

THE DESIGN AND PRODUCTION OF A SEXUAL SIGNAL: HOODS AND HOOD BUILDING BY MALE FIDDLER CRABS *UCA* *MUSICA*

by

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(Acc. 14-VI-2001)

Summary

Courting male fiddler crabs *Uca musica* sometimes build hoods at the entrances of their burrows to which females come for mating. Females differentially orient to burrows with hoods and thereby show a mate preference for hood builders. Here we describe how this mode of sexual selection may affect hood design and building. Larger males built generally larger but not higher hoods. Small males may build relatively high hoods so that they will be conspicuous to females of all sizes and construction or other costs may limit hood height. Most males built only one hood each biweekly reproductive cycle, typically on a day that many females chose mates, and they finished construction before females began mate searching. Both patterns fit predictions based on applying ideal free theory to the timing of sexual signaling. Sexual selection may favor more frequent hood building but the timing of hood building appears to be optimal.

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⁵⁾ We thank Thomas Kreuter for his assistance in the field and Bill Eberhard, Michael Jennions and Jochen Zeil for constructive criticism of an earlier draft of this manuscript. The Smithsonian Tropical Research Institute and the Japanese Ministry of Education, Culture and Science generously supported this research.

Introduction

Males of some species of birds (Gilliard, 1969; Andersson, 1991; Kusmierski *et al.*, 1997), cichlid fish (McKaye *et al.*, 1990; Taylor *et al.*, 1998) and ocypodid crabs (Linsenmair, 1967; Jones, 1972; Crane, 1975; Christy *et al.*, in press) build bowers, arenas, pyramids and other typically elaborate and decorated structures at mating sites. Unlike male-built nests or burrows, neither sex uses these structures when caring for eggs or young. Lacking a utilitarian role in breeding, they may be signals that attract receptive females or repel intruding males.

Courting males of the fiddler crab *Uca musica* sometime build sand hoods at the entrances to their burrows to which they attract females for mating (Crane, 1975). Males of 17 (Christy, 1988a; Christy *et al.*, in press) of the approximately 100 species in the genus *Uca* (Rosenberg, 2000) build structures at their burrow openings; relative to male body size, the hoods of *U. musica* are the largest (Fig. 1a). We have demonstrated experimentally that hood building is sexually selected because females differentially approach hoods and mate with their builders (Christy *et al.*, in press). We showed that hoods attract females by removing hoods from builders' burrows, adding hood models to non-builders burrows and recording the effects of these manipulations on female behavior and male courtship success. Thus, we treated hood building as a discrete behavior with two states and hoods as signals that were present or absent. This was appropriate for demonstrating sexual selection for hood building but not for understanding how such selection may affect hood structure and the frequency and timing of hood building. Here we describe the hoods and hood building behavior of male *Uca musica* and interpret both with regard to their function for mate attraction.

Reproductive behavior of Uca musica

Uca musica (≈ 1 cm carapace width) lives in burrows in mixed-sex colonies on intertidal sand flats and bars in the tropical Eastern Pacific where it breeds year-round (Crane, 1975). Except when mating, crabs occupy burrows alone. They are active on the surface for about 6 h daily when their habitat is exposed to the air by the daytime semidiurnal tide. *U. musica* rarely emerge at night and surface activity is minimal for 2-3 consecutive days every two weeks when both semidiurnal low tides occur during twilight. Courtship and

