ORIGINAL ARTICLE

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The effect of food availability on the semilunar courtship rhythm in the fiddler crab *Uca lactea* (de Haan) (Brachyura: Ocypodidae)

Abstract Semilunar or lunar reproductive rhythms that follow tidal cycles are common in marine animals. For brachyuran crabs, an adaptive explanation for the synchronous release of larvae in phase with the tidal cycle is that females release larvae when their offspring are best able to escape predators. As a corollary to this hypothesis, the synchronous male reproductive cycle is selected to be in phase with female receptivity. As an alternative hypothesis, we propose that variation in food abundance influences the onset and intensity of the semilunar courtship cycle. We tested this hypothesis in male fiddler crabs (*Uca lactea*) by experimentally manipulating food availability for 4 weeks. Food-supplemented males built more semidomes and waved for more days than did food-deprived males or untreated control males. Moreover, food-supplemented males began courtship earlier and the median courtship day advanced with an increase in food. Courtship intensity was not related to crab size. These results provide the first evidence in marine animals that changes in food abundance due to the tides, and hence in phase with the semilunar cycle, influence male reproductive rhythm.

Keywords Fiddler crab · Courtship · Food availability · Reproductive cycle · Semilunar tidal rhythm

Introduction

The reproductive synchrony of marine animals in phase with the lunar or semilunar cycles has invoked much interest among field researchers (Palmer 1974, 1995; Neumann 1981; Thresher 1984; Ali 1992). Although several theories have been suggested to explain this

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phenomenon (Amano 1988; Robertson et al. 1990; Omori 1995; Tyler and Stanton 1995), there is as yet no single theory that synthesizes all these hypotheses. In brachyuran crabs, however, predation was proposed as the most important cause of selection on reproductive timing (Christy 1978, 1982, 1986; Morgan and Christy 1994, 1995; Christy and Morgan 1998; Kellmeyer and Salmon 2001). The theory states that females have evolved their endogenous reproductive cycle to release larvae usually in spring tides when both they and their larvae are least vulnerable to predators. In accordance with this scenario, male courtship synchronization was understood as a corresponding adaptation to female receptivity to increase reproductive success (Christy 1978; Salmon and Hyatt 1983; Moritto and Wada 1997; Christy et al. 2001). Despite accumulating information on the female reproductive cycle, however, there is a lack of studies on the cause of reproductive synchrony of males. It is not certain that female receptivity is the crucial factor that governs male reproductive activity.

In the context of sexual selection, the expression of a male sexual signal was suggested to evolve to be condition-dependent (Zahavi 1977; Nur and Hasson 1984; Johnstone 1995). Given that sexual signals are condition-dependent, environmental changes are predicted to influence the timing of sexual signaling. For example, under conditions that food availability changes, the male endogenous reproductive rhythm might have adapted to show flexibility in signal expression. Although many empirical studies showed that sexual-signal intensity is dependent on food quality or quantity (Griffith et al. 1999; David et al. 2000; Kotiaho 2000; Kotiaho et al. 2001; but see Candolin 1999), there are few studies that address whether food availability influences male reproductive timing (e.g., Abrahams 1993). Despite increasing concern in the mechanisms of expressing condition-dependent signals under stressful conditions, there are few empirical studies on the behavioral adaptation (Buchanan 2000).

The semi-terrestrial fiddler crab, *Uca lactea* (family Ocypodidae) (Rosenberg 2001), lives on the upper intertidal mudflat and, like all fiddler crabs, is famous

for the exaggerated claw on one side in males (Yamaguchi 1971; Crane 1975). In the mating season, males build low semidomes as courtship ornaments out of mud at their burrows, and then wave their large claws to females in order to mate in their burrows (Yamaguchi 1971, 2001a, 2001b; Murai et al. 1987). Male courtship and females' burrow sampling occur synchronously following the semilunar tidal cycle (Yamaguchi 1971).

