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ORIGINAL ARTICLE

Males are attracted by their own courtship signals

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Abstract Courting male fiddler crabs *Uca terpsichores* (1 cm carapace width) sometimes build mounds of sand called hoods at the entrances to their burrows. Males wave their single enlarged claws to attract females to their burrows for mating. It was shown previously that burrows with hoods are more attractive to females and that females visually orient to these structures. In this study, we test whether males also use their hoods to find their burrows. We first determined the maximum distance that males can see and find a burrow opening without a hood. Males were removed from their burrows and placed on the sand at a range of distances from a burrow opening. If they were more than about 8 cm (seven units of eye-height) away, they were unable find the burrow. In contrast, males that were burrow residents used a non-visual path map to return to their burrows from much greater distances. To determine if hoods help males find their burrows when there are errors in their path maps, we moved residents 1–49 cm on sliding platforms producing errors equal to the distances they were moved. Males with self-made hoods or hood models at their burrows relocated their burrows at significantly greater distances than did males with unadorned burrows. Hood builders also relocated their burrows faster. Hence, hoods have two functions: they attract females and they provide a visual cue that males use to find their burrows quickly and reliably when their path maps fail.

Keywords Sensory trap · Landmark orientation · Sexual selection · Hood building · *Uca*

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Introduction

A sensory trap (West-Eberhard 1984) operates during courtship when the signaling individual, usually the male, possesses a trait that elicits a response in the receiver, usually the female, that increases the signaler's chance of mating but has evolved for a function other than mate choice (Christy 1995). Examples include male morphological and behavioral traits that females approach because they mistake them for food (Proctor 1991; Rodd et al. 2002; Garcia and Ramirez 2005) as well as objects males make that attract females because they look like young (Stålhandske 2002) or safe places (Christy et al. 2003b).

Most research on sensory traps has been directed at understanding how selection has shaped receiver's responses in both the mating and non-mating contexts.

Far less attention has been given to the possible functional origins of the male traits that currently elicit sensory trap preferences. During a study of the courtship of the fiddler crab *Uca terpsichores* (Christy et al. 2002), we accidentally discovered a possible second current function for a sensory trap male courtship signal that attracts females for mating. In this paper, we document this second function and discuss the implications of this finding for understanding the evolution of the signal.

The signal is a sand hood, a tall, wide, arching structure that courting males sometimes build at one edge of the opening to their burrow to which they attract females for mating (Christy et al. 2001). Females visually orient to these structures and preferentially approach courting males with hoods, increasing the mating rates of hood builders, (Christy et al. 2002). Hence, hoods are attractive courtship signals. Several lines of evidence (Christy et al. 2003a,b) suggest that this preference is based on landmark orientation (Herrnkind 1983), a behavior sometimes shown by male and female fiddler crabs of species that do and do not build structures (Christy 1995; Christy et al. 2003b) when they are moving on the surface away from the safety of a burrow. Without immediate access to a refuge, a fiddler crab will either follow another crab to its burrow or it will approach and stand momentarily motionless with its body against any protruding object (e.g., shell, stone, plant part, lump of sediment). Landmark orientation is thought to reduce the risk that the crab, while next to the object, will be detected by visual predators, primarily birds (Koga et al. 2001). With notable exceptions (Yoder et al. 2005), fiddler crabs forage near their burrows and show burrow fidelity. Burrows are refuges (Frix et al. 1991) to which crabs run when predators come near (Zeil and Layne 2002). Fiddler crabs can orient to their burrows using vision but, due to perspective foreshortening and to the geometry and configuration of their eyes, crabs cannot recognize the dark image of a burrow entrance when they are more than about ten body lengths from it (Zeil and Layne 2002). To relocate their burrows from greater distances, they construct non-visual path maps (Vannini and Cannicci 1995) to their burrow opening. Path maps are based on an egocentric spatial frame of reference and an idiothetic source of information (Layne et al. 2003) that probably uses leg odometry (Zeil and Layne 2002). Errors in path maps, revealed by off-target return orientation, may be introduced whenever a crab loses contact with the surface, such as when males fight and physically flip each other, or when males make complex movements while courting.

