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Why do fiddler crabs build chimneys?

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Chimneys are mud mounds built by fiddler crabs that encircle the entrance to their burrow. Their function in many species is unknown. In *Uca capricornis*, crabs of both sexes and all sizes build chimneys, but females do so disproportionately more often. There are no differences in the immediate physical or social environments between crabs with and without a chimney. Chimney owners spend less time feeding and more time underground than non-owners. We show experimentally that burrows with a chimney are less likely to be located by an intruder. It is possible that some crabs construct chimneys around their burrow to conceal the entrance and reduce the risk of losing it to an intruder.

Keywords: fiddler crab; chimneys; structure building

1. INTRODUCTION

Many animals build structures: birds build nests, beavers construct dams and bees make honeycombs. Animals can adaptively modify their environment to create a structure whose function is obvious, such as a bed (gorilla nests: Aschemeier 1922), a trap (spider webs: Gould & Gould 2007), a lung (termite mounds: Gould & Gould 2007) or a mate-attracting device (fiddler crab hoods: Christy *et al.* 2003). It is, however, sometimes difficult to see how a structure benefits the builder. One such case is that of the chimneys built by fiddler crabs.

Chimneys are circular walls of mud that surround the entrance to a crab's burrow (Crane 1975; Thurman 1984). At least 11 fiddler crab species build chimneys, but the proposed functions vary greatly among species (Wada & Murata 2000; Shih *et al.* 2005). In *Uca arcuata*, juveniles and adults of both sexes build chimneys (Wada & Murata 2000). In other fiddler crab species, chimneys tend to be built by a specific size class or sex. In *Uca formosensis*, chimneys are built only by males that have recently attracted a female into their burrow to mate. They are assumed to hide the male from rivals while he expands his burrow for the female (Shih *et al.* 2005). By contrast, only large reproductive females build chimneys in *Uca thayeri*, *Uca urvillei*, *Uca coarctate* and *Uca forcipata* (Crane 1975; Salmon 1987). The adaptive value of chimneys is unknown for all but one species: in *U. arcuata*, the chimney decreases the likelihood of burrow intrusion by wandering crabs (Wada & Murata 2000). Thurman (1984) proposed that chimneys may act as temperature or humidity regulators in *Uca subcylindrica*.

The Australian fiddler crab *Uca capricornis* also builds chimneys. Here, we determine (i) which individuals build chimneys and when they build them, (ii) whether there are behavioural or local environmental differences (social or physical) between chimney builders and non-builders, and (iii) whether chimneys conceal the burrow entrance from intruders who might otherwise usurp the burrow.

2. MATERIAL AND METHODS

We studied *U. capricornis* at East Point Reserve, Darwin, Australia in November–December 2007. This species is notable for its carapace colouring which undergoes distinctive changes with each successive moult (Detto *et al.* 2008). Division of crabs into colour classes is therefore very similar to identifying distinct age classes.

We documented the sex and colour class distribution for 77 chimney-owning crabs. We compared these to a population sample obtained by noting details of all crabs within a 25 m^2 grid placed in the centre of the study site. We measured the height and width of 70 chimneys. The position of 41 chimneys was marked and we noted whether the burrow owner rebuilt it the following day (chimneys are destroyed by the incoming tide).

We matched 35 chimney owners with nearby non-owners of the same sex and colour class and watched each pair simultaneously for ± 30 min. We noted the time spent feeding or inside the burrow (each as a proportion of the observation period) and how often the crab was chased back to its burrow by an intruder (the resident ran quickly away from the wandering crab and the wanderer followed it for at least a short distance). We measured the distance to the nearest conspecific neighbour and noted its sex. We counted how many burrows were in a 35×35 cm area centred on the focal crab's burrow. We documented the physical environment around each focal burrow, noting the distances to the nearest mangrove pneumatophore, standing water and tree trunk. We noted how many mangrove pneumatophores were within a 35×35 cm quadrat around the burrow. The adjacent mud viscosity was measured by dropping a 20 g rod with 5 mm graduations vertically from a height of 40 cm. The depth of penetration into the substratum was our index of viscosity.

