production or through indirect benefits by their offspring's survival and reproductive success. The effect of size on female choice for large and/or competitively superior males has been shown in several species, among which fishes such as bicolour damselfish (Pisces, Pomacentridae: *Pomacentrus partitus* Poey, 1868) (cf. Schmale, 1981), mottled sculpin (Cottidae: *Cottus bairdi* Girard, 1850) (cf. Downhower et al., 1983), cichlids (Cichlidae: *Nannacara anomala* Regan, 1905) (cf. Noonan, 1983), two pipefish species (Syngnathidae: *Syngnathus typhle* Linnaeus, 1758 and *Nerophis ophidion* Linnaeus, 1758) (cf. Berglund et al., 1986), river bullhead (Cottidae: *Cottus gobio* Linnaeus, 1758) (cf. Bisazza & Marconato, 1988), browncheek blenny (Chaenopsidae: *Acanthemblemaria crockeri* Beebe & Tee-Van, 1938) (cf. Hastings, 1988), and Japanese medaka (Adrianichthyidae: *Oryzias latipes* Temminck & Schlegel, 1846) (cf. Howard et al., 1998).

Many studies have shown that larger males tend to win in male contests, hold higher quality territories, and gain greater access to females, such as in Japanese medaka (Pisces, Adrianichthyidae: *Oryzias latipes* (cf. Howard et al., 1998), freshwater angelfish (Cichlidae: *Pterophyllum scalare* Lichtenstein, 1823) (cf. Chellappa et al., 1999), and Siamese fighting fish (Belontiidae: *Betta splendens* Regan, 1910) (cf. Jaroensutasinee & Jaroensutasinee, 2001). For species in which some males can prevent other males from mating, it is difficult to disentangle the effects of female choice and male-male competition and the relative impact that each may have upon the maintenance of the trait. Some studies have examined female mate choice by preventing males from interacting and allowing females to associate with preferred males (e.g., Zuk et al., 1990; Jaroensutasinee & Jaroensutasinee, 2001). However, female behaviour might permit mate choice within the context of male-male competition for mates. Some studies have demonstrated that female choice of mates is not limited by male behaviour (Westneat et al., 1990; Birkhead & Moller, 1992; Ahnesjö et al., 1993; Poston, 1997).

Sexual selection favouring larger males in fiddler crabs, *Uca paradussumieri* Bott, 1973, could be due to female choice, male-male competition, or both. If females have higher reproductive success when mating with large males, selection should favour females that mate preferentially with large males. Our study was designed to investigate the impact of female choice and male-male competition for large male body size in the fiddler crab, *U. paradussumieri*, based on the following hypotheses: (1) if females preferred larger males as mates, then the accepted males should be larger than the rejected males and copulation time should be shorter in cases where females were larger than males; and (2) if male contest played an important role in mating success in this species, then larger males should win the fight.

Fiddler crab biology

The fiddler crab, *Uca paradussumieri*, is a highly social crustacean inhabiting sandy mudflats in tropical zones (Crane, 1975). The mating system in *U. paradussumieri* can be characterized as resource free and promiscuous. Females are receptive at most times. Female fiddler crabs actively sample several males before mating (e.g., Crane, 1975; Christy, 1983; Backwell & Passmore, 1996). Surface copulation usually happens when a male climbs the carapace of the female from the rear. The receptive female remains in a rest position with her carapace horizontal. The male advances until his front is at the level of the female's mesogastric region. He strokes the anterior part of the female carapace with the minor cheliped. Only the tips of the gonopods are inserted into the gonopores. The crabs remain in contact for periods up to several minutes and then the males leave (Crane, 1975; Christy & Salmon, 1991).

Males defend their burrows from conspecific intruders. The burrow serves as a shelter from predators and during high tide when they remain underground. Males use their large major claw to signal to females and to threaten or fight other males. Male combat is very common throughout the year (Hyatt & Salmon, 1978; Christy & Salmon, 1984). Many of the combats are between adjacent and burrow-owning males.

Both intruders and residents initiate three kinds of forceful combat: manus-push, heel and ridge, and forceful interlace (Crane, 1975; Hyatt & Salmon, 1978). Manus-push is defined as holding the 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 involves gripping, overturning, and throwing the opponent that can be turned upside down, levered into the air, and flung several centimetres away.

MATERIALS AND METHODS

Data collection

A study was made of a population of *Uca paradussumieri* on Lanta Island, Krabi, Thailand, from June to October 2001. The study site was an intertidal muddy sand flat on the Andaman Sea. All observations of fighting and copulation were made in the field during low tide through a pair of 8 × 30 binoculars from a distance of 4-5 metres.

For the female choice test, 66 receptive females were observed while encountering courting males of varying sizes. The numbers of accepted and rejected males

were recorded. A receptive female wandered past several displaying males before choosing to copulate with the accepted male on the surface. Acceptance by females was signalled by allowing the males to climb onto their carapace from the rear to begin copulation. Some of the accepted males had a successful copulation. Courtship ritual and duration were observed and recorded. Females signalled rejection by walking away from the courting males or using their claws to chase the courting males. At the conclusion of the mate choice event, female and male fiddler crabs were captured, and their carapace length and breadth measured to the nearest 0.1 mm using Vernier callipers.