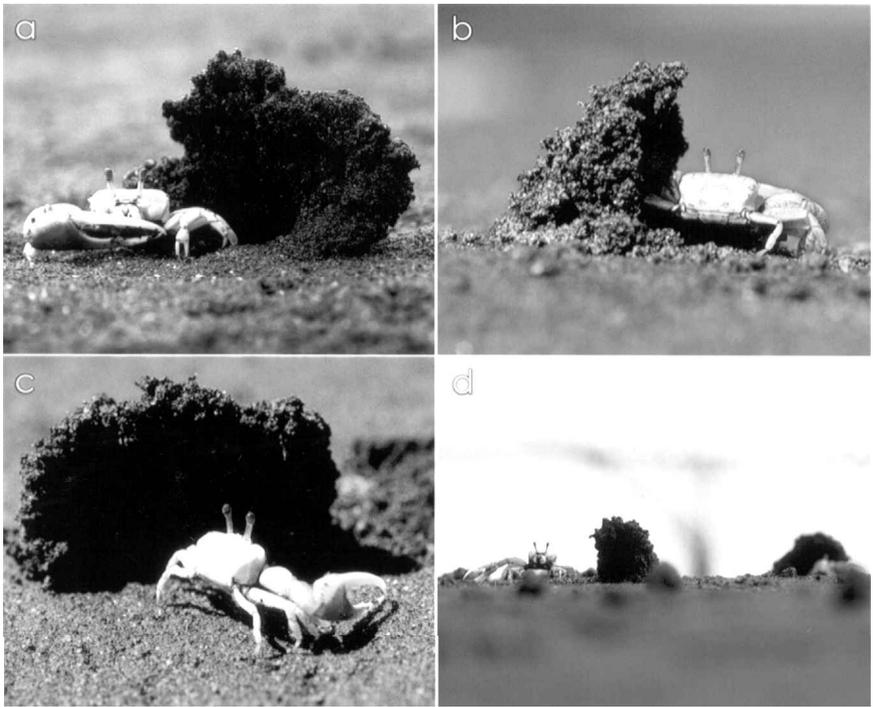


Fig. 1. Courting male *Uca musica* and their sand hoods. (a) Relative to male size, hoods are the largest structures built by male fiddler crabs. (b) Hoods arch over the burrow entrance. (c) Unusually broad hoods become walls that are asymmetrical relative to the burrow entrance. (d) An approximately crab's-eye view of hoods. Hoods are tall enough to be seen above the visual horizon of mate searching females. The objects in foreground are balls of sand made during burrow excavation by another fiddler crab species.

mating follow a biweekly cycle with a monthly modulation at some locations (Zucker, 1976, 1978).

Reproductively active males court from and defend burrows in the middle to upper intertidal zones (Zucker, 1984). Each day during the 8-10 day biweekly mating period, some courting males build hoods (Fig. 1a; Zucker, 1978). Hoods collapse when they are covered by the tide so males build them anew daily. Hood builders usually blanch to white by the time of low tide and they allocate relatively less time to feeding and more time to courtship than do darker non-builders (Zucker, 1976; Christy *et al.*, in press). Pillar building male *Uca beebei* also court more and feed less than do non-builders (Christy, 1988b) and Backwell *et al.* (1995) demonstrated experimentally that better

fed males more often build pillars. Structure building probably is a costly and condition-dependent behavior.

Males may increase the benefit (attractiveness) to cost (time and energy) ratio of hood building by building when they are most likely to encounter mate-sampling females. Two temporal scales are relevant — the daily tidal activity cycle and the biweekly reproductive cycle. We suggest that loss rates on investments in courtship signals to attract females are analogous to mortality rates in models of the competitive timing of life history events for reproductive advantage (Milinski & Parker, 1991). For example, a hood that lasts but a day and a male insect that soon dies after emergence present similar timing problems. The expected investment patterns in hood building on the tidal activity and biweekly temporal scales may correspond to the two ESS extremes predicted by application of ideal free theory to the timing of male insect emergence — one extreme when mortality rates (loss rates on investments) are very low, the other when they are very high (Iwasa *et al.*, 1983; Parker & Courtney, 1983). Fights at burrows, predatory birds and the wind sometimes destroy hoods but the hood loss rate is low during a given activity cycle. With a low loss rate, the ESS is for males to build their hoods before females begin mate sampling so that they 'cover' the activity cycle. In contrast, the tide destroys hoods daily so that a male's investment in hood building on a given day never yields a gain on subsequent days. Under these high loss rate conditions the ESS is for the daily male investment in hood building to be directly proportional to the daily intensity of mating. We therefore expected that males would build hoods early in the activity cycle, before receptive females begin mate sampling, and that there would be a constant proportional relationship between the number of hoods and the number of matings during the biweekly reproductive cycle.

Sexually receptive female *U. musica* leave their burrows, move through the area with courting males and stop at, on average, 17 males' burrows before they stay in one for mating (Christy *et al.*, in press). Courting males either stay within a few cm of their burrow entrances and direct lateral-circular claw waving to distant females, or they move as much as 1 m from their burrows, closely approach females (<5 cm) and lead them with rapid vertical waves back to their burrows. By removing males' hoods and replacing them with models positioned about 3 cm away from the burrow opening, we showed that females visually orient to hoods primarily when males court from a distance and do not lead them to their burrows (Christy

et al., in press). Studies of fiddler crab vision (Land & Layne, 1995; Zeil & Al-Mutairi, 1996) and visual and non-visual orientation mechanisms (Herrnkind, 1983; Langdon & Herrnkind, 1985; Cannicci *et al.*, 1999; Zeil & Layne, in press) suggest that hoods may be conspicuous and attractive because they are tall, vertical structures. Sexual selection might favor tall but not necessarily wide or thick hoods. We therefore predicted that hoods should vary less in height than in width and that courting males of all sizes should build tall hoods.

Methods

Study period and sites

We conducted this study in February-April and August-November 1995, April 1998 and January-June 1999. We observed crabs at various locations on several sand bars and associated flats on the west bank of the Pacific entrance to the Panama Canal about 0.75 to 1 km up-stream of the Bridge of the Americas.