Serendipitous observations during a previous study revealed that males sometimes orient to their own hoods, especially after venturing far away to court distant females. In addition, males without hoods sometimes are unable to find their burrows and subsequently become wandering rogues (Christy et al. 2002). The purpose of the present study was to determine experimentally if hoods enable males to find their burrows reliably and quickly after errors have been introduced in their path maps.

Materials and methods

Study site and species

The study was conducted on a sand beach on the western shore of Culebra Island located 5 km SE of the Bridge of the Americas at the Pacific entrance to the Panama Canal. *U. terpsichores* is abundant in the upper intertidal zone along about 40% of this beach (about 4×60 m) with the standing population estimated at between 5,000 and 7,000 adults (20–30 crabs/m^2 (J.H. Christy, unpublished). Hood building and the reproductive cycles of this species have been monitored daily at this site for 2.5 years (J.H. Christy and J.R. Rissanen, unpublished).

Visual detection of burrow openings

To evaluate whether hoods allow males to relocate their burrows when errors are introduced in their path maps, we first established the maximum distance (in units of eye-height) at which males can detect the opening of a burrow using vision only. Male crabs were captured from their burrows at low tide, their carapace length was measured (0.02 mm accuracy) and they were placed individually on a crab-free area of sand near an artificial burrow (1 cm deep) that we had made. Relatively large males were chosen (mean carapace length=6.41 mm, S.D.=0.18, n=91). Using a fitted linear regression (see the "Background data" section below), the diameter of the artificial burrow (0.05 mm accuracy) was adjusted to correspond to that occupied by males of their size.

Each male (used once) was positioned upon release so that its transverse axis was oriented as closely as possible toward the opening and so that its front was facing away from the observer. The observer immediately moved 2 to 3 m away from and behind the crab and sat nearly motionless until the crab either found or did not find the burrow and walked away. A video camera, positioned directly above the scene, recorded the crab's movement. Males were released over a range of distances within and beyond the expected burrow detection distance based on male size. To compare our results to those of Zeil and Layne (2002) we expressed the distance between the crab and the artificial burrow in units of eye-height. For this, we estimated the relationship between eye-height and carapace length (see the "Background data" section below).

To evaluate whether crabs found the burrow because they bias their first movement with respect to their transverse axis, we performed a preliminary experiment on 37 males using the same methods but without providing an artificial burrow. We determined from video tape recordings the initial direction that the crab moved relative to its transverse axis and the position of the observer (directly behind the crab).

Burrow relocation success and searching time

To determine if males more often or more quickly relocate their burrows if they have hoods, we performed translocation experiments (Vannini and Cannicci 1995) in which crabs were moved on sand-covered platforms. These experiments change the crab's location without the crab walking to the new position. Visual but not proprioceptive cues of the movement are available to the crab. Thus, translocation produces an error in the crab's non-visual perception of the location of its burrow. The error is equivalent to the difference in the location of the crab before and after it is moved.

Two thin acrylic platforms (20×30 cm) were placed on both sides of a male's burrow (approximately 5 cm apart) and covered with a thin layer of sand collected from the surface nearby (Fig. 1a). The platforms were positioned so that their long axes were approximately perpendicular to the direction that the male resident usually exited his burrow as determined by the orientation of the upper burrow shaft. A video camera was positioned directly over the scene. Thin lines were tied to the platforms by which they could be pulled in either direction along their long axes. A receptive female was tethered on the platform in "front" of the burrow at a distance of 15 to 20 cm from the opening (Fig. 1b).

The female usually attracted the male to her. However, some males walked on the opposite platform. An observer sat nearly motionless holding the control lines (guided by bamboo sticks in the sand) about 4 to 5 m from the male. When the male walked away from his burrow over one of the platforms, it was pulled relatively quickly in one direction so that the male was moved to a new position further away from his burrow entrance. Crabs were moved different distances by varying the time at which the observer moved the platforms. The males responded to the movement of the platform by running to where their burrows would have been if the burrow had been also moved.

From the video recordings we measured (1) the distance between the position of the male before and after the platform was moved, (2) whether the male found his burrow or walked away, and (3) the time it took him to do this. The experiment was performed using 37 hood-building males with their hoods intact, 37 non-builders that had no hoods, and 42 non-builders that had hood models of average size (Christy et al. 2002) placed at their burrow entrances. All male crabs were used once.