For the male-male competition test, 46 pairs of males were observed while engaged in fighting behaviour. Observation was made of the three types of forceful combat between fighting pairs (manus-push, heel and ridge, and forceful interlace), fighting duration, and the winner's identity. The outcome of the contest for each fighting pair was defined for each combatant as a win or a loss. A combatant was classified as a winner if it remained within the area and subsequently engaged in feeding and courting behaviour. Losers walked quickly and erratically away from the combat area. When a combat ended, the winner's identity was recorded, and both combatants were captured. The major claw length and carapace breadth and length were measured to the nearest 0.1 mm using Vernier callipers.

Data analysis

The ratio between carapace breadth and length of the pairs was calculated as the smaller breadth (or length) divided by the larger breadth (or length) (Jennions & Backwell, 1996). Fighting duration was log transformed. Parametric statistics were used when underlying assumptions were met, otherwise non-parametric tests were used. Independent two-sample t-tests with separated variance and Bonferroni adjustment were used to compare accepted and rejected males. Exact binomial probability tests were used to test for the number of fights won by the larger males. All significant tests were two-tailed.

RESULTS

Size relationship between males and females

All *Uca paradussumieri* collected in the field were measured for body weight and for carapace length and breadth. Males were heavier but had a shorter carapace than females (table I). Male weight correlated highly with carapace length and breadth (Pearson correlation coefficient: carapace length: $r_{54} = 0.81$, $P < 0.001$; carapace breadth: $r_{54} = 0.82$, $P < 0.001$). Female weight also correlated highly with carapace length and breadth (Pearson correlation coefficient: carapace length: $r_{54} = 0.67$, $P < 0.001$; carapace breadth: $r_{54} = 0.69$, $P < 0.001$).

TABLE I

The mean ± S.D. of weight, carapace length and carapace breadth of fiddler crabs, *Uca paradussumieri* Bott, 1973; N represents sample size; t-tests were independent two-sample tests with separated variance and Bonferroni adjustment; $^*P < 0.05$

Body measurement	Males	Females	t-test	d.f.
Weight (g) ($N = 54$)	6.86 ± 3.52	5.85 ± 1.20	−2.00*	65.10
Carapace length (mm) ($N = 70$)	16.18 ± 2.76	17.04 ± 2.24	2.01*	132.46
Carapace breadth (mm) ($N = 70$)	25.78 ± 3.87	25.05 ± 2.45	−1.34	116.57

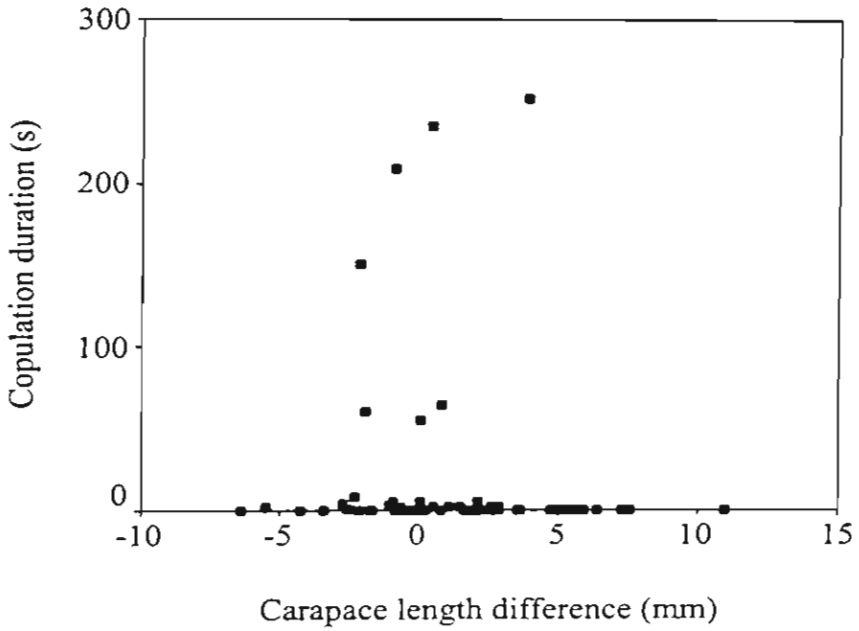

Fig. 1. Relationship between carapace length difference (mm) and copulation duration (s) in *Uca paradussumieri* Bott, 1973. Each point represents one encounter pair. Carapace length difference was calculated as female carapace length minus male carapace length.

Female choice

Females rejected courting males in more than 50% of courtship encounters (43 out of 66 courting males, Chi-square test: $\chi^2_1 = 6.061$, $P < 0.05$). Time duration of 23 accepted males that females allowed to stay on top of them varied from 1.30 to 252 s. Only 7 out of 23 accepted males had a successful copulation. Copulation time was shorter in cases where females were larger than males (Spearman rank correlation: carapace breadth: $r_s = -0.318$, $N = 65$, $P < 0.01$; carapace length: $r_s = -0.343$, $N = 65$, $P < 0.005$ (fig. 1)). Accepted males had a longer carapace than rejected males (table II). Accepted males had a longer and wider carapace than the females of the pairs (table II, fig. 2a, b: Carapace breadth difference and Carapace length difference). This suggests that females preferred