In many fiddler crabs that show reproductive synchrony, male courtship usually peaks around spring tides. In a previous study, however, we found that their courtship rhythm was different from that of the same species in Japan (Kim 2002, Kim et al. 2003). The courtship peaks did not occur at spring tides but nearer to neap tides. We noted that there is a difference in habitat characteristics linked to tidal height. Everyday, tides flood over the habitat in Japan, but in our study site, the tide does not flood the habitat during neap tides. Crabs cannot feed on dried mudflat because they need water for feeding (Miller 1961). We supposed that the discrepancy in courtship rhythm between two places would be due to the different food-supply condition. Males living in Kanghwa Island might delay courtship timing in order to feed in the advancing waters of the spring tide to compensate for the food deficiency that arises during neap tides.

Thus, we hypothesized that food availability influences the intensity and timing of male reproductive behavior. Although previous studies in other fiddler crabs showed that male-courtship intensity is dependent on food availability (Backwell et al. 1995; Jennions and Backwell 1998), the effect of variation in food abundance on the timing of male courtship has never been studied. The objective of this study was to investigate if the amount of food influenced both male-courtship intensity and timing, by manipulating food availability. In addition, we studied if male size, which is known to be influenced by food availability (Smith and Palmer 1994; Jennions and Backwell 1998), is also related to male-courtship activity.

Methods

Study site and species

The study was carried out on a 20×20 m area of intertidal mudflat in Choji-ri, Kanghwa Island, off the west coast of South Korea (37°35′N 126°32′E) from 20 May to 30 July 2001. The maximum tidal range at spring tides was approximately 9 m (from 0 to 9.0 m in tidal height) and the minimum at neap tides was approximately 3.5 m (from 2.8 to 6.3 m in tidal height). U. lactea lives on the upper intertidal mudflat from 7 to 8.5 m high in the tidal range covering 400–500 m². This area is not inundated by flood tides for 6–8 days during each semilunar cycle (Fig. 1). Crabs emerge from their burrows and are active on the surface for about 6 h each day during the diurnal low tide. They were not active on the surface before sunrise, after sunset or in heavy rain.

Food manipulation

In May 2001, three 1×1 m² cages were constructed on the same line of tidal height (about 8 m) in the middle of their habitat. Each cage
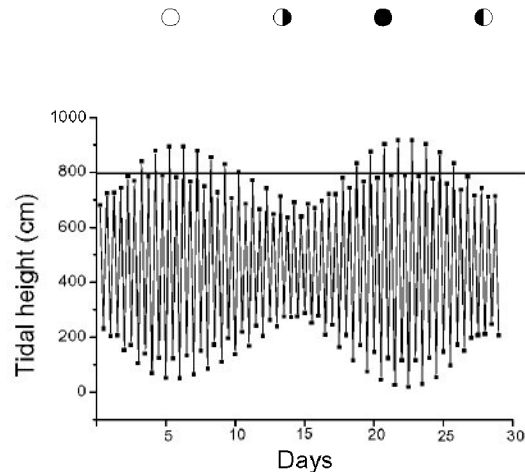
Fig. 1 Tidal amplitude of the study site in June 2001. The *straight line* indicates the tidal height of the experimental plots; symbols represent full moon, last quarter, new moon and first quarter, respectively

was made from four 30×100 cm stainless-steel mesh walls with less than 0.5 mm mesh size. The cages were inserted 15 cm into the sediment. PVC pipes (diameter=3 cm) were slit and threaded on the top of the edges and connected by PVC elbows at the corner to prevent crabs from escaping. We removed all crabs inside the enclosures.

When males were not yet ready to begin courtship display, we captured them by reaching with a 1.2-m-long bamboo stick (diameter=1 cm) to block their burrow entrances before they could escape below the surface or by digging burrows with a shovel. Each male's carapace width, carapace length, and major claw length were measured to the nearest 0.1 mm with vernier calipers. We marked them individually on the dorsal carapace by using both color paint markers and numbering stickers. No male was observed to molt during the experiment.

Twenty artificial burrows were made at the same distance apart from each other using a 1-cm-diameter bamboo stick, and 20 males were introduced into the burrows of each plot a week before food manipulation; 20 males/m² was the optimal density of this population (Murai et al. 1987). There was no significant difference in male size between plots (Kruskal Wallis test, carapace width $H=0.67, P=0.7$; carapace length $H=1.81, P=0.40$; major claw length $H=1.52, P=0.46$). Ten females were also introduced to each plot to stimulate male-courtship behavior.