To test whether burrows with chimneys were less conspicuous to conspecifics than those without, we matched 38 pairs of chimney and non-chimney burrows that were less than 2 m apart and had occupants of the same sex and colour class. We temporarily surrounded each burrow with a plastic fence (8 cm high, 19 cm diameter) and placed a male ($n=20$) or female ($n=18$) that was at least as large as the burrow owner in a release container within the arena. We released the intruder and noted how long it took to locate the focal burrow. The trial was terminated if it had not located the burrow after 5 min. We used the same intruder for both arenas in paired trials, but a different intruder for each new pair. Trial order was randomized. Summary statistics are presented as mean ± s.d.

3. RESULTS

Most chimneys were owned by females (73%, 56/77). Females made up 48 per cent of the population sample ($n=69$) so they are disproportionately often chimney owners (Fisher's exact probability test: $p<0.001$). Chimneys were owned by crabs in all colour classes except for the plain black class (the largest, oldest crabs). In both sexes, small brown and white-mottled crabs most often had chimneys. There is, however, no difference in the distribution of colour classes between the population sample and that of chimney owners ($\chi^2_2=4.31$, $p=0.12$, $n=77, 69$).

Chimneys are built early in the low tide period, shortly after the tide recedes. It takes approximately 10 min for a chimney to be built. A crab collects mud from the sediment surface and carries it to the burrow entrance with its legs. The mud is piled up around the entrance (figure 1) to a height of 11±5 mm (range: 3–27 mm) with a width of 17.2±6 mm (range: 5.8–33 mm) ($n=70$). Of 41 chimneys, 18 (44%) were rebuilt the following day. The greatest

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Figure 1. *Uca capricornis* male on his chimney.

number of consecutive days of chimney building by the same crab was four.

Chimney owners spent more time underground than non-owners (15 versus 7.8% of the observation period; Wilcoxon signed-rank test: $Z=2.61$, $p=0.009$, $n=35$ pairs). Chimney owners also spent less time feeding than non-owners (54.6 versus 60.4% of the observation period; $Z=3.78$; $p<0.001$), even when we corrected for the amount of time spent on the surface ($Z=2.40$, $p=0.016$). Chimney owners were less likely than non-owners to be chased by an intruding crab (6/35 owners were chased one or more times; 20/35 non-owners were chased one or more times; Fisher's exact probability test, $p=0.001$) but not when we corrected for the relative amounts of time spent on the surface ($Z=1.66$, $p=0.098$). Both chimney owners and non-owners were seen to display (claw wave), but chimney owners never displayed from the top of their chimney.

The sex of the nearest neighbour did not differ between chimney owners and non-owners (owners: 6/16 females; non-owners: 11/21 females; Fisher's exact probability test: $p=0.29$). If chimneys were important in reducing burrow intrusions, we might expect more chimneys in high density areas; however, this was not the case (table 1). The local physical environment may influence chimney building if chimneys regulate temperature or humidity, or can be built only under certain conditions (e.g. mud viscosity). We found no difference between the local physical environment around chimney owners and that of non-owners in terms of the distance to the nearest mangrove pneumatophore, standing water or tree, nor in the local density of pneumatophores around their burrows, nor in the mud viscosity (table 1).

Finally, intruders more often located and entered a burrow without a chimney than one with a chimney (31/38 versus 16/38 trials; Fisher's exact probability test, $p<0.001$). It took significantly longer to locate a burrow with a chimney than one without (chimney: 217 ± 104.7 s; non-chimney: 115 ± 105.3 s; Kaplan–Meier survival analysis: $\chi_1^2=15.2$; $p<0.001$).

4. DISCUSSION

Uca capricornis build chimneys at the start of the daily low tide period. Both sexes build chimneys but females do so more often. Most burrows with a chimney were occupied by small, brown-mottled crabs but no more so than expected as this is the most common age/size/colour class in the population. Chimneys were equally likely to be built by crabs of all sizes and crabs rebuilt chimneys for 1–4 consecutive days.

