

Chimney Building by Male *Uca formosensis* Rathbun, 1921 (Crustacea: Decapoda: Ocypodidae) after Pairing: A New Hypothesis for Chimney Function

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Hsi-Te Shih, Hin-Kiu Mok, and Hsueh-Wen Chang (2005) Chimney building by male *Uca formosensis* Rathbun, 1921 (Crustacea: Decapoda: Ocypodidae) after pairing: a new hypothesis for chimney function. *Zoological Studies* 44(2): 242-251. The construction of a chimney after pairing is first described for *Uca formosensis* Rathbun, 1921, a fiddler crab endemic to Taiwan. After attracting a female into his burrow, the male builds a chimney averaging 9.2 cm high and 7.7 cm in diameter at the base within a 4- or 5-d period before the next neap tide. It is not related to sexual attraction because the chimney does not appear prior to or during courtship. To build the chimney, the male excavates the burrow which probably widens the shaft and, more importantly, deepens the burrow so that it reaches the water table, thus providing a moist chamber in which the female can incubate her eggs. The mudballs dug out from within the burrow are piled around the entrance and form the chimney, which herein is assumed to function as a way for the builder to hide from its enemies. The sex ratio of *U. formosensis* present on the surface was also recorded and is discussed. <http://www.sinica.edu.tw/zool/zoolstud/44.2/242.pdf>

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Some crabs (and other crustaceans) build structures (pillars, hoods, chimneys, etc.) next to their burrows (Powers and Bliss 1983). Some of these structures have been shown to function for sexual attraction, e.g., pillars (*Uca*: Christy 1988a b), hoods (*Uca*: Zucker 1974 1981, Christy et al. 2002 2003), mudballs (*Uca*: Oliveira et al. 1998), and pyramids (*Ocypode*: Linsenmair 1967, Hughes 1973); some are related to disturbance (fighting or burrow occupation) caused by neighbors, e.g., hoods (*Uca*: Zucker 1974 and *Cleistostoma*: Clayton 1988), chimneys (*Uca*: Salmon 1987, Wada and Murata 2000), and barricades (*Ilyoplax*: Wada 1984); and some are related to environmental regulation, e.g., hoods (*Uca*: Powers and Cole 1976), chimneys (*Uca*: Crane 1975: 524, Thurman

1984), and igloos (*Dotilla*: Takeda et al. 1996). Crane (1975) reviewed these structures in fiddler crabs of the world, and chimneys were found in some subgenera: *Deltuca* (*U. dussumieri*, *U. arcuata*, *U. forcipata*, *U. coarctata*, and *U. urvillei*), *Thalassuca* (*U. tetragonon*), *Amphiuca* (*U. chlorophthalmus*), *Boboruca* (*U. thayeri*), *Minuca* (*U. vocator*), and *Celuca* (*U. cumulanta* and *U. stenodactylus*). Other fiddler species were also reported to build chimneys, e.g., *U. elegans* of the subgenus *Australuca* (George and Jones 1982) and *U. subcylindrica* of the subgenus *Minuca* (Thurman 1984) (reviewed in Table 1).

Uca formosensis Rathbun, 1921 is a species of fiddler crab endemic to Taiwan. This species is poorly known except for its morphological charac-

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ters (see Shih et al. 1999). From preliminary observations, many large chimneys were periodically found in the habitat of *U. formosensis*. The chimneys of this species have not been described in detail before (Shih et al. 1999). In this paper, we describe results based on successive observations in Changhua, west-central Taiwan, and on data recorded on mudflats along the western coast of Taiwan. A chimney of *U. formosensis* is built by the male of a pair after he has attracted a female into his burrow for underground mating, and it therefore is not a courtship signal. The function of chimney building is proposed and discussed in this study. The chimneys built by *U. arcuata* (de Haan, 1835) are also recorded for comparison. In addition, we also recorded and discuss the sex ratio of *U. formosensis* present on the surface.

