私立東海大學生命科學系

碩士論文

指導教授： 林惠真　博士

Dr. Hui-Chen Lin

論文題目：弧邊招潮蟹煙囪功能之新假說

A new hypothesis on the function of the chimney of the fiddler crab, *Uca arcuata*

研究生：　蘇國強

Kuo-Chiang Su

中華民國九十六年六月二十一日

私立東海大學生命科學系碩士論文

論文題目：弧邊招潮蟹煙囪功能之新假說

A new hypothesis on the function of the chimney of the fiddler crab, *Uca arcuata*

研究生：　蘇國強

Kuo-Chiang Su

指導教授：林惠真　博士

Dr. Hui-Chen Lin

中華民國九十六年六月二十一日

CONTENTS

中文摘要

某些招潮蟹會在其洞口堆置洞口堆積物。在前人的研究中，這些堆積物的功能有幾項假說被提出。本研究的實驗物種－弧邊招潮蟹（*Uca arcuata*），其煙囪建構的行為並不能以上述各假說來解釋。在此研究的前半部分，最顯著影響建構煙囪與否的因子為具探洞行為的其他種螃蟹（此指台灣厚蟹及德氏仿厚蟹）的數量。野外觀察發現，某些種類的螃蟹在地表活動時會有探洞行為，推測此種行為對於該洞螃蟹會造成干擾。另外，觀察也發現當地表活動的螃蟹遇到阻擋其行進路線的障礙物時，會有繞行的行為。因此我提出新的假說並嘗試去測試。我的假說是網紋招潮蟹的煙囪可能具有降低因被探洞所造成的干擾之功能。實驗從三方面著手：第一、若煙囪有降低干擾的功能，則預期網紋招潮蟹建構煙囪的頻率及速度會隨探洞螃蟹的密度而增加。實驗以設置三種台灣厚蟹密度處理樣區進行。在 12 個樣區中記錄連續 5 天各樣區中出現的煙囪數量，以了解煙囪出現的數量及速度是否會隨台灣厚蟹的密度而增加。結果顯示，高厚蟹密度處理的樣區中，網紋招潮蟹建構煙囪的數量顯著較無厚蟹處理的樣區多。煙囪出現的速度也和台灣厚蟹的密度成線性增加的關係。第二、預期會探洞的螃蟹在面對有煙囪及無煙囪的洞口時，進入無煙囪洞口的頻率會較高。實驗以人為釋放的方式測定台灣厚蟹及雙齒近相手蟹在釋放後，進入有煙囪及沒有煙囪洞口的比例。結果顯示，此兩種螃蟹進入沒有煙囪洞口的比例均較進入有煙囪的洞口高。第三、預期有煙囪的洞口被探洞的頻率會比無煙囪洞口低。利用洞口陷阱測試的結果顯示，有煙囪

洞口被探洞的頻率極顯著低於無煙囪洞口。28 隻被陷阱所捕獲的探洞螃蟹中有 18 隻為台灣厚蟹（64.29%），5 隻為網紋招潮蟹（17.86%）。這三個實驗均支持此研究中所提出的新假說。

ABSTRACT

Some fiddler crabs (genus *Uca*) build structures at their burrow entrances. In the previous studies, several hypotheses on the functions of these structures have been proposed. For *Uca arcuata*, the chimney-building behavior could not be explained by any of these hypotheses. In the first part of this study, the number of visiting crabs (ie., *Helice formosensis* & *Helicana doerjesi*) was one of the most important factors for the chimney-building behavior in *U. arcuata*. Field observations revealed that some crabs have a burrow-visiting behavior, suggesting that this behavior may be interference to the resident crabs. Furthermore, crabs usually make a detour if there is a roadblock. Hence, I proposed a new hypothesis that chimneys will reduce inter-specific interference due to burrow-visiting. To test this hypothesis, three experiments were conducted. First, the frequency and the rate of chimney building would increase when there are more visiting crabs around. Twelve enclosures were constructed and three densities of *H. formosensis* were manipulated. The number of chimney in each enclosure was recorded for the following 5 consecutive days. The number of chimney in the high density enclosures was significantly greater than that in the no *H. formosensis* treatment. And there was a linear relation of density to the rate of chimney emergence. Second, if the chimney can reduce interference, then it is expected that the visiting crabs are more likely to enter a burrow without a chimney.

I recorded the frequency of burrows, with and without chimneys, visited by *H. formosensis* and *Perisesarma bidens* after artificial releases. The results indicated that both species entered burrows without chimneys significantly more frequently. Third, the visited frequency is expected to be lower in the burrows with a chimney than in those without a chimney. The result of the burrow trap experiment confirmed this prediction. The burrow-visited frequency was significantly lower in burrows with a chimney. And eighteen of the 28 visiting crabs captured by burrow traps were *H. formosensis*, and 5 were *U. arcuata*. These three experiments supported the new hypothesis of this study.

INTRODUCTION

Extra-burrow structures are found in some crab species. Among the nearly 100 species of fiddler crab (genus *Uca*), males of 16 species build extra-burrow structures at their burrow entrances (Christy et al. 2002). According to their shapes, the structures can be divided into four types. The first type is called mudballs (Oliveira et al. 1998; Burford *et al*. 2001). Crabs that build this structure usually put some mudballs near their burrow entrances. The second type is called a chimney (Wada & Murata 2000; Shih et al. 2005) which is built around a burrow entrance (Wada & Murata 2000). The third type is called a hood (Zucker 1981; Christy *et al.* 2001 2002 2003ab), a semi-dome (Kim et al. 2004) or a shelter (Zucker 1974). This is a semi-circle structure built at the burrow entrance. And the fourth type is called a pillar (Christy 1988ab) which is also built at the burrow entrance and is narrower than a hood. In previous studies, various hypotheses were proposed to explain the possible functions of these structures (Table 1).

Uca arcuata is a common fiddler crab species in Taiwan. It is also widely distributed in north-east Asia, ranging through Japan, Korea and China (Crane 1975). The chimney-building behavior is one of the activities in some *U. arcuata* during ebb tides. When building a chimney, most mud material was collected from the area outside of the burrow (Fig. 1). Therefore, a chimney of *U. arcuata* is not a by-product from burrow excavation, and should have served a certain function. In her classic book, Crane (1975) described that both males and females build a chimney at their burrow entrance. In addition, females and small males build a chimney more often than large males (Yeh 1996; Wada & Murata 2000). Therefore, the hypotheses that focused on the male-female attraction and male-male territorial interactions (the first 3 functional hypotheses in Table 1) were not applicable to *U. arcuata* (Wada & Murata 2000).

There were at least two studies focused on the functions of chimneys built by *U. arcuata*. However, they were proposed from field observations and the results did not fully explain the function of chimneys in *U. arcuata*. In Yeh's study (1996), after the chimney was artificially moved to the area near the burrow entrance, the resident crab was still able to go back to its own burrow immediately, and none of the crabs in the experiment entered the chimney which was replaced near the burrow entrance. In addition, after being artificially released, there was no significant difference between the proportions of the released crabs that approached the burrows with and without chimneys in either male or female *U. arcuata* (Wada & Murata 2000). Thus, the chimneys of *U. arcuata* may not serve as a guidepost.

In his master's thesis, Yeh (1996) found more chimneys in the high tidal zone. Yeh (1996) hypothesized that the chimney in *U. arcuata* may function to maintain the moisture and the temperature within the burrow. But the author provided no direct evidence to support this hypothesis. The burrow depth of *U. arcuata* is about 50-100 cm (personal observation), and the height of a chimney is about 1.77 cm (0.41-4.01 cm, n = 53, pilot experiment of this study). The effect of such a small structure on the microhabitat improvement of a deep burrow should be limited. Therefore, this hypothesis by Yeh (1996) may not be applicable to *U. arcuata*.

Wada and Murata (2000) recorded the response of *U. arcuata* to a burrow with or without a chimney. They found that the artificially released *U. arcuata* entered a burrow without a chimney significantly more frequently. This was found in all size categories regardless of their sex. Since burrow usurpation by conspecific wanderers is common in *U. arcuata* (Murai 1992), Wada and Murata (2000) proposed that a chimney might protect the owner *U. arcuata* against burrow encroachment by wandering crabs. To support this hypothesis, it is expected that the chimney abundance is positively correlated to the number of wandering conspecifics. However, Wada and Murata did not find a significant positive correlation between the daily fluctuations of the number of wandering *U. arcuata* and the chimney-building frequency. This implies that the chimney of *U. arcuata* may serve other function but not only in preventing burrow intrusion by conspecific *U. arcuata* as Wada and Murata's hypothesis.