We left the crabs for 1 week to stabilize the experimental groups. They showed no difference in activity among the plots. No males built semidomes and waved to females for a week. Thus we assumed that all enclosures were alike in their environment.

On 1 June, we began the experimental treatments. The treatments were done everyday from 1 to 30 June after the tide receded during daylight hours and before crabs emerge from their burrows. For the food-supplemented treatment, we added food to one plot. Food consisted of 5 g anchovy flakes mixed with 0.5 l seawater. Prior to the food manipulation, it was confirmed that crabs ate anchovy flakes diluted with seawater in laboratory experiments. In the food-deprived plot, the upper film (1–3 mm) of the sediment was scraped using a 10×30 cm plastic panel. This removed much of the food source such as diatoms and other microparticles supplied by the tide (Jennions and Backwell 1998). In addition, we added 0.5 l seawater as a control for that added to the food-supplemented plot. In the untreated control plot, we added only 0.5 l seawater. On days when the tide did not cover the plots (11–14 and 27–28 June), the sediment became too dry for crabs to build semidomes. On those days, we poured 10 l seawater into each plot to extend the days possible for semidome building. For all

treatments, semidomes built on the previous day were artificially destroyed.

Observation

We observed the plots from 3 h before to 3 h after low tide for 30 consecutive days during 1–30 June . From 7 June, when males began to build semidomes (a courtship signal), we gathered behavioral data. On those days when low tide was at sunset (15–18 June) or it rained heavily (24, 29–30 June), courtship behavior was nil and the days were excluded from the analyses. Because crabs did not court on 1 July, we terminated the observation. Our manipulation included two semilunar cycles. From a chair 1.5 m away, we recorded the behaviors of the crabs in one plot at a time for 15 min per plot per hour. In order to measure the frequency of courtship activity in males in the different treatments over the course of the lunar cycle, we recorded the following: each active male's identity, whether each male was waving or had built a semidome, and the total number of semidomes. Males that were observed more than once on different days during the manipulation test are called "resighted males".

The initiation day and median day for the two courtship activities (semidome building and waving) were measured relative to the day of the nearest spring tide. The median day is a measure of the midpoint of activity, and it was only measured for those males that showed waving or semidome building at least twice during a semilunar cycle.

As measures of courtship intensity, the durations of "semidome-building bout" and "waving bout" were calculated as the numbers of days between the start and finish of these activities, permitting a maximum 1-day gap without these activities. The "semidome building cycle" and "waving cycle" were measured as the number of days between the consecutive starts of these activities in two semilunar cycles.

To test whether courtship intensity depends on male size, we used both carapace width and relative claw size as size parameters. Relative claw size was calculated as a standardized residual from a least squares regression of major claw length on carapace width (Smith and Palmer 1994).

Statistical analyses

For the food manipulation experiment, we collected independent data daily for 17 days. To test if food manipulation influences the activity of males, we used repeated measures ANOVA. We used a Kruskal-Wallis test to examine the influence of food treatment on each male's semidome building and waving days by comparing the initiation day and median day. All analyses were carried out using STATVIEW 5.01 for Windows (SAS Institute). All tests were two-tailed; the significance level was set at 0.05, and summary statistics are presented as means±SD. We used many statistical tests in tables. Therefore, we used sequential Bonferroni correction to adjust the probability levels to correspond to the number of tests performed (Rice 1989).

Results

Food availability and courtship intensity

Males in all food treatments showed semilunar cycles in semidome building and waving. The frequencies of semidome builders and wavers were dampened with a reduction in food (Fig. 2). Out of 30 days, males did not show courtship activity on the first 6, and they were not active on the 7 days that it rained heavily or when tides occurred at sunset. The percentage of semidome builders and wavers differed significantly among treatments (Table 1), even though treatments did not differ in the proportion of males resighted. In the food-deprived plot, 63–68% of the males were semidome builders or wavers, whereas 90–95% of the males in the food-supplemented and control plots courted at least once. The number of males active each day differed significantly among the three plots. Both the number of semidomes built on each day and the number of wavers per day increased as the available food increased (Table 2).

