

Muramatsu: Costs of possessing a sand ornament in *Uca lactea*

TO BUILD, NOT TO BUILD, OR TO DESTROY THE SEXUAL ORNAMENT: SAND

STRUCTURE CONSTRUCTION OF *UCA LACTEA*

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INTRODUCTION

In many animals, males possess secondary sexual traits, ornaments, that are used to attract mates (Andersson, 1994). These ornaments are often costly to produce and maintain (Walther and Clayton, 2004; Allen and Levinton, 2007), and only high-quality males can possess the ornaments (Zahavi, 1975). Like bowers of bowerbirds, ornaments can exist physically apart from the animals (external ornament; see Andersson, 1991). In such cases, males that hold an ornament must be sufficiently aggressive to fend off rival males who attempt ornament destruction (Borgia, 1985).

Males of at least 18 species of fiddler crabs (*Uca*) construct sand structures at the entrances to their burrows (Christy and Backwell, 2006). In several fiddler crab species it has been shown that sand structures attract females for mating (Christy, 1988a; Christy, et al. 2001, 2002, 2003a, b), and thus the structures function as a sexual ornament (Christy et al., 2002). Despite the mating benefit gained by possessing a structure, a considerable number of males do not construct structures (Yamaguchi 1971; Zucker 1974, 1978, 1981; Greenspan 1982; Christy 1988a, b; Backwell et al. 1995). Sand structures may be costly, and for some males, costs of building or owning a structure may exceed its benefits (Christy 1988a).

Based on the fact that food supplementation increases the frequency of sand structure construction, the sand structure of *U. beebei* (Crane, 1941) is energetically expensive and thus may act as an indicator of condition-dependent male quality (Backwell et al. 1995). Kim

and Choe (2003) also reported that food supplementation increases the frequency of structure construction in *U. lactea* (de Haan, 1835). However, constructing a structure itself does not seem energetically expensive (Christy 1988a; Backwell et al. 1995; Koga et al. 1998; Yamaguchi et al. 2005). Therefore, other costs associated with possession of a structure may account for the condition-dependence of structure construction (Christy 1988a; Backwell et al. 1995).

Sand structures are sometimes destroyed by the males that built them with apparent intent (Christy 1988b). Males might gain benefit by damaging the structures of rival males, (see Borgia 1985), but the reason why males destroy their own structures remains unknown. One possible explanation is that sand structures may impose some costs on male fiddler crabs. To test this, I removed or emplaced sand structures of *U. lactea* and observed how structure builders and non-builders responded to these manipulations.

METHODS

All observations and experiments were carried out in a dense colony of *U. lactea*, which was approximately 3500 m² in area, centered on an intertidal mudflat in the estuary of the Yabusa River, Kagoshima, Japan (31° 41' N, 130° 17' E). There was no vegetation in this area. Crabs emerged from their burrows and were active on the mudflat surface during the diurnal low

tide. Some males constructed sand structures at the entrances to their burrows. The entire study site was covered by the semidiurnal high tide, and sand structures constructed by crabs were destroyed by the tide. The experiments were carried out in the middle of the breeding season, between 12 June and 16 August 2004.

To randomly select burrows for the experiments, 10 sampling lines spaced 2 m apart were established at the study site. Both sides of each line were marked with 1-m-long, 4-mm-diameter wooden poles, which were placed vertically into the sediment, leaving approximately 5 cm above the surface. The distance of the two poles was 5 m. Each day one sampling line was chosen in random order, and crabs that had their burrow near (less than 20 cm from) the sampling line were used for the observations. I remained stationary beside the burrows for a while to identify the sex of the residents. Sand structures were removed from or emplaced at the burrows by hand with the help of an L-shaped 0.4-mm thin aluminum scraper. To avoid blocking the path, sand structures were emplaced on the side opposite to the direction where the residents emerged. To make it possible to relocate these burrows later, I marked the burrows with symbols written on the sediment. Burrow marking and manipulation of sand structures, which took approximately 1 hour, were carried out by the time of lowest tide. Two hours after the lowest tide, the numbers of constructed or destroyed structures were counted. The following six types of manipulations of the structures were performed:

- (1) Builders with no manipulations: Males that had their own structures (no manipulation).
- (2) Structure-replaced males: Sand structures were removed from males that had a sand structure, and structures of other males were emplaced at their burrows.
- (3) Structure-emplaced males: Sand structures of other males were emplaced at the burrows of males that did not have their structures.
- (4) Structure-emplaced females: Sand structures of other males were emplaced at the females' burrows.
- (5) Non-builders with no manipulations: Males that did not have their own structures (no manipulation).
- (6) Structure-removed males: Sand structures were removed from males that had their own structures.