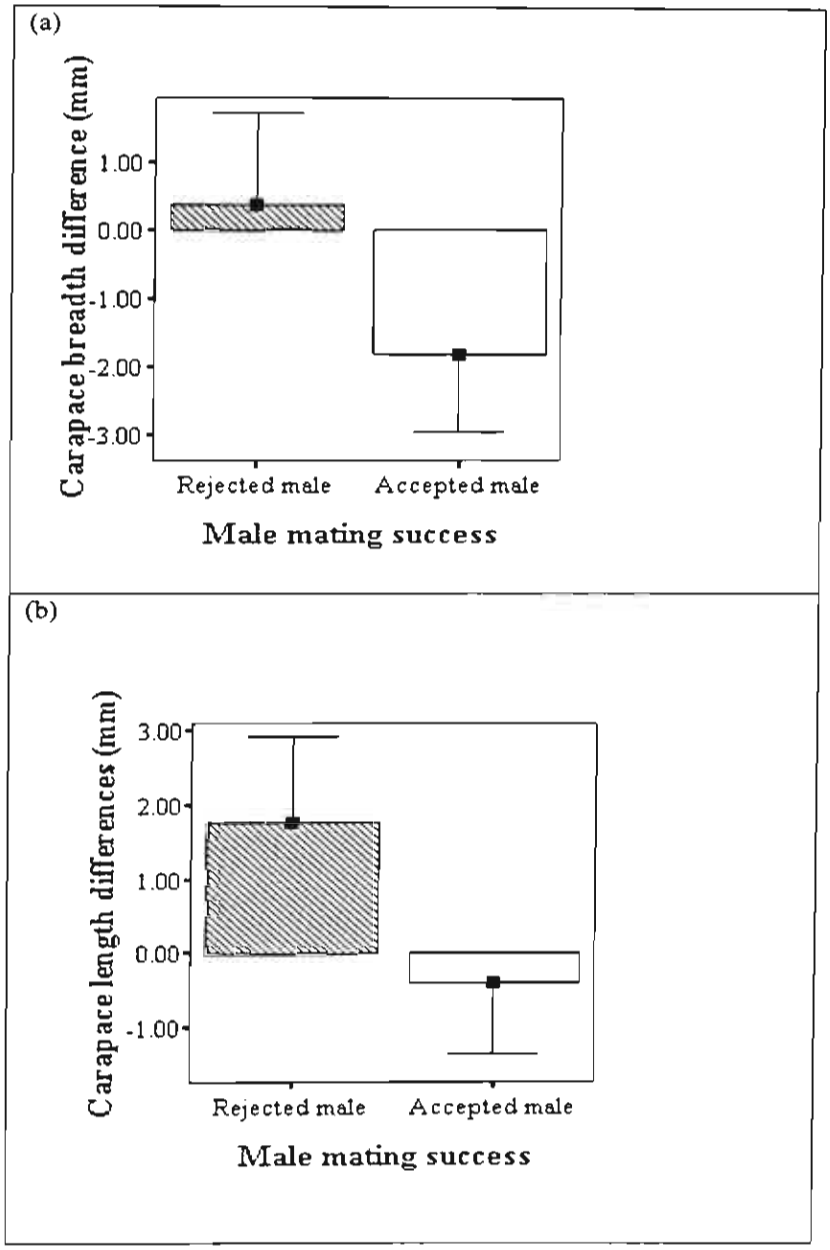

Fig. 2. a, carapace breadth difference (mm); and b, carapace length difference (mm), between males rejected and accepted by females of *Uca paradussumieri* Bott, 1973. Carapace length difference was calculated as female carapace length minus male carapace length.

TABLE II

The mean ± S.D. of measurement of accepted and rejected males by females of *Uca paradussumieri* Bott, 1973; N represents sample size; t-tests were independent two-sample tests with separated variance and Bonferroni adjustment; carapace length difference was calculated as female carapace length minus male carapace length; $^{*}P < 0.05$; $^{**}P < 0.005$

Measurement	Accepted males ($N = 23$)	Rejected males ($N = 43$)	t-test	d.f.
Carapace length (mm)	17.18 ± 1.80	15.65 ± 3.12	−2.53*	63.58
Carapace breadth (mm)	26.09 ± 2.81	25.43 ± 4.41	−0.74	61.87
Carapace length difference (mm)	−0.40 ± 2.19	1.77 ± 3.72	2.98**	63.33
Carapace breadth difference (mm)	−1.81 ± 2.67	0.37 ± 4.46	2.48*	63.07
Copulation duration (s)	46.01 ± 85.20	2.70 ± 12.38	−2.32*	20.41

mating with males that were larger than themselves. Variation in their carapace breadth and length are also larger than are those values for rejected males (table II).

Male-male competition

Of the 46 pairs observed in fighting, the larger combatant won in over 50% of the antagonistic encounters (Exact binomial probability: carapace breadth: $N = 37$ of 46 pairs, $P < 0.001$; major claw length: $N = 40$ of 46 pairs, $P < 0.001$). The average fight duration between males was 15.81 ± 15.40 s (mean ± S.D.). There was no association between the ratio of carapace length difference or the ratio of carapace breadth difference and log fighting duration (Pearson correlation: carapace length: $r_{46} = -0.08$, n.s.; carapace breadth: $r_{46} = 0.05$, n.s.).