The behavior of intertidal crabs was affected by many environmental factors. For example, the tidal rhythm and the light-dark cycle affected the reproductive behavior of intertidal crabs (Morgan & Christy 1994), and the predation risk affected the mating behavior of *U. beebei* (Koga et al. 1998). The chimney-building behavior in *U. arcuata* may also be affected by certain environmental factors. A systematic survey is needed to identify these factors and to hypothesize the function of a chimney in *U. arcuata*. Therefore, in the first part of this study, I recorded as many as 14 environmental factors and verified which factors appear to be related to the chimney building behavior in *U. arcuata*. My results suggested that the number of a certain species of visiting crabs was the most important factor in the chimney-building behavior. Therefore, I proposed a new hypothesis that the inter-specific interaction was more important than the intra-specific interaction in the chimney-building behavior.

To support this new hypothesis, I had the following three predictions. First, the chimney-building frequency increases when there are more visiting crabs around. Second, upon confronting burrows with and without a chimney, the visiting crabs are more likely to enter the burrow without a chimney. And third, under a natural situation, the visited frequency is lower in the burrow with a chimney than in that without a chimney.

METHODS

The relationship between environmental factors and the chimney-building behavior

The observations were conducted on the mudflat near the estuary of the Dadu River, Taiwan (24°12'N, 120°29'E) from early July to mid-August, 2003. The mudflat was inside an embankment and covered by some grass and mangroves (*Kandelia obovata*). It is hypothesized that the chimney-building behavior is affected by certain environmental factors. To screen out the environmental factors, some *U. arcuata* burrows on the mudflat were randomly selected. A 1.5 m × 1.5 m frame was placed on the surface with the selected burrow located in the center, and a total 14 biotic and abiotic parameters within this frame were recorded. They are listed in Table 2. I collected the soil around the burrow entrance with about 15 cm in diameter and 20 cm in depth, and measured the soil water content. The water content in the soil was estimated by the following equation, soil water content = $(W_w - W_d) / W_d \times 100\%$, where the W_w is the wet weight of the soil and the W_d is the dry weight of the soil. The dry weight was measured after the soil was dried at 105 °C for 24 hours. The inner temperature was the temperature about 15 cm deep in the burrow, whereas the outer temperature was the surface temperature of the burrow entrance under sunshine. The habitats were divided into five types according to the vegetation, crab component and pool presence. The first type of habitat was partially covered by grass and water pool, and there were many *U. arcuata* inhabiting it. The second type was wet and muddy due to the presence of a pool next to it. A species of mud crab (*Macrophthalmus banzai*) was the most common species in this habitat. The third type of habitat was drier with no vegetation covering it. There were a lot of *Uca formosensis* and *Helice formosensis* inhabiting this area. The fourth type of habitat was a mudflat without any vegetation, and was inhabited mostly by *U. arcuata*. The final one was a mudflat outside the embankment and in direct contact with the branch of the Dadu River Estuary. This habitat was flushed by the tide directly.

The observations were taken in two stages. The first stage was conducted from 7th to 20th July, 2003. During this period, 30 burrows were recorded and analyzed by a multiple logistic regression model to evaluate the factors that would be important to initiate the chimney-building behavior. The preliminary result led us to exclude the following six parameters from further study, including the distances from the selected burrow to the closest burrows of both male and female *U. arcuata* and to other crab species, the soil water content, and the inner and outer temperature. The second stage was conducted from 25th to 30th July, 2003. During this stage, I only recorded eight parameters. They were the densities of male and female *U. arcuata*, the density of other species of crabs, the number of the visiting crabs, the sex and the carapace width of the focal individual, the density of chimneys and the habitat type. A total of 53 crabs were included in the examination. I combined these 53 observations with the 30 ones collected previously from the first stage. Therefore, 83 observations were analyzed by a multiple logistic regression model to determine the factors that were important for the chimney-building behavior.

To evaluate the different chimney-building frequencies in different size categories and sex, the sex and the carapace width of the focal individual were further analyzed. The crabs were categorized as small if they had a carapace size below the 20^{th} percentile value of the size distribution and as large if it was above the 80^{th} percentile. Therefore, the small size individuals were those with their carapace width smaller than 19.5 mm in males and smaller than 14.5 mm in females, the middle ones were from 19.5 mm to 35.5 mm in males and from 14.5 mm to 25.5 mm in females, and the large ones were those larger than 35.5 mm in males and larger than 25.5 mm in females. The analyses were separated for the size and sex. The relationship between chimney-building frequency and size was analyzed by a Mantel-Haenszel correlation statistic (Stokes et al. 2001), and a Cochran-Armitage trend test (Stokes et al. 2001) was performed to evaluate the trend of the correlation between chimney-building frequency and size. For the sex, the Fisher's exact test was performed to evaluate the relationship between chimney-building frequency and sex.

Density effect of *Helice formosensis* on chimney-building frequencies

To determine whether the density of *Helice formosensis* affects the chimney building frequencies, the experiment was conducted in 12 (1.5 m × 3 m) enclosures on the mudflat (Fig. 2b) by the estuary of the Dadu River in July 2005. The edge of each enclosure was made by wood boards 20 cm in height with 5 cm protruding above ground (Fig 2a). In addition, a 20-cm wood board was buried perpendicular to the edge of the enclosure (Fig 2a). This will prevent the crabs from digging to escape. A 20-cm wide window fence (1-mm wire mesh) was used and the bottom 5 cm of the fence was stapled to the edge of the wood board (Fig 2a). Plastic boards 20 cm wide covered the top of the fence to avoid the escape of crabs (Fig. 2a). Crabs within the enclosures were removed as thoroughly as possible before 10 male and 10 female *U. arcuata* were colonized in each enclosure. This was to simulate the local density on the mudflat. The carapace width of *U. arcuata* was 25.90 ± 2.78 mm (ranging from 20.11 to 29.98 mm, n = 240). Each crab was provided with an artificial burrow. The artificial burrows were created by sticking a plastic rod 2 cm in diameter into the mudflat. After a week of recovery, three densities of *H.*

formosensis were established in these 12 enclosures. Each of the four high density (HD) treatment enclosures had 15 *H. formosensis*. There were five *H. formosensis* in each of the four low density (LD) treatment enclosures, and this was the average density of the local area. No *H. formosensis* was in the four control (C) enclosures. The arrangement of these treatments is shown in Fig. 2b. At the same time of density manipulation, all chimneys in the enclosures were removed before recording. The numbers of chimney in each enclosure were recorded daily for the following five consecutive days. Because the mudflat was located inside an embankment, the tidal force was weak and the chimney can last for at least a half month and this allowed us to record the number of chimney consecutively with no chimney collapsed. The difference of the chimney-building frequency between the three treatments was analyzed by a randomization ANOVA with Tukey's test as a post hoc test.

The behavior of visiting crabs

If the function of the chimney is to reduce the burrow-visiting frequency, it is expected that the visiting crabs are more likely to enter a burrow without a chimney. I set up a 1 m × 1 m enclosure with 4 wooden boards (Fig. 3) on the mudflat near the estuary of the Dadu River. Each board was 20 cm in height, and the bottom 5 cm was buried in the mud. The bottom of the enclosure was covered with 1 mm mesh to prevent the presence of other crabs in the enclosure. A circular setting of 10 artificial burrows was prepared within the enclosure (Fig. 3). The artificial burrows were created by sticking a plastic rod 2 cm in diameter into the mudflat. The diameter of the setting was about 25 cm. Five artificial chimneys were placed onto the artificial burrows alternately among the 10 burrows. The artificial chimneys were made of a mixture of concrete and mud with 2 cm inner diameter, 5 cm outer diameter and 2.5 cm height (Fig. 4).

Two species of the grapsid crabs, *Helice formosensis* and *Perisesarma bidens*, were used as the visiting crabs in this experiment. These two species were commonly seen on the same intertidal mudflat where *U. arcuata* was found, and the burrow-visiting behavior was frequently found (personal observation). These crabs were collected locally and each crab was tested only once in this experiment.