Hood structure

We measured seven features (Table 1) of 100 hoods in an area with abundant courting males. We noted whether the scrape marks males make when they collect sand to build their hood were to the right or left of a line that was perpendicular to the frontal plane of the hood and

TABLE 1. *Hood structure and hood-building behavior*

Hood structure ($N = 100$ hoods)						
Height (mm)	Width at base (mm)	Width at 1 cm (mm)	Depth at base (mm)	Depth at 1 cm (mm)	Acute angle of back	Asymmetry to L or R
23.2 ± 3.17	33.3 ± 5.35	28.4 ± 6.06	21.2 ± 3.96	16.4 ± 3.41	66.2 ± 5.97	0.57 ± 0.061
Hood building behavior ($N = 20$ males)						
Duration of building (min)	Number of loads	Time per load (s)	Time between loads (s)	Minimum distance to scrapes (cm)	Maximum distance to scrapes (cm)	
36.1 ± 12.96	56.5 ± 11.26	5.5 ± 2.25	17.5 ± 7.64	2.1 ± 1.93	7.4 ± 3.21	

Values are means \pm one standard deviation. Asymmetry: the proportion of the total width of the wider half of the hood, either to the left or to the right of center. The means of the time per load of sand and time between loads are the averages of the means of ten measurements per male.

bisected the burrow opening. We dug the males out of their burrows, noted their handedness, and measured (calipers, 0.1 mm precision) their carapace width and length, and the length of the propodus ('hand' and 'fixed finger') of their large cheliped.

Hood building behavior

On each of 9 days, we recorded the time it took 2 or 3 males to build their hoods and the number of loads of sand they used. We also measured the time it took each male to collect and deposit 10 sequential loads of sand and the time between loads. We noted how males built their hoods, how they responded to other crabs during construction and the time they blanched to white relative to when they finished construction. After males completed their hoods, we measured them and their hoods, recorded the position of the scrapes marks the males made when they collected sand and measured the distance from the burrow to the nearest and farthest edge of the scraped area.

Frequency and timing of hood building

Daily activity cycle — Since hood loss rates are low, we predicted that males would build their hoods before females begin mate sampling. We recorded when males built hoods and when females searched for mates on three days with morning low tides. Beginning soon after crabs emerged, each of two observers continuously watched one of two contiguous 8×2 m rectangular areas. Each area was divided into eight 1×2 m plots and extended from the upper to the lower limit of the distribution of courting males in a high-density colony (see Christy *et al.*, 1998). We divided our continuous observations into 15 min intervals during which we sketched on scale maps the locations of each new hood and counted the number of times we saw females stop at ('visit') the burrows of courting males. Individual females usually visited several males but we did not attempt to assign visits to individuals. Hence, we recorded the intensity of mate sampling, not the number of mate-sampling females. We stopped about 20 min before tidal immersion, 4–5 h after we began. On two days, after males built their hoods, we counted the number with and without hoods in the sixteen 1×2 m plots.

We also counted female visits to males during a 'hood addition' experiment but we did not record when males built hoods (see Christy *et al.*, in press). On each of four days we recorded, at 10 min intervals, the number of times females visited males with and without natural and model hoods (30–40 males per group). We began at low tide and ended about 2.5 h later, about 30 min before immersion at this lower site.

Biweekly cycle — Hood building undoubtedly is costly and hoods do not 'survive' from one day to the next. Hence, we expected that the daily tendency for individuals to build hoods, and the number of hoods built per day, would track the biweekly breeding cycle. From 13 February to 23 March 1995 we captured and individually marked 39 males in the high-density colony. Except for days with dawn and dusk low tides, each day during the hour after low tide we recorded the color (dark or white) of each male, whether he predominantly fed or claw waved and whether he built a hood. We also noted when any marked male mated. We saw 8 males almost daily for 2 or more weeks, long enough to detect possible biweekly cycles in their reproductive activity. During the same period we counted daily, at 1 h past low tide, the total number of hoods along both sides of a sandbar, about 100 m long and 6 m wide, that extended from but did not include the area where we watched the marked males.

We studied how the proportion of hood builders varied with the biweekly cycle by counting daily the total number of courting males and the number with hoods in seven 1 m² fixed plots. The plots were positioned to sample the entire distribution at the high-density site — an area about 175 m² that was delimited by natural boundaries and contained the two 16 m² plots described above. Our counts spanned two biweekly breeding periods.

We determined how the intensity of hood building and mating varied over the biweekly cycle by counting daily, over a two-month period, the total number of open and plugged hooded burrows in the high-density area. We made these counts at 3 h past low tide, approximately 1 h before immersion and after most females have chosen mates (Fig. 4). At this time, a plug in a burrow of a courting male reliably indicates a mating.

