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Eat Better to Look Better: The Relationship between Food Availability, UV Brightness of the Major Claw, and Mating Success of the Fiddler Crab *Austruca lactea*

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Many factors affect male fiddler crab courting and female choice during underground mating, including claw-waving patterns, claw-waving frequency, hood structures, burrow quality, and visible and ultraviolet signals of the major claw. Under food-limited conditions, fiddler crabs decrease their investments in reproduction—*e.g.*, lower their claw-waving frequency. However, the effect of food availability on the visible or ultraviolet signals important for courtship success is unknown, not only for fiddler crabs, but for crustaceans in general. This is the first study to explore the influence of food availability on the early stages of female choice in *Austruca lactea*. In the present study, we tested (1) the effect of food availability on the UV brightness of *A. lactea*'s major claw and burrow quality and (2) the correlation between *A. lactea* courtship success and the UV brightness of its major claw. Our results showed that higher food availability increased the UV brightness of the major claw and enhanced the male's burrow quality. The UV component to the signal is important for courtship success. The males with a UV component of signal on their major claw had a higher courtship success. This is an indication that food availability may affect the attractiveness of male fiddler crabs.

Key words: *Austruca lactea*, UV brightness, Food availability, Mate choice, Fiddler crab, Courtship behavior.

BACKGROUND

The reproductive behavior of animals is influenced by food availability (Kim and Choe 2003; Kim et al. 2010; Sofaer et al. 2012). Animals will decrease their reproductive investment and tend to search for more food when they are under food-limited conditions (Schneider et al. 2013). For example, when food is scarce, hamsters prefer to search and hoard food rather than choose a mate, even if the hamsters are on their estrous cycle (Klingerman et al. 2010). Some studies also indicate that sexual signals (visible and ultraviolet signals) may reflect the body condition of an organism; this, too, is influenced by food availability. Some well-known signals include the beak color of the avian species *Turdus merula* (Faivre et al. 2003), foot color of the courting blue-foot booby *Sula nebouxii* (Torres and Velando 2003; Velando et al. 2006), UV component to the signals on the wings of the butterfly *Colias eurytheme* (Kemp and Rutowski 2007), and fluorescent signaling on the palpus of the jumping spider *Cosmophasis umbratica* (Painting et al. 2017).

When it comes to the reproductive behavior of fiddler crabs, there are two mating strategies: surface

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mating and underground mating (Christy 2007). During surface mating, a mature male leaves his burrow and approaches a nearby female, courting with vibrational signals by stroking its own walking legs (Takeshita and Murai 2016). In underground mating, the female leaves her burrow and mates inside a male's burrow. The female samples several males' burrows before the underground mating takes place. Male crabs wave their major claw to attract the wandering females; factors that increase the probability that a female crab undergoes underground mating include the type of claw-waving (Muramatsu 2011a b), claw-waving frequency (Reaney et al. 2008), visible and ultraviolet signals of the major claw (Detto 2007; Detto and Backwell 2009), extra-burrow structures (Kim et al. 2004 2009), and burrow quality. The factors reported previously for determining burrow quality includes the volume (Goshima and Murai 1988; Clark and Backwell 2016), the number of burrow branches (Backwell and Passmore 1996), and the width (Derivera 2005; Reaney and Backwell 2007; Kerr et al. 2012). Underground mating occurs in two courtship stages—in the first stage, the male waves its major claw to attract the wandering female; in the second stage, the female visits the male's burrow (Christy 2007).

Fiddler crabs also decrease their reproductive investment under food-limited conditions. Male *Austruca annulipes* and *Austruca lactea* decrease their claw-waving frequency during the first stage of courtship (Jennions and Backwell 1998; Kim and Choe 2003; Kim et al. 2008). Similarly, under food-limited conditions, the angular distribution of the male *Leptuca terpsichores* courtship activity (Kim et al. 2010) and the number of extra-burrow structures will both decrease (Backwell et al. 1995; Kim and Choe 2003; Kim et al. 2008). However, no study has investigated how food availability affects the visible or ultraviolet signals that are important for courtship success in any crustacean. In addition, during the second stage of courtship behavior, whether the factors related to the burrow quality of the courting male are affected by food availability is not known.

In recent years, studies on the courtship success of fiddler crabs have mostly examined the factors for underground mating, such as types of claw-waving (Muramatsu 2011a b), claw-waving frequency (Reaney et al. 2008), visible signals of major claw (Detto 2007; Detto and Backwell 2009), hood structures (first stage of female choice, Kim et al. 2004 2009), and burrow quality (second stage of female choice, Goshima and Murai 1988; Backwell and Passmore 1996; Derivera 2005; Reaney and Backwell 2007; Kerr et al. 2012; Clark and Backwell 2016). However, only one study has been conducted on the relationship between the UV component to the signals of the major claw and courtship success a male fiddler crab (*Austruca mjoebergi*; Detto and Backwell 2009).