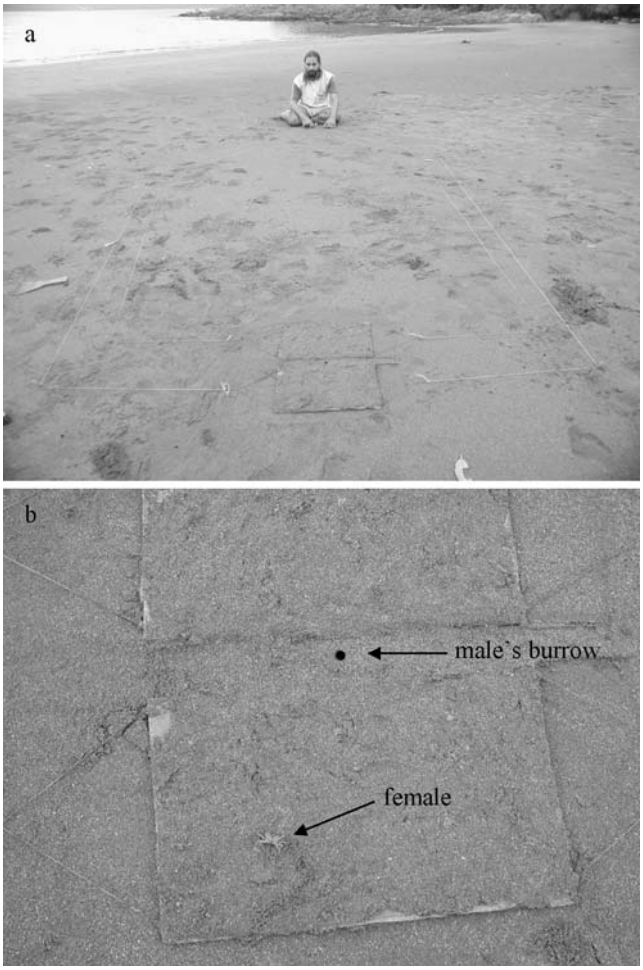

Fig. 1 Set up for translocation experiments. **a** Two thin acrylic platforms (20×30 cm) were placed on both sides of a male's burrow (approximately 5 cm apart) and covered with a thin layer of sand. The long axes of platforms were approximately perpendicular to the direction that the male resident usually exited his burrow. *Thin lines* were tied to the platforms by which they could be pulled in either direction along their long axes. **b** A receptive female that was tethered on the platform in "front" of the burrow at a distance of 15 to 20 cm from the opening

Background data

Relationship between size of crabs and burrow opening diameter

A linear regression was constructed to adjust the diameter of the artificial burrow (*Di*) to the carapace length (*Cl*) of the crab. For this we captured 54 male crabs from their burrows during the low tide and measured the carapace length (0.02 accuracy) and the diameter of the

burrow (0.05 accuracy) before we captured the crabs. The fitted regression was: $Di = 1.08 + 0.01\ Cl$; $1^2 = 0.89$; M.S.E.= 0.1853.

Relationship between eye-height and carapace length

The relationship between male eye-height (*Eh*) and male carapace length (*Cl*) was determined using video recordings of males that had been placed in a narrow glass chamber with a 1-mm grid fixed to the back wall. Each male (n=102) was collected from a burrow and its carapace length (0.02 mm precision) was measured. The axis of the lens of the camera was approximately at the expected level of the male's eyes when erect, and it was less than 20 cm from the male, minimizing possible parallax errors. The magnification was set so that scene was about 5 cm wide with the male in the middle. A recording was made until at least a few seconds of tape were obtained in which the crab appeared to be in a normal, relaxed upright posture. The height of the eyes above the surface on which the crab stood was then measured to the nearest 0.02 mm using calipers calibrated against the background grid. All recordings were made in the field with freshly collected crabs that were immediately returned to the beach after they were taped. The fitted regression was: $Eh = 2.18 + 1.33\ Cl$; $R^2 = 0.64$; M.S.E.=0.4949.