A single visiting crab was placed at the center of the circle. It was covered by a bowl for 30 seconds before release. When the bowl was removed, the crab could have at least three kinds of responses, including entering a burrow with a chimney, entering a burrow without a chimney and passing in between burrows without entering. There were 68 trials for *H. formosensis* from September 2004 to August 2005, and 21 trials for *P. bidens* in September 2005.

Burrow-visiting frequencies in burrows with or without a chimney

A burrow trap was designed to determine the burrow-visiting frequency in burrows with and without a chimney. The burrow trap consisted of a plastic cup covered with a plastic disc with a 17 mm hole at the center. A plastic straw plugged the hole to prevent the mud from falling into the trap before a mud channel was created. A trap set is defined as a pair of two burrow traps buried about 15 cm apart (Fig. 5). One burrow trap of the trap set was buried about 3 cm down from the surface, and the other was about 1 cm from the surface. The condition was left for recovery for five days before the straw was removed. Therefore, simulated mud channels like those in the burrows of *U. arcuata* were formed. Then I collected natural chimneys from the local area and measured several parameters before removal onto the burrow traps. The parameters were the inner diameter, the outer diameter and the height of the chimneys. A natural chimney was placed on the shallower trap (buried 1-cm below ground) of the trap set. Because most chimneys built by *U. arcuata* were about 2 cm in height (average: 1.77 cm, range from 0.41 to 4.01 cm, n = 53, pilot experiment of this study), the lengths of both mud channels were about 3 cm (Fig. 5). I left the trap set for three days. Most chimneys and burrow channels were still intact when I dug out the burrow traps for recording. I identified the species and the number of the crabs which were collected in the trap sets.

During 17th and 18th August 2006, 64 trap sets were prepared and allocated to four lines on the mudflat of the estuary of the Daan River (24°26’N, 120°37’E). The distance between each two trap sets was 2 m. I removed straws and completed all trap sets on 23rd August 2006, and recorded data on 25th August 2006.

The two burrow traps of a trap set were very close to each other in the field. Therefore, I treated them as a single pair. The data were analyzed by the Wilcoxon matched-pairs signed-ranks test to evaluate the difference of the number of visiting crabs within a trap set.

To further exclude the possibility that the species and the number of crabs were captured randomly by the burrow traps, a 1.5 m × 1.5 m frame was constructed to record local species composition and density. The frame was placed on the mudflat, and observations by binoculars were taken about three meters away from it. After five minutes of recovery, the crabs on the surface were identified and the numbers of crabs counted. A total of 12 observations were conducted during 24th and 26th October 2006. Each observation was five meters away from each other along the four lines on which the trap sets were located.

The *G*-test was applied to evaluate the difference between the proportion of the captured crabs and the species component of the local area.

RESULTS

The relationship between environmental factors and the chimney-building behavior

A multiple logistic regression model was developed to assess the independent contribution of factors in distinguishing the burrows with chimneys from those without ones. Among the eight factors, the first three factors, which were the number of the visiting crabs ($\chi^2 = 8.70$, n = 83, $P < 0.01$, Table 3), the carapace width of the focal individual ($\chi^2 = 8.09$, n = 83, $P < 0.01$, Table 3), and the male *U. arcuata* density ($\chi^2 = 4.18$, n = 83, $P < 0.05$, Table 3) significantly affected the chimney-building behavior. The importances of these three factors were further evaluated in the following experiments. The remaining five factors were not statistically significant.

In male *U. arcuata*, the chimney-building frequency was different among size categories (Mantel-Haenszel Chi-Square = 6.96, n = 42, $P < 0.01$, Table 4). Small individuals built a chimney more frequently than middle ones, and most large individuals did not build a chimney (Cochran-Armitage trend test, Z = -2.67, n = 42, $P < 0.01$). In females, there was no significant difference in the chimney-building frequencies among the three size categories (Mantel-Haenszel Chi-Square = 1.90, n = 41, $P = 0.17$, Table 4). That is, most females were found to build a chimney regardless of their size category (Cochran-Armitage trend test, Z = -1.39, n = 41, P = 0.16).

In the small and middle categories, there was no significant difference between sexes (Fisher's exact test, small: n = 19, P = 0.16; middle: n = 43, P = 0.20, Table 5). Most small individuals were found to build a chimney. However, in the large category, females built a chimney significantly more often than males (Fisher's exact test, n = 21, P = 0.009, Table 5).

Density effect of *Helice formosensis* on chimney-building behavior

The highest chimney-building rate was found in the HD treatment and the lowest was in the C treatment during the first three recording days (Fig. 6). The building rates slowed down on the fourth and fifth days. This is an indication that the chimney building rate increased as the *H. formosensis* density increased.

The density of *H. formosensis* also affected the chimney-building frequency. There was a significant difference in the number of chimneys among the three manipulated density treatments (randomization ANOVA, simulations = 5000, $F_{2, 21}$ = 3.56, $P < 0.05$). The number of chimneys in the HD treatment was significantly higher than that in the C treatment (Tukey test), whereas there was no significant difference between C vs. LD, and LD vs. HD (Fig. 6). There was a positive linear relation between the density of *H. formosensis* and the frequency of chimney building.

The behavior of visiting crabs

Both species of visiting crab, *Helice formosensis* and *Perisesarma bidens*, significantly entered a burrow without a chimney. In 57 out of 68 trials, *H. formosensis* entered a burrow without a chimney, but it never entered a burrow with a chimney (fig. 7a). The responses of *P. bidens* were similar to that of *H. formosensis*. In 10 out of 21 trials, *P. bidens* entered a burrow without a chimney, and none entered a burrow with a chimney (fig. 7b).

Burrow-visiting frequencies in burrows with or without a chimney

Only 1 chimney collapsed Among the 64 trap sets. Crabs were captured in 23 of the remained 63 trap sets, and the 40 trap sets which captured no crab were excluded from the analysis. The total number of visiting crabs captured by the trap sets was 28 individuals, and 22 of them were in the burrows without chimneys. The Wilcoxon matched-pairs signed-ranks test was used to evaluate the difference of the captured number between the 2 burrow traps of a trap set. The result revealed that the burrow-visiting frequency was significantly lower in the burrow with a chimney (Wilcoxon matched-pairs signed-ranks test, $n = 23$, $z = 2.235$, $P < 0.05$).

Among the 28 captured crabs, there were 18 *Helice formosensis* (64.29%), 2 *Helicana doerjesi* (7.14%), 3 *Perisesarma bidens* (10.71%) and 5 *Uca. arcuata* (17.85%) (Fig. 8). The average local density in each species in a square meter was 22.15 *Uca lactea*, 0.74 *H. formosensis*, 0.3 *H. doerjesi*, 0.07 *P. bidens* and 13.19 *U. arcuata* (Fig. 9). Because no *U. lactea* was captured by the trap sets, it was excluded from the analysis. The proportion of the captured crabs was significantly different from that of the local density (G-test, $G = 97.527$, $P < 0.001$). Therefore, it is not a random capture either in the species composition or in the numbers of each species caught.

DISCUSSION

The chimney of *U. arcuata* is not a by-product from burrow excavation. Burrow excavation is one of the activities during the ebb tide in *Uca tangeri* (Burford et al. 2001), and it is also found in *U. arcuata*. However, *U. arcuata* always removes the muddy substrate from the burrow and puts it away from the burrow entrance during burrow excavation (Crane 1975). When building a chimney, most mud material was scraped and collected from the area out of the burrow and around the entrance (Crane 1975). The time available for surface activity of the intertidal organisms is restricted by the daily tidal rhythm. Any time and energy not spent directly for survival or reproduction is costly. Therefore, such a chimney in *U. arcuata* must serve some functions and is not just a by-product.