The two aims in the present study are to examine whether (1) UV signal and burrow quality are affected by food availability and (2) the UV signal of the major claw influences *A. lactea*'s courtship success. Fiddler crabs are deposit feeders and feed on organic matter on mud using the specialized maxillipeds (Lim and Goh 2021). *Austruca lactea* populations are mainly distributed in the upper tidal zone, and organic material becomes limited during the neap period when seawater does not flood the mudflat for several days. Some studies also indicated that organic content and chlorophyll-*a* at the top mudflat gradually decreased with distance to the upper tidal zone (Murai et al. 1982; Allen and Levinton 2014). Since most organic contents are found at low tide, *A. lactea* may be confronted with limited food during that period. Previous studies showed that reproductive investments and sexual signals may be related to an individual's body condition and food intake (Velando et al. 2006). Our first aim was to test whether food availability can affect the UV brightness of *A. lactea*'s major claw and its burrow quality. This is the first study to explore the influence of food availability on both the first and the second stages of *A. lactea* female choice. In the other hand, we conducted a pilot test in our laboratory, measured the body reflectance of *A. lactea*, and were surprised to find that the major claw had the highest UV brightness of the body parts measured. The waveform trend of UV brightness on the major claw was much higher than those of two fiddler crab species (*Afruca tangeri* and *Austruca mjoebergi*) reported in the literature (Cummings et al. 2008; Detto and Backwell 2009). Therefore, our second aim for this study was to test whether the UV brightness of the major claw correlates to *A. lactea* courtship success.

MATERIALS AND METHODS

The effect of food on the structure of male burrow

We established nine 100 × 100-cm^2 quadrate plots for the three treatments (food-added, food-limited, and control) from July to September near Gaomei wetland, Taichung, Taiwan (24°17'52.9"N, 120°32'44.8"E). There was no significant difference in crab density among the three treatments—30.4 ± 3.5 (mean ± SD) for males and 23.4 ± 4.2 for females. We buried a mesh net around the quadrate to prevent the crabs from escaping. The mesh was buried 20 cm underground to 20 cm aboveground. In the food-limited treatment, we used the plastic plate

to remove the 5 mm of mud and sand on the surface. In the food-added treatment, we scratched the mud surface first before spraying it with 5 g of fish powder (D-50 PLUS, Tropical, EU) and adding 0.5 L sea water onto the quadrate. In the control and food-limited treatment, we sprayed 0.5 L sea water onto the quadrate. The three treatments in the low tide area were conducted during three consecutive tidal cycles for 43 days. At the end of the experiment, we applied a foaming agent (puff dino pu foam, Chung Tai Sing the domestic professional environmental sanitation chemical producer, Taiwan) to prepare the burrow model. The burrow volume, burrow entrance diameter, maximum burrow width, burrow deep and burrow length were recorded.

The UV brightness of the male *A. lactea*'s major claw

Austruca lactea males were captured near Gaomei wetland and immediately placed into 80% iced EtOH to prevent any color change. The reflectance of the major claw (pollex) was measured using a USB4000 spectrometer (USB4000, Ocean Optics, USA) within twenty-four hours, and the highest measurement was recorded. Each claw manus was measured twice, and the average of the two recordings became the reflectance of the claw. Ultraviolet brightness of the claw was defined as the integral area of claw reflectance at 300–400 nm (Kemp et al. 2008).

The integral equation is as followed. If $f(x)$ is the continuous function of [a, b] and $F'(x) = f(x)$, so we can obtain the total UV area using a general formula: $\int_a^b f(x)\,dx = F(b) - F(a)$. We first substituted the equation for the trend line over a wavelength of 300–400 nm into $f(x)$, then integrated $f(x)$ to get $F(x)$. Next, we substituted 300 and 400 into a and b, respectively. Finally, the total UV brightness was obtained as the difference between $F(400)$ and $F(300)$.

The organic content among three tidal levels

The habitat of *A. lactea* was covered by the mangrove, so we changed the study site to an intertidal mudflat with the similar environment in Dadu Estuary, Taichung, Taiwan (24°12'10"N, 120°29'17.8"E). During low tide, three transect lines perpendicular to the waterline were used to collect surface sediment samples at 2–3 mm deep. We collected the samples from three tidal levels including low tidal level (near the waterline), middle tidal level (20 m away the waterline), and high tidal level (40 m away the waterline) in each transect line. In each tidal level we collected 50 g sediment from five locations.

The organic content values were obtained by the high temperature ashing method. The sample were dried in an oven at 60°C and placed to an ashing furnace (500°C) for 4 hours. The organic content (C_o) of the soil samples was $C_o = [(W_{60} - W_{500}) / (W_{60} - W_p)] \times 100\%$ (Crisp 1984). W_{60} is the sample weight with container after dried in 60°C oven; W_{500} is the weight with container after ashing in 500°C; W_p is the weight of the container.

