the experimental area was significantly higher among crabs that walked on both areas than among those that walked on either of the two areas (Chi-square test: $\chi^2 = 4.972$, $P = 0.0258$).

The length of time taken for soldier crabs to begin burrowing differed significantly among individuals that showed the five categories of such behavior in the three experiments (ANOVA: $F_{(14, 264)} = 27.4235$, $P < 0.0001$) (Fig. 4). In general, the times were divisible into two groups: the lengths of time taken for soldier crabs to begin burrowing in the control area, in the experimental area, and at the border between them after walking on either of the two areas, and in the control area and in the experimental area after walking on both areas. The length of time taken for soldier crabs to begin burrowing after walking on either of the two areas did not differ among the three experiments (ANOVA: $F_{(8, 195)} = 0.7467$, $P = 0.6502$). The range of the mean times was between 2.2–7.7 s, suggesting that the individuals swiftly burrowed into the sediment to evade any danger. The time required tended to be longer after walking on both of the two areas than after walking on either of them alone. The length of time taken for soldier crabs to begin burrowing after walking on both areas was shorter in the experiment using sediment conditioned through feeding by soldier crabs than in that using sediment conditioned through being walked on by soldier crabs (Tukey-Cramer test: $P < 0.05$).

Carapace length did not differ among individual crabs that showed the five different categories of behavior when the sediment had been conditioned by fiddler crabs (ANOVA: $F_{(4, 94)} = 0.5171$, $P = 0.7233$), when it had been conditioned through being walked on by soldier crabs ($F_{(4, 77)} = 0.1884$, $P = 0.9438$), or when it had been conditioned through feeding by soldier crabs ($F_{(4, 93)} = 1.7775$, $P = 0.4299$).

DISCUSSION

Previous field surveys of the distribution of soldier crabs during the daytime low tide indicated that, after walking on the tidal flat during the previous night-time low tide, large individuals burrowed into the sediment of their upper habitat where conspecific juveniles and young crabs inhabited (Takeda & Murai, 2004; Takeda, 2005).

In the fenced enclosure that included one area surfaced with sediment that had been conditioned by fiddler crabs, or through being walked on by soldier crabs after migration to the shoreline, and another area surfaced with sediment that had not been thus conditioned, the proportion of soldier crab individuals that burrowed into the conditioned sediment was equal to that of individuals that burrowed into the non-conditioned sediment after walking on the two areas. In contrast, the proportion of individuals that burrowed into sediment conditioned through feeding by conspecific crabs was significantly higher than that of individuals that burrowed into the non-conditioned sediment. Moreover, the length of time taken for soldier crabs to begin burrowing into sediment conditioned through feeding by conspecific crabs was about half that taken until they began burrowing into sediment conditioned through having been walked on by conspecific crabs, or by fiddler crabs. These results strongly suggested that conditioning of the surface sediment through feeding by conspecific crabs was related to sediment selection by soldier crabs when burrowing. In other words, the presence of sediment conditioned through feeding by conspecific crabs prompted soldier crabs to burrow swiftly. In the fenced enclosure that included one area with sediment conditioned through feeding by soldier crabs and a non-conditioned area, the short length of time taken for soldier crabs to begin burrowing in the non-conditioned area after walking on both the two areas may have been related to earlier walking on sediment that had been conditioned.

At least two behaviors are related to the return of soldier crabs to their upper habitat in the tidal flat during the night-time low tide after moving to the shoreline from their burrows during the daytime low tide (e.g., Chiussi & Díaz, 2001; Murakami *et al.*, 2018). One behavior is to determine the direction of the upper

Table 1. Number of individuals that burrowed in the control and experimental areas, and at the border between the two areas after walking on either of the two areas, and in the control area and the experimental area after walking on both areas in the enclosure that had been included in half of the sediment conditioned by fiddler crabs *Austruca perplexa*, or through walking or feeding by soldier crabs *Mictyris guinotae*.