DISCUSSION

Many studies have reported female choice in fiddler crab species such as *Uca rapax rapax* (Smith, 1870), *U. pugilator* (Bosc, 1802), *U. beebei* (Crane, 1941), and *U. lactea annulipes* (A. Milne-Edwards, 1837), but those female choices are based on other characteristics, such as size-assortative mating (Greenspan, 1980), burrow structures, and building pillar (Christy, 1983, 1987, 1988), or leading signals and synchronous waving displays (Backwell et al., 1999). Our study is the first investigation to show that female fiddler crabs discriminate by rejecting smaller males outright. Females may use the rejection response as a mate assessment exercise whereby they test the ability of males to withstand rejection during pre-mating encounters. Larger males may be able to withstand a rejection response for longer, resulting in female acceptance when the cost of rejection exceeds the costs of mating. This has been proposed as an explanation for the large male mating advantage in many species such as water striders (Insecta,

Gerridae: *Gerris odontogaster* Zetterstedt, 1828) (cf. Arnqvist, 1992; Rowe et al., 1994), seven seaweed-fly species (Coelopidae: *Coelopa frigida* Fabricius, 1805 (cf. Gilburn & Day, 1996), *C. ursina* Wiedemann, 1824 (cf. Crean & Gilburn, 1998), *C. nebularum* Aldrich, 1929, *C. vanduzeei* Cresson, 1914, *C. pilipes* Haliday, 1838, *Gluma musgravei* McAlpine, 1991, and *G. nitida* McAlpine, 1991 (cf. Crean et al., 2000), and crickets (Orthopteroidea: *Gryllus bimaculatus* De Geer, 1773) (cf. Bateman et al., 2001).

Our study shows that larger males have longer copulation times than smaller males, as is the case in other species such as damselflies (Insecta, Chlorocyphidae: *Platycypha caligata* Selys, 1853) (cf. Jennions, 1998), seed beetles (Bruchidae: *Stator limbatus* Horn, 1873) (cf. Savalli & Fox, 1998), and crickets (Orthopteroidea: *Gryllus bimaculatus*) (cf. Bateman et al., 2001). Many studies show that copulation duration is under female control. Females could terminate or prolong copulatory events based on male characteristics or resource gains from mating such as nuptial prey (Thornhill, 1976), male size (Jennions, 1998; Savalli & Fox, 1998), and spermatophore size (Bateman et al., 2001).

Our study shows that male *Uca paradussumieri* use size asymmetry to settle conflicts between males. Many studies of aggression in crustaceans clearly demonstrate that the larger combatant has an advantage in winning fights (e.g., Hazlett, 1968; Schein, 1975; Dingle & Caldwell, 1969; Hyatt & Salmon, 1978; Jennions & Backwell, 1996). It is of interest that large size confers a mating advantage in a species in which adult males and females are similar in size. Therefore, these data support the contention of Downhower et al. (1983) that male mating advantage based on large size is not in itself sufficient to account for a pattern of sexual size dimorphism in which adult males are on the average larger than adult females.

Empirical studies of sexual selection commonly show that either female choice or male-male competition drives the evolution of secondary sexual characteristics (reviewed in Andersson, 1994). Our findings show that male body size has a significant influence on both female choice and male-male competition in *Uca paradussumieri*. However, the intensity of sexual selection from female choice and male-male competition still needs further study.

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สาขาวิชา
■ ชีวภาพ และการแพทย์
☐ กายภาพ และวิศวกรรมศาสตร์
☐ สังคมศาสตร์ และมนุษยศาสตร์

Species diversity and morphological variations of fiddler crabs in Trang, Krabi and Phuket.

Mullica Jaroensutasinee, and Pitiwong Tuntichodok

Fiddler crabs were collected from 3 provinces: Trang, Krabi and Phuket. Species diversities were different among these three provinces. I collected five localities from Trang, 3 localities from Krabi and 2 localitie from Phuket with 10 replicates each. In Trang, I found seven *Uca* species: *U. dussumieri spinata*, *U. forcipata*, *U. lactea annulipes*, *U. triangularis bangali*, *U. urvillei*, *U. vocans hespiriae*, and *U. rosea*. In Krabi, I only found six Uca species: *U. dussumieri spinata*, *U. forcipata*, *U. lactea annulipes*, *U. triangularis bangali*, *U. urvillei*, and *U. vocans hespiriae*. Surprizingly, I only found three species in Phuket: *U. lactea annulipes*, *U. vocans hespiriae* and *U. tetragonon*. However, *U. tetragonon* was endemic only to the rocky shore in Phuket. The carapace width, carapace length, propodus length, and manus length were different in some species in both males and females. There were highly correlated between carapace width and its length, and between propodus length and manus length in all 8 species.