The effect of food availability on the UV component of the signal

This experiment was conducted from July to August. Eighteen plastic containers (50 × 50 × 30 cm^3) were set up, each representing one of three food treatments: food-added, food-limited, and control. The containers were buried from 15 cm under to 15 cm above the mudflat surface. To prevent fiddler crabs from escaping the rearing boxes, the rearing box was covered with 1 mm mesh. Furthermore, all crabs were removed after setting up the rearing boxes, and 15 or 20 *A. lactea* male crabs were placed into rearing boxes after one week of recovery.

Field work was conducted daily 1 hour before low tide. Two-mm surface soil was removed by scraping with a plastic plate for the food-limited treatment. For the food-added treatment, we scratched but did not remove the surface soil with a plastic plate, then added 5 grams dry shrimps (Tropical, Poland) and 5 grams fish food (Haifeng, Taiwan). Lastly, for the control treatment we scratched but did not remove the surface soil. After keeping the *A. lactea* males for three weeks in the enclosures, we brought them back to the laboratory and measured their UV brightness. We used a USB4000 spectrometer to measure the UV reflectance of male *A. lactea*. Four parts of the major claw were measured with a spectrometer: the front end of the dactyl, middle of the dactyl, front end of the pollex, and middle of the pollex (Fig. 1). We applied a definite integral and obtained the

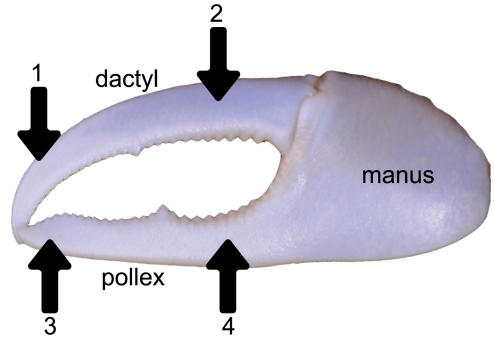

Fig. 1. Four parts of the major claw were measured by a spectrometer: 1-front end of the dactyl, 2-middle of the dactyl, 3-front end of the pollex, and 4-middle of the pollex.

area with a UV brightness wavelength of 300–400 nm.

How the UV component of the signal affects courtship success

Our preliminary test indicated that the sunscreen we were using (UV perfect spray sunscreen, Biore, Japan) effectively inhibited the reflectance of UV components with a wavelength of 300–400 nm (Fig. S1). The brightness of visible light changed slightly with this sunscreen treatment. Therefore, we collected 50 crabs to test how sunscreen affects the brightness of the major claw in the sensitive visible light component of the signals (wavelengths 510–540 nm; Horch et al. 2002). The brightness was 1973.18 ± 303.07 before sunscreen was applied and 2050.20 ± 516.94 after it was applied, a change that was not significant (paired sample *t*-test, $t = 1.09$, $p = 0.28$, $n = 50$).

Field work was conducted daily 1 hour before the low tide in the Dadu Estuary wetland. We used binoculars to search for two nearby resident male crabs with similar carapace widths that were simultaneously displaying courtship (lateral-circular) waving toward the same female. Both males were caught carefully without destroying their burrows and placed in a plastic container before measuring their carapace width and claw length with a vernier caliper (CD-6 PSX, Mitutoyo, Japan). The 50 × 50 × 10 cm^3 wooden plots were placed around the center of the two males' burrows. The maximum side length of the plot was less than 50 cm to ensure the male crabs could meet the female (Booksmythe et al. 2008). The outside burrow structure ("hoods"), of the two crabs were removed to avoid the possible effects of sensory traps (Christy et al. 1995). The burrows of all the surrounding crabs except the two courting males inside the plot were removed to avoid interference during the study period.

The two males were treated with different sunscreen treatments. The major claw of one male crab was sprayed with sunscreen to block the UV component to the signals, while the other male crab was treated with sunscreen on the carapace to prevent the artificial product effect. After applying sunscreen treatment for 10 minutes, the two crabs were returned to their burrows for at least 10 minutes to recover. Crabs change their body color—especially the carapace—under stressful conditions (Takeshita 2019). Their bodies returned to their previous color during the recovery time. The wandering and reproductively mature females with a carapace width over 7 millimeters (Severinghaus and Lin 1990; Yamaguchi 2001) were collected and released equidistant from the burrows of the two male crabs.

We recorded the fiddler crab courtship behaviors for 15 minutes with a camera (HDR-XR350, Sony, Japan). It was reported that *A. lactea* courtship lasts an average of 10 minutes before underground mating occurs, and our 15 minutes of recording were sufficient to capture the courtship of fiddler crabs (Goshima and Murai 1988; Yamaguchi 2001). We recorded four courtship parameters: (1) courtship success of the males (in bouts), (2) time needed for successful courtship (in seconds), (3) male claw-waving frequencies (in times per second) and (4) distance between male and female crabs (in cm).