The chimney-building behavior in *U. arcuata* was associated with some environmental factors. Among them, the number of visiting crabs was the most significant factor to the behavior. In the field, burrow-visiting behavior can be found in some crabs such as *Helice formosensis*, *Helicana doerjesi* and *P. bidens* (personal observation), and these crabs were considered as visiting crabs. The purpose and benefits of this visiting behavior are still unknown, but it is suggested that this visiting behavior may be a disturbance to the resident crab. The disturbance might include burrow usurpation (Wada & Murata 2000) or predation. A burrow is an important resource to an intertidal crab, for example, it provides the crab a refuge to hide from predators (Crane 1975), water supply (Murai 1992) and body temperature maintenance (Eshky et al. 1995) during ebb tides. Temporary burrow occupation by wanderers in fiddler crabs is a frequent phenomenon (Murai 1992), and it may make the resident crab lose its own burrow. Predation on *U. arcuata* by *H. formosensis* had been recorded during my field observation. I manipulated the density of *H. formosensis*, and found that the density of *H. formosensis* was positively correlated to the chimney-building frequency of *U. arcuata*. The presence of *H. formosensis* could be regarded as a higher chance of disturbance. Furthermore, it is observed that crabs usually make a detour if there is a roadblock such as a stone or a piece of wood on the surface. These observations and results suggested that the chimney is built by *U. arcuata* to reduce the inter-specific disturbance. Previous studies have indicated that chimney-building frequencies in *U. arcuata* were different between male and female, and between different size categories (Yeh 1996; Wada & Murata 2000). Females built chimney more frequently than males (Wada & Murata 2000), and smaller individuals built chimney more often than larger ones (Yeh 1996; Wada & Murata 2000). Additionally, ovigerous females constructed chimneys at their burrow entrances (Yeh 1996). In the study by Wada and Murata (2000), they hypothesized that the chimney in *U. arcuata* was to protect the burrow owner from burrow occupation by conspecific wandering males, but the authors did not explain why the chimney-building frequency did not correspond to the number of wandering males present.

In the density effect study, an average of 5.88 ± 1.56 chimneys was recorded in the control enclosure where there were 10 male *U. arcuata* but no *H. formosensis.* That is, male *U. arcuata* also affected the chimney-building behavior as suggested by Wada and Murata (2000). However, the chimney-building frequency in control treatment was not significantly different from that of the low density treatment. It is an indication that the chimneys are important not only intraspecifically but also interspecifically.

In the present study, it is the number of visiting crabs, rather than the male density, which affected the chimney-building behavior more significantly. This result supported the hypothesis that the function of the chimney was more significant in reducing inter-specific disturbance.

After the visiting crabs, *H. formosensis* and *P. bidens*, were released, both species entered a burrow without a chimney significantly more frequently. In fact, not a single crab entered a burrow with a chimney. The artificial releases in this experiment may be a shock to the crabs and it may result in seeking to hide quickly. However, no matter why the visiting crabs entered the burrow, the core of the question was the kind of burrows the visiting crabs tended to enter upon confronting burrows with or without chimneys. The fact is that the crab reaching down the burrow is a disturbance to the resident crab. Burrows sometimes serve as refuges (Crane 1975) when encountering predators such as birds. Artificial release can be regarded as a sudden appearance of a predator, and the released crab takes refuge in an emergency situation. From my results, the disturbance in the burrows without a chimney was significantly higher than that in the burrows with a chimney. A similar release experiment was also performed in Wada and Murata's study (2000). Therefore, the results this release experiment supported the hypothesis that a chimney was able to reduce the disturbance from the burrow-visiting behavior by other crabs.

The results of the burrow trap experiment further supported this hypothesis. There were more crabs captured in the burrows without a chimney, and this was direct evidence that a chimney was able to reduce the visiting-frequency of a burrow in a natural situation. The captured crabs were not randomly falling into the traps for at least two reasons. The first reason is about the design of the trap. Although the traps were below the surface, there was still about a three centimeter depth of mud channel connecting to each trap. If a crab were active on the surface and fell into a trap entrance accidentally, it could still climb out through the mud channel. But when a crab visited a burrow, it would enter the entrance of a burrow trap, go through the mud channel and finally fall into the trap. In other words, the mud channel was able to prevent the crabs from falling into the trap randomly. Second, the proportion of the crabs captured by the traps was significantly different from that of the local density. If the captured crabs were falling into the traps accidentally, the proportions of the captured crabs and of the local density should be similar. This is why a pit-fall trap is workable in a lot of ecological survey studies. *U. lactea* was the most abundant species in the study site (22.15 individuals per m^2; about 60.77%), but none was captured by the traps. In contrast, the number of *H. formosensis* in the local area was very few (0.74 individuals per m^2; about 2.03%), but it was the species most captured by the traps. Furthermore, in the result mentioned above, the number of *H. formosensis* had the most significant relationship with the chimney-building behavior in *U. arcuata*. This is strong evidence to support the hypothesis that inter-specific disturbance reduction is the major function of the chimney.

The mechanism by which a chimney is able to prevent intrusion from other crabs is unknown and deserves further study. There are at least two possible mechanisms. The first one is based on a visual cue. As mentioned earlier, crabs usually make a detour when some objects are present on the way. A chimney may simulate an object on the surface, and make the other crabs pass around the chimney. The second possible mechanism is based on the tactile sense. A burrow of a crab is a hollow structure, and the other crabs could detect the burrow entrance by the tactile sense of their legs. On the contrary, a chimney is able to cover a hollow signal of the burrow entrance and prevent the detection of the burrow, and therefore reduce the burrow-visiting frequency. These are two hypothetical mechanisms, and are able to be tested experimentally in a future study.

The carapace width of the focal individual also significantly affected the chimney-building behavior in the multiple logistic regression model of this study. In some previous studies (Yeh 1996; Wada & Murata 2000) and this study, larger male *U. arcuata* built chimneys less frequently than conspecific females and smaller males. An enlarged claw of a male fiddler crab serves multiple functions such as fighting during male-male combat (Levinton et al. 1995), male-female attraction (Backwell et al. 1999; Pope 2000), burrow defense (Hyatt & Salmon 1978; Jennions & Backwell 1996) and assessment of the quality of an opponent (Jennions & Backwell 1996). Furthermore, based on the disturbance reduction hypothesis in this study, I suggest that the lesser chimney-building frequency in larger males is because of the possession of a larger major claw which is considered a more powerful weapon. Again, this can be tested in the future by estimating the relationship between the claw size and the chimney-building frequency.

In conclusion, this study supported the hypothesis that a chimney in *U. arcuata* may also in reducing the inter-specific disturbance. This hypothesis is not mutually exclusive with Wada and Murata's hypothesis on protecting from burrow usurpation by wandering *U. arcuata* (Wada & Murata 2000). My hypothesis not only would further explain the conflict in their study but also provide a better discussion on the role of chimneys in *U. arcuata*.

REFERENCES

Backwell, P. R. Y., Jennions, M. D., Christy, J. H. & Passmore, N. I. 1999. Female choice in the synchronously waving fiddler crab *Uca annulipes*. *Ethology*, **105**, 415-421.

Burford, F. R. L., McGregor, P. K. & Oliveira, R. F. 2001. Mudballing revisited: further investigations into construction behaviour of male *Uca tangeri*. *Behaviour*, **138**, 221-234.

Christy, J. H. 1988a. Pillar function in the fiddler crab *Uca beebei*. I. Effects on male spacing and aggression. *Ethology*, **78**, 53-71.

Christy, J. H. 1988b. Pillar function in the fiddler crab *Uca beebei*. II. Competitive courtship signaling. *Ethology*, **78**, 113-128.

Christy, J. H., Backwell, P. R. Y. & Goshima, S. 2001. The design and production of a sexual signal: hood and hood building by male fiddler crabs *Uca musica*. *Behaviour*, **138**, 1065-1083.

Christy, J. H., Backwell, P. R. Y., Goshima, S. & Kreuter, T. 2002. Sexual selection for structure building by courting male fiddler crabs: an experimental study of behavioral mechanisms. *Behavioral Ecology*, **13**, 366-374.

Christy, J. H., Backwell, P. R. Y. & Schober, U. 2003a. Interspecific attractiveness of structures built by courting male fiddler crabs: experimental evidence of a sensory trap. *Behavioral Ecology and Sociobiology*, **53**, 84-91.

Christy, J. H., Baum, J. K. & Backwell, P. R. Y. 2003b. Attractiveness of sand hoods built by courting male fiddler crabs, *Uca musica*: test of a sensory trap hypothesis. *Animal Behaviour*, **66**, 89-94.

Crane, J. 1975. *Fiddler Crabs of the World. Ocypodidae: genus* Uca. Princeton, New Jersey: Princeton University Press.

Eshky, A. A., Atkinson, R. J. A. & Taylor, A. C. 1995. Physiological ecology of crabs from Saudi Arabian mangrove. *Marine Ecology Progress Series*, **126**, 83-95.

Hyatt, G. W. & Salmon, M. 1978. Combat in the fiddler crabs *Uca pugilator* and *Uca pugnax*: a quantitative analysis. *Behaviour*, **65**, 182-211.