Results

Hood structure and hood building behavior

Hoods are cupped, rounded, asymmetrical walls, about two-thirds as high as wide, that rise sharply from a thick base and arch over the burrow entrance (Fig. 1a, b; Table 1). They were significantly less variable in height than in width (*z*-test (Zar, 1999, p. 145); *CV* height = 13.624, *CV* width = 16.095, *z* = 123.5, *p* << 0.001). Wider hoods were higher (*r* = 0.45, *p* < 0.01, Fig. 2a) and more asymmetrical (*r* = 0.58, *p* < 0.01, Figs 1c, 2b) with the

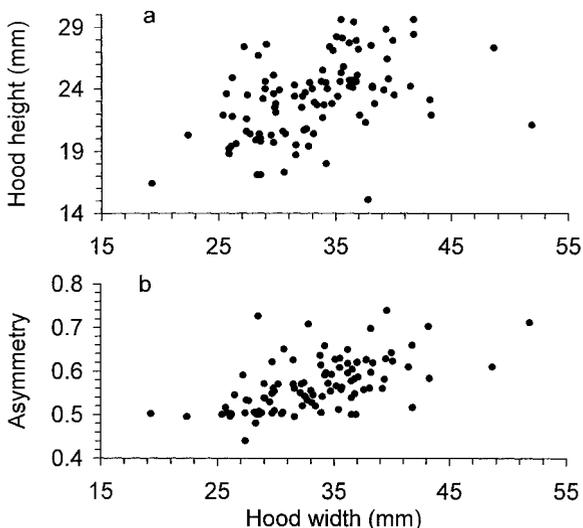


Fig. 2. Hood height (a) and asymmetry (b) in relation to hood width. Asymmetry is the proportion of the total hood width made up by the wider part of the hood measured from the center of the burrow opening to the right and left lateral edges.

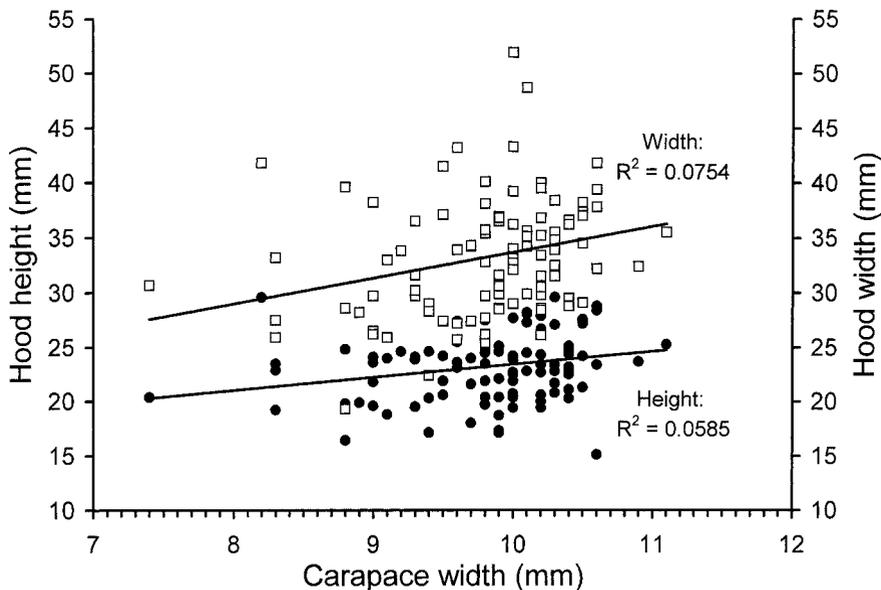


Fig. 3. Hood width (open squares), and hood height (filled circles) in relation to male carapace width. Hood height increased only slightly with male size, perhaps because small males built relatively high hoods.

larger wall almost always (97 of 100 cases) on the same side of the hood as the oblong patch of scrapes males made when they collected sand for their hood. The scraped patch always ($N = 30$) was opposite the side of the male with the large claw. Larger males built higher and wider hoods (height = $11.36 + 1.207 \times \text{carapace width}$, $F_{1,98} = 6.0887$, $p = 0.015$; width = $10.23 + 2.35 \times \text{carapace width}$, $F_{1,98} = 7.9949$, $p = 0.006$, Fig. 3) but these relationships are weak as male size explains only about 6% and 8% of the variation in hood height and width, respectively.

Males built their hoods in one to three bouts of construction activity in which they collected sand from very near their burrows, always with the legs on the side with the large claw, and deposited it at the entrance at a rate of about 2.5 loads per minute (Table 1). Males did not feed during the approximately 35 min construction period and none blanched to white, though a few (5/20) began to lighten as they finished construction. The 20 males courted only 4 females during the 12 male-hours of observation but 15 males waved from a few to many times without there being an apparent receiver. Hood dimensions, male size and building behavior were recorded for 17 cases.

Significant positive correlations (Pearson's r , Bonferroni correction) were found between male size (carapace width and propodus length) and hood width ($r = 0.48$ and 0.59) and depth ($r = 0.67$ and 0.65), between hood height and the number of loads ($r = 0.49$) and between the time for each load and the time between loads ($r = 0.58$). Hence, larger males built more robust, but not higher hoods, higher hoods took more loads, but not more time to build, and the slower a male collected and deposited sand, the longer he paused between loads.