A successful courtship event in *A. lactea* was defined as a male crab performing the lateral-circular waving to attract a female crab, and the female either approaching the courting male (Detto 2007; Detto and Backwell 2009) or reaching the burrow of the male (Kim et al. 2007 2009; Zhu et al. 2012). A courtship event was considered to have failed when the female ignored the courtship waving signals from the males. Three kinds of male courtship waving events were recorded: 1) only the male without sunscreen exhibiting courtship waving behavior, 2) only the male with sunscreen exhibiting courtship waving behavior, and 3) both males exhibited courtship waving behavior. The following events were considered invalid and not recorded: both males staying inside their own burrows for the entire recording period, neither male waving to the female crab, the female crab hiding in her burrow for the entire recording period, or the female crab moving away from the plot.

The successful courtship time in this study was defined as the time needed for a male crab to perform the lateral-circular waving toward a particular female crab until the female reached that male's burrow. Claw-waving frequency was defined as the number of waves per second during the courting period. Lastly, the distance between males and the female was the shortest distance at which the male crab started the lateral-circular waving to court the female.

Statistical analysis

The Kruskal-Wallis test was used to compare the differences in burrow characters among the three food treatments. The data on UV brightness were normally distributed, but the variance was unequal across treatments. Therefore, analysis of variance (Welch) was used to analyze the UV brightness among three food treatments and Dunnett post hoc test was used to compare the differences among the three treatments. Kernel density estimation was used to compare the distribution of UV brightness among the three treatments. Under the probability density function, the total area of each treatment within the curve was 1. Hence, we compared the area of overlap within the curve to analyze the distribution of UV brightness

between two treatments. If the area of 95% confidence interval did not overlap with the curve of kernel density between two treatments completely, then the distribution of UV brightness between the two treatments was different. Logistic regression analysis was used to examine the factors that might affect the courtship success, including application of sunscreen onto the major claw of male crabs, male carapace width, major claw length of the male crabs, distance between male and female crabs, and male claw-waving frequencies.

The *Chi*-square test of independence was used to analyze the sunscreen effect on courtship successfulness in only one male courting event. The *Chi*-square goodness of fit test was used to analyze the sunscreen effect on courtship success in both males courting simultaneously. The time needed for successful courtship was not a normal distribution, and the Kruskal-Wallis test was used for further analysis, and the Dunn post hoc test was used to compare the differences among the three food treatments.

RESULTS

The effect of food on the structure of male burrows

The males in the food-added treatment had the largest burrow volumes (Kruskal-Wallis test, *Chi*-square = 15.1, *d.f.* = 2, $p < 0.01$; food addition: 81.9 ± 31.7 ml, food limited: 41.3 ± 16.2 ml, control: 56.9 ± 19.4 ml) and maximum diameters (Kruskal-Wallis test, *Chi*-square = 9.2, *d.f.* = 2, $p < 0.01$; food addition: 3.6 ± 0.8 cm, food limited: 2.9 ± 0.8 cm, control: 2.9 ± 0.5 cm). Under both food-added and control treatments, males had significantly greater burrows depths (Kruskal-Wallis test, *Chi*-square = 11.79, *d.f.* = 2, $p < 0.01$; food addition: 23.0 ± 5.8 cm, food limited: 16.3 ± 5.2 cm, control: 23.0 ± 2.8 cm) and burrow lengths (Kruskal-Wallis test, *Chi*-square = 10.37, *d.f.* = 2, $p < 0.01$; food addition: 28.1 ± 6.6 cm, food limited: 21.3 ± 4.9 cm, control: 27.0 ± 2.7 cm).

The food availability changed the diameters of the females' burrow entrance. The food-limited females had smaller diameters than those from the other treatments (Kruskal-Wallis test, *Chi*-square = 7.34, *d.f.* = 2, $p = 0.03$; food addition: 1.1 ± 0.1 cm, food limited: 0.9 ± 0.1 cm, control: 1.0 ± 0.1 cm). Food availability did not, however, affect females' burrow volumes (Kruskal-Wallis test, *Chi*-square = 1.25, *d.f.* = 2, $p = 0.53$), depth (Kruskal-Wallis test, *Chi*-square = 0.64, *d.f.* = 2, $p = 0.73$), lengths (Kruskal-Wallis test, *Chi*-square = 0.76, *d.f.* = 2, $p = 0.68$), or maximum diameters (Kruskal-Wallis test, *Chi*-square = 0.007, *d.f.* = 2, $p = 0.99$).

Organic content among the three tidal levels

The organic content at the surface of the mudflat significantly decreased with distance to the upper tidal zone. The organic content was highest at the low tide level (34.28 ± 1.25 mg/g), followed by the middle (23.03 ± 0.84 mg/g) and high tide levels (21.84 ± 0.65 mg/g) (Table 1).