Data analysis

Walking bias

We used circular statistics (Zar 1999) to evaluate a possible bias in the direction males walk relative to their body axis when they do not have a burrow. The frequency distribution of the walking direction vectors, and confidence limits (95%) for the mean of the vectors were calculated. Following the von Mises distribution (a natural distribution for circular data; for a review, see Fisher 1993) we calculated the probability that the mean direction vector was 0° or 180° (the directions to the artificial burrows in the experiment on visual detection of burrow openings).

Visual detection of burrow openings

The horizontal distances between crabs and the artificial burrows at the time of release were expressed in units of eye height. We measured each male and used the regression of eye height on male size to obtain the mean expected eye height for each crab. We calculated the distance between the crab and the burrow in units of eye height by dividing the horizontal distance by the mean expected eye height.

A logistic regression was fitted to evaluate the relationship between the success and failure of finding a burrow in relation to the distance (in units of eye height) to the burrow opening. The logistic regression model was:

$$ln\left(\frac{P_i}{1-P_i}\right) = a + b \cdot D_i$$

where p_i is the probability that a male crab will find a burrow at a distance D_i (in units of eye height).

Maximum likelihood estimates (for a review, see Hilborn and Mangel 1997; McCallum 2000) were obtained for a and b parameters. As a measure of the ability of crabs to detect burrows visually, we estimated the distance at which crabs have 0.5 probability of detecting the burrow, which corresponds to the $-a/b$ parameter ratio. Bootstrap 95% confidence limits were constructed for the $-a/b$ parameters ratio. We also estimated the probability that a crab would detect a burrow opening located beyond ten units of eye height. We compared these estimates with the theoretical predictions of Zeil and Layne (2002).

Burrow relocation success and searching time

For each male treatment (male without hoods, males with hoods they built, and males with model hoods added to their burrows) a logistic regression was fitted to evaluate the burrow relocation success in relation to the distance the male was moved. Maximum likelihood estimates were obtained for a and b parameters, and likelihood ratio tests (for a review, see Cerrato 1990; Hilborn and Mangel 1997) were performed to evaluate whether the relationships were similar for the three males' treatments. A likelihood ratio test is performed calculating (1) the joint negative log-likelihood for the three models fitting the data independently for each male treatment, and (2) the joint negative log-likelihood for the three models fitting the data assuming either the three male treatments have similar a and b parameters, or two male treatments have similar a and b parameters. Two times the difference in the negative log-likelihood follows a χ^2 distribution with degrees of freedom equal to the number of restricted parameters. Joint confidence limits (95%) for both parameters were constructed using the likelihood profile (Hilborn and Mangel 1997). The distance at which crabs have 0.5 probability of finding their burrow was calculated from $-a/b$ parameters ratio, and bootstrap 95% confidence limits were constructed. Likelihood ratio tests were performed to compare the $-a/b$ parameter ratios between male treatments.

The relationship between the searching time (*St*) and the translocated distance (*Td*) was fitted as:

$$St = a \cdot Td^b + e$$

where *a* and *b* are the parameters and *e* is an error term. As search time can never be negative, *St* was fitted to a log-normal distribution. Maximum likelihood estimates were obtained for *a* and *b* parameters, likelihood ratio tests were performed to compare parameters between male treatments, and 95% joint confidence limits for parameters were constructed for each model/male treatment.

Results

Walking bias

Male crabs that were released on bare sand without a burrow tended to walk forward away from the motionless observer (Fig. 2). The probability that the crabs walked in a direction aligned with their transverse body axis (mean vector of 0° or 180°) was estimated to be 0.0018 (von Mises distribution: circular variance=0.073, concentration parameter=7.156). Hence, it is highly unlikely that males given artificial burrows aligned with their transverse axis would find them because they are biased to walk toward them.

Maximum distance for visual detection of a burrow opening

The maximum horizontal distance at which crabs detected the opening to an artificial burrow was 8 cm, which corresponded to 7.18 eye-height units of the average-sized male used in our experiments (Fig. 3). The distance (in units of mean eye height) at which crabs have 0.5 probability of detecting the burrow was estimated to be