Conditioning	Either of two areas			Both areas		Total
	Control	Experimental	Border	Control	Experimental	
Fiddler crabs	35	32	6	15	11	99
Walking by soldier crabs	20	24	3	19	16	82
Feeding by soldier crabs	36	42	6	2	12	98

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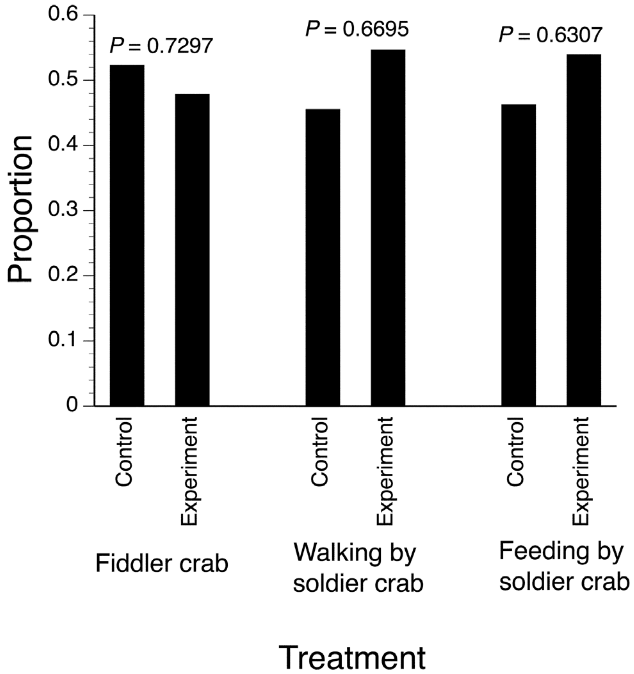

Figure 2. Proportion of individual soldier crabs *Mictyris guinotae* that burrowed into the sediment in the control area or an experimental area containing sediment that had been conditioned by fiddler crabs *Austruca perplexa*, or by being walked on or through feeding by conspecific crabs after walking on either of the two areas within the fenced enclosure (*P* values: Chi-square test).

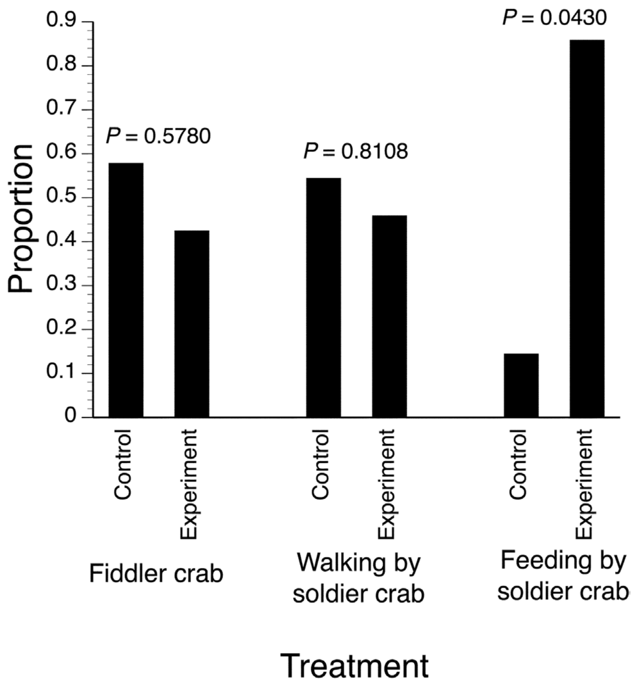

Figure 3. Proportion of individual soldier crabs *Mictyris guinotae* that burrowed into the sediment into the control area or an experimental area containing sediment that had been conditioned by fiddler crabs *Austruca perplexa*, or by being walked on or through feeding by conspecific crabs after walking on both of the areas within the fenced enclosure (*P* values: Chi-square test).

area on the tidal flat, and the other is to distinguish the location of the burrow on the upper tidal flat. In the first approach, soldier crabs probably use y-axis orientation, celestial and terrestrial cues,