UV brightness of the major claw of male *A. lactea*

We collected 96 males and obtained the UV brightness of the major claw of *A. lactea*. The UV brightness was not correlated with carapace width (Fig. 2), an indication that its UV brightness is influenced by other factors.

The effect of food availability on the UV brightness of the major claw

After male crabs were maintained in the enclosure for three weeks, the UV brightness of male *A. lactea* was almost—but not—statistically different among the three food treatments (Analysis of variance (Welch), $F_{2,164} = 2.76$, $p = 0.07$, $n = 167$) (Fig. 3). However, UV brightness tended to be higher in the food-added treatment than the control one, and UV brightness in the control treatment was higher than in the food-limited one.

The kernel density estimation that showed the distributions of UV brightness on the major claw between food-added and food-limited treatments were significantly different, and the 95% confidence interval between the two treatments did not overlap completely

Table 1. Organic content in the top mudflat among the three different distances to the water line ($n = 5$)

Distance to the water line	Organic content of soil (mg/g)
0 m (low tide level)	34.28 ± 1.25
20 m (middle tide level)	23.03 ± 0.84
40 m (high tide level)	21.84 ± 0.65

(Kernel density analysis, $p = 0.01$, $n = 104$) (Fig. 4A).

The probability density was concentrated at 7000 UV brightness in food-limited treatments, and 7000 and 9000 UV brightness in the food-added treatment (Fig. 4A). There was a clear bimodal distribution in food-added treatment. The distribution of UV brightness on the major claw was also significantly different between the food-added and control treatments, and the 95% confidence interval between the two treatments did not completely overlap with the curve of kernel density (Kernel density analysis, $p = 0.05$, $n = 115$) (Fig. 4B). The distribution of UV brightness on the major claw between the control and food-limited treatments was not significantly different, and the 95% confidence interval between the two treatments completely overlapped with the curve of kernel density (Kernel density analysis, $p = 0.53$, $n = 115$) (Fig. 4C).

The effects of the UV component of signal on courtship success

We recorded 100 videos, including 62 valid videos with at least one successful courtship event. Among the factors recorded to test the courtship success of the fiddler crabs, the most important was the sunscreen treatment, which blocked the UV signal of the major claw (Logistic regression analysis, Wald-statistic = -2.163, $p < 0.05$, $n = 125$) (Table 2).

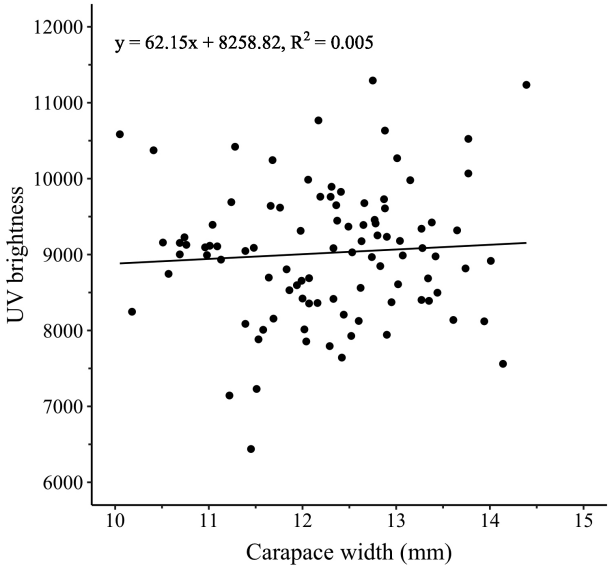

Fig. 2. The UV brightness on the major claw of *A. lactea*. The UV brightness in *A. lactea* has no correlation with carapace width (n = 101).

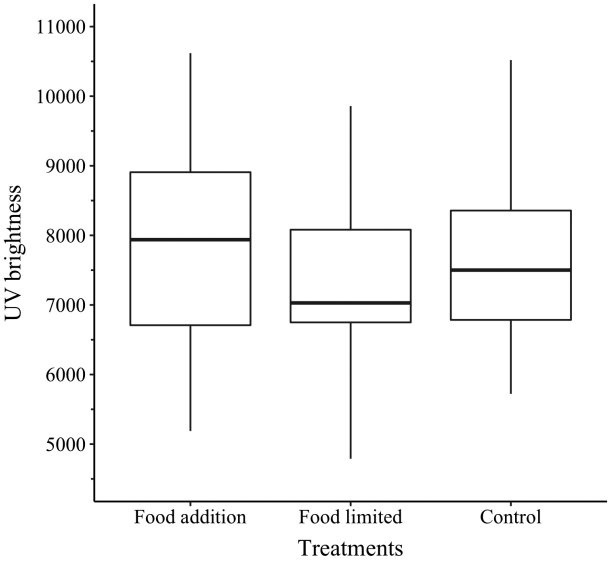

Fig. 3. The UV brightness on the major claw of male *A. lactea* among the three food treatments (food-added, food-limited, and control).