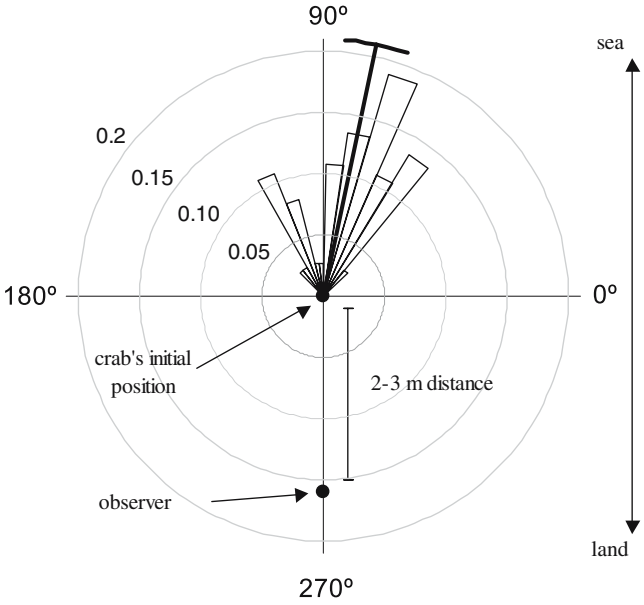

Fig. 2 Directions crabs first moved following release on the sand without a nearby burrow. The angles are expressed relative to the crabs' transverse axis (0–180°). The *bars* indicate the relative frequency distribution of the direction vectors. *Concentric circles* show the values for the relative frequencies. The *black line* indicates the mean of the direction vector (78.07°) and the 95% confidence limits (70.90–85.23°)

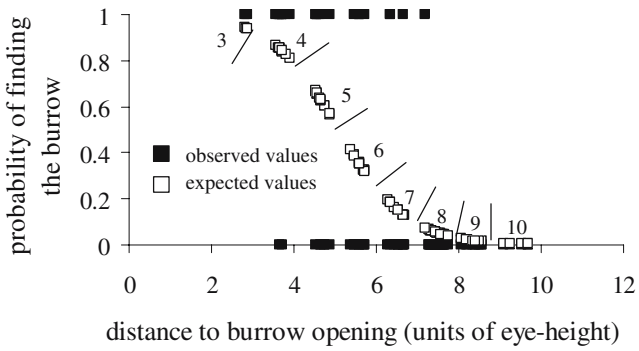

Fig. 3 Probability of finding burrow in relation to the distance from the burrow opening in units of eye-height. *Filled boxes* are observed values and represent success (1) or failure (0) in finding the burrow. *Blank boxes* are expected values of the probabilities from the fitted logistic regression. *Numbers* inside the *graph* indicate the horizontal distance, in centimeter, between the crab and the found burrow

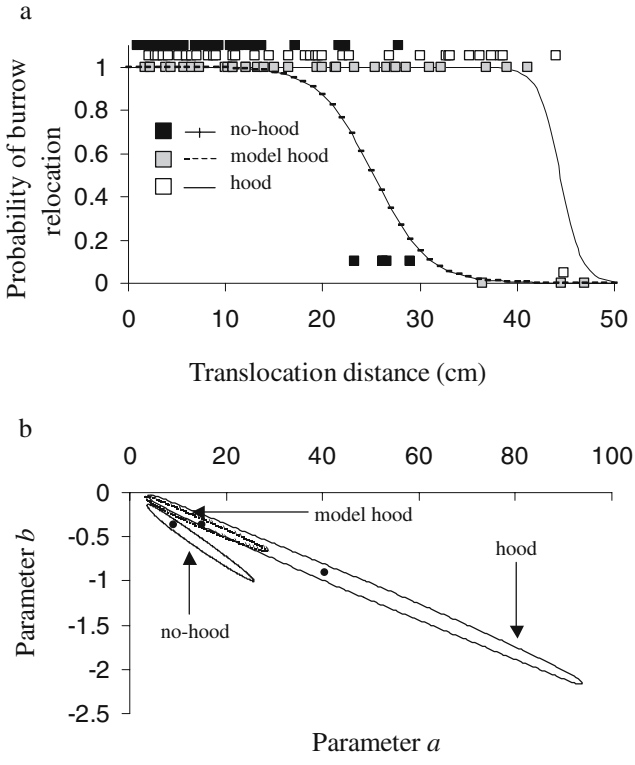

Fig. 4 **a** Probability of relocating a burrow in relation to the distance a male crab was moved. *Boxes* show success (1) or failure (0), but for an easier graphical interpretation, different treatments were slightly separated along the vertical. *Lines* show the fitted logistic regression. **b** *Ellipsoids* of 95% joint confidence limits for both *a* and *b* parameters for the logistic regressions. *Circles* inside joint confidence limits correspond to the maximum likelihood estimates for each model. Hood = males with hood around their burrow openings, model hood = males without hoods but with model hoods added around their burrow openings, No-hood = males without hoods

