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Biological and Physical Factors in Population Distribution and Territorial Defence of Fiddler Crabs, *Uca vocans hesperiae*

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ABSTRACT

The study investigated the physical and biological factors relating to population distribution and territorial defence of *Uca vocans hesperiae* habitat in Libong non-hunting area, Trang Province, southern Thailand. The area under study was divided into 3 zones: Zone 1, Zone 2, and Zone 3 that were 2, 4, and 6 m from the water edge respectively. Zone 1 contained higher levels of organic matter, moisture content, population density, male feeding rate, and more burrows than the other two zones. Zone 1 also had 1:1 adult sex ratio of male to female compared with the more female biased ratios for Zone 2 and Zone 3. Males had greater carapace width and length than females. Male territorial defenders had larger and longer carapaces, propodus, and dactylus than the average males in the population. The amount of organic matter did not have a direct bearing on the physical dimensions of territorial males in this species.

Key words: Territorial defence - Fiddler crabs - *Uca vocans hesperiae* - Organic matter - Population density - Adult sex ratio

INTRODUCTION

Several factors are known to affect the distribution of fiddler crab populations including grain size, organic matter and moisture content (1,2,3,4,5). High soil moisture content can minimise the desiccation rate especially in small fiddler crabs (6,7). Robertson et al (8) showed the increasing gradient of available food from the supratidal to the low intertidal zones, and suggested that *Uca pugilator* were present in large numbers in low intertidal areas in response to increased levels of food in the sediment.

Combatants that are physically larger than their opponents tend to be stronger. Consequently they inflict greater costs on their rivals and incur lesser costs to themselves (9). Contests over resources won by larger males have been demonstrated in many species such as fiddler crabs *Uca annulipes* (10), *U. vocans hesperiae* (11), *U. paradussumieri* (12), crayfish *Cherax cuspidatus* (13) and cichlid *Tilapia zillii* (9).

This study examined the influence of the physical and biological factors affecting the population distribution and the male territorial defenders of *U. v. hesperiae*. The following hypotheses were investigated:

(1) If the amount of organic matter and moisture content affects the fiddler crab distribution, then more fiddler crabs should inhabit the areas with high levels of organic matter and moisture content than those with less organic matter and moisture content.

(2) If male territorial defenders are stronger than their opponents, then they should have wider and longer carapaces than the average males in the population.

MATERIALS AND METHODS

Fiddler Crab Biology

Fiddler crabs, *U. v. hesperiae* Crane, 1975 are highly social crustaceans inhabiting sandy mudflats in tropical zones, e.g. East Africa, India, Myanmar, and Malaysia (11,14,15). Males defend their burrows from conspecific intruders. The burrow serves as a shelter from predators, and a refuge at high tide when they remain underground. Males use their major claw to signal to females and to threaten or fight other males. Male combat is very common throughout the year (16,17,18). Many fights are between wanderers and burrow-owning males, but a few are between adjacent burrow-owning males (16).

U. v. hesperiae males can initiate three kinds of forceful behaviours: manus-push, heel and ridge, and forceful interlace (14,15,16). Manus-push is defined as holding chelipeds flexed with the chelae partly opened through a slight lifting of the dactyls. The lower halves of the mani are pushed against each other. Heel and ridge is defined as a male placing his dactyl outside the manus of the opponent, while the pollex is passed to the inner or palm side. Forceful interlace includes grips, flings, and upsetting the opponent. The crabs can be turned upside down or levered into the air or flung several centimetres away.

Data Collection

We studied a population of *U. v. hesperiae* Crane, 1975 at Libong non-hunting area (7° 25′ N, 99° 38′ E), Trang Province, southern Thailand, from January 2003 to January 2004. The study site was an intertidal muddy sand flat on the shore of the Andaman Sea. All field observations were made during low tide.