MATERIALS AND METHODS

Uca formosensis is distributed on the west coast of Taiwan, including the Penghu Archipelago (the Pescadores) (Shih et al. 1999). From 7 to 21 July 1996, successive observations on chimney building were conducted in Shengang, Changhua County. Two plots (2 x 2 m) were selected in which to monitor the crabs' behavior. From 08:00 to 18:00, numbers of males and females in each plot and 3 temperature readings were recorded each hour, except for the period when the habitat was covered by water at high tide. The 3 temperatures recorded were the ground temperature in sunshine (sun temperature), ground temperature under the shade of some object (shade temperature), and soil temperature at a depth of about 12 cm by inserting the probe of a Digital Thermo (Digital Taschen-Thermometer). The sex ratio, males/females, appearing on these plots was also calculated each hour. One hour's data in 21 July are not included as sex ratio was 16:0.

The process of chimney building and other

Table 1. A summary of chimneys built around burrow entrances by *Uca* fiddler crabs

Species	Subgenus defined by Crane (1975)	Materials	Builder	References
<i>U. formosensis</i>	? ^a	from within the burrow	mostly male and seldom female	this study
<i>U. arcuata</i>	<i>Deltuca</i>	mostly from the surface	both sexes	Crane 1975, Yeh 1996, Wada and Murata 2000
<i>U. coarctata</i>	<i>Deltuca</i>		both sexes	Crane 1975
<i>U. coarctata flammula</i>	<i>Deltuca</i>			Crane 1975
<i>U. dussumieri</i>	<i>Deltuca</i>		both sexes	Crane 1975
<i>U. paradussumieri</i>	<i>Deltuca</i>			Ng and Sivasothi 1999
<i>U. forcipata</i>	<i>Deltuca</i>	from within the burrow	female	Crane 1975
<i>U. urvillei</i>	<i>Deltuca</i>	from within the burrow	male (?) and female	Crane 1975
<i>U. elegans</i>	<i>Australuca</i>			George and Jones 1982
<i>U. tetragonon</i>	<i>Thalassuca</i>	from the surface	female	Crane 1975
<i>U. chlorophthalmus crassipes</i>	<i>Amphiuca</i>		female	Crane 1975
<i>U. chlorophthalmus</i>	<i>Amphiuca</i>		female	Crane 1975
<i>U. thayeri</i>	<i>Boboruca</i>	from the surface (?)	female	von Hagen 1970, Crane 1975, Salmon 1987, Kellmeyer and Salmon 2001, Weaver and Salmon 2002
<i>U. galapagensis</i>	<i>Minuca</i>		male	von Hagen 1968
<i>U. minax</i>	<i>Minuca</i>			Montague 1980
<i>U. pugnax</i>	<i>Minuca</i>			Montague 1980
<i>U. subcylindrica</i>	<i>Minuca</i>	from within the burrow (?)		Thurman 1984
<i>U. vocator</i>	<i>Minuca</i>		both sexes	Crane 1975
<i>U. cumulanta</i>	<i>Celuca</i>			Crane 1975
<i>U. stenodactylus</i>	<i>Celuca</i>		female (?)	Crane 1975

^aBased on Shih et al. (1999).

related behaviors were recorded on video tape. Reproductive behaviors (e.g., courtship, surface mating, underground mating, etc.) and other behaviors (e.g., fighting, feeding, etc.) were recorded by ad libitum sampling (Martin and Bateson 1993). If a certain behavior pattern was observed, it was recorded until it ceased. Some burrows with chimneys were dug out, and the sex and carapace width (CW) of the pair were measured, as well as the reproductive condition of the female. The depth of the burrow and its relative distance to the high tide mark were also recorded. Behaviors related to chimney building in Jhuwei (Taipei County), Jinshuei (Hsinchu City), Haishangu (Hsinchu City), Shengang (Changhua Co.), Dongshih (Chiayi Co.), Budai (Chiayi Co.), and Cigu (Tainan Co.) from Sept. 1994 to Apr. 1997 were also recorded to supplement the results.

Uca arcuata (de Haan) is another species in Taiwan that frequently builds chimneys. Its chimney building behavior was also recorded and is described for comparison.

RESULTS

Chimneys of *U. formosensis* appeared on the mudflats of the high intertidal zone during the period of the neap tide in the warm season (Mar. to Oct.) in Taiwan (Fig. 1A).