Table 1 Maximum likelihood estimates for the parameters of the logistic regressions evaluating the probability that a male will relocate its burrow in relation to the distance it was translocated

	Parameters		Bootstrap estimation for $-a/b$			Negative log-likelihood of models
	a	b	Mean	SE	95% confidence limits	
Males without hoods	9.21	−0.36	25.23	2.20	21.61–29.32	6.57
Males with hoods	40.46	−0.91	43.37	1.42	40.99–44.45	1.04
Males with model hoods	14.99	−0.37	40.58	3.00	34.06–45.76	3.61

The $-a/b$ parameter ratio corresponds to the translocation distance at which crabs have a 0.5 probability of relocating their burrow

5.10 (95% confidence limit: 4.99–5.17). The probability that a crab will detect a burrow beyond ten units of eye height was estimated to be 0.0026.

Burrow relocation success and searching time

Crabs that were translocated ran to where their burrows should have been if they too had been moved on the platform. This was revealed by the slight pause males made at the expected burrow location while they probed for the opening with their dactyls. The males then walked back and forth in the vicinity until they either located their burrow or moved away. Translocated males evidently did not initially use visual cues present in the general visual scene to find their burrows.

The logistic regressions fitting the probability of burrow relocation in relation to the translocation distance (Fig. 4a; Table 1) differed for the different males' treatments (Table 2). Likelihood ratio tests (Table 2) and joint confidence limits (Fig. 4b) indicate that both a and b parameters were similar for males with hoods and males with model hoods, but different for males without hoods. Crabs with hoods or with model hoods found their burrows at significantly greater distances (see confidence limits in Table 1) than did crabs without hoods (see likelihood ratio tests for $-a/b$ ratio in Table 2).

The rate of increase in the searching time in relation to the translocation distance differed between the male treatments (Fig. 5a; Table 3). Likelihood ratio tests (Table 4) and 95% joint confidence limits (Fig 5b) indicate that the equations for males without hoods and males with hoods were different, while the equation for males with model hoods was similar to males with hoods (and different to males without hood) or similar to males without hoods (and different to males with hood).

Discussion

Our results are generally consistent with previous estimates of the maximum distance at which crabs can locate a burrow visually. Based on the geometry and resolution power of their eyes, crabs should be able to detect a burrow opening when it is up to 10–15 eye heights away (Zeil and Layne 2002); under natural conditions, background visual noise is expected to reduce that distance considerably (Zeil and Layne 2002). Our results may confirm this. The maximum distance for burrow recognition was 7.18 eye-

Table 2 Summary of likelihood ratio tests comparing logistic regression parameters between males without hoods (*nh*), males with hoods (*h*), and males with model hoods (*m*)

Null hypothesis tested	Negative log-likelihood upon null hypothesis	Chi^2	*df*	*P* value
a) Similarity of both parameters				
$a_{nh}=a_h=a_m$ and $b_h=b_h=b_m$	26.26	30.10	2	<0.0001
$a_{nh}\neq a_h=a_m$ and $b_{nh}\neq b_h=b_m$	12.44	2.46	2	0.2929
$a_{nh}=a_h\neq a_m$ and $b_{nh}=b_h\neq b_m$	24.09	25.76	2	<0.0001
$a_{nh}=a_m\neq a_h$ and $b_{nh}=b_m\neq b_h$	19.70	16.97	2	0.0002
b) Similarity of $-a/b$ parameters ratio				
$-a_{nh}/b_{nh}=-a_h/b_h=-a_m/b_m$	19.55	16.67	1	<0.0001
$-a_{nh}/b_{nh}\neq-a_h/b_h=-a_m/b_m$	11.69	0.95	1	0.3303
$-a_{nh}/b_{nh}=-a_h/b_h\neq-a_m/b_m$	19.21	15.99	1	0.0001
$-a_{nh}/b_{nh}=-a_m/b_m\neq -a_h/b_h$	17.92	13.42	1	0.0002