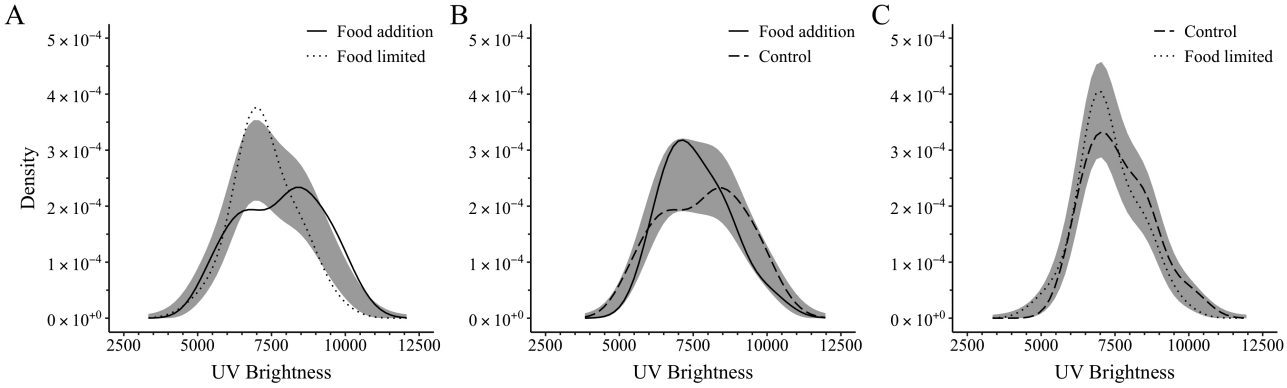

Fig. 4. Distribution of UV brightness on the major claw between two treatments. A, The distribution of UV brightness between food-added and food-limited treatments; B, between food-added and control treatments; C, between control and food-limited treatments. The gray area shows the overlap of the 95% confident interval between two treatments.

From the two only one male court events, we found the courtship success was not influenced by the UV signal on the major claw (Fig. 5A; *Chi*-square test, $\chi^2 = 0.28$, *d.f.* = 1, $p = 0.59$). The successful percentage was similar between the male with (50.31%) and without (55.22%) sunscreen treatments. However, the time needed for successful courtship was shorter in the male with sunscreen (Kruskal-Wallis test, $\chi^2 = 4.5$, *d.f.* = 1, $p = 0.03$).

When both males exhibited the courtship behavior, the percentage of courtships that were a success was 51.61%, similar to that of one male court events. However, the males without the sunscreen treatment on the major claw successfully mated 2.2 times more than the UV-blocked males (Fig. 5B; *Chi*-square test, $\chi^2 = 0.28$, *d.f.* = 1, $p = 0.59$). The time needed for successful courtship was longer than the two events in which only one male was courting (Fig. 6; Kruskal-Wallis test, $\chi^2 = 19.38$, *d.f.* = 2, $p < 0.01$).

DISCUSSION

The role of visual signals among different species

Visual signals play different roles among species, including in species recognition (Takeda 2006; Secondi and Théry 2014), in fighting ability (Stapley and Whiting 2006), and as an indicator of good gene quality