Each male's courtship intensity also increased as the food level increased (summarized in Table 3). The number of days that each resighted male constructed a semidome increased significantly with food availability, even though the number of days that resighted males were active on the surface did not differ between treatments. Furthermore, resighted males waved on more days as food increased, even though the number of days that they were active was not different between treatments. For semidome builders or wavers, the number of days that they built semidomes or waved increased with food availability.

Food availability and courtship timing

In the first semilunar cycle, there was no significant difference in any measure of semidome construction or waving, including initiation and median days (summarized in Table 4). In contrast, during the second semilunar

Table 1 Percentage of male activity and sexual signaling in enclosed plots with different food treatments for 30 days. *Males resighted* refers to all males seen on the sediment

	Food treatment			Statistics	P
	Supplemented	Untreated	Deprived		
Total number of semidomes built	85	54	22	$\chi^2=43.91$	<0.0001*
Percentage of males resighted	100% $n=20$	100% $n=20$	95% $n=19$	$\chi^2=2.03$	0.36
Percent semidome builders (of males resighted)	95% $n=19$	95% $n=19$	63% $n=12$	$\chi^2=10.10$	<0.01*
Percent waving males (of males resighted)	95% $n=19$	90% $n=18$	68% $n=13$	$\chi^2=5.97$	0.02*

* $P<0.05$ sequential Bonferroni correction, $n=4$ tests.
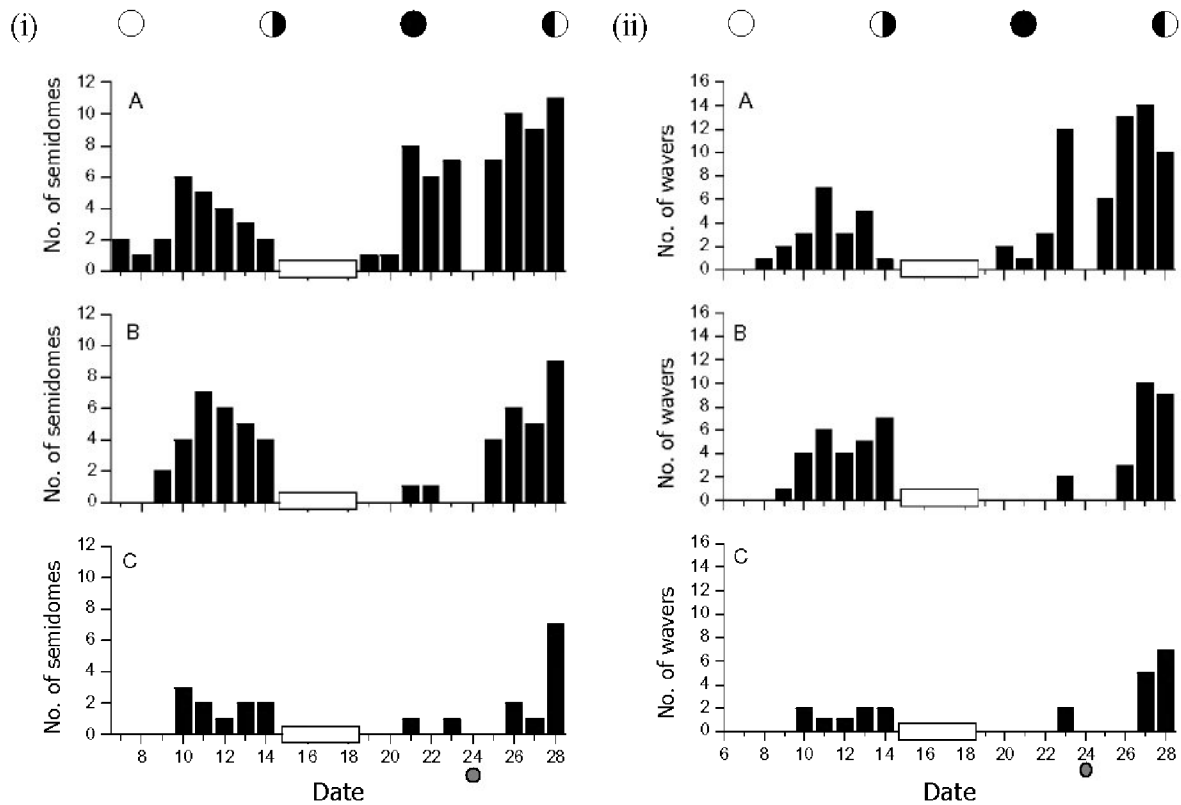
Fig. 2A–C Distribution of the number of (i) semidomes and (ii) waving males under **A** food-supplemented, **B** untreated, **C** food-deprived condition during the manipulation test. The *boxes* on the *x-axis* represent days when low tide was at sunset (15–18 June). On 24 June (*dashed circle*), crabs were not observed on the mudflat because it rained heavily