The physical and biological factors relating to habitat use of *U. v. hesperiae* were investigated. The study area was divided into three zones: Zone 1, Zone 2, and Zone 3 that were 2, 4, and 6 m from the water edge respectively. Data were collected every three months with a total of five collecting periods, i.e. January, April, August, November 2003, and February 2004. Fifteen individual 4 m^2 (2×2 m^2) plots were marked on the ground surface at each zone. Three substrate samples were collected at a depth of 5-10 mm for each plot in each zone at each collecting period for laboratory measurement and analysis of their physical and biological factors. Physical factors comprised organic matter, moisture content, and grain size. Three hundred grams of each sample were dried for 72 h at 80°C or until there was no change in weight, and then reweighed to determine the moisture content. One hundred grams of each dried

sample were then grade sieved for 20 min in an automatic sieving machine. Sieve hole diameters were >2,000, 1,000-2,000, 500-1,000, 250-500, 125-250, 63-125 and <63 μm respectively. Each resultant grain size sample was weighed to 0.1 g of accuracy. To determine organic content, fifty grams of each dried sample were heated at 550°C for 1 h and then reweighed. Final weight was subtracted from the initial weight to give gram organic content.

Observing all *U. v. hesperiae* present in each plot through 10×35 binoculars, we counted and sexed the crabs to determine population density and adult sex ratio without catching or disturbing them. Adult sex ratio was calculated as the number of sexually active males divided by the total number of sexually active adults of both sexes in the plot (19). The crabs were then captured and marked. For all males, their carapace width and length, manus, propodus, and dactylus were measured. For all females, measurement was taken of their carapace width and length. Handedness and the number of brachychelous and leptochelous claws were then recorded. Brachychelous claws are identified by the relatively short and broad pollex and dactyl of the major cheliped and more pronounced tubercles in the gap in comparison with most individuals in the same species of similar carapace size (14,15,20). Leptochelous describes an unusually long, slender, and regenerated major cheliped beset with reduced tubercles (14,15,20). Carapace width and length were measured to the nearest 0.1 mm using Vernier callipers. Most crabs with a carapace length of less than 3.5 mm were difficult to identify and/or sex satisfactorily. Therefore, these small crabs were referred to as juveniles, although the carapace length of 3.5 mm was not regarded as the point at which juvenile fiddler crabs became sexually distinguishable adults.

Crab behaviour was classified as either territorial or non-territorial. Territorial males were defined as male crabs that went up and down the burrow, fed in the area nearby, fended other males off their burrow area, and tried to entice females into their burrow. Non-territorial males were defined as those males that walked and fed without defending a burrow. Each plot was marked and divided with strings on the ground surface into 10×10 cm^2 grids. At each plot, we observed the territorial males defending their territory from 4-5 m away. The ground area defended by the males was plotted on paper in order to estimate the size of the territory. This was done by measuring its width (a), length (b) and calculated with the ellipsoid equation ($A = \pi ab$).

All variables were tested for normality using Levene's tests and transformed when necessary. One-way ANOVA and *t*-tests were used to test the differences between parameters. Non-parametric tests were used where normality or other assumptions of parametric tests were not met. All significance tests were two tailed.

RESULTS

Zone 1 had the highest levels of organic matter, moisture content, population density, male feeding rate, and more burrows than Zone 2 and Zone 3 **(Table 1)**. Zone 1 also had 1:1 adult sex ratio of male to female compared with the more female biased ratios for Zone 2 and Zone 3 **(Table 1)**. Differences in grain size among the three zones were observed in five out of seven grain size categories **(Table 1, Figure 1a-g)**. Zone 3 had larger grain sizes than Zone 1 and Zone 2 **(Figure 1b, c, d, f and g)**. There was no difference between Zone 1 and Zone 2 in terms of territorial size and defence rate **(Table 1)**.

Territorial males had larger and longer carapaces, propodus, and dactylus than non-territorial males in the population but there was no difference in the size of manus **(Table 2)**. No difference in the incidence of handedness between territorial and non-territorial males was observed **(Table 2)**. However, fewer territorial males had Brachychelous claws compared with the non-territorial males **(Table 2)**. Males had greater carapace width and length than females in this species **(Table 3)**.

DISCUSSION

Our results showed that *U. v. hesperiae* tend to inhabit areas like Zone 1 with high levels of organic matter and moisture content. This tendency has been observed in other *Uca* species such as *U. pugilator* (21), and *U. uruguayensis* (22). Generally, higher intertidal zones are sandier, have less food and get drier during low tide than mid-low intertidal substrata. Organic detritus is frequently buried in intertidal sediment which is also kept moist during low tide (23).