The joint negative log-likelihood for the three models fitting each male type independently was 11.22 (sum of the negative log-likelihood of each model in Table 1). a: Comparison of both a and b parameters together. b: Comparison of the $-a/b$ parameter ratios (estimators of the translocation distance at which the crabs have a 0.5 probability of relocating their burrow)

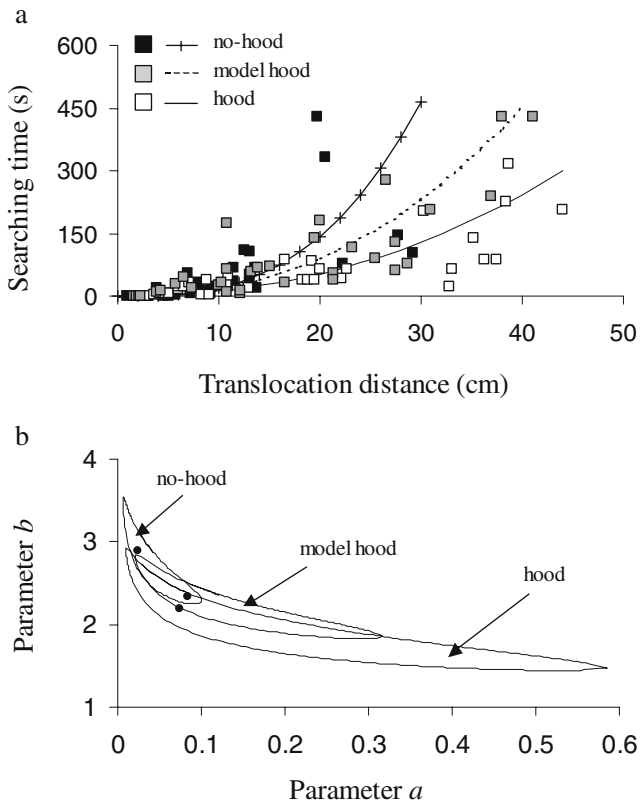

Fig. 5 **a** Time to relocate a burrow after errors were introduced into crabs' path maps. *Lines* represent the expected values from the fitted relationships. **b** *Ellipsoids* of 95% joint confidence limits for both *a* and *b* parameters for the logistic regressions. Circles inside joint confidence limits show the maximum likelihood estimates for each model. Hood = males with hood around their burrow openings, model hood = males without hoods but with model hoods added around their burrow openings, no-hood = males without hoods

height units, or 8 cm between the burrow and the center of the average-sized crab. These values may be proportionately less for juveniles, as they have fewer facets in their eyes compared to adults (Land and Layne 1995). Fiddler crabs have a surprisingly limited range at which they can see their burrow. Yet they regularly move far beyond this range and still find their burrows. To do this they use their non-visual path integration mechanism. This mechanism is generally reliable but occasionally fails leading to burrow loss (Christy et al. 2002 and below).

The presence of a hood at the entrance of a burrow improved the ability of resident males to relocate their burrows when they had errors introduced into their path maps. This was true for both hood-builders with natural hoods and non-builders with model hoods. Hence, the act of hood-building does not increase a male's tendency to orient toward the hood marking his burrow. However, hood-builders relocated their burrows faster compared to non-builders with or without model hoods. Hood building may decrease a male's response threshold for landmark orientation in the event that his non-visual path map fails. Alternatively, since structure building is condition-dependent (experimentally well-fed males build structures more often: Backwell et al. 1995; Taewon Kim, unpublished), structure-builders simply may walk faster and find their burrows sooner.

Predation often may limit the development of male sexual signals under directional selection by female choice (reviewed by Jennions et al. 2001; Kotiaho 2001). In contrast, our studies suggest that natural and sexual selection on hood-building is not countervailing forces. Hood-building is sexually selected by a female preference (Christy et al. 2002); the presence of a hood, but perhaps not its size (Christy and Backwell 2006, in press), increases the rate that females approach courting males and the mating success of hood builders. This study suggests that selection due to predation on courting males may favor those that build hoods. The vulnerability of a fiddler crab to predation is controlled mainly by its escape reaction to an approaching predator (Backwell et al. 1995; Koga et al. 2001).