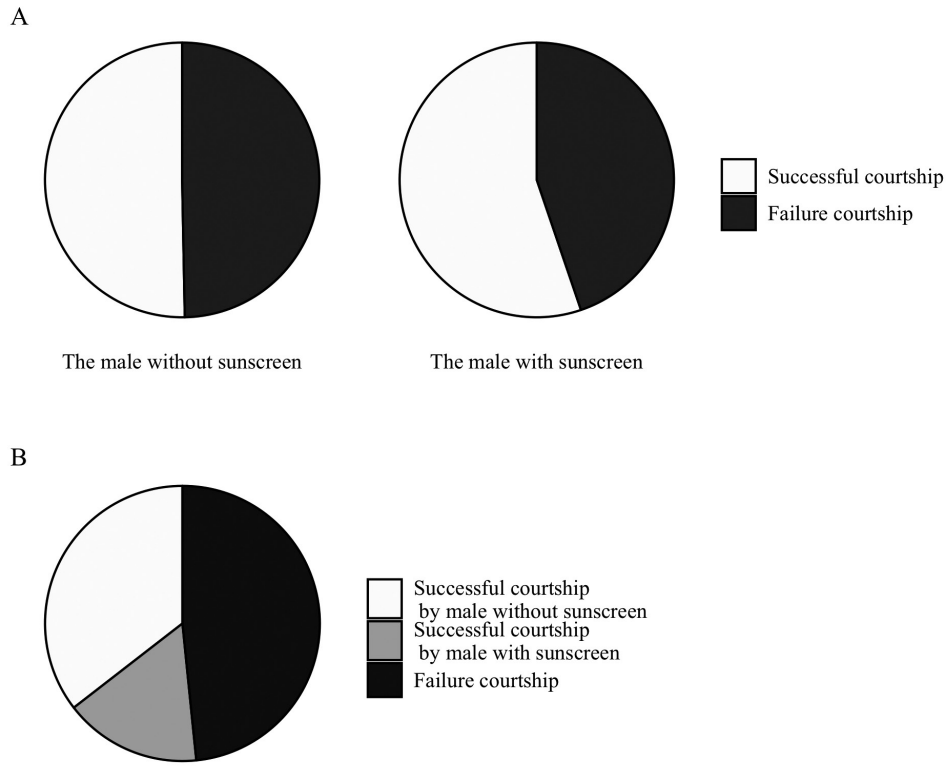

Fig. 5. Courtship results of the three events presented as pie chart with percentages. A, only one male courting; B, two males courting simultaneously. The filled color represents the results of the courtships.

Table 2. Factors affecting the courtship success of fiddler crabs

Coefficient	Estimation	Std. err.	Wald-statistic	*p*-value
Intercept	-0.339	1.876	-0.180	0.857
Sunscreen	-0.968	0.448	-2.163	0.031*
Carapace width	0.028	0.063	0.443	0.658
Distance	-0.050	0.032	-1.578	0.115
Claw-waving frequency	0.223	1.178	0.189	0.850

*indicates *p* value < 0.05 based on logistic regression analysis.

(Szigeti et al. 2007; Henderson et al. 2013) and body condition (Torres and Velando 2003; Velando et al. 2006; Kemp and Rutowski 2007; the present study). Two newt species—*Lissotriton vulgaris* and *Lissotriton helveticus*—can recognize each other by their body UV signals during courtship (Secondi and Théry 2014). Visual signals on the *Platysaurus broadleyi* throat is an indication of its fighting ability. One male lizard with a low UV brightness on its throat will cause other male lizards to launch a fierce attack (Stapley and Whiting 2006). Females of the lizards *Lacerta agilis* and *Cnemidophorus ocellifer* also prefer males with higher UV brightness on their throats (Olsson et al. 2011; Lisboa et al. 2017). Visual signals can also be an indicator of good gene quality. Females of two tit species—*Parus caeruleus* and *Cyanistes caeruleus*—have a UV component to the signals on their crowns, and their egg size (fitness of offspring) is positively related to the UV brightness of the crown (Szigeti et al. 2007; Henderson et al. 2013). Lastly, visual signals can be an indicator of body condition. Foot color of the male blue-footed booby *Sula nebouxii* varies with body condition, and females prefer males with bright green feet during courtship (Torres and Velando 2003; Velando et al. 2006). The butterfly *Colias eurytheme* has a UV component to the signals on its wings, and the brightness of that UV indicates its body condition (Kemp and Rutowski 2007). In many cases, the color recognition ability makes animals identify conspecifics, choose mates, and avoid fight through the color pattern variation. And the UV brightness is related to the mating success. Both of them are important visual signals.

In the study of fiddler crabs, Crane (1975) found there are conspicuous coloration. The coloration is important for interspecific and intraspecific recognition and mate attraction (Detto et al. 2006; Detto 2007; Takeda 2006; Dyson et al 2020). Detto and his colleges (2006) found *Tubuca capricornis* could recognize neighbors by the carapace color pattern and female *Austruca mjoebergi* was attracted not only by male *A. mjoebergi* painted with yellow color, its original claw color, but also by the other species, *Tubuca signata*, painted with yellow paint. In the white-based color fiddler crab, *Austruca perplexa*, Takeda (2006) found females prefer males with white body color. On the other hand, the UV signal is important in mate selection, females have preference for males with UV reflectance on its large claw. It was also reported on *A. mjoebergi* (Detto and Backwell 2009) and *Leptuca leptodactyla* (Silva et al. 2021). As for *A. lactea*, Takeshita (2019) found the coloration of carapace and claw may have different function. He found the carapace color would change when under the stressful condition or when the season changed but the claw is always lighter than the carapace. Thus, it is suggested that the function of carapace color is related to thermoregulation and/or camouflage, while the claw color is for courtship. In the present study, we also found females of *A. lactea* prefer males with UV signal during courtship (Fig. 5). In addition, the UV signal on the male's major claw is influenced by food availability (Fig. 4). A male *A. lactea* with a good nutritional status will have a high UV brightness. On the other hand, when there is only one male, regardless of whether or not it has a UV signal, that male can still successfully attract females. Hence, the UV signal on the *A. lactea* major claw is not used for species recognition, but as an important indicator of male body condition.