Chimney structure

After a male *U. formosensis* had attracted a female to stay inside his burrow for underground mating, the male began to build a tower-like cylindrical structure, a chimney (average height, 9.2 (range, 4~14) cm; average diameter at the base, 7.7 (range, 3~13 cm); $n = 26$) (Fig. 1C, D), around the burrow entrance. The chimney was composed of large wet soil pellets (i.e., mudballs). The material for the chimney was carried up from within the burrow (Fig. 1G), not from the surface substrate near the burrow as with the chimney building of *U. arcuata* (Fig. 1K). Therefore, the color of the chimney and the substrate generally differed. Sometimes, both the entrance of the chimney (and also the entrance of the burrow) would become plugged by mudballs (Fig. 1E, F; see below). In addition, because the builder did not trim the chimney like *U. arcuata* does (see "Discussion"), its surface was rugged, and generally there were several large gaps among the mudballs.

Twelve females were observed to excavate mudballs from within the burrow and five of these females were ovigerous. The female piled up the mudballs loosely beside, but not around, the burrow, and the resulting structure resembled a pyramid (Fig. 1H), not a cylinder like the male's chimney.

Chimney building

We determined the process and timing of chimney building from successive 15 d observations conducted in Shengang, Changhua, Taiwan.

1. During the period of a neap tide, the amount of time that the tide covered the habitat of *U. formosensis* (in the high intertidal zone) decreased each day. About 1 or 2 d before the tide did not cover its habitat, males began courting wandering females. When a female stayed inside his burrow, the male began to build a chimney. The male excavated mudballs from inside the burrow, carrying them using its ambulatories on the minor side (Fig. 1G), and piled them on one side of the burrow entrance. The crab did not place mudballs on the other side until the chimney was finished. Therefore, the structure appeared hood-shaped while it was being built (Fig. 1B, G). The original entrance was plugged by mudballs to 3~5 cm in depth (Fig. 1E), while the entrance of the chimney sometimes became plugged by 1 or 2 mudballs (Fig. 1F). Meanwhile, the female stayed inside the burrow, and it was assumed that she did not participate in the building process. A chimney could be finished in 1 d.

2. On the day the tide first failed to cover the habitat (e.g., during the day on 10 July, Fig. 2C), most chimneys had already been built. A few individuals of *U. formosensis* without chimneys came to the surface by the side of their burrow entrances but were generally inactive. On the following days, the ground temperature of the sand gradually increased, and no *U. formosensis* (or any other crab species) was observed on the surface during this period (10~13 July, Fig. 2A). The mudflats became cracked (Fig. 1I), and salt crystallized on the surface (Fig. 1J). The highest sun, shade, and soil temperatures measured were 45.9, 39.7, and 41.1°C, respectively, on 13 July. This drought period lasted for 4 or 5 d until the tide returned to its normal levels.

3. When the tide again covered the habitat (14 July), the chimneys were destroyed by the water due to their loose structure. Then, increasing numbers of individuals began emerging from



Fig. 1. Chimney building of *Uca formosensis*. (A) Numerous chimneys of *U. formosensis* protruding above the mudflat when the habitat was not covered by the tide, at which time it became extremely dry (Shengang, Changhua, Taiwan). (B) A hood-shaped chimney in the middle stage of chimney building. (C and D) Two types of chimneys. (E) The burrow entrance also becoming plugged (arrow) by mudballs to about 3–5 cm in depth after removing the chimney. (F) The entrance of a chimney having become plugged (arrow) by mudballs. (G) A male building a chimney. (H) A chimney built by an ovigerous female. Note that it is loose and without a distinct shape. (I and J) Mudflats having become cracked, and salt having crystallized on the surface. (K) For contrast, a chimney built by *U. arcuata* with many scraping traces on its surface (arrow). Scale = 5 cm.

their burrows (Fig. 2A), and they mainly fed and fought, but courtship was rare. The tides were high enough to periodically cover the habitat for 10 to 11 d, during which time, chimneys were rare. When the next neap tide occurred, the chimney building processes began again, synchronized with the semilunar cycle.