It was found that male feeding rate was higher in Zone 1, i.e. closer to the water than in Zone 2 and Zone 3. Several Ocypodid crabs tend to feed in response to sediment food content. Zimmer-Faust (24) reported that the sand bubbler crab, *Scopimera inflata* was capable of detecting sediment food quality. Other studies have shown that fiddlers such as *U. vocans* (25), and *U. pugilator* leave their burrows in the high intertidal zone and travel downslope across the mid intertidal zone to feed near the water edge in response to increased levels of food in the sediment (8,14,21,26).

The adult male to female sex ratio was 1:1 in Zone 1, and became more female biased in Zone 2 and Zone 3. This result suggests that females tend to inhibit the upper zone which is drier, has larger grain size and less organic matter. This could be due to two possible reasons. First, females avoid being eaten by mudskippers. Macintosh (27) found that in peninsular Malaysia *U. paradussumieri* and *U. rosea* were eaten predominantly by two species of mudskippers: *Periophthalmodon schlosseri* and *Periophthalmus argentilineatus*. These mudskippers consumed mostly female and smaller male fiddler crabs because they could not crush the larger males. *P. schlosseri* learn to avoid the larger male fiddler crabs on shore. Secondly, males might avoid being eaten by coastal bird predators by living in high density near the water edge for dilution effect. Koga et al (28) suggested that males might suffer a greater predation risk than females due to their lighter colours and elaborate courtship display both of which made them more conspicuous than the cryptic females. Birds feeding on male crabs often capture the crab by the large claw that easily breaks off requiring them to recapture the prey.