Table 2 Repeated measures ANOVA of daily activity and sexual signaling (with comparison based on data from the observation of 17 days)

	Food treatment			Statistics	P
	Supplemented	Untreated	Deprived		
No. of active males/day	13.2 (±3.2)^a	13.4 (±3.7)^a	10.5 (±4.0)^b	$F_{2,16}$=3.34	0.04*
No. of semidomes/day	5.1 (±3.3)^c	3.2 (±2.9)^{c,d}	1.3 (±1.8)^d	$F_{2,16}$=18.49	<0.0001*
No. of wavers/day	4.9 (±4.7)^e	3.0 (±3.4)^{e,f}	1.3 (±2.0)^f	$F_{2,16}$=7.38	<0.001*

* $P<0.05$ sequential Bonferroni correction, =3 tests. Values with same *letter* are not significantly different from each other at 0.05 levels (Fisher's PLSD test).

Table 3 Kruskal-Wallis tests of each male activity and sexual signaling in enclosed plots with different food treatments

	Food treatment			Statistics	P
	Supplemented	Untreated	Deprived		
Days seen/male (for males resighted)	11.3 (±3.1)	11.4 (±3.8)	9.3 (±3.2)	H=4.12	0.12
Semidome building days/male (for males resighted)	4.3 (±3.1)	2.7 (±1.9)	1.2 (±1.3)	H=17.31	<0.001*
Waving days/male (for males resighted)	4.2 (±2.5)	2.6 (±2.1)	1.5 (±1.5)	H=12.37	<0.005*
Days seen/semidome builder	11.6 (±3.0)	10.1 (±2.4)	11.5 (±2.6)	H=2.38	0.3
Semidome building days /semidome builder	4.5 (±3.0)	2.8 (±1.9)	1.8 (±1.3)	H=10.60	<0.005*
Days seen/waver	11.6 (±3.0)	11.4 (±2.6)	10.8 (±2.2)	H=0.56	0.755
Waving days/waver	4.4 (±2.4)	2.8 (±2.1)	2.2 (±1.3)	H=8.14	0.01*

* $P<0.05$ sequential Bonferroni correction, n=7 tests.

Table 4 Male courtship in two semilunar cycles during the food manipulation test [initiation day and median day were counted from the day at spring tide (1st cycle: 6 June, 2nd cycle: 23 June, respectively)]

		Food treatment			Test statistic	P
		Supplemented	Untreated	Deprived		
First semilunar cycle	Semidome building					
	Initiation day	3.9 (±1.7) n=10	5.1 (±1.4) n=12	4.9 (±1.2) n=7	H=2.15	0.341
	Median day	4.8 (±1.6) n=7	5.4 (±0.8) n=8	6.3 (±0.4) n=2	H=2.69	0.260
	Waving					
	Initiation day	4.8 (±1.5) n=10	5.5 (±1.8) n=11	5.0 (±1.7) n=6	H=0.75	0.686
	Median day	4.8 (±1.4) n=6	5.7 (±1.2) n=9	5.7 (±0.8) n=3	H=1.14	0.565
Second semilunar cycle	Semidome building					
	Initiation day	0.4 (±2.7) n=17	3.1 (±1.8) n=16	3.1 (±2.7) n=8	H=9.82	0.007*
	Median day	1.7 (±2.2) n=16	3.6 (±1.1) n=8	3.8 (±1.9) n=3	H=6.64	0.03
	Waving					
	Initiation day	0.4 (±2.0) n=17	3.4 (±0.7) n=18	3.0 (±1.5) n=12	H=16.01	<0.0005*
	Median day	2.6 (±1.7) n=15	4.1 (±0.9) n=12	H=12.05 n=6	0.004*	
Semidome building cycle		12.5(±3.1) n=8	15.2(±2.3) n=10	[a]	t=−2.12	0.05
Waving cycle		12.5 (±1.6) n=8	14.9 (±1.9) n=10	14.7 (±2.3) n=3	H=5.97	0.05