Relationships between the number of crabs on the surface and temperatures each hour are shown in Fig. 2A. The number of crabs was negatively correlated with sun temperature ($R = -0.37$, $p < 0.001$) and shade temperature ($R = -0.28$, $p = 0.005$), but not soil temperature ($R = 0$, $p = 0.99$; d.f. = 98) on an hourly basis. However, R values were higher if the average number of crabs and temperatures each day were used (sun temperature: $R = -0.54$, $p = 0.11$; shade temperature: $R = -0.70$, $p = 0.02$; soil temperature: $R = -0.58$, $p = 0.08$; d.f. = 9). The most-significant negative correlation with the number of females (thick line in the lower part of Fig. 2A) was with the sun temper-

ature ($R = -0.79$, $p = 0.006$, d.f. = 9), and for the number of males (thin line in the lower part of Fig. 2A) was with the shade temperature ($R = -0.64$, $p = 0.04$).

When the tide covered the habitat after the drought period, crabs emerged from their burrows. A greater number of males (with an average sex ratio of males: females of 4.68, and a range of 1.81~10.02, Fig. 2B) always appeared on the mudflats. During the time when the habitat was covered by the tide at least once a day (Fig. 2C), female numbers increased to a maximum (16 July), followed by the maximum of male numbers which occurred 3 d later (Fig. 2A). The sex ratio of crabs appearing on the mudflats also showed a tendency to fluctuate with the tide. The ratio increased to its highest value (of 10.02) 7 d after the tide began covering the habitat again (Fig. 2B). It is apparent that the increasing value of the sex ratio was caused by an increase in the numbers of males, although it decreased slightly after 20 July,