ความหลากหลายของสปีชีส์และลักษณะของรูปร่างที่ต่างกันของปูก้ามดาบที่จ.ตรัง จ.กระบี่และจ.ภูเก็ต

มัลลิกา เจริญสุธาสินี และ ปิติวงษ์ ตันติโชดก

ปูก้ามดาบเก็บจาก 3 จังหวัดดังนี้ ตรัง กระบี่และ ภูเก็ตมีความหลากหลายของสปีชีส์ที่ต่างกัน ได้ทำการเก็บตัวอย่างจาก 5 ตำแหน่งที่ตรัง 3 ตำแหน่งที่กระบี่ และ 2 ตำแหน่งที่ภูเก็ต ที่ตรังนั้นได้พบปูก้ามดาบจำนวน 7 สปีชีส์ดังนี้ *U. dussumieri spinata*, *U. forcipata*, *U. lactea annulipes*, *U. triangularis bangali*, *U. urvillei*, *U. vocans hespiriae*, และ *U. rosea* ที่จ.กระบี่ได้พบปูก้ามดาบจำนวน 6 สปีชีส์ดังนี้ *U. dussumieri spinata*, *U. forcipata*, *U. lactea annulipes*, *U. triangularis bangali*, *U. urvillei*, และ *U. vocans hespiriae* ที่น่าประหลาดใจก็คือที่ จ. ภูเก็ตได้พบปูก้ามดาบเพียง 3 สปีชีส์เท่านั้น ดังนี้ *U. lactea annulipes*, *U. vocans hespiriae* และ *U. tetragonon* แต่อย่างไรก็ตาม *U. tetragonon*เป็นปูก้ามดาบที่พบเฉพาะหาดหินที่จ.ภูเก็ตเท่านั้น ขนาดความยาวของกระดอง ความกว้างของกระดอง ขนาดของpropodus และ ขนาดของ manus มีความแตกต่างกันระหว่างสปีชีส์ ความยาวและความกว้างของกระดองมีความสัมพันธ์กันอย่างมีนัยสำคัญทั้ง 7 สปีชีส์ ขนาดความยาวของ propodusและ manusมีความสัมพันธ์กันอย่างมีนัยสำคัญทั้ง 7 สปีชีส์

INDEX KEY WORDS fiddler crab, Uca Sp., morphological variations

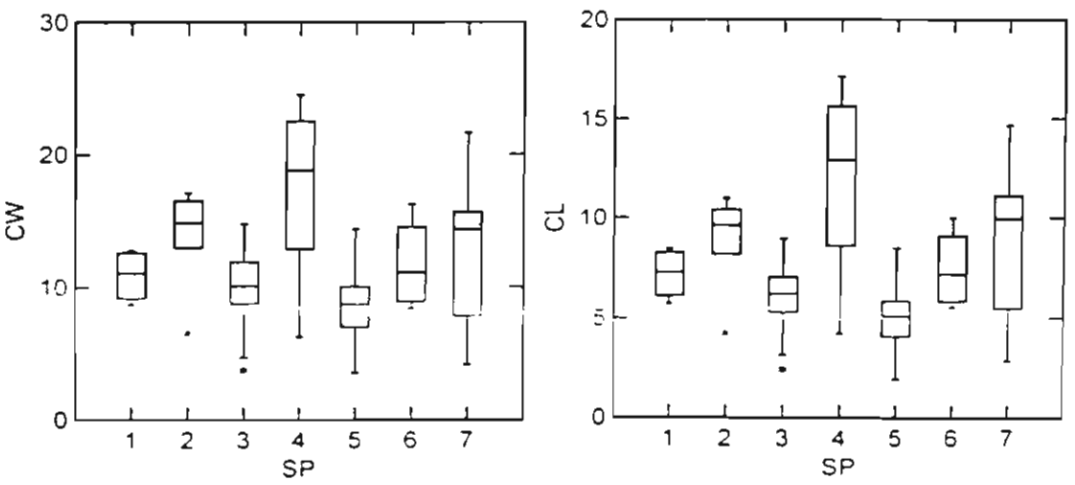
ชื่อเรื่อง (ภาษาอังกฤษ) Species diversity and morphological variations of fiddler crabs in Trang, Krabi and Phuket.