* P<0.05 sequential Bonferroni correction, n=8 tests.
[a] No males built semidomes in all two cycles.

Fig. 3A–D The number of semidomes in relation to **A** carapace width and **B** relative claw size, and waving days in relation to **C** carapace width and **D** relative claw size (✚ food-supplemented, ◯ untreated, ▽ food-deprived)
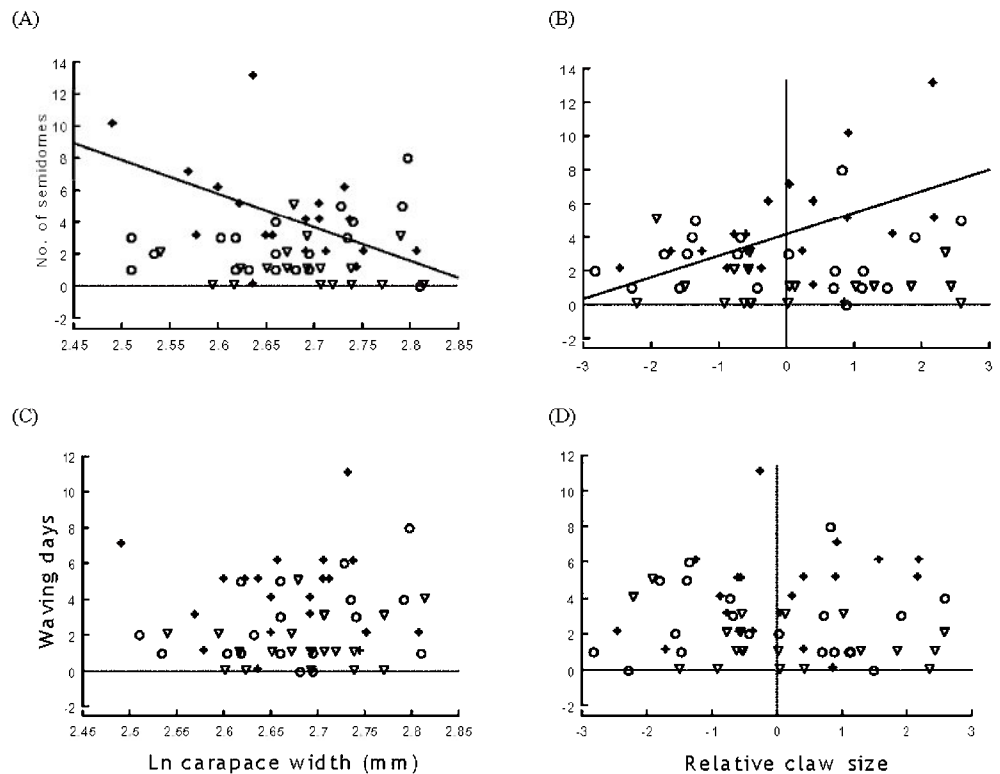
cycle, the initiation of semidome building and waving by food-supplemented males was advanced on average 2.7 and 3.8 days, respectively, relative to the untreated or food-deprived groups. Food-supplemented males showed a rapid increase in waving and they differed significantly from the control and food-deprived groups in the median days. They also had more semidome-building bouts than did untreated or food-deprived males. Food supplementation appeared to decrease the length of the semidome-building cycle and waving periods relative to no treatment by an average of 2.7 and 2.4 days, respectively.