The numbers of destroyed structures were compared between the following pairs: (1) Builders with no manipulations vs. (3) Structure-emplaced males, (2) Structure-replaced males vs. (3) Structure-emplaced males, (1) Builders with no manipulations vs. (4) Structure-emplaced females, (2) Structure-replaced males vs. (4) Structure-emplaced females, and (3) Structure-emplaced males vs. (4) Structure-emplaced females, using Wilcoxon's signed rank tests with Bonferroni correction. The numbers of constructed structures were compared

between (5) Non-builders with no manipulation vs. (6) Structure-removed males, using Wilcoxon's signed rank test.

Crabs were captured after the observations, marked by painting on their carapace, and released to their own burrows after they were kept for 5 minutes in a plastic cup to allow the paint to dry. Marked males were not used for the observation to avoid pseudoreplication.

RESULTS

Comparisons of the frequency of structure destruction (Fig.1)

For each manipulation, 145 crabs were observed (five crabs, 29 days). (3) Structure-emplaced males destroyed structures more frequently than (1) Builders with no manipulations (Wilcoxon's signed rank test; $Z=-4.017$; $P<0.001$) and (2) Structure-replaced males (Wilcoxon's signed rank test; $Z=-3.858$; $P<0.001$). (4) Structure-emplaced females destroyed the structures more frequently than (1) Builders with no manipulations (Wilcoxon's signed rank test; $Z=-4.330$; $P<0.001$) and (2) Structure-replaced males (Wilcoxon's signed rank test; $Z=-4.257$; $P<0.001$). There was no significant difference of the number of structures destroyed between (3) Structure-emplaced males and (4) Structure-emplaced females (Wilcoxon's signed rank test; $Z=-1.225$; $P=0.221$).

Comparisons of the frequency of structure construction (Fig. 2)

For each manipulation, 145 crabs were observed (five crabs, 29 days). (6) Structure-removed males constructed structures more frequently than (5) Non-builders with no manipulation (Wilcoxon's signed rank test; $Z=-2.719$; $P=0.007$).

DISCUSSION

The results obtained here suggest that sand structures of *U. lactea* are costly to possess.

Males that did not have their own structures destroyed experimentally replaced structures more frequently than males that originally possessed a structure. Females, which do not build structures, also destroyed experimentally replaced structures more frequently than males that originally possessed a structure. Thus, the presence of sand structures is detrimental to crabs that do not build structures, irrespective of their sex. It is possible to suppose that non-builders and females destroyed the replaced structures because the structures that were not built by themselves were unfamiliar to them. However, males that originally possessed structures rarely destroyed structures even when their structures were replaced with other males' structures. Therefore, unfamiliarity may not have been a reason for the destruction of the structures.

The costs of the structures can be divided into three categories: costs to build the structure, costs to maintain the structure, and costs associated with the possession of the structure.

Structure destruction cannot be explained by the costs to build or maintain them. Therefore, the possession of structures alone can be costly. The fact that at least some structure builders destroyed their own or experimentally replaced structures indicates that builders as well as non-builders may incur the costs of structures. Sand structures are able to attract females (Christy 1988a; Christy et al. 2001, 2002, 2003a, b), but the structures may also attract males and non-receptive females (Christy 1988a; Backwell et al. 1995). Builders thus incur greater costs than non-builders in time, energy, and risk of burrow loss due to the greater frequency of facing crabs other than receptive females (Christy 1988a). Therefore, it is possible that only the fraction of males that can afford the costs may build structures. In this scenario, sand structures may function as an indicator of the present quality of males. Indeed, males that have lost their major claw rarely construct structures even though they are physically capable of constructing structures without their major claw (Muramatsu, unpublished work).