Chimney building does not appear to be a response to local environmental conditions. Burrows with and without chimneys were equally far from mangrove trees, pneumatophores and standing water and in areas with mud of similar viscosity. This suggests that chimneys do not function in temperature or humidity regulation. There was also no effect of the immediate social environment. There was no difference between burrows with and without chimneys in the surrounding crab density or sex of their nearest neighbour, suggesting that chimneys do not function in territorial disputes with neighbours. Chimney building is also unlikely to have a reproductive function, since many builders were pre-reproductive (T. Detto 2008, personal communication). As the tendency to build chimneys differed between the sexes, time to moulting is unlikely to account for the observed patterns of chimney building.

The behaviour of crabs with and without a chimney differs markedly. Chimney owners spent less time feeding and more time underground. They were also less likely to be chased by intruders than those without a chimney. These results suggest that chimney owners are possibly 'shy' crabs (Reaney & Backwell 2007). Whether these behaviours are directly affected by the presence of a chimney is unclear and would require comparison of the behaviour of chimney owners whose chimney is left intact or removed.

Both male and female intruders were less likely to find the burrow of a chimney owner than that of a non-owner. Furthermore, even when intruders did locate a burrow with a chimney, it took them longer to do so. This suggests that a chimney hides the entrance to the burrow it surrounds. This is supported by field observations of burrowless crabs approaching and even feeding off chimneys, apparently without recognizing the burrow inside it. We suggest that the main function of chimneys is to disguise the burrow entrance. In *U. arcuata*, Wada & Murata (2000) similarly showed reduced intrusion rates into burrows with a chimney and proposed that chimneys confer protection against wandering crabs.

There are two further potential functions for chimneys but they are unlikely in this species. Chimneys may act as landmarks for burrow relocation; however, chimney owners spend most of their time on top of or within a few cm of the chimney. Alternatively, chimneys may function to reduce predation; however, the only observed predators (grapsid crabs) caught only wandering, burrowless crabs.

A burrow is an extremely important resource for a fiddler crab. It offers refuge from predators and the high tide, provides water, a place to thermoregulate and a site for egg incubation. It is therefore unsurprising that crabs attempt to conceal their burrow entrance from potential intruders. What is surprising, however, is how few crabs construct chimneys each

Table 1. Differences between chimney owners and non-owners in the local social and physical environments.

	chimney owner (mean ± s.d.)	non-owner (mean ± s.d.)	*Z* Wilcoxon signed-rank test	*p*-value
local crab density (total in 35 × 35 cm quadrat)	7.4 ± 5.9	8.1 ± 7.0	0.51	0.61
distance to nearest pneumatophore (cm)	2.56 ± 2.19	2.25 ± 1.89	0.55	0.58
distance to nearest standing water (cm)	44.11 ± 34.81	51.32 ± 35.77	0.84	0.40
distance to nearest tree trunk (cm)	201.88 ± 69.42	190.68 ± 81.24	1.65	0.10
local density of pneumatophores (total in 35 × 35 cm quadrat)	29.85 ± 10.40	29.30 ± 10.17	0.12	0.90
mud viscosity (in mm; see text)	1.03 ± 1.06	0.95 ± 0.86	0.43	0.67

day: less than 5 per cent of surface active crabs. Why do not all crabs build chimneys every day?

It may be a costly behaviour that is condition dependent, as is the construction of sand pillars by *Uca beebei* (Backwell *et al*. 1995). Possibly well-fed crabs, who need to forage less, can better afford the time and energy costs associated with chimney construction. In our study, chimney owners fed less than non-owners, which is consistent with this claim. The decrease in feeding time cannot be fully accounted for by chimney construction and repair itself, since chimneys are quick to build and are not repaired after damage.

It is interesting that chimney owners were more likely to be females. Females might benefit more from disguising their burrows as they have a poor ability to fight off intruding males (deRivera *et al*. 2003) while, as more efficient feeders (Valiela *et al*. 1974), females may be more able to sustain time or energy costs associated with building.

In sum, we have shown that chimneys lower the rate at which intruders locate burrow entrances. This is not because the intruders avoided the chimneys. In fact, they often approached and fed off the chimneys. It appears that they do not associate a chimney with a burrow entrance and this is likely to reduce the rates of burrow loss for chimney owners.

This study conformed to Australian and university animal ethics requirements.

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