Body size and courtship intensity

In the food-supplemented plot, the number of semidomes constructed by each male was negatively correlated with its carapace width (Fig. 3A; no. of semidomes= 60.16−20.931×Ln carapace width; $r=-0.507$, $N=20$, $P=0.022$) and positively correlated with relative claw size (Fig. 3B; no. of semidomes=4.185+1.28×Relative claw size; $r=0.503$, $N=20$, $P=0.02$). In the other plots, however, there were no significant correlations between male carapace size and the number of semidomes built (Fig. 3A; untreated: $r=0.369$, $N=20$, $P=0.110$; deprived: $r=0.084$, $N=19$, $P=0.734$), or between relative claw size and the number of semidomes built (Fig. 3B; untreated: $r=0.105$, $N=20$, $P=0.659$; deprived: $r=0.097$, $N=19$, $P=0.691$). Combining males in all plots, neither carapace size nor relative claw size were predictors of semidome construction ($N=59$, $r=0.159$, $P=0.229$, and $r=0.179$, $P=0.174$, respectively).

Male carapace size did not determine the number of waving days for all males (Fig. 3C; $r=0.094$, $N=59$, $P=0.477$) or in each treatment (supplemented: $r=0.035$, $N=20$, $P=0.885$; untreated: $r=0.367$, $N=20$, $P=0.112$; deprived: $r=0.134$, $N=19$, $P=0.583$). Relative claw size and the number of waving days were not significantly correlated either in total (Fig. 3D; $r=0.014$, $N=59$, $P=0.917$) or in each plot (supplemented: $r=0.277$, $N=20$, $P=0.237$; untreated: $r=0.004$, $N=20$, $P=0.986$; deprived: $r=0.347$, $N=19$, $P=0.146$).

Discussion

With an experimental change in the availability of food, we have found that the onset and intensity of male courtship in *U. lactea* also changes. Without replicating the experiment, we cannot exclude the possibility that differences in male-courtship activities observed between cages were not due to some unforeseen difference in the cages themselves. However, we have every reason to believe that the environment within the cages was identical due to the homogeneity of the mudflat upon which they were built.

The intensities of both semidome building and claw waving as courtship signals were different between food treatments, which supports the view that these behaviors depend on the male's physiological state which is influenced by food availability. Although a previous study on pillar building in *U. beebei* suggested that pillar building is condition-dependent, not all males built the courtship structure (Backwell et al. 1995). Except for food-deprived males, 95% of the males built ornaments at least once in our experiment. This clearly indicates that most males have the ability to build semidomes.

Food availability influenced the onset of courtship timing in *U. lactea*. During the second semilunar cycle, food-supplemented males started to build semidomes and wave approximately 3 days earlier than males in other treatments. Median courtship days also occurred earlier in food-supplemented males. It seemed to take approximately 2 weeks for food manipulation to have a salient effect on the physiological state of males. The lack of a significant difference between the untreated and food-deprived plot in the initiation and median of courtship activities was due in part to a reduction in the number of reproductively active males in the food-deprived plot. In the food-deprived environment, about half the males did not delay but suspended their courtship altogether (compare the sample sizes of the treatments in Table 2).

In a related study, food availability varied naturally. During July 2001, the monsoon season began in Korea. During rainfalls, crabs were inactive on the surface and feeding activity was reduced. Courtship activity in the middle of July started 5 days after the spring tide, and thus was delayed 2–3 days from a typical month (T.W. Kim, unpublished data). The reduction in days available for feeding might have delayed their courtship activity. This observation further supports our hypothesis that courtship activities are flexible and respond to variation in food availability.

This courtship rhythm flexibility could be regarded as an adaptation of *U. lactea* to the environmental variability in food supply. In estuaries, food is most abundant in the lowest intertidal zones (Teal 1958; Robertson et al. 1980). There, some fiddler crabs living on upper intertidal mud or sand flats form droves (or herds), moving to feed in the lower zone in order to compensate for food deficiency (e.g., *U. tangeri*, *U. pugilator*, Crane 1975; *U. vocans*, Murai et al. 1983). Although *U. lactea* lives in the upper intertidal mudflat, they do not form droves but usually feed solitarily close to their own burrows (Crane 1975). They rarely leave their burrows unless they are aggressively displaced or when females search for mates.