The data obtained here about the frequency of structure construction revealed that structure-removed builders constructed structures more frequently than non-builders. However, the fraction of builders that rebuilt their structures was only 11.7 %. In *U. lactea*, males construct structures in the earlier half of their daily activity period, and the ratio of structure reconstruction following structure removal decreases with the passage of time

(Yamaguchi et al. 2005). Christy (1988b) reported that some males of *U. beebei* knocked over their structures near the end of their daily activity period. There might be few mate-searching females left at that time. If the benefits associated with the possession of a structure decrease with the time left, the costs of structure possession may outweigh its benefits near the end of the activity period. This may explain the low frequency of rebuilding by builders whose structures were removed in the middle of their daily activity period.

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FIGURE CAPTIONS

Fig. 1: Frequency of sand structure destruction by *U. lactea*.

Numerals on the bars represent the number of crabs that destroyed structures. "Builders" indicate males that originally possessed a structure. Valves obtained for pairs marked with an asterisk were significantly different. "N.S." denotes that the difference was non-significant.

Fig. 2: Frequency of sand structure construction by *U. lactea*.

Numerals on the bars represent the number of crabs that constructed structures. "Non-builders" indicate males that originally did not possess a structure. An asterisk denotes that the difference between the indicated valves was statistically significant.

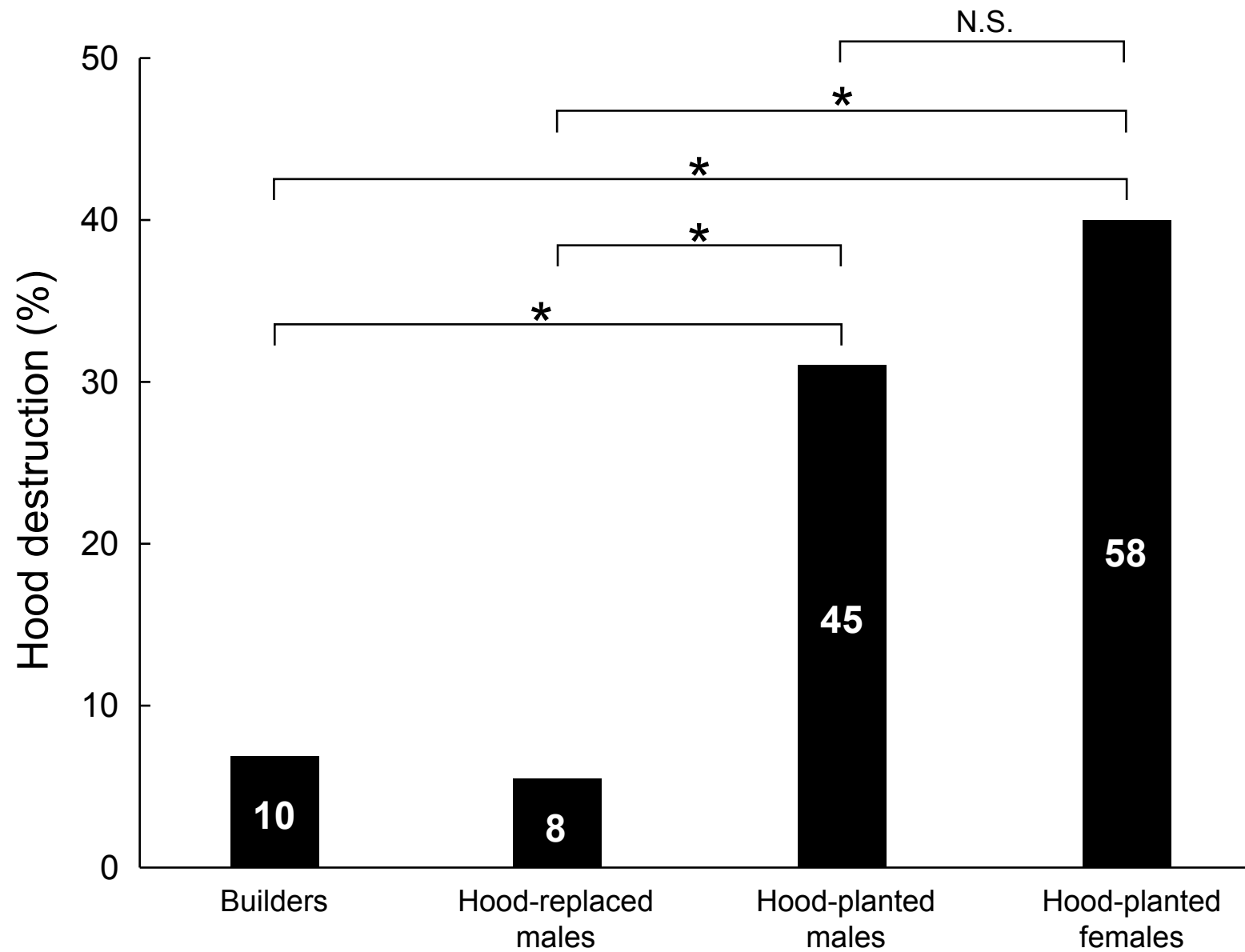


Fig. 1

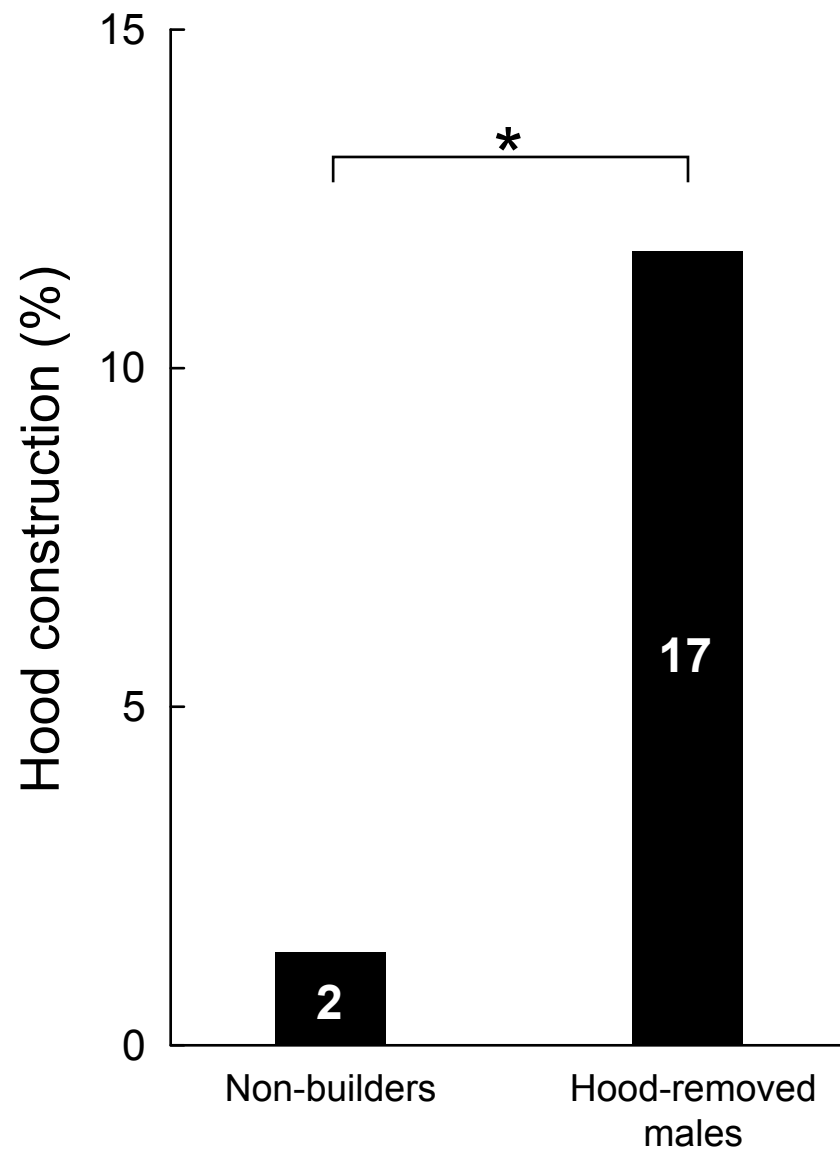


Fig. 1