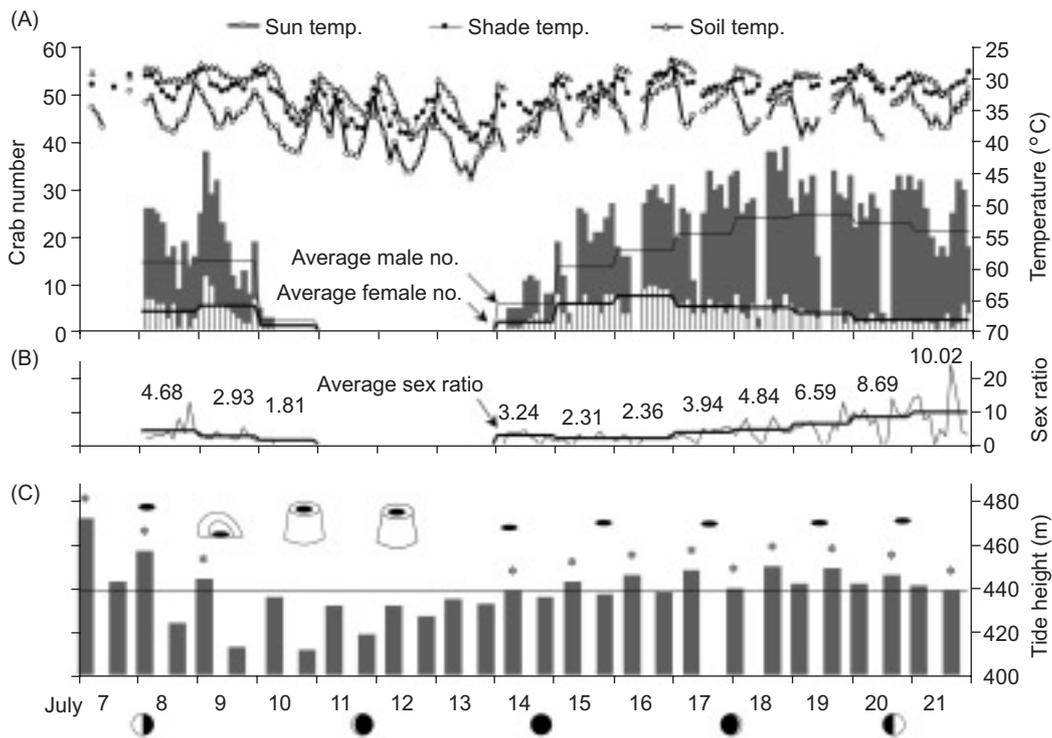


Fig. 2. Relationships among temperatures, the number of *Uca formosensis*, sex ratio, and tide height recorded in the study areas in Shengang, Changhua, Taiwan. (A) Sun, shade, and soil temperatures each hour shown in the upper part. The gray and white bars in the lower part represent the number of males and females appearing on the surface, respectively. The average number of males (thin line) and females (thick line) each day is also shown. (B) The sex ratio (number of males/females) each hour (thin line) and its average value each day (thick line with values shown above it). (C) Icons at the bottom indicating the moon phase. The gray bars are the tidal height, days and nights, each day; the horizontal line is the height estimated for the study areas; the asterisk (*) above the gray bar indicates when the study area was covered by tide in the daytime; and icons in the upper part represent the processes of chimney building. See text for further explanations.

and there was also a decrease in the number of females.

Twenty-one burrows with chimneys were dug up and their depths measured. The relationship between burrow depth and the relative distance to the high intertidal line is shown in fig. 3. A crab dug a deeper burrow if the burrow was nearer the high intertidal line ($R = 0.62$, $p = 0.003$, d.f. = 20). There was also a tendency for smaller males to live nearer the higher intertidal line ($R = 0.58$, $p = 0.015$, d.f. = 16), however, the relationship between male body size and burrow depth was not significant ($R = 0.21$, $p = 0.42$, d.f. = 16). The per-

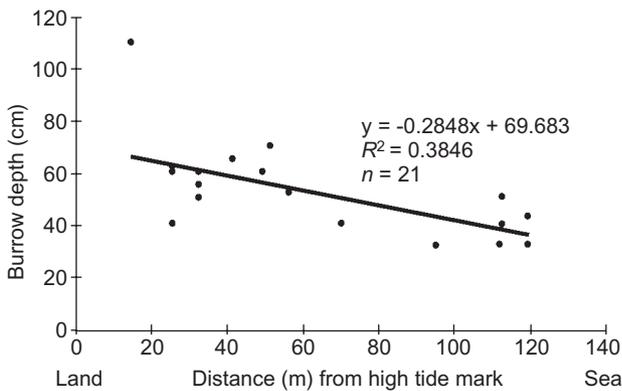


Fig. 3. Relationship between the relative distance from the high intertidal zone (m) and burrow depth (cm) of the burrows with chimneys of *Uca formosensis*.

centage of burrows with depths exceeding 40 cm was 85.7% (18 of 21 burrows).

Reproductive condition of resident females

Twenty-eight burrows with chimneys were dug up to examine the residents. Among them, 21 burrows contained a single pair (among which 1 female was ovigerous), and 7 burrows contained only 1 female (among which 2 females were ovigerous). In addition, from the videotapes, an additional 5 females (among which 3 were ovigerous) were individually recorded building chimneys. Among the *U. formosensis* pairs excavated, the relative vertical locations inside the burrows of the 18 pairs were recorded. More males were found to be nearer the entrance (15/18), and of the 3 cases for which the female was above the male, 1 female was ovigerous.

Chimney building by *Uca arcuata*

In contrast, both male and female *U. arcuata* frequently build chimneys around their burrows. Sediment to build the chimney is scraped up from the surface near the burrow entrance (Fig. 1K), and mudballs are carried by the ambulatory legs of either side (including by the male). Mudballs are placed around the entrance, and the walls of the chimney are trimmed using the ambulatory legs

Table 2. Comparison of chimneys built by *Uca formosensis* and *U. arcuata*

	<i>U. formosensis</i>	<i>U. arcuata</i>
Materials	from the interior burrow	from near the surface
Chimney size	generally large and high (average height, 9.2 cm; highest, 14.0 cm)	most are small and low (Taiwan ^b : average height, 2.9 cm; highest, 4.9 cm; Japan ^c : average height, 1.1 cm; highest, 3.7 cm)
Appearance	only piled up as large mudballs, no trimming	after adding a mudball, builder trims it until it is smooth, especially at the entrance of the burrow
Solidity	destroyed easily by the tide	still solid after the tide retreats
Builder	most are males (paired); a few are females (unpaired)	more young than adults; more females than males ^{b,c}
Inhabitants of a burrow	generally a pair, sometimes a single female	1 male or female
Timing	after successful courtship	year round ^c
Maintenance	after plugging, builder does not emerge for several days	builder repairs chimney immediately after it is damaged or broken
Possible function	1. hiding the excavating behavior of the male 2. by-product of excavation for hatching eggs of ovigerous female	microhabitat regulation ^a ; burrow protection against wandering crabs ^c

^aCrane (1975); ^bYeh (1996); ^cWada and Murata (2000).

and both chelipeds. If a chimney becomes damaged or broken, the builder repairs it immediately. A new chimney can be finished in less than 30 min, even if it had been badly damaged (see Table 2).