In *U. lactea*, males appeared to have adapted to food variation by delaying their reproductive timing rather than moving to the lower intertidal flat. They might control their reproductive timing flexibly to compensate for food deficiency during the neap tidal periods. This is clearly supported by the fact that the male courtship rhythm is different between the same species in dissimilar environments. In a population of *U. lactea* in Japan, the male courtship cycle peaked 2–3 days before spring tides (Yamaguchi 1971, 2001a). The habitat in Japan is flooded even in neap tides and does not suffer from sediment dryness (M. Murai, personal communication). If crabs

living in the upper intertidal zone generally have evolved to drove to feed in the lower zone, *U. lactea* might have lived in the environment where food was not scanty even without migration.

Food availability might also influence female reproductive receptivity (e.g., Tyler and Stanton 1995; Byrne et al. 1998) such that the males are responding directly to the reproductive rhythm of the females. In these studies, it is very difficult to determine which factor, food availability or female receptivity, is the causative agent because females should be included in the experimental plots. In our experiment, however, females apparently showed no receptive difference among treatments. We did not observe them sampling males' burrows as a normal mating sequence. We only found surface mating in the plots during experiments. When they mated on the surface, males neither built semidomes nor waved to females (*N*=16 out of 17 cases, unpublished data). Surface-mating females have also been reported to be sexually non-receptive (Murai et al. 1987).

We here suggest that food availability is an important factor influencing male reproductive rhythm in marine animals. Male reproductive rhythm in synchrony with the female lunar or semilunar reproductive cycle has been suggested as an adaptation to female reproductive activity (Christy 1978; Omori 1995; Rahman et al. 2000). In intertidal crabs, previous studies supported this theory by showing that male courtship synchronously corresponds to female receptivity (e.g., Greenspan 1982; Salmon and Hyatt 1983; Salmon 1987; Christy et al. 2001). However, reproductive synchrony is not sufficient to show that female receptivity controls male reproductive activity. Male courtship could also trigger female responses. Interestingly, the timing of female larval release of *U. lactea* follows not the semilunar but the lunar tidal cycle, which does not match with males' semilunar courtship rhythm (Yamaguchi 2001a). If male courtship rhythm is controlled by female receptivity, male and female reproductive cycles should be synchronized. Male-courtship synchrony might be a consequence of complex interactions among female receptivity (Christy 1978), male-male competition (Backwell et al. 1998), and food availability, as shown in our study.

Although male claw size was suggested to be influenced by food availability in some crabs (Smith and Palmer 1994), neither relative claw size nor carapace size appeared to affect the duration or intensity of sexual signaling in *U. lactea*. Except in the case of correlation between relative claw size and semidome building days in the food-supplemented plot, the numbers of semidomes and waving days were not correlated with either male carapace width or relative claw size. This implies that short-term food availability could directly influence male-courtship intensity rather than long-term food availability affecting the difference in claw size. In a separate study, the outcome of fighting in *U. lactea* usually depends on male size (T.W. Kim, unpublished data). Although the larger males tend to take control of territories and prevent neighbors from courting on the ground, their suppression probably had little effect on the small males' investment in feeding and courting.

In conclusion, to our knowledge, we have provided the first evidence among marine animals that food availability influences not only male reproductive intensity but also the onset of courtship. Male reproductive rhythm might have evolved to increase reproductive success. Entrainment of reproductive rhythm is necessary for efficient mating. However, if males do not know the female reproductive cycle or male courtship could initiate female endogenous receptivity, extending the duration of advertising sexual characters could also be an important strategy for increasing mating chances (Backwell et al. 1995). In this regard, this experiment shows that male reproductive rhythm can be influenced by food variation rather than female receptivity. It is striking that the male reproductive signal has not evolved to be fixed to show synchrony controlled by female receptive cycle but to be flexible depending on food availability. More studies are needed to learn if a proximate endogenous timing mechanism is involved in this adaptation (Neumann 1981). We suggest that reproductive synchrony should be viewed in the context of ecological factors including food variation, as well as the female reproductive cycle.

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