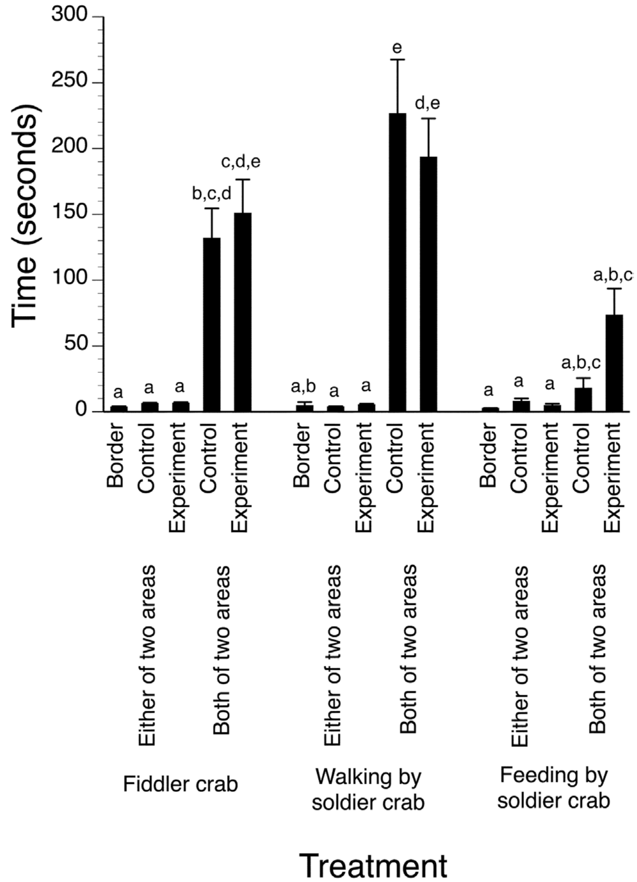

Figure 4. Length of time (mean + SE) taken for soldier crabs *Mictyris guinotae* to begin burrowing into the sediment in the control area or an experimental area containing sediment that had been conditioned by fiddler crabs *Austruca perplexa*, through feeding or by being walked on by conspecific crabs, or at the border between the two areas after walking in either or both of the areas within the fenced enclosure as an indicator of sediment selection by the soldier crab. Values with different letters in each column are significantly different (Tukey-Cramer test: $P < 0.05$).

as is the case for fiddler crabs (e.g., Chiussi & Díaz, 2001). In the second behavior occurring on the upper tidal flat, chemical cues in the sediment conditioned by conspecific crabs may play an important role in distinguishing the location for burrowing, especially during the period of emergence at the night-time.

ACKNOWLEDGEMENTS

I thank Dr. M. Murai, Mr. Y. Nakano, and Mr. S. Kadena, and other staff of Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyu, for their help and for facilitating my work. I am also grateful to the two anonymous reviewers for their invaluable suggestions to the manuscript.

REFERENCES

Altervogt, R. & von Hagen, H.O. 1964. Über die Orientierung von *Uca tangeri* Eydoux im Freiland. *Zeitschrift für Morphologie und Ökologie der Tiere*, **53**: 636–656.

Bosc, L.A.G. 1802. *Histoire naturelle des crustacés, contenant leur description et leurs moeurs; avec figures dessinées d'après nature*, **Vol. 1**. Déterville, Paris.

Cameron, H.S. & Forward, R.B. Jr. 1993. Direction orientation of the sand fiddler crab *Uca pugilator* (Bosc) in water: onshore escape response. *Marine Behaviour and Physiology*, **22**: 75–88.

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Chiussi, R. & Díaz, H. 2001. Multiple reference usage in the zonal recovery behavior by the fiddler crab *Uca cumulanta*. *Journal of Crustacean Biology*, **21**: 407–413.

Christy, J.H. 1982. Burrow structure and use in the sand fiddler crab, *Uca pugilator* (Bosc). *Animal Behaviour*, **30**: 687–694.