Timing of hood building and mate sampling

We recorded the timing of hood building and mate sampling on three days just before a biweekly peak in hood building (28-30 March, 1995; Fig. 6). Most males built their hoods before females began to move and respond to courtship, and 76-99% of hoods were built by the time females had made half of the total number of visits to courting males (Fig. 4). The time of low tide advance from 0749 h on the first day to 0926 h on the third when emergence, hood building and mate sampling occurred about 45 min earlier

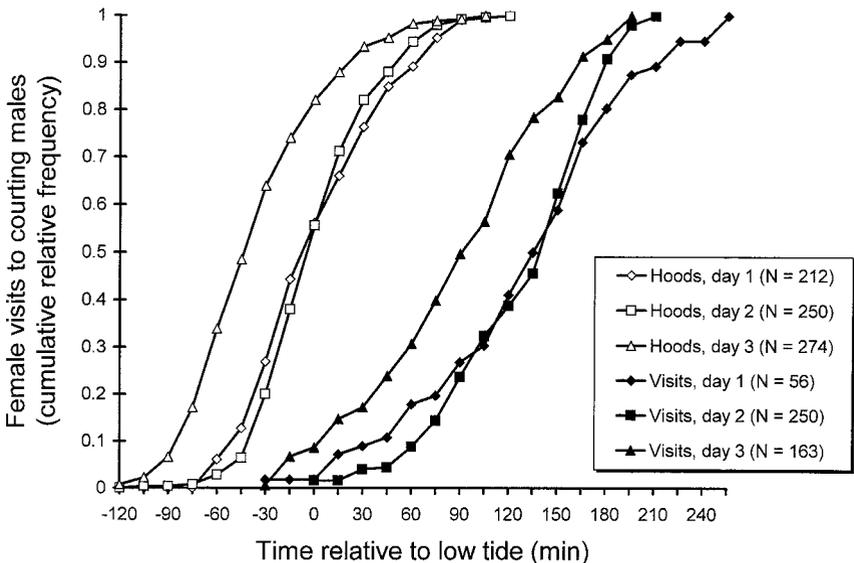


Fig. 4. The timing of hood building (open symbols) and female visits to courting males (filled symbols) in the tidal activity cycle on three days with early morning low tides.

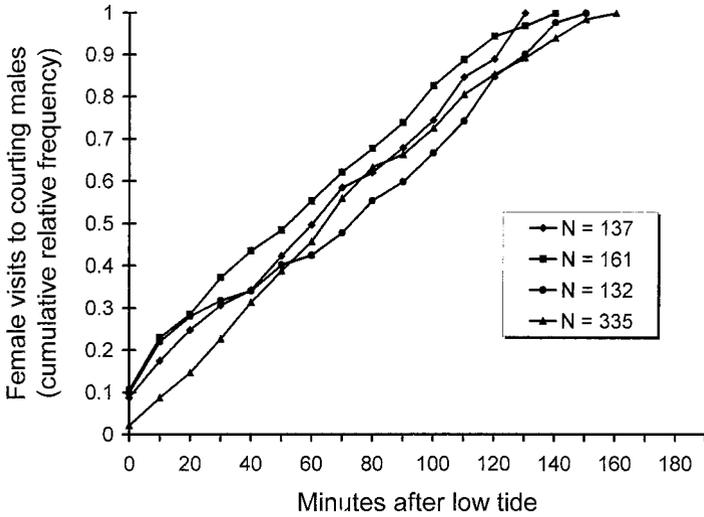


Fig. 5. The timing of females visits to courting males on four days with mid to late morning low tides.

relative to the time of low tide. The timing of 765 visits to 525 males over a 4-day period with low tides from 0915 to 1136 (Fig. 5) suggests that the latter pattern is typical. On 29 and 30 March, mean (\pm SD) male density ($N = 16$ plots) was 12.2 ± 3.08 and 12.8 ± 3.78 m^{-2} and the proportion of hood builders averaged 0.65 ± 0.183 and 0.66 ± 0.124 .

The 8 marked males we observed for 2 or more weeks courted intensively for a few days twice each month (Fig. 6). All but one (#3) built at least one hood and only one (#6) build a hood on successive days. Hood building by these males and those on the adjacent sand bar showed a biweekly pattern with peaks around the full and new moons (Fig. 6).

Later in the year, hood building in a 175 m^2 portion of the high-density site, which included all the courting males, again followed a biweekly pattern, but relatively few males built hoods in August and September when it often rained (Fig. 7). The daily average proportion of hood builders in the seven 1 m^2 plots, which were positioned throughout this larger area, peaked on 27 August at 0.21 ± 0.137 , with 11.0 ± 3.91 males m^{-2} and on 9 September at 0.28 ± 0.959 , with 10.4 ± 3.31 males m^{-2} . These proportions are about 40% of those during the March hood-building peak when male densities were slightly higher. There was no relationship in the seven plots between the daily total number of hoods and the daily average male density (excluding