Jennions, M. D. & Backwell, P. R. Y. 1996. Residency and size affect fight duration and outcome in fiddler crab *Uca annulipes*. *Biological Journal of the Linnean Society*, **57**, 293-306.

Kim, T. W., Christy, J. H. & Choe, J. C. 2004. Semidome building as sexual signaling in the fiddler crab *Uca lactea* (Brachyura: Ocypodidae). *Journal of Crustacean Biology*, **24**, 673-679.

Koga, T., Backwell, P. R. Y., Jennions, M. D. & Christy, J. H. 1998. Elevated predation risk changes mating behaviour and courtship in a fiddler crab. *Proceedings of the Royal Society of London, series B*, **265**, 1385-1390.

Levinton, J. S. Judge, M. L. & Kurdziel, J. P. 1995. Functional differences between the major and minor claws of fiddler crabs (*Uca*, family Ocypodidae, Order Decapoda, Subphylum Crustacea): A result of selection or developmental constraint? *Journal of Experimental Marine Biology and Ecology*, **193**, 147-160.

Morgan, S. G. & Christy, J. H. 1994. Plasticity, constraint, and optimality in reproductive timing. *Ecology*, **75**, 2185-2203.

Murai, M. 1992. Courtship activity of wandering and burrow-holding male *Uca arcuata*. *Ethology*, **92**, 124-134.

Oliveira, R. F., McGregor, P. K., Burford, F. R. L., Custódio, M. R. & Latruffe, C. 1998. Functions of mudballing behaviour in the European fiddler crab *Uca tangeri*. *Animal Behaviour*, **55**, 1299-1309.

Pope, D. S. 2000. Testing function of fiddler crab claw waving by manipulating social context. *Behavioral Ecology and Sociobiology*, **47**, 432-437.

Shih, H. T., Mok, H. K. & Chang, H. W. 2005. Chimney building by male *Uca formosensis* rathbun, 1921 (Crustacea: Decapoda: Ocypodidae) after pairing: a new hypothesis for chimney function. *Zoological Studies*, **44**, 242-251.

Stokes, M. E., Davis, C. S. & Koch, G. G. 2001. *Categorical Data Analysis Using the SAS System.* 2nd ed. SAS Institute Inc., Cary, NC. pp. 78-86.

Su, Y. C., Su, S. H. & Lin, H. C. 1996. The possible functions of chimney in *Uca* *formosensis*. *Senior Research Theses in Biological Literature, Department of Biology, Tunghai University*, pp. 15-23.

Wada, K. & Murata, I. 2000. Chimney building in the fiddler crab *Uca arcuata*. *Journal of Crustacean Biology*, **20**, 505-509.

Yeh, C. L. 1996. Observations of chimney function and territorial behavior in the fiddler crab *Uca arcuata* De Haan, 1835. *Master Thesis of Fujen Catholic University*.

Zucker, N. 1974. Shelter building as a means of reducing territory size in the fiddler crab, *Uca terpsichores* (Crustacea: Ocypodidae). *The American Midland Naturalist*, **91**, 224-236.

Zucker, N. 1981. The role of hood building in defining territories and limiting combat in fiddler crabs. *Animal Behaviour*, **29**, 387-395.

Table 1. Current hypotheses on the function of differenct burrow structures in fiddler crabs.

Function	Structure type	Species	Reference
Attractiveness to female	mudballs	*Uca tangeri*	Oliveira et al. 1998
	hood	*U. musica*	Christy et al. 2001
			Christy et al. 2002
			Christy et al. 2003a
			Christy et al. 2003b
	semidome	*U. lactea*	Kim et al. 2004
	pillar	*U. beebei*	Christy 1988b
Territory spacing	mudballs	*U. tangeri*	Oliveira et al. 1998
			Burford et al. 2001
Reduction in territory size	shelter	*U. terpsichores*	Zucker 1974
Guidepost	pillar	*U. beebei*	Christy 1988a
Microhabitat improvement	chimney	*U. formosensis*	Su et al. 1996, in Chinese
			Shih et al. 2005
	chimney	*U. arcuata*	Yeh 1996, in Chinese
Intra-specific burrow protection	chimney	*U. arcuata*	Wada & Murata 2000

Table 2. A list of the biotic and abiotic factors recorded for the focal burrow

Recorded parameters
Biotic factors
Sex of the focal individual
Carapace width of the focal individual
Density of chimneys
Density of male *Uca arcuata*
Density of female *U. arcuata*
Density of other crab species
Number of visiting crabs
Distance between the selected burrow and the closest burrows of male *U. arcuata*
Distance between the selected burrow and the closest burrows of female *U. arcuata*
Distance between the selected burrow and the closest burrow of other crab species
Abiotic factors
Soil water content of the selected burrow
Inner temperature of the selected burrow
Outer temperature of the selected burrow
Habitat type

Note: Visiting crabs were *Helice formosensis* and *Helicana doerjesi*

Soil water content = $(W_w – W_d) / W_d \times 100\%$

Table 3. Multiple logistic regression model on the relationship between environmental factors and the burrows with or without chimneys (n = 83).

Source	***df***	χ^2	**Pr >** χ^2
Intercept	1	1.22	0.27
Habitat type	1	1.61	0.21
Sex	1	1.00	0.32
Carapace width	1	8.09	0.005*
Male density	1	4.18	0.041*
Female density	1	3.17	0.08
Chimney density	1	2.98	0.08
Number of visiting crabs	1	8.70	0.003*
Density of other crabs	1	0.98	0.32

Note: Visiting crabs were *Helice formosensis* and *Helicana doerjesi*

* means the *P* value was < 0.05

Table 4. Chimney-building frequencies in different size categories of males and females.

Sex	Size category	Chimney builder	Non-builder	Total	*P*-value
Male	Small	6	2	8	0.008**
	Medium	12	10	22	
	Large	2	10	12	
Female	Small	11	0	11	0.17
	Medium	16	5	21	
	Large	7	2	9	

** means the *P*-value < 0.01 with Mantel-Haenszel Chi-Square test.

Table 5. Chimney-building frequencies in different sexes within a size category.

Size category	Sex	Chimney builder	Non-builder	Total	*P*-value
Small	Male	6	2	8	0.16
	Female	11	0	11	
Medium	Male	12	10	22	0.20
	Female	16	5	21	
Large	Male	2	10	12	0.009**
	Female	7	2	9	

** means the *P*-value < 0.01 with Fisher's exact test.

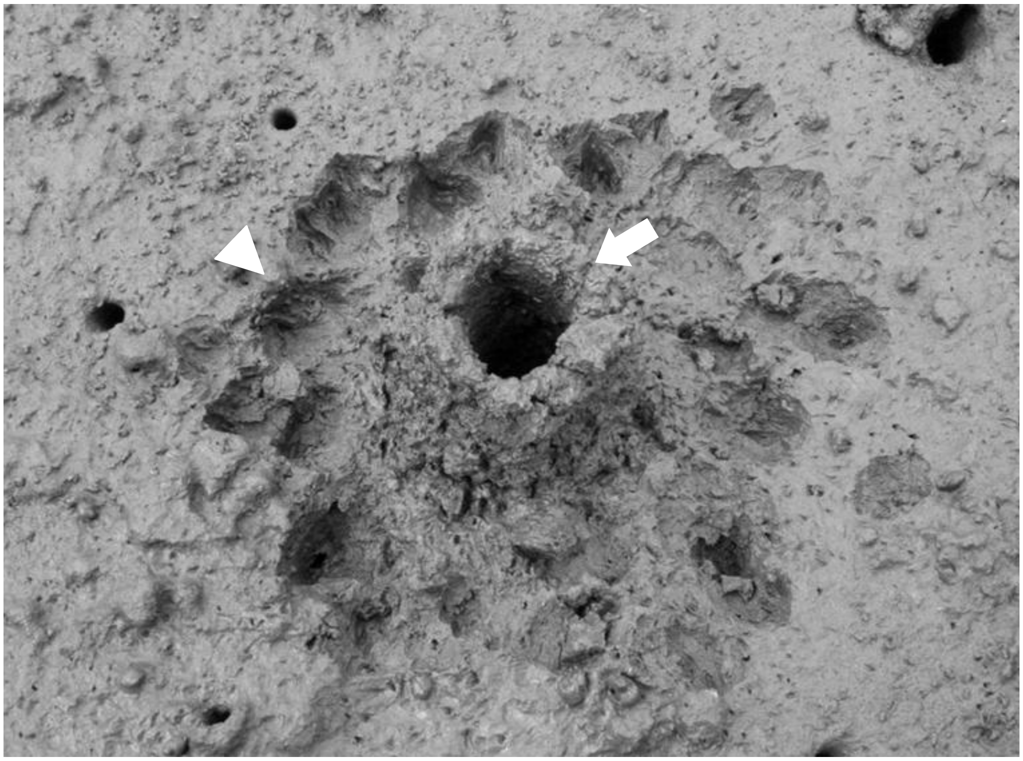

Figure 1. Picture of a chimney in *U. arcuata*. A chimney is a mud structure around a whole burrow entrance (arrow). The scratches show the collection of the mud to build a chimney (arrow head).