DISCUSSION

Chimney building by *Uca formosensis* was observed daily during 15 d periods. However, chimneys were destroyed by the tide, so subsequent observations of the behavior of chimney builders and their mates were impossible. According to Nakasone and Murai (1998), the pairing time (the time which a male and female stay together within a burrow after successful courtship) of narrow-fronted fiddlers (e.g., 5.7 (range, 3~9) d for *U. rosea*, Murai et al. 1996; and 5.2 (range, 4~8) d for *U. tetragonon*, Goshima et al. 1996) is much longer than that of broad-fronted species (e.g., 1.8 (range, 1~3) d for *U. pugilator*, Christy 1978; and 2.0 (range, 1~5) d for *U. lactea*, Goshima and Murai, 1988). At our study site, the habitat of *U. formosensis* was not covered by the tide for 4 to 5 d (Fig. 2C), and the male was seen to leave its burrow once the chimney had been destroyed by the tide (pers. obs.). The amount of time that the narrow-fronted *U. formosensis* spent in mate-guarding was presumed to match this drought period. It is possible that the female *U. formosensis* stays inside the burrow until the eggs hatch after the male has left. The incubation duration in most female fiddler crabs ranges from 12 to 15 d (Zucker 1978, Christy and Salmon 1984, Salmon 1987, Salmon and Zucker 1988), except for the incubation duration of *U. tetragonon* which is 28 d (Goshima et al. 1996). Females of several *Uca* species that live in the upper intertidal zone release larvae during the largest-amplitude nocturnal high tide of the lunar month (Morgan and Christy 1995). During this study, only 1 ovigerous female was seen feeding on the surface, and other ovigerous females were seen piling up mudballs (Fig. 1H). Therefore, when the chimney was destroyed by the tide, we presumed that the female *U. formosensis* stayed underground for a further 16 to 18 d until the night of the next spring tide.

The number of crabs appearing on the mudflats each day was negatively correlated with the sun, shade, and soil temperatures (Fig. 2A). When the temperature was too high, *U. formosensis* did not appear on the surface. However, tem-

perature, sediment dryness, and food availability are likely interrelated, and without further study, it is unclear which factors most affect crab activity.

Johnson (2003) suggested that the male-biased sex ratios in *U. pugilator* may be due to differential mortality between the sexes. During the present study, individuals of *U. lactea* and *U. arcuata* were seen being eaten by birds, and discarded chelae of the 2 species were frequently found, but not of individuals of *U. formosensis* (Shih 1997). However, individuals of *U. formosensis* were observed being attacked by other crabs during the study. Both cases occurred at dusk when the light was weak. In one case, an adult male *U. formosensis* was preyed upon, and his viscera were eaten by a *Helice formosensis*. In another case, a young male *U. formosensis* was attacked by a young *H. wuana*, but the fiddler autotomized his major cheliped and escaped after his cheliped plunged into the legs of the attacker (Shih 1997). While the differential mortality caused by the defensive chela weapon may be a possible factor for explaining the male-biased sex ratio of *U. formosensis*, other factors related to the mortality of females cannot be excluded. The sex ratio of *U. formosensis* on the surface tended to fluctuate with the tide (ranging from 1.81 to 10.02, Fig. 2B). When the number of females began decreasing, the number of males began to dramatically increase (decreasing slightly after 20 July) (Fig. 2A). One day after the tide had risen to periodically cover the habitat, female numbers increased to a maximum which may have been because the females were maximizing their food intake in preparation for breeding after a period of inactivity. When the sun temperature increased, the females spent less time on the surface possibly to escape lethal temperatures.