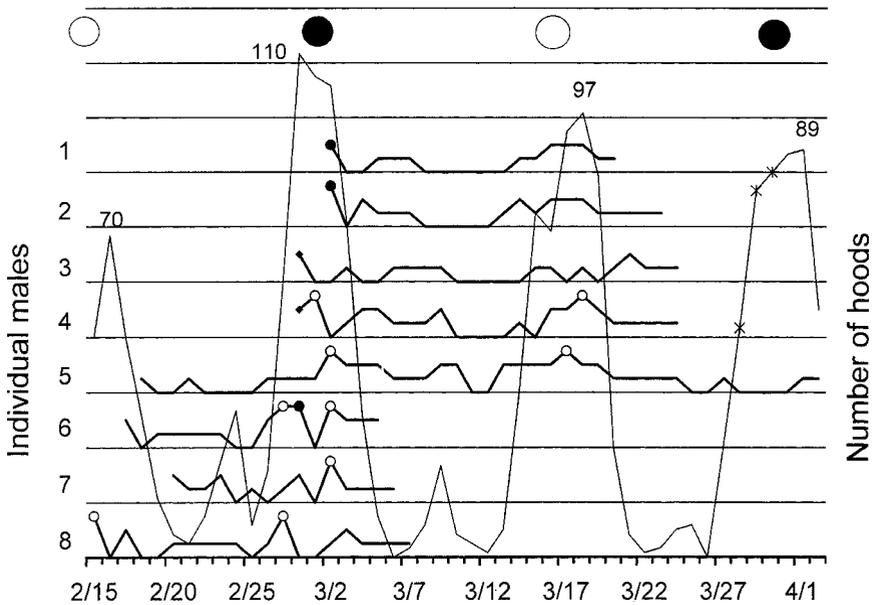


Fig. 6. Hood building in a fixed area of an open population and the reproductive activity of eight marked males over a 1.5-month period in 1995. The maximum numbers of hoods are given for each biweekly cycle. The stars in late March on the hood-building curve show the days on which we measured the timing of hood building and mate sampling (see Fig. 4). Each day marked males were classified relative to four levels of increasing reproductive activity: inactive, feeding during low tide, waving during low tide, waving and built a hood (circles; filled or open). Filled symbols show when males mated.

days with rain and low tides before 0800 and after 1700; $R^2 = 0.048$, $F_{1,16} = 0.8107$, $p = 0.381$, Fig. 8). Hence, variation in the proportion of hood builders, not male density, probably produced the temporal pattern in hood abundance. Considering days with >150 hoods (*e.g.* days with good weather and activity; Fig. 7) the number of hood builders who mated in the 175 m^2 area increased significantly with the number of hoods ($F_{1,27} = 68.178$, $p < 0.001$) but the proportion who mated did not ($F_{1,27} = 2.066$, $p > 0.15$). Hood builder mating rates were nearly constant over a three-fold range in hood abundance with $9.0 \pm 2.07\%$ of the hood-builders mating daily (Fig. 9).

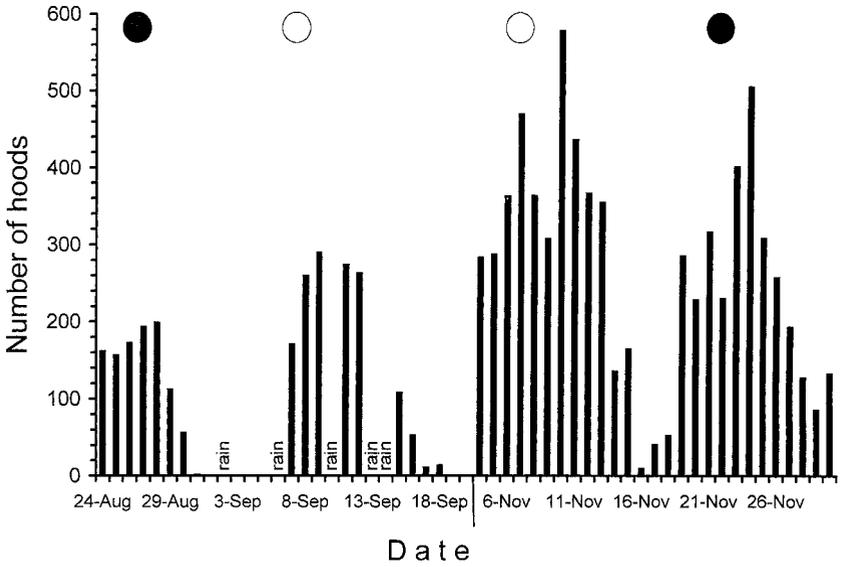


Fig. 7. Daily counts of the number of hoods in a fixed area within a larger population over four biweekly periods in 1995.