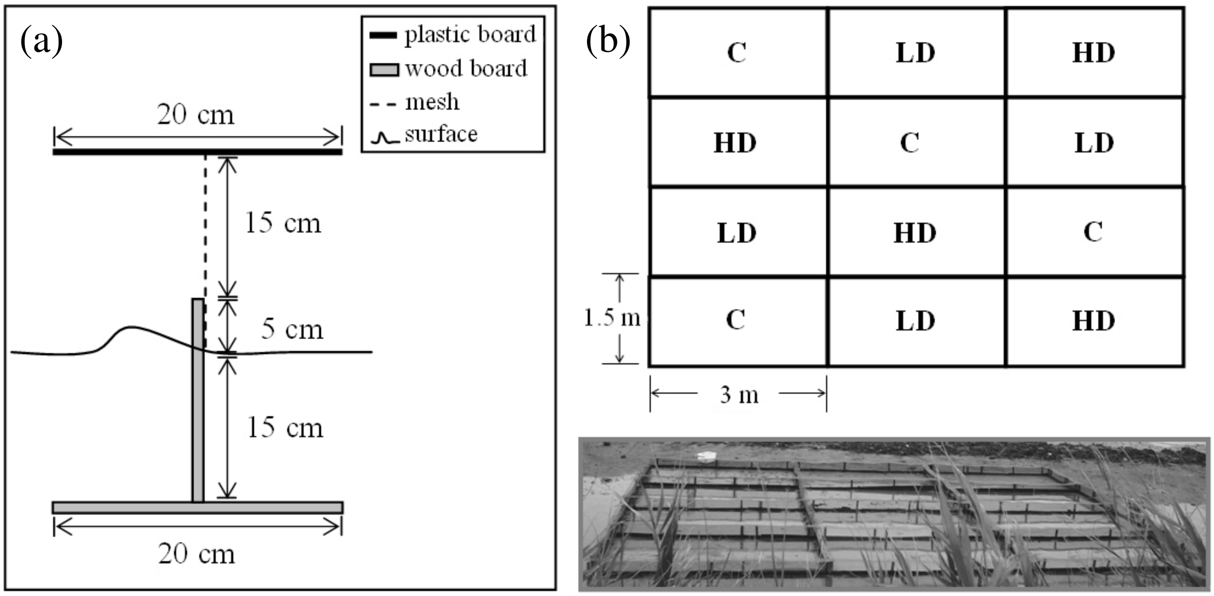

Figure 2. Diagram and picture of the enclosures for the density manipulation experiment. (a) a cross-sectional view of the edge design of the enclosure. (b) the arrangement of the treatments (above). HD: high density treatment. LD: low density treatment. C: control, and the picture of the enclosure (below).

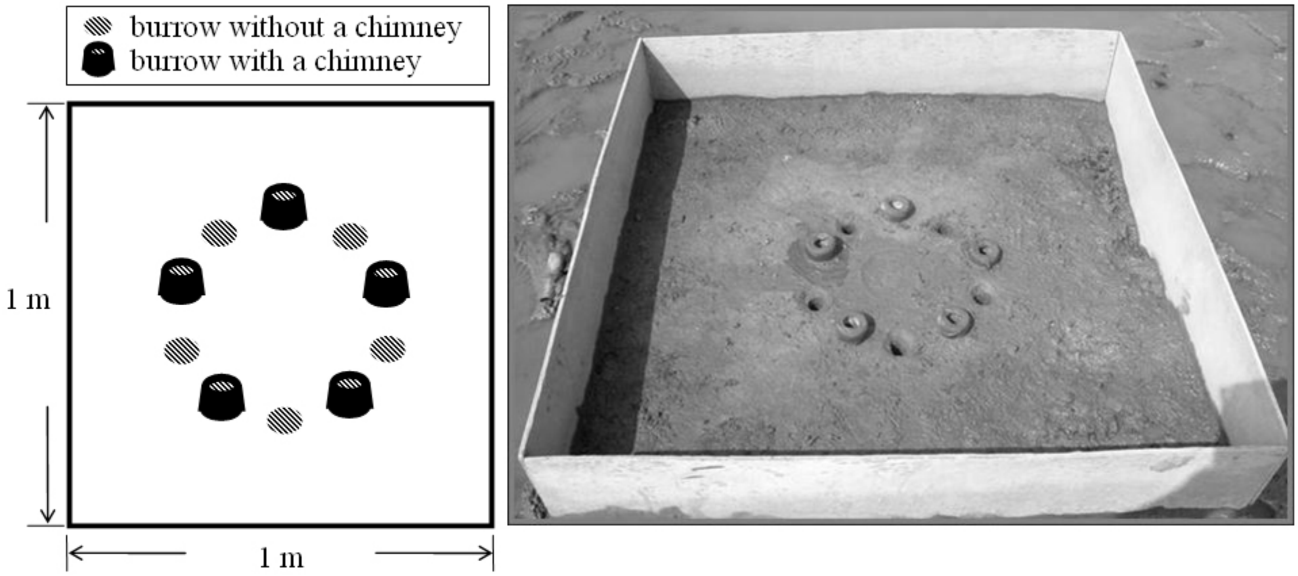

Figure 3. Diagram and picture of the enclosure in the choice-of-burrow experiment.

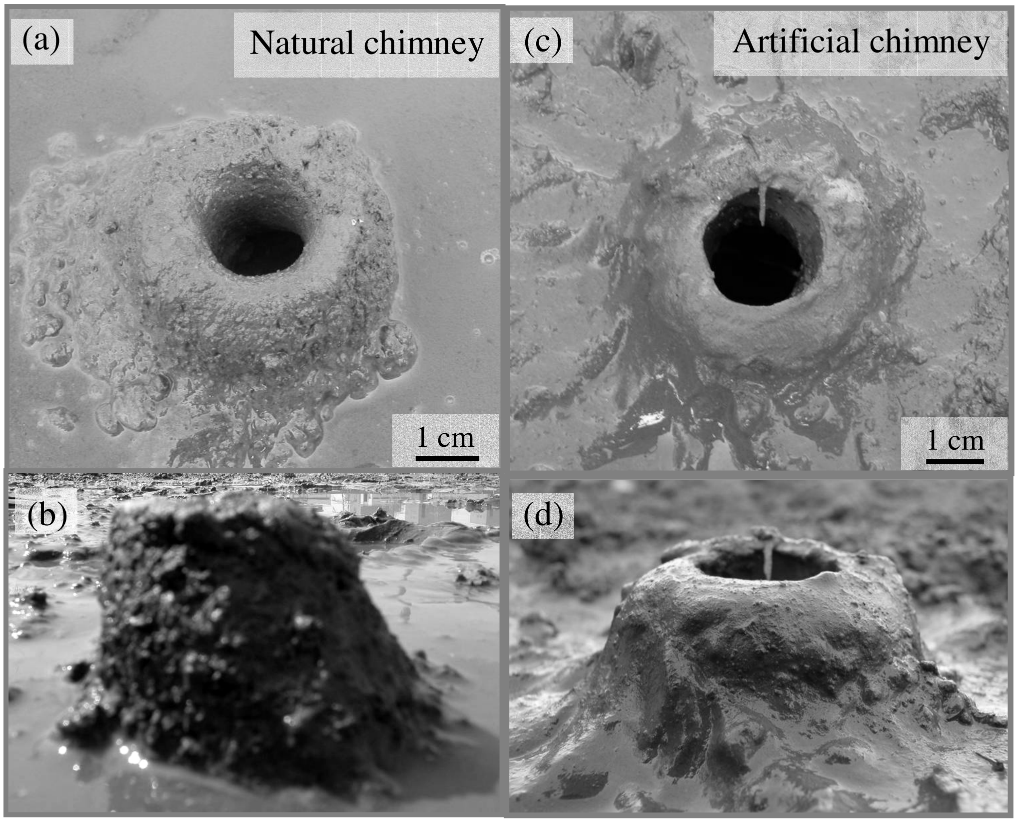

Figure 4. Pictures of a natural chimney (a: aerial view; b: side view) of *Uca arcuata* and a artificial chimney (c: aerial view; d: side view).