ขั้นตอนการวิจัย

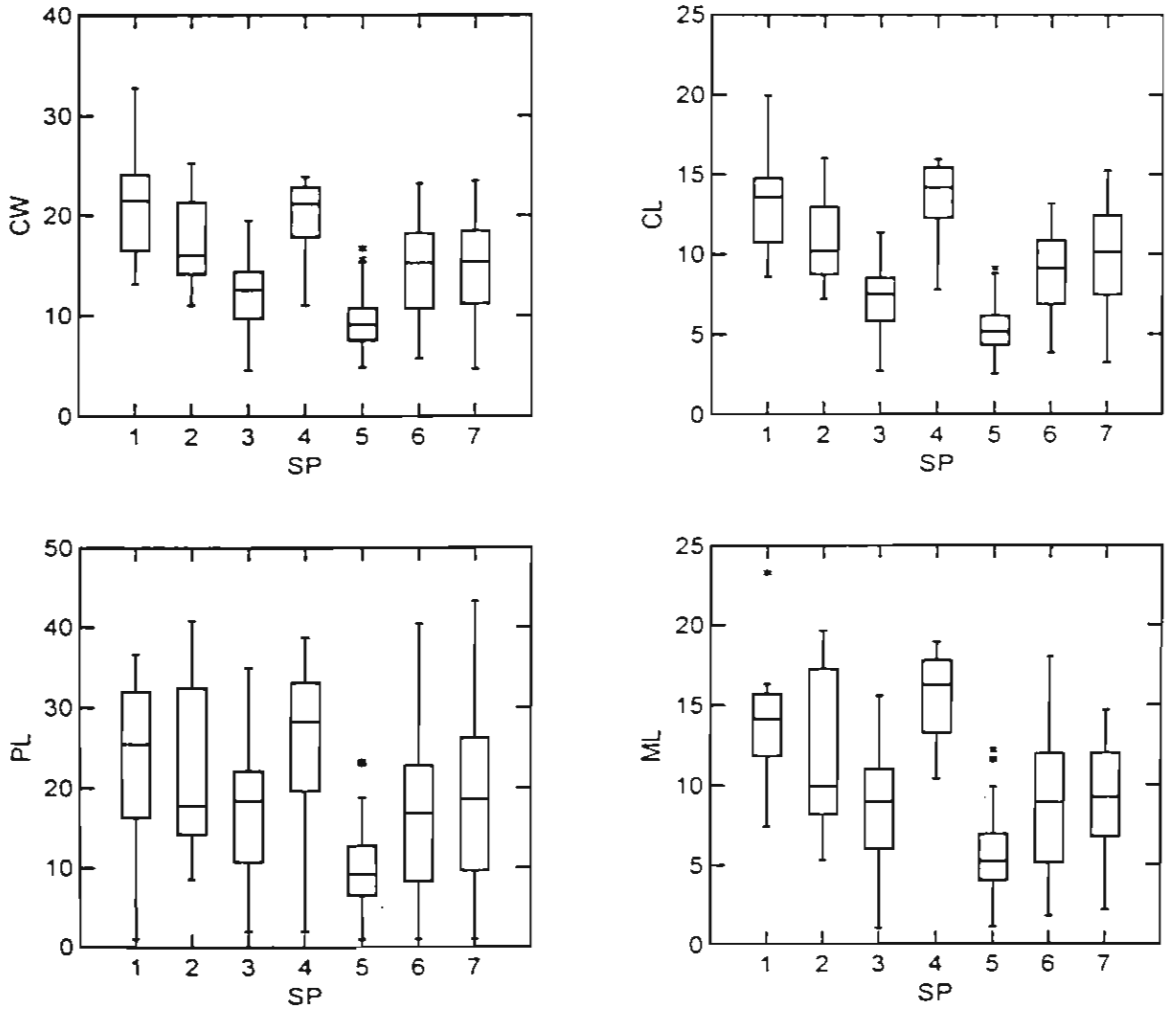
1. กำหนดบริเวณที่จะเก็บตัวอย่างทั้ง 3 จังหวัดภาคใต้ ได้แก่ จังหวัด กระบี่ ภูเก็ต และ ตรัง
2. เลือกเก็บตัวอย่างจากบริเวณที่มีลักษณะทางนิเวศวิทยาที่แตกต่างกัน ได้แก่ บริเวณป่าโกงกาง ป่าชายเลน หาดทราย หาดหิน หาดเลนที่อยู่ตามปากแม่น้ำ เป็นต้น โดยเก็บตัวอย่างตำแหน่งละ 10 ซ้ำ
3. สุ่มตัวอย่างใช้ quadrat (sampling quadrat on transect) โดยใช้ quadrat ขนาด 0.5x0.5 เมตรในแต่ละบริเวณ ใช้เสียมขุดดิน ภายใน quadrat ลึกลงไป 0.1 เมตร ร่อนแยกดินออกโดยใช้ตะแกรงขนาดตา 0.25 ตารางเซนติเมตร
4. นำตัวอย่างที่เก็บได้มาแช่ในฟอร์มาลิน 10% เพื่อแยกเพศ และนำไปวัดสัดส่วนของความยาวและความกว้างของกระดอง ความยาวของ propodus และ ความยาวของ manus
5. จำแนกชนิดในห้องปฏิบัติการต่อไป ตัวอย่างที่ผ่านการจำแนกแล้วนำมาดองด้วยแอลกอฮอล์ 70% และเก็บตัวอย่างที่ผ่านการแยกชนิดไว้ การจำแนกชนิดของปูก้ามดาบยึดหลักของ Crane (1975) และบรรพวิจิตร (2522) โดยอาศัยลักษณะความแตกต่างของอวัยวะเพศ ก้ามข้างใหญ่และกระดองของปูตัวผู้เป็นหลักในการจำแนก
6. ใช้การวิเคราะห์ทางสถิติถึงขนาดของปูก้ามดาบทั้งเพศผู้และเพศเมีย เช่น ค่าความแปรปรวน (ANOVA) เพื่อทดสอบความแตกต่างระหว่างสปีชีส์ และ Post Hoc-test (Bonferroni adjustment).

ผลการทดลอง

รูปที่ 1. แสดงค่าเฉลี่ยของความยาว (CL) และความกว้างของกระดองปูก้ามดาบตัวเมีย (CW) ทั้ง 7 สปีชีส์เรียงตามลำดับดังนี้ *U. dussumieri spinata, U. forcipata, U. lactea annulipes, U. tetragonon, U. triangularis bangali, U. urvillei* และ *U. vocans hespiriae*