deRivera and Vehrencamp (2001) suggested that the degree of synchrony of receptive females (to the tidal height of the habitat) and female gametic investment (clutch size) can explain the sex ratio. An upper intertidal fiddler species breeds more synchronously than lower intertidal species (Morgan and Christy 1995), and the sex ratio approaches 1 (deRivera and Vehrencamp 2001). Females of fiddler species with large clutch sizes produce a male-biased sex ratio because the female's cycle length of reproduction is longer (i.e., females spend more time underground during the hatching period, and fewer females appear on the surface) (Christy and Salmon 1984). However, these 2 parameters are interrelated in a way that cancels out their influences, because smaller fid-

dler species tend to have larger clutch sizes and inhabit areas higher in the tidal zone. *Uca formosensis* is a large-sized species (CW > 30 mm, Shih et al. 1999) and inhabits the high intertidal zones, but the sex ratio did not approach equality based on the 2 parameters, indicating that the female gametic investment as incubation days instead of clutch size better explains the high male-bias sex ratio of *U. formosensis*.

Here we propose and discuss some possible hypotheses to explain the functions of the chimneys built by *U. formosensis*. The 1st is the sexual attraction hypothesis. Because the chimney of *U. formosensis* is built after a male has successfully attracted a female into his burrow, all possible functions, direct or indirect, of construction for sexual attraction, e.g., the hood of *U. musica terpsichores* (Zucker 1974, Christy et al. 2002) and the pillar of *U. beebei* (Christy 1988a b), are excluded. The 2nd is the sunshade effect hypothesis. It seems likely that the large chimney of *U. formosensis* provides a sunshade effect for lowering the temperature of the burrow underneath. However, since the bottom of the burrow is not directly under its entrance, and nearly 86% of burrows were more than 40 cm deep (Fig. 3); the sunshade effect of lowering burrow temperatures is probably negligible. The 3rd is the ventilation hypothesis. The chimney of *U. formosensis* is generally loosely constructed from mudballs, and many large gaps remain in the walls of the chimney; thus, the wind can easily ventilate the burrow through these gaps. However, after the chimney is finished, the burrow entrances can become plugged (Fig. 1F), a behavior also seen in other species of *Uca* (Salmon and Zucker 1988), and thus a ventilatory function of the chimney is highly unlikely. The 4th is the hypothesis of warding off intruders. McCann (1938) proposed that the function of the castle built by the terrestrial (freshwater) crab, *Paratelphusa (Barytelphusa) guerini* (H. Milne Edwards) on Salsette I., India, was to keep intruders away during estivation, because it acted as a bluff which is mistaken for a clod of earth. Silas and Sankarankutty (1960) also cited McCann's opinion to explain the castle built by the land crab, *Cardisoma carnifex* (Herbst). The burrow with paired fiddler crabs was found to be usurped by other males (e.g., *U. rosea*, Murai et al. 1996, and *U. lactea perplexa*, Nakasone and Murai 1998). Wada and Mutata (2000) also considered that the function of the chimney of *U. arcuata* was to protect the burrow from usurpation by wandering crabs. Therefore, the function of the chimney

of the mating burrow may possibly be to keep intruders away to prevent usurpation. However, in the case of the chimney of *U. formosensis*, after the chimney was finished, the environment on the mudflats greatly deteriorated (no tide covered it and temperatures increased, see Fig. 2), and no crab was seen on the surface during that period. It is unlikely that a pair inside a burrow would be disturbed by other crabs. Therefore, the chimney of *U. formosensis* does not seem to play a defensive role. The last possible hypothesis is that the chimney hides the burrower. There are 2 reasons why males need to excavate their burrows after attracting a mate. First, a male's burrow is for a single crab before pairing (Fig. 4A). After pairing, the diameter of the burrow shaft, at least the space near the bottom, must be enlarged to accommodate 2 individuals (Fig. 4B(1)). Second, it is important to dig a deeper burrow to reach the water table for the female, because the neap tide is approaching (with lower water levels at that time), and moisture or water in the burrow is necessary for incubation (Kellmeyer and Salmon 2001, Weaver and Salmon 2002; Fig. 4B(2)). Generally 2 types of chimneys, with either a wide or slender diameter (Fig. 1C, D), were constructed by *U. formosensis*. The burrow depth was correlated with the tidal level (Fig. 3), but was not related to male