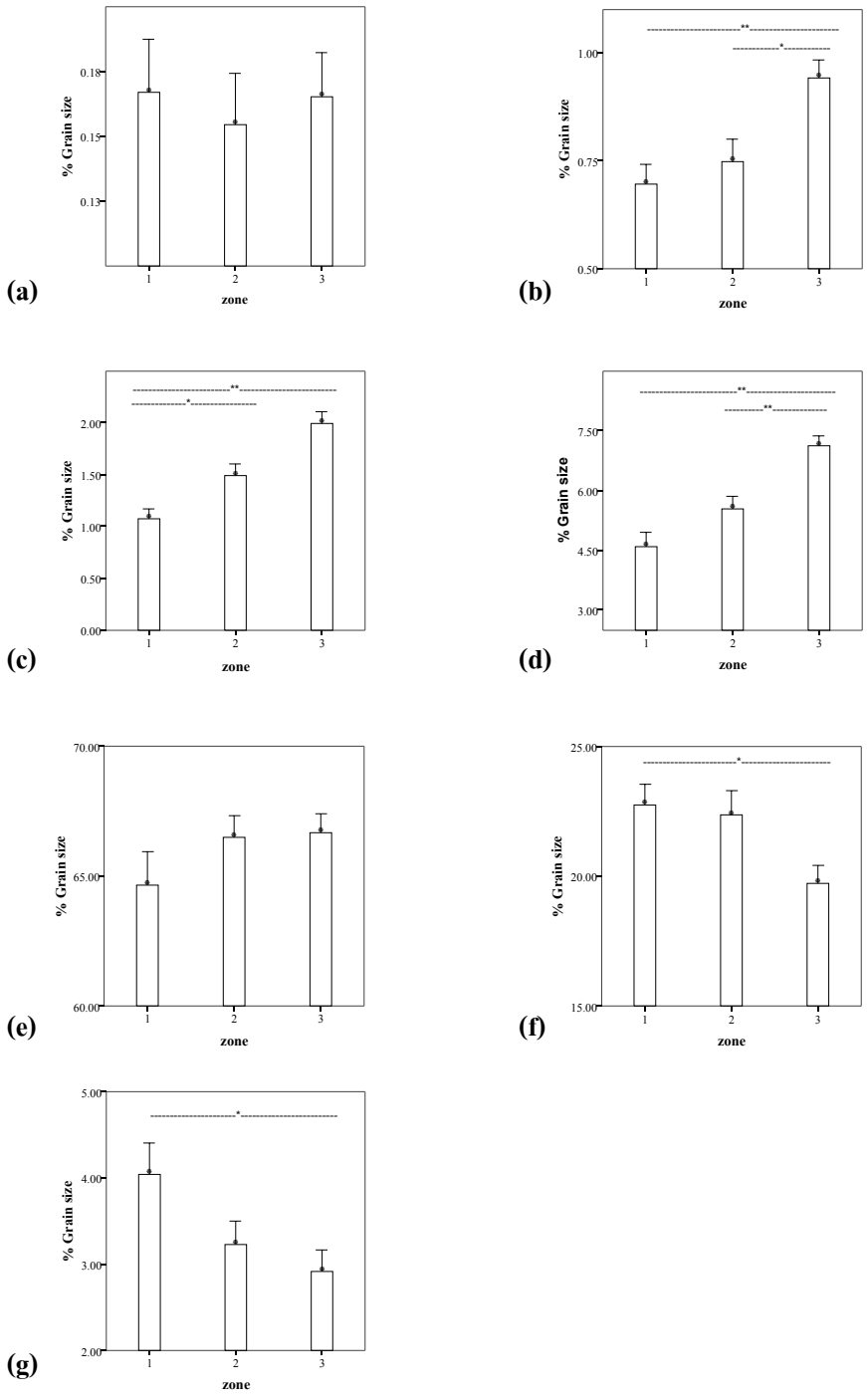

Figure 1. Percentage of grain size at three zones. (a) >2,000 μm, (b) 1,000-2,000 μm, (c) 500-1,000 μm, (d) 250-500 μm, (e) 125-250 μm, (f) 63-125 μm and (g) <63 μm. **P*<0.05, ***P*<0.001.

Table 1. ($\bar{x} \pm$ S.D.) of physical and biological factors of three zones of *Uca vocans hesperiae* habitat. **P*<0.05, ***P*<0.001.

Factor	Zone 1	Zone 2	Zone 3	Statistical test
Organic matter (%)	0.20± 0.21	0.07±0.27	0.02±0.17	$F_{2,309} = 18.78$**
Moisture content (%)	0.55±0.08	0.45±0.17	0.41±0.20	$x^2_2 = 43.51$**
Grain size (%)				$F_{2,966} = 0.66$
>2,000 μm	0.16±0.14	0.15±0.13	0.17±0.12	$F_{2,138}$=0.13
2,000-1,000 μm	0.70±0.31	0.74±0.36	0.94±0.27	$F_{2,138}$=7.89**
1,000-500 μm	1.07±0.66	1.49±0.82	2.00±0.75	$F_{2,138}$=18.21**
500-250 μm	4.59±2.45	5.54±2.07	7.13±1.66	$F_{2,138}$=17.71**
250-125 μm	64.64±8.61	66.515±0.56	66.65±5.04	$F_{2,138}$=1.32
125-63 μm	22.72±5.62	22.36±6.49	19.73±4.63	$F_{2,138}$=3.96*
<63 μm	4.03±2.52	3.22±1.88	2.91±1.74	$F_{2,138}$=3.68*
Density (Individual/m^2)	7.06±4.38	1.17±1.77	0.02±0.22	$F_{2,883}$=570.60**
Adult sex ratio	0.51±0.19	0.34±0.37	0.02±0.14	$F_{2,883}$=290.15**
Territory size (m^2)	0.72±0.44	0.79±0.51	-	$F_{1,56}$=0.26
Feeding rate (time/min)	102.73±14.25	63.93±16.14	-	$F_{1,100}$=164.17**
Number of burrows/zone	7.78±3.74	1.4±2.35	-	$F_{2,59}$=50.77**
Territorial defend rate (time/min)	0.16±0.13	0.14±0.27	-	$F_{1,53}$=0.21

Table 2. Body measurement ($\bar{x} \pm$ S.D.), handedness and claw type of males and territorial males in *Uca vovans hesperiae*. **P*<0.005, ***P*<0.001.

	Males	**Territorial males**	***t*-test**
Body measurement ($\bar{x} \pm$ S.D.)			
Carapace width (mm)	22.63 ± 3.22	24.75 ± 2.42	t_{99} = -6.286**
Carapace length (mm)	15.13 ± 2.04	16.35 ± 1.44	t_{105} = -6.026**
Propodus (mm)	35.19 ± 9.21	40.40 ± 6.93	t_{99} = -5.405**
Manus (mm)	16.23 ± 5.175	17.49 ± 5.26	t_{514} = -1.858
Dactylus (mm)	22.52 ± 7.44	27.19 ± 6.13	t_{93} = -5.582**
Handedness			χ_1^2 = 0.99
Right handed males	442	8	
Left handed males	55	0	
Claw type			χ_1^2 = 12.07*
Brachychelous claw	374	35	
Leptochelous claw	76	20	

Table 3. Carapace size ($\bar{x} \pm$ S.D.) of males and females *Uca vocans hesperiae*. **P*<0.001.