Christy, J.H. & Wada, K. 2015. Social ethology in Brachyura. In: *Decapoda: Brachyura, Treatise on Zoology – Anatomy, Taxonomy, Biology* (P. Castro, P. Davie, D. Guinot, F.R. Schram & J.C. von Vaupel Klein, eds.), **Vol. 9C-I**, pp. 417–468. Brill, Leiden, The Netherlands.

Crane, J. 1943. Crabs of the genus *Uca* from Venezuela. *Zoologica*, **28**: 33–44.

Crane, J. 1975. Fiddler crabs of the World. Ocypodidae: Genus *Uca*. Princeton University Press, Princeton, NJ, USA.

Davie, P.J.F., Shih, H.-T. & Chan, B.K.K. 2010. A new species of *Mictyris* (Decapoda, Brachyura, Mictyridae) from the Ryukyu Islands, Japan. In: *Studies on Brachyura: a homage to Danièle Guinot* (Castro, P., Davie, P.J.F., Ng, P.K.L. & Richer de Forges, B., eds.), *Crustaceana Monographs*, **11**: 83–105.

Gherardi, F., Russo, S. & Lazzara, L. 2002. The function of wandering in the sand-bubbler crab, *Dotilla fenestrata*. *Journal of Crustacean Biology*, **22**: 521–531.

Haan, W. de. 1833–1850. Crustacea. In: *Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jußu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suscepto, Annis 1823–1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit* (P.F. von Siebold, ed.). Lugduni-Batavorum [= Leiden].

Henmi, Y. 1984. The description of wandering behavior and its occurrence varying in different tidal areas in *Macrophthalmus japonicus* (De Haan) (Crustacea: Ocypodiae). *Journal of Experimental Marine Biology and Ecology*, **84**: 211–224.

Henmi, Y. 1989. Factors influencing drove formation and foraging efficiency in *Macrophthalmus japonicus* (De Haan). *Journal of Experimental Marine Biology and Ecology*, **131**: 255–265.

Herrnkind, W.F. 1968. Adaptive visually-directed orientation in *Uca pugilator*. *American Zoologist*, **8**: 585–598.

Herrnkind, W.F. 1983. Movement patterns and orientation. In: *The biology of Crustacea*, **Vol. 7**, Behavior and ecology (Vernberg, F.J. & Vernberg, W.B., eds.), pp. 41–105. Academic Press, New York.

Le Conte, J. 1855. On a new species of *Gelasimus*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **7**: 402–403.

Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. **Vol. 1**, Edn. 10. Reformata. Laurentii Salvii, Holmiae [= Stockholm].

Milne Edwards, H. 1852. Observations sur les affinités zoologiques et la classification naturelle des crustacés. *Annales des Sciences Naturelles. Zoologie*, Série 3, **18**: 109–166.

Montague, L.C. 1980. A natural history of temperate western Atlantic fiddler crabs with reference to their impact on salt marshes. *Contributions in Marine Science, University of Texas*, **23**: 25–55.

Murai, M., Goshima, S. & Nakasone, Y. 1983. Adaptive droving behavior observed in the fiddler crab *Uca vocans*. *Marine Biology*, **76**: 159–164.

Murakami, H., Tomaru, T. & Gunji, Y.-P. 2018. Exclusive shift from path integration to visual cues during the rapid escape run of fiddler crabs. *Animal Behaviour*, **144**: 147–152.

Nakasone, Y. 1982. Ecology of the fiddler crab *Uca (Thalassuca) vocans vocans* (Linnaeus) (Decapoda: Ocypodidae) 1. Daily activity in warm and cold seasons. *Research on Population Ecology*, **24**: 97–109.

O'Connor, N.J. 1991. Flexibility in timing of the metamorphic molt by fiddler crab megalopae *Uca pugilator*. *Marine Ecology Progress Series*, **68**: 243–247.