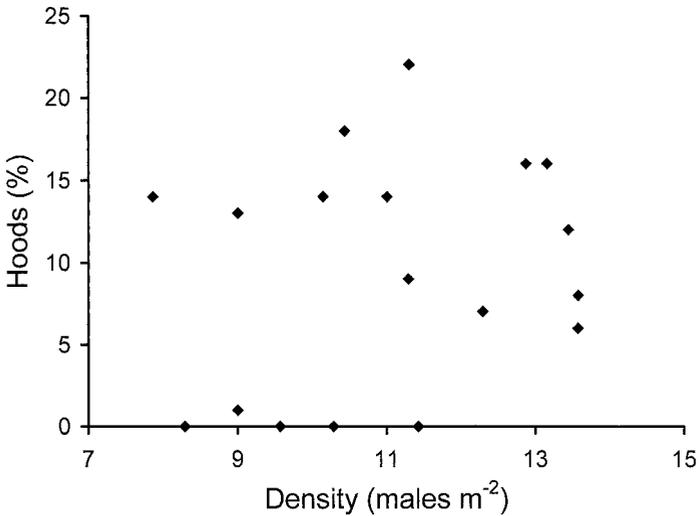


Fig. 8. The percentage of hood builders in relation to male density. Each point is a daily average ($N = 7$, 1 m^2 plots) of each variable.

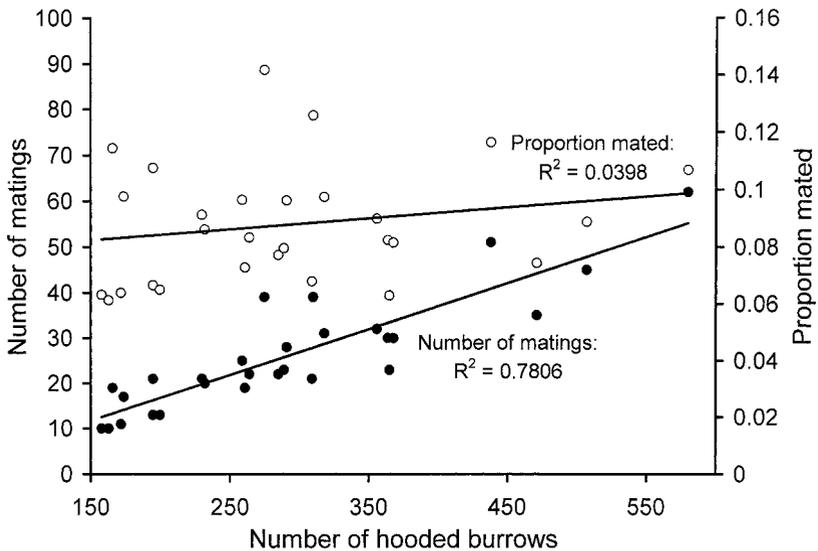


Fig. 9. The number (filled circles) and the proportion (open circles) of hood builders that mated in relation to the number of hooded burrows.

Discussion

Hood structure and signal design

The effects of hood height and width on attractiveness can be profitably understood by considering how females respond to hoods (Christy *et al.*, in press) and features of fiddler crab vision and orientation behavior. Females differentially orient to burrows with hoods when they leave one male's burrow and move to another and are not closely led to that burrow by its owner. However, after females have stopped at males' burrows, they are just as likely to stay and mate with builders, as they are with non-builders. Hence, a hood on a burrow increases the chance that a female will approach and mate with the burrow resident but females don't use hoods to discriminate between acceptable and unacceptable mates.

As they move away from a burrow, crabs use a non-visual mechanism (Zeil, 1998), which probably is based on leg odometry (Zeil & Layne, in press), to track the location of the burrow entrance so that they can return quickly and directly to it. As females move between burrows they must switch their orientation reference from the burrow they are leaving to a new one. Hoods may attract females in this context because they elicit landmark

orientation (Herrnkind, 1983), the tendency for burrowless crabs to orient visually to vertical objects, over objects of the same angular size but different shapes (Langdon & Herrnkind, 1985). Landmark orientation is thought to be adaptive because it leads crabs to parts of plants and other natural objects that provide temporary cover. However, it has not been shown that orientation to vertical objects is especially beneficial; crabs that hide against objects of other shapes might be equally difficult for predators to detect.

Hoods, pillars and other vertical objects may be differentially attractive simply because crabs are better able to resolve objects in the vertical than in the horizontal plain. Fiddler crab eyes have equatorial zones (approximately $\pm 10^\circ$) of acute vertical resolution which crabs keep aligned with the horizon (Land & Layne, 1995; Zeil *et al.*, 1986; Zeil & Al-Mutairi, 1996). Hoods may be most conspicuous if they are tall enough so that their upper edge, a line of contrast between the dark hood and the generally bright horizon (Fig. 1d), is imaged within the zone of acute resolution of the eyes of approaching females. This appears to be the case. Hoods are taller than the eyes of their builders (Fig. 1) and the sexes are comparable in size. More importantly, hood height increases only slightly with male size (Fig. 3). Smaller males may build relatively high hoods so that they will be conspicuous even to the largest females. Conversely, larger males may build relatively low hoods because the cost of construction may increase more rapidly with hood height than does conspicuousness. The most conspicuous hood per unit of construction cost may be one that is tall enough so that most females, at typical female-to-burrow distances, will see its upper edge in their zone of acute vertical resolution. Thus, males may build hoods that are tall enough to be conspicuous to most females, and the relatively small variation in hood height ($CV = 14\%$) may little affect hood attractiveness.