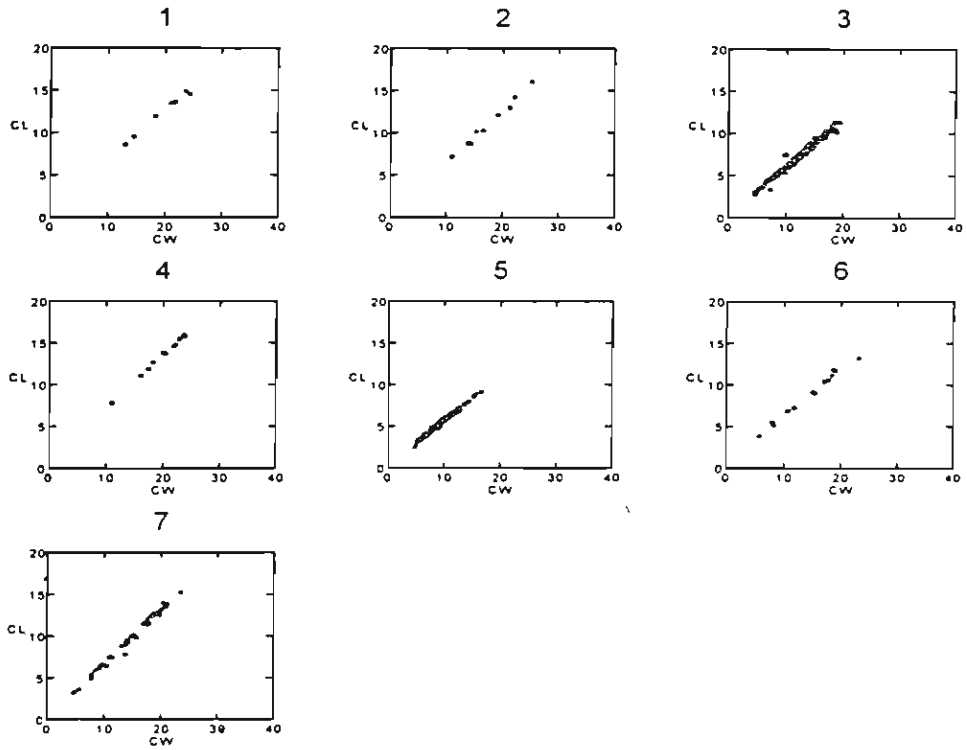


ชื่อเรื่อง (ภาษาอังกฤษ) **Species diversity and morphological variations of fiddler crabs in Trang, Krabi and Phuket.**



รูปที่ 2. แสดงค่าเฉลี่ยของความยาวกระดองปูก้ามดาบตัวผู้ (CL), ความกว้างของกระดองปูก้ามดาบตัวผู้ (CW), ขนาดของ propodus (PL), และขนาดของ manus (ML) ทั้ง 7 สปีชีส์เรียงตามลำดับดังนี้ *U. dussumieri spinata, U. forcipata, U. lactea annulipes, U. tetragonon, U. triangularis bangali, U. urvillei* และ *U. vocans hespiriae*

ชื่อเรื่อง (ภาษาอังกฤษ) **Species diversity and morphological variations of fiddler crabs in Trang, Krabi and Phuket.**



รูปที่ 3. แสดงความสัมพันธ์ระหว่างความยาวกระดองปูก้ามดาบตัวผู้ (CL), และความกว้างของกระดองปูก้ามดาบตัวผู้ (CW), ทั้ง 7 สปีชีส์เรียงตามลำดับดังนี้ *U. dussumieri spinata, U. forcipata, U. lactea annulipes, U. tetragonon, U. tnangulans bangali, U. urvillei* และ *U. vocans hespinae*

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TITLE: THE EFFECT OF SIZE AND RESIDENCY ON FIGHTING DURATION AND OUTCOME IN FILDDLER CRABS, *Uca hesperiae*

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Objective: To examine the affect of size and residency on the outcome of fights and fighting duration in *Uca hesperie*.

Methods: We studied a population of *U. hesperiae* in Pakmeng beach, Trang, Thailand from April to May 2001. We observed 100 pairs of males naturally engaged in fighting behaviors and recorded fighting duration and the identity of the winner. We captured both intruder and resident males to measured major claw length and carapace width to its nearest 0.1 mm using vernier calipers.

Results: There was a positive correlation between both major claw length and carapace width of fighting pair males (major claw length: $r = 0.70$, $P<0.01$; carapace width: $r = 0.58$, $P<0.01$). Males of the same handedness were more likely to encounter each other ($\chi^2_1 = 70.56$, $P<0.001$). The larger of the pair won the fight more than 50% (Exact binomial probability: major claw length: n = 78 of 100, $P<0.001$; carapace width: n = 64 of 100, $P < 0.01$). There was an interaction between major claw size and resident-intruder status (Fisher's exact test, $P<0.001$). When the intruders won the fight, they were larger than the resident in 40 of 47 fighting pairs (exact binomial probability, $P <0.001$). When the residents won the fight, they also were larger than the intruders in 38 of 53 fighting pairs (exact binomial probability, $P<0.005$). There were negative correlations between carapace width difference and fighting duration ($r =-0.234$, $P<0.05$) and major claw length and fighting duration ($r =-0.211$, $P<0.05$)

Conclusion: Large *U. hesperiae* males tend to win fights regardless of residency status. Fighting duration was shorter when size difference between males was greater than when the size difference was smaller.

WINNER	Major Claw Length		Total
	Intruder>residence	Residence>intruder	
Intruder wins (n)	40	7	47
Resident wins (n)	15	38	53
Total (n)	55	45	100

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Keyword: fighting, residency, male size, fiddler crab, *Uca hesperie*

ขนาดปูก้ามดาบเพศผู้มีผลต่อความชอบของปูเพศเมียและการแข่งขันระหว่างปูก้ามดาบเพศผู้ *UCA SPINATA*

MALE BODY SIZE INFLUENCES FEMALE CHOICE AND MALE-MALE COMPETITION IN THE FIDDLER CRAB, *UCA SPINATA*.