O'Connor, N.J. 1993. Settlement and recruitment of the fiddler crabs *Uca pugnax* and *Uca pugilator* in a North Carolina, USA, salt marsh. *Marine Ecology Progress Series*, **93**: 227–234.

O'Connor, N.J. 2005. Influence of extracts of adult crabs on molting of fiddler crab megalopae (*Uca pugnax*). *Marine Biology*, **146**: 753–759.

O'Connor, N.J. & Gregg, A.S. 1998. Influence of potential habitat cues on duration of the megalopal stage of the fiddler crab *Uca pugnax*. *Journal of Crustacean Biology*, **18**: 700–709.

O'Connor, N.J. & Judge, M.L. 1997. Flexibility in timing of molting of fiddler crab megalopae: evidence from in situ manipulation of cues. *Marine Ecology Progress Series*, **146**: 55–60.

O'Connor, N.J. & Judge, M.L. 1999. Cues in salt marshes stimulate molting of fiddler crab *Uca pugnax* megalopae: more evidence from field experiments. *Marine Ecology Progress Series*, **181**: 131–139.

O'Connor, N.J. & Judge, M.L. 2004. Molting of fiddler crab *Uca minax* megalopae: stimulatory cues are specific to salt marshes. *Marine Ecology Progress Series*, **282**: 229–236.

O'Connor, N.J. & Van, B.T. 2006. Adult fiddler crabs *Uca pugnax* (Smith) enhance sediment-associated cues for molting of conspecific megalopae. *Journal of Experimental Marine Biology and Ecology*, **335**: 123–130.

Salmon, M. & Hyatt, GW. 1983. Spatial and temporal aspects of reproduction in North Carolina fiddler crabs (*Uca pugilator* Bosc). *Journal of Experimental Marine Biology and Ecology*, **102**: 167–181.

Smith, S.I. 1870. Notes on American Crustacea. No. 1. Ocypodoidea. *Transactions of the Connecticut Academy of Arts and Science*, **2**: 113–176.

Takeda, S. 2005. Sexual differences in behaviour during the breeding season in the soldier crab (*Mictyris brevidactylus*). *Journal of Zoology* (London), **266**: 197–204.

Takeda, S. 2010. Habitat partitioning between prey soldier crab *Mictyris brevidactylus* and predator fiddler crab *Uca perplexa*. *Journal of Experimental Marine Biology and Ecology*, **309**: 160–168.

Takeda, S. 2019. Predation by male fiddler crabs *Gelasimus vocans* (Linnaeus, 1758) (Brachyura: Ocypodidae) on soldier crabs *Mictyris guinotae* Davie, Shih & Chan, 2010 (Brachyura: Mictyridae) in relation to burrow occupation. *Journal of Crustacean Biology*, **39**: 274–278.

Takeda, S. & Murai, M. 2003. Morphological and behavioural adaptations to the rocky substratum by the fiddler crab, *Uca panamensis* (Stimpson, 1859): preference for feeding substratum and feeding mechanism. *Journal of Experimental Marine Biology and Ecology*, **287**: 179–191.

Takeda, S. & Murai, M. 2004. Microhabitat use by the soldier crab *Mictyris brevidactylus* (Brachyura: Mictyridae): interchangeability of surface feeding and subsurface feeding through burrow structure alternation. *Journal of Crustacean Biology*, **24**: 327–339.

Takeda, S., Poovachiranon, S. & Murai, M. 2004. Adaptations for feeding on rock surfaces and sandy sediment by the fiddler crabs (Brachyura: Ocypodidae) *Uca tetragonon* (Herbst, 1790) and *Uca vocans* (Linnaeus, 1758). *Hydrobiologia*, **528**: 87–97.

Yamaguchi, T. 1976. A preliminary report on the ecology of the sand bubbler crab, *Mictyris longicarpus* Latreille. *Benthos Research*, **11/12**: 1–13 [in Japanese].

Young, D.Y. & Ambrose, H.W. 1978. Underwater orientation in the sand fiddler crab, *Uca pugilator*. *Biological Bulletin*, **155**: 246–258.

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