The horizontal resolving power of fiddler crabs' eyes, which is poor compared to the vertical resolving power, is relatively evenly distributed around the eye (Zeil *et al.*, 1986). Hence, hood conspicuousness, as determined by horizontal angular size, may increase continuously but slowly with hood width. Larger males built wider, thicker and more asymmetrical hoods, the most exaggerated examples of which are better described as walls (Fig. 1c). Hood attractiveness is likely to increase with hood width but at substantial cost.

Hood building, timing and frequency

Hoods mediate sexual communication, but hood building does not and this behavior lacks features common to visual displays that have evolved for mate attraction (Bradbury & Vehrencamp, 1998, p. 577-585). For example, hood building is not stereotyped. The coefficients of variation of the elements of building behavior we measured (Table 1) range from about 20-90% compared to about 20% or less for the structural features of hoods and for components of the claw waving display of *Uca pugilator* (Hyatt, 1977). Nor are the movements made during hood building obviously exaggerated for signal function. A probable case of signaling by modified and exaggerated sand deposition behavior has been described for a ghost crab (Schober & Christy, 1993). The origin of the collect-and-deposit behavior that is the basic element of structure building by fiddler crabs is not clear; it does not appear to be related to burrow excavation.

Sexual selection due to competition to attract females may strongly affect the timing and frequency of hood building. Given low mortality rates, models of the timing of male insect emergence to most profitably encounter and mate with emerging females (Iwasa *et al.*, 1983; Parker & Courtney, 1983) led us to expect that male *U. musica* would build hoods before most females wander and choose mates in the tidal activity cycle; indeed, this was the case (Fig. 4). It could be argued that males build early because they cannot wave while building and they would miss courtships if they built later when many females are mate sampling. Although few females moved during the hood-building period, some males waved extensively indicating that hood building and waving are not incompatible. Instead, we suggest that males build early because the longer they wait, the greater the chance that the females they court will be differentially attracted to the hoods of early building neighbors. Signal competition may favor males who are prepared with the most attractive signal when females begin mate sampling. Since the hood loss rate is low during a given activity period, males who build early are unlikely to lose their investment before they benefit from it.

Also as predicted by models of the competitive timing of life history events, but with high mortality rates (Iwasa *et al.*, 1983; Parker & Courtney, 1983), hood building closely tracked biweekly variation in the intensity of female receptivity and mate choice. Since males build hoods daily before females begin mate sampling, a daily male response to the number of mate-sampling females can not contribute to the phase match between male and

female reproductive cycles. The converse, that female mate sampling tracks the intensity of hood building, is contradicted by extensive comparative evidence that predation on females and their larvae during and soon after larval release has shaped the timing of reproduction by intertidal crabs (Morgan & Christy, 1995). Endogenous rhythms in both sexes that are phase set by the same cues (Zucker, 1976) may best explain why male and female reproductive cycles of *U. musica* coincide. Such a mechanism would ensure that male cycles follow female cycles (von Hagen 1970; Christy, 1978) as females track safe times for larval release (Zucker, 1978; Morgan & Christy, 1994).

Endogenous rhythms and hood building by neighbors both may affect a male's tendency to build a hood (Zucker, 1974, 1981). However, in this study, the proportion of males who built hoods did not increase with male density (Fig. 8) indicating that social facilitation of building did not occur. Males courted synchronously for 3 to 4 days each biweekly cycle and most built only one hood (Fig. 6). Male *U. beebei* court and build pillars for 4 to 6 days (Backwell *et al.*, 1995) and male *U. pugilator* defend burrows and court without feeding for about 6 days each biweekly period (Florida, west coast; Christy, 1978). *U. beebei* has a relatively broad reproductive cycles (Morgan & Christy, 1994) but, like *U. musica*, reproduction in *U. pugilator* shows strong synchrony (Christy, 1978, 1982). The duration of breeding periods at the population level must reflect both the degree of synchrony among males and the mean duration of individual periods of reproductive activity.

A remarkable result for males of the coincidence between male and female cycles is that, on average, the value of building a hood, as measured by the daily relative mating rate at hooded burrows, is constant (with substantial variance) and independent of hood abundance (Fig. 9). This is analogous to 'input matching' in continuous-input ideal free models of competition for resources in space (Milinski & Parker, 1991). However, the mechanisms thought to give rise to this pattern in space (*e.g.*, complete knowledge about food input rates and movement without cost between patches) are entirely different than those that probably produce phase matching of male and female endogenous reproductive rhythms in *U. musica*. Equal average hood builder mating rates across days does not mean that all males are equal competitors; those who build on more days than others (Fig. 6) should mate more often. Thus, variance in male reproductive success in *U. musica* that can be attributed to hood building may be determined largely by the

frequency with which individual males build hoods, not by when they build them.

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