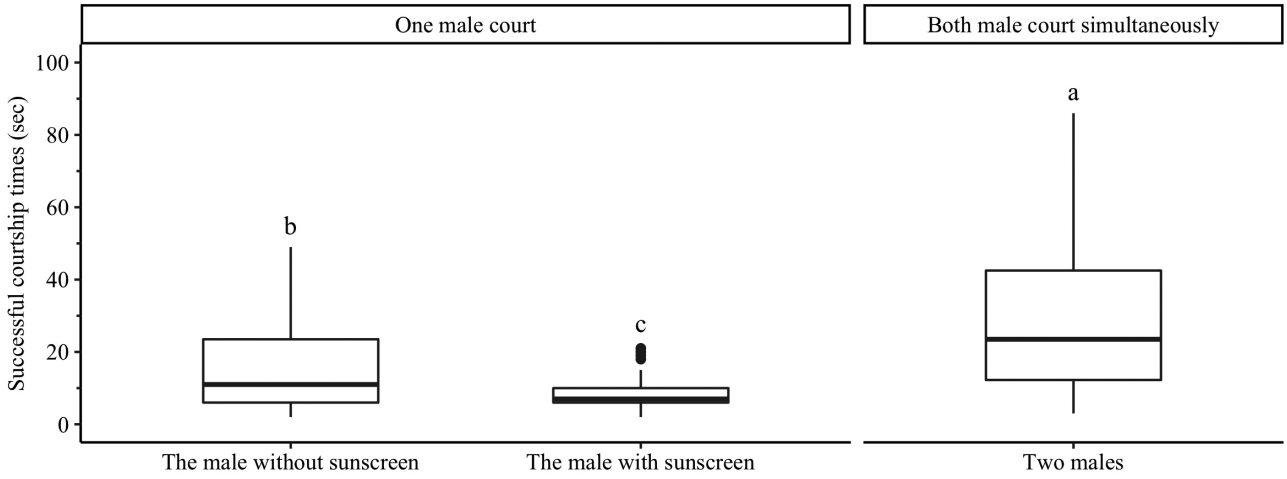

Fig. 6. The time needed for successful courtship among the three courtship events. The time usage was significantly different among events (Kruskal-Wallis test, $\chi^2 = 19.38$, $d.f. = 2$, $p < 0.001$, $n = 133$). The text in the plot shows the Dunn post hoc test results.

High-quality food may increase male burrow quality

With regard to mating success, the male fiddler crab needs to perform a series of costly behaviors, such as waving claw, constructing its hood, and enlarging its burrow. The female fiddler crab will choose the male with the highest quality performance. Backwell and Passmore (1996) found that female *Austruca annulipes* choose males based on burrow quality. A higher quality burrow includes larger burrow volume, higher maximum burrow width, and higher burrow minimum width. Similarly, Goshima and Murai (1988) reported that the burrow volume of *A. lactea* is larger for underground mating. After mating underground, male *A. lactea* leaves his burrow and the female stays until she leaves to release her larvae. Fiddler crabs exhibit food storage behavior (Kim 2010). This was also found in *A. lactea* in our pre-test. It is likely that larger burrows store more food for consumption during the female incubation period. In this study, we found that the burrow volumes of males in the food-added treatment were two-fold larger than those from the food-limited treatment. This implies that, with more energy, males can perform costly behaviors and gain more opportunities for mating success.

Austruca lactea males may wander to the edge of the stream for food

Austruca lactea males with a good nutritional status have a high UV brightness on their major claw (Fig. 4). This begs the question of how *A. lactea* males obtain high quality resources in their environment. During our field experiment, we found that males moved to the edge of water line to forage. Our results also indicate that organic content decreases with distance to the upper tidal zone, and the highest organic content was found at the low tide level. Hence, we propose that *A. lactea* males' wandering to the edge of the stream may be related to a high quality diet. Some previous studies also support this statement. Takeda (2003) mentioned that *A. perplexa* males abandon their burrows at the high tide and wander to the low tide level to forage. Murai et al. (1982) examined the wandering behavior of *A. lactea* males and found a correlation between body size and the likelihood of wandering along the edge of the waterline during low tide. They also indicated that the water's edge has more organic particles than the mudflat around *A. lactea* burrows (Murai et al. 1982). In addition, chlorophyll-a gradually decreased with distance to the low tidal zone (Allen and Levinton 2014). Thus, male *A. lactea* maybe obtain high quality resources by wandering to the water's edge during low tide.

CONCLUSIONS

In summary, our study shows that food availability affects courtship investment in *A. lactea* in terms of both the male's behavior and its physical status. The visual signal of the male fiddler crab's major claw acts as an important indicator of body condition. Males with higher UV reflection on their major claw wave more and have higher burrow quality; they are thus more attractive to females and have high reproductive success. However, the effect of a loss in UV signal remains unknown. Further studies should focus on reproductive success in this species without the UV signal.

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Supplementary Materials

Fig. S1. The reflectance on the major claw of male *A. lactea* with sunscreen treatment. This plot showed the wavelength from 300 to 550 nm. (download)