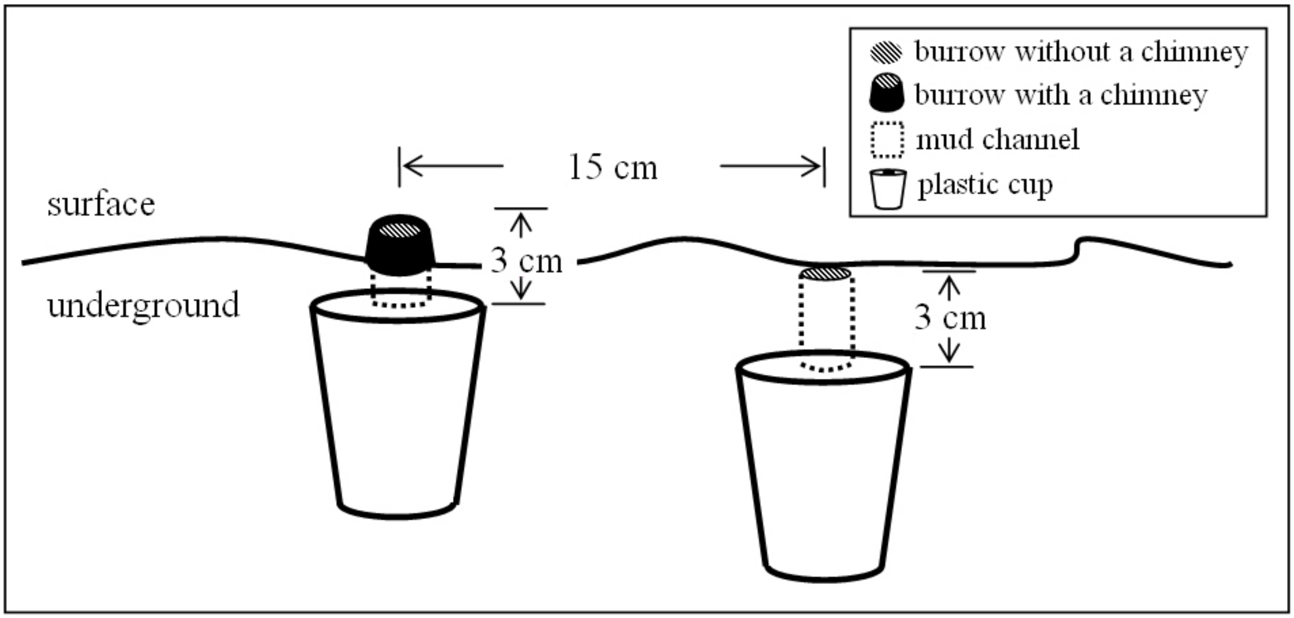

Figure 5. A cross-sectional view of the burrow trap set. The distance between the two traps of a trap set was 15 cm, and the length of both mud channels was 3 cm.

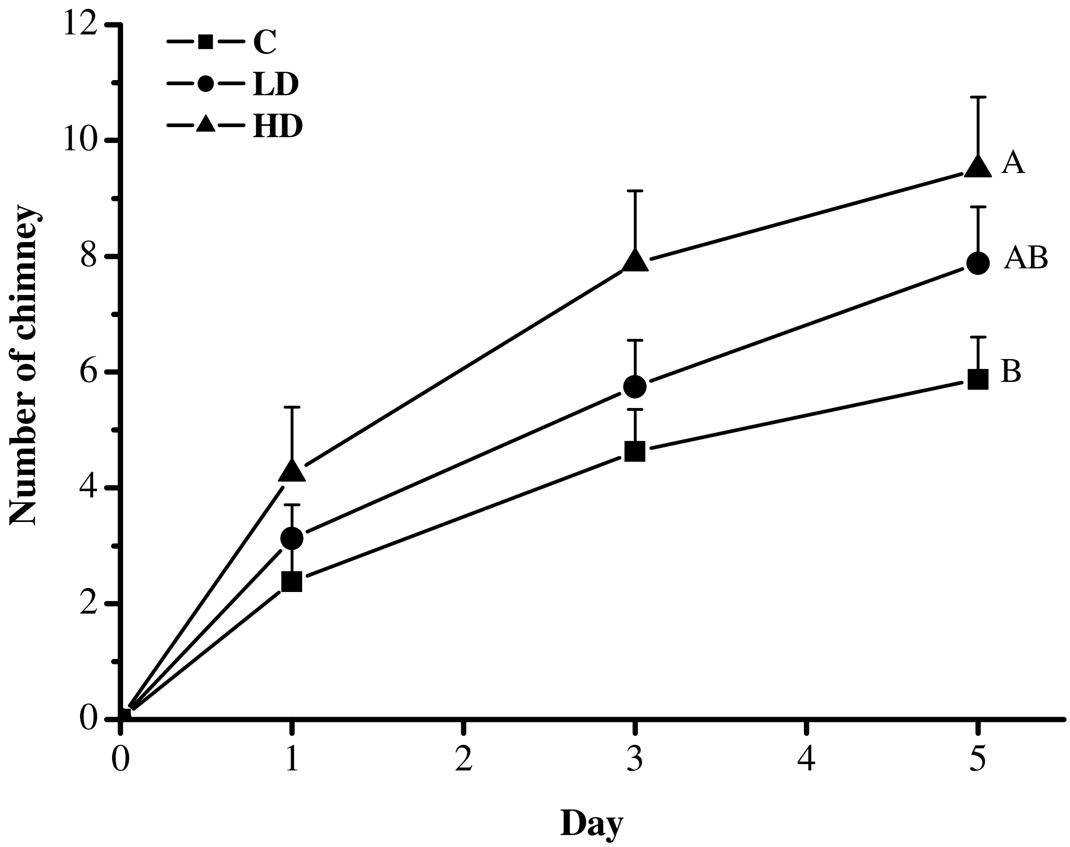

Figure 6. The chimney-building rate in the three manipulated density treatments. Each point was the mean± SE number of the chimneys on the surface in the enclosure (n = 8 in each treatment). HD: high density treatment. LD: low density treatment. C: control. The capital letters show significant difference between C and HD (Tukey's test).