Carapace size (mm)	**Males**	**Females**	***t*-test**
Carapace width	22.63 ± 3.22	19.83 ± 2.91	t_{388} = -10.77*
Carapace length	15.13 ± 2.04	14.05 ± 1.50	t_{476} = -7.40*

The study has confirmed the findings of previous studies that larger males tend to win fights and hold territories such as in *U. annulipes* (10), *U. v. hesperiae* (11) and *Heloecius cordiformis* (29). Our results showed that males were larger than females. Other fiddler crab species in southern Thailand in which males are larger than females include *U. perplexa*, *U. triangularis bengali*, *U. forcipata*, *U. lactea annulipes*, and *U. v. hesperiae* (15).

Our study supports Jaroensutasinee & Jaroensutasinee's findings (15) that *U. v. hesperiae* were mainly right-handed. There are other fiddler crab species that are mainly right-handed, including *U. tetragonon*, *U. t. bengali*, and *U. forcipata* (15, 30,31,32,33). The relative frequencies of left-handedness and right-handedness of the male major chela can vary from population to population (34). Williams and Heng (35) reported that *U. v. vocans* in Australia and Singapore were 95% or more right-handed throughout their range. The high repeatability of the percentage of right-handedness in the genus *Uca* can be used as an aid in taxonomic grouping within this genus (32).

Our study showed that the percentage of territorial males with brachychelous claws was lower in comparison with the non-territorial males in a population. This finding suggests that territorial males tend to lose their major claw (brachychelous claw) and then regenerate a new claw with leptochelous characteristics that is lighter and requires less energy to move. This could be due to two possible reasons. First, as these territorial males are engaged in fighting and defending territory more frequently than non-territorial males, they are more likely to lose their brachychelous claw while fighting their opponents. Since leptochelous claws are just as effective as a means of

displaying superior fighting ability and attracting females for mating (20), territorial males have no need to regenerate brachychelous claws that require more energy to produce. Secondly, these territorial males might be more likely to be captured by bird predators while being engaged in elaborate courtship activities and territorial defence. The only part of the male fiddler crab body that coastal wading birds can feed on is the large claw (27). Thus the males tend to lose their major claw (brachychelous claw) and then regenerate a new one with leptochelous characteristics.

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บทคัดย่อ

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ปัจจัยทางชีวภาพและกายภาพที่มีอิทธิพลต่อพฤติกรรมการป้องกันอาณาเขตของปูก้ามดาบ *Uca vocans hesperiae*

การศึกษาครั้งนี้ได้ทำการศึกษาลักษณะทางกายภาพและชีวภาพของแหล่งอาศัยและปัจจัยที่มีอิทธิพลต่อพฤติกรรมการป้องกันอาณาเขตของปูก้ามดาบ *Uca vocans hesperiae* บริเวณเขตห้ามล่าสัตว์ป่าหมู่เกาะลิบง จังหวัดตรัง เราได้ทำการแบ่งพื้นที่ศึกษาออกเป็น 3 โซนคือ โซนที่ 1, 2 และ 3 ซึ่งห่างจากชายน้ำ 2, 4 และ 6 เมตร ตามลำดับ พบว่าโซนที่ 1 มีปริมาณสารอินทรีย์อุดมสมบูรณ์ ความชื้นในดินสูง มีประชากรปูอยู่หนาแน่น อัตราการกินของปูก้ามดาบเพศผู้สูงและจำนวนรูปูก้ามดาบมากกว่าโซนอื่นๆ ส่วนอัตราส่วนทางเพศในโซนที่ 1 เท่ากับ 1:1 และในโซนที่ 2 และ 3 จะมีปูเพศเมียมากกว่าเพศผู้ ปูก้ามดาบเพศผู้มีกระดองกว้างและยาวกว่าเพศเมีย ปูก้ามดาบเพศผู้ที่ป้องกันอาณาเขตจะมีขนาดความกว้างและยาวของกระดอง ขนาด propodus และขนาด dactylus ที่ใหญ่กว่าเพศผู้ในประชากรโดยเฉลี่ย ปริมาณสารอินทรีย์ไม่มีผลต่อขนาดอาณาเขตของปูก้ามดาบเพศผู้ในสปีชีส์นี้

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