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บทคัดย่อ: ทำการทดสอบผลของขนาดของปูก้ามดาบเพศผู้ต่อความชอบของปูเพศเมียและการแข่งขันระหว่างปูเพศผู้ในปู *Uca spinata* พบว่าการคัดเลือกทางเพศทั้ง 2 ประเภทได้รับผลกระทบจากขนาดของปูเพศผู้ กล่าวคือปูเพศเมียชอบปูเพศผู้ที่มีขนาดใหญ่ เวลาในการผสมพันธุ์จะสั้นในกรณีที่ปูเพศเมียมีขนาดใหญ่กว่าเพศผู้ เมื่อเปรียบเทียบระหว่างปูเพศผู้ที่ถูกปฏิเสธและปูเพศผู้ที่ได้รับเลือกจากปูเพศเมีย พบว่าปูเพศผู้ที่ได้รับเลือกเป็นคู่ครองจะมีขนาดความกว้างและความยาวของกระดองมากกว่า ปูเพศผู้ที่มีขนาดใหญ่กว่าก็มักจะประสบความสำเร็จในการต่อสู้กับปูเพศผู้ที่เล็กกว่า แต่ขนาดของปูเพศผู้นี้ไม่มีผลต่อระยะเวลาในการต่อสู้ระหว่างเพศผู้ด้วยกัน

Abstract: Male body size was tested for its influence on female choice and male-male competition among fiddler crabs, *Uca spinata*. Both modes of sexual selection had an influence on male body size. Females preferred larger males as mates. Copulation time was shorter in cases where females were larger than males. Compared with rejected males, accepted males had greater carapace breadth and length. Larger males were more successful in competition against smaller males, but body size had no effect on fighting duration.

Methodology: We studied a population of *U. spinata* at Lanta Island, Krabi, Thailand from June-October, 2001. The study site was an intertidal muddy sand flat on the Indian Ocean. All observations were made in the field. We sat quietly 4-5 meters from where fighting and copulation was taking place and observed all behaviour through 8x30 binoculars. All observations were made in the field during low tide.

For the female choice test, we observed 70 females encountering courting males. These courting males varied in size. We recorded the number of accepted males and rejected males. A receptive female wandered past several displaying males and then chose to copulate with the accepted male on the surface. Females accepted the males as mates by allowing the accepted males to climb onto their carapace from the rear following which surface copulation began. We recorded their courtship duration. For rejected males, receptive females walked away from the courting males. After mate choice ended, we captured crabs of both sexes to measure carapace length and breadth to the nearest 0.1 mm using vernier callipers.

For the male-male competition test, we observed 46 pairs of males naturally engaged in fighting behaviour. We recorded three forceful combats between fighting pairs (i. e. manus-push, heel and ridge and forceful interlace), the fighting duration, and the identity of the winner. The outcome of the contests was defined for each individual as a win or loss. An individual was classified as a winner if he remained within the area and subsequently undertook feeding and courting behaviour. Losers left the area with fast or erratic walk. After the fights ended and the identity of the winner was recorded, we captured both crabs to measure major claw length, carapace breadth and length to the nearest 0.1 mm using vernier callipers.

Results, Discussion and Conclusion: All the fiddler crabs, *U. spinata*, collected in the field were measured for body weight, and carapace length and breadth. Males were heavier but had a smaller carapace length than females (Table 1). Male weight correlated highly with carapace length and breadth (Pearson correlation coefficient: carapace length: $r_{54} = 0.81$, $P<0.001$; carapace breadth: $r_{54} = 0.82$, $P<0.001$). Female weight also correlated highly with carapace length and breadth (Pearson correlation coefficient: carapace length: $r_{54} = 0.67$, $P<0.001$; carapace breadth: $r_{54} = 0.69$, $P<0.001$).

Females preferred to mate with males that were larger than them. Copulation duration was shorter in cases where females were larger than males (Spearman rank correlation: carapace breadth: $r_s = -0.318$, N = 65, $P<0.01$; carapace length: $r_s = -0.343$, N = 65, $P<0.005$ (Fig. 1). Comparing accepted and rejected males, accepted males had a larger carapace breadth and length than rejected males. They also had less carapace breadth and length difference than rejected males (Table 2; Fig. 2a, b).

From 46 pairs of males naturally engaged in agonistic behaviour, the larger of the pairs won the fight in over 80% of encounters (Exact binomial probability: carapace breadth: n = 37 of 46 pairs, $P<0.001$; major claw length: n = 40 of 46 pairs, $P<0.001$). The average fight duration between males was 15.81 ± 15.40 s (mean ± SD). There was no association between the ratio of carapace length difference or the ratio of carapace breadth difference and log fighting duration (Pearson correlation: carapace length: $r_{46} = -0.08$, ns; carapace breadth: $r_{46} = 0.05$, ns).

Empirical studies of sexual selection commonly show that either female choice or male-male competition drives the evolution of secondary sexual characteristics. Our findings show that both female choice and male-male competition act upon male body size in *U. spinata*. However, the intensity of sexual selection from each mode still needs further study.

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Keywords: female choice, male-male competition, fighting duration, male size, fiddler crab, *Uca spinata*.