Hood building may reduce male predation rates because hoods allow males to find their burrows more quickly and reliably when errors arise in their non-visual path maps. How often do such errors put males at risk? Previously, we found (Christy et al. 2002) that males oriented to hood models that were offset by about 3 cm from their burrow openings in 8 of 213 courtships (3.8%). Hence, path map errors sufficient to cause males to lose their non-visual spatial reference to their burrow arise naturally during roughly 4 of every 100 courtships. Males then rely on their hoods, if present, to find their burrows using landmark orientation. Actively courting males ("rouges") that do not

Table 3 Maximum likelihood estimates for the relationship between searching time (*St*) and the translocation distance (*Td*)

	Parameters		SD of log(*St*)	Negative log-likelihood of models
	a	*b*		
Males without hoods	0.02	2.90	1.19	53.21
Males with hoods	0.07	2.19	1.44	56.00
Males with model hoods	0.08	2.33	1.06	49.31

The relationship was fitted as: $St = a \cdot Td^b + e$, where *e* is an error term with a log-normal distribution and standard deviation estimated from log (*St*)

Table 4 Likelihood ratio tests evaluating differences in the relationship between searching time (*St*) and the translocation distance (*Td*) between males without hoods (*nh*), males with hoods (*h*), and males with model hoods (*m*)

Hypothesis tested	Negative log-likelihood upon null hypothesis	Chi^2	*df*	*P* value
$a_{nh}=a_h=a_m$ and $b_h=b_h=b_m$	161.92	6.79	2	0.0335
$a_{nh}\neq a_h=a_m$ and $b_{nh}\neq b_h=b_m$	159.76	2.49	2	0.2883
$a_{nh}=a_h\neq a_m$ and $b_{nh}=b_h\neq b_m$	161.52	6.01	2	0.0496
$a_{nh}=a_m\neq a_h$ and $b_{nh}=b_m\neq b_h$	159.99	2.94	2	0.2303

The relationship was fitted as: $St=a\cdot Td^b+e$, where *e* is the residual following a log-normal distribution. The joint negative log-likelihood for the three models fitting each male type independently was 158.52 (see Table 3)

have a burrow but follow females as they respond to other males can be seen every day in the field. At least some of these males wander because they are unable to relocate their hood-less burrows after venturing far from them (Christy et al. 2002).

Fights in which males are lifted entirely from the surface (flipped) also are a source of path map errors causing males to fail to relocate their burrows. As they search and fight for a new burrow, they are unable to run quickly into a burrow for safety if a predator approaches. By building a hood, a male may minimize the chance it will lose its burrow and have to search for a new one at an elevated risk of predation. Contrary to the general rule for sexual traits (Jordão and Oliveira 2001; Koga et al. 2001), hood-building probably makes a male less rather than more vulnerable to predation. A direct positive effect of sexual ornaments on male survival may be more common than is currently recognized (Bildstein et al. 1989; Ribeiro et al. 2003).

Hood-building may also be favored by male–male competition for, and defense of burrows, which are required for mating in *Uca terpsichores* (Christy et al. 2001). Clearly, a male that loses its burrow for any reason will not attract a mate until it digs a new burrow or wins one in a fight. Lost courtship time during a mating peak may be a cost of burrow loss that contributes to selection for hood-building.

The tendency of both mate-searching females (Christy et al. 2002, 2003a,b) and male burrow owners (this study) to approach hoods appears to be based on landmark orientation, a behavior that probably is selected by predation and that is exhibited by many species of fiddler crabs, including some that do not build courtship structures (Christy 1995; Christy et al. 2003b). If landmark orientation evolved before structure building, which seems likely, then hood-building probably was favored from its inception by natural selection (predation) on males as well as sexual selection by female choice and perhaps for resource holding ability. Males of many species of fiddler crabs attract females to their burrows for mating (deRivera and Vehrencamp 2001), yet relatively few make courtship structures. To understand why some species do and some do not build structures, we suggest it will be necessary to identify the causes of errors in the non-visual path maps of males, how these vary between species, and how selection consequent to burrow loss and female preferences based on landmark orientation combine to favor structure building.

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