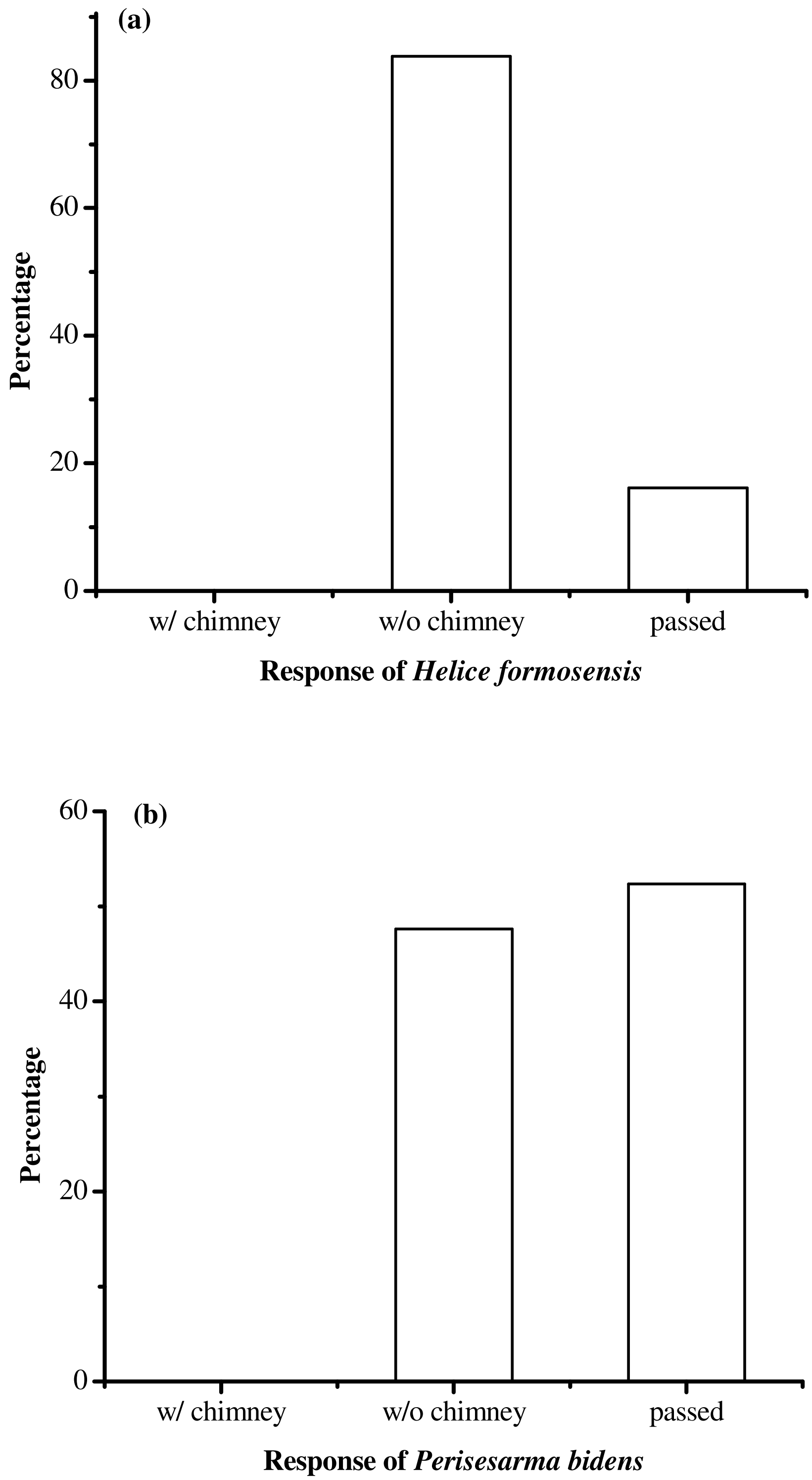

Figure 7. The responses of (a) *Helice fomosensis* (n = 68) and (b) *Perisesarma bidens* (n = 21) in the choice-of-burrow experiment. The responses were as follows: the crab entered a burrow with a chimney (w/ chimney), without a chimney (w/o chimney), and passed between burrows (passed).

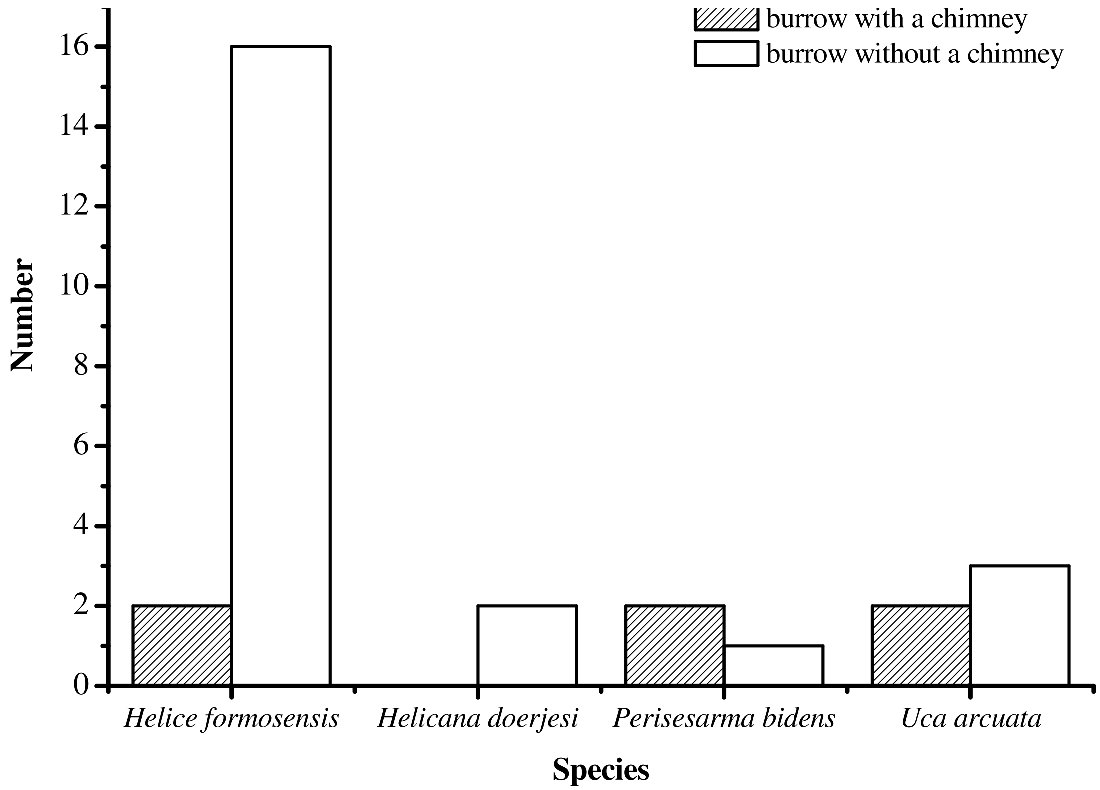

Figure 8. The number of captured crabs in each species. The total number of captured crabs was 28 individuals, including 18 *Helice formosensis*, 2 *Helicana doerjesi*, 3 *Perisesarma bidens* and 5 *Uca arcuata*.The hatched bar is the number of crabs captured in the burrow traps with a chimney, and the open bar is the number of crabs captured in the burrow traps without a chimney.

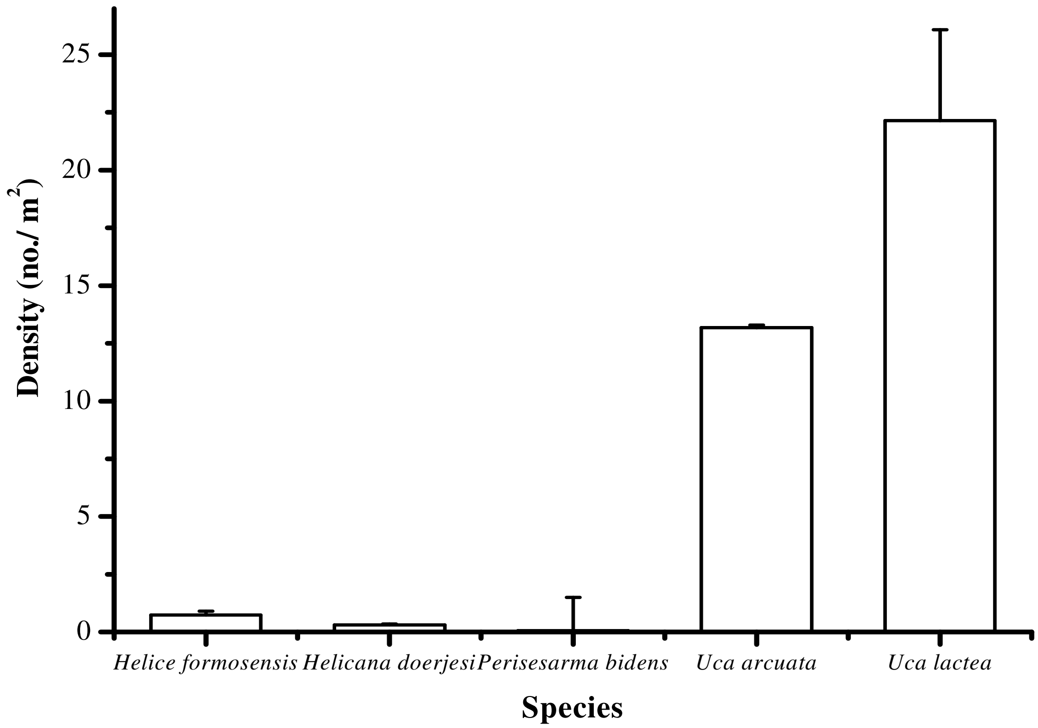

Figure 9. The crab density (no. / m^2) in the study site (a mudflat near the estuary of the Daan River, Taiwan). The survey sample size, n = 12, and each survey was collected from a 1.5 m × 1.5 m quadrate on the mudflat.