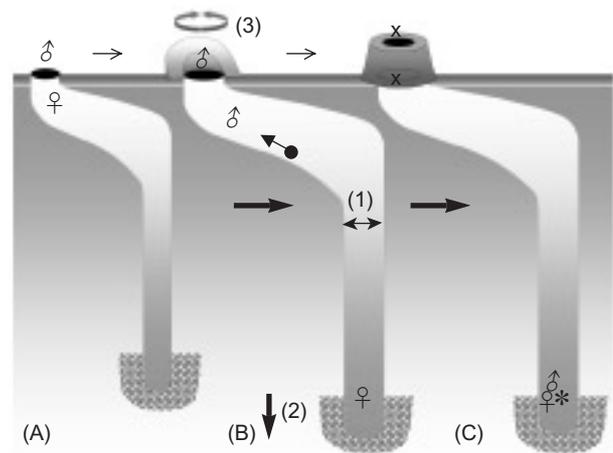


Fig. 4. A possible mechanism of chimney building by *Uca formosensis*. (A) Diagrammatic representation of a typical burrow of a male without a chimney before pairing. (B) After pairing. The shaft of the burrow must be enlarged (1), the bottom of the burrow is dug deeper until it reaches the water table (2), and the male piles the mudballs around the burrow entrance to hide himself while excavating (3). (C) After the excavation behavior is completed. The male may plug the entrances of both the chimney and burrow. See "Discussion" for further explanations.

body size ($p = 0.42$). Therefore, we predict that the width of a chimney is positively related to the size of the female and/or male while the height of the chimney is positively related to the vertical distance to the water table.

This is a new hypothesis for chimney building by *U. formosensis*, and it also has implications for more-terrestrial species that have to burrow to the water table on dry beaches. When the male *U. formosensis* carries the mudballs to the surface, he is faced with the danger of predation, or usurpation of the burrow and/or female by other males. One possible solution for him is to pile mudballs around the burrow entrance using his major cheliped, while the ambulatories of the minor side clasp onto the entrance, thus hiding himself behind the wall of the chimney so that he can rapidly withdraw into the burrow if necessary (Fig. 4B(3)). In *U. rosea*, after a pair enters a burrow, the male also repeatedly carries mud from the burrow and drops it onto the surface a short distance from the entrance until he plugs the entrance (Murai et al. 1996). It is possible that *U. formosensis* has evolved chimney building to hide the male from predators or other crabs that may attempt to usurp the burrow and female. The chimney structure here is hypothesized to be a by-product of burrowing. After the excavating behavior is completed, the male may plug the entrances to both the chimney and burrow (Figs. 1E, F, 4C) to prevent any enemy from entering at that moment and also to maintain the moist environment within the burrow during the 4 to 5 d period of drought.

This hypothesis can also explain the excavating behavior by the ovigerous (or assuming it will soon be ovigerous) female of *U. formosensis*. A female may excavate mudballs from within a burrow because the male of the pair has disappeared (e.g., killed by a predator). A more-plausible explanation is that the female had already been fertilized in surface mating, and she needs to dig a deeper burrow by herself in order to reach the water table for incubation, which is similar to the male's work in underground mating. However, the female was unable to build a structure like the male's chimney (Fig. 1H).

When burrows of *U. formosensis* were dug out, most males were found to be above the female at the bottom in paired burrows (15 of 18 burrows). This phenomenon had previously been noted, and of all pairs excavated, males were nearer the entrance in those observations (von Hagen 1962, Nakasone et al. 1983, Yamaguchi 1998). Yamaguchi (1998) suggested that the rela-

tive position of *U. lactea* has to do with the mating behavior process. In this study, there was generally a large space inside the burrow of *U. formosensis*, and a pair could meet each other and exchange their positions inside the burrow (pers. obs.). Therefore, it is possible that we were misguided by the relative positions of the crabs when the burrow was dug out. However, the female should generally be in the lower position near the bottom, because an ovigerous female needs a moist, even water-containing, environment. As another explanation, some predators or other crabs may enter the burrow, and so the male may generally maintain an upper position for defensive purposes (Nakasone and Murai 1998).

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