

To paddle or not: context dependent courtship display by male blue crabs, *Callinectes sapidus*

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SUMMARY

The nature of the courtship signalling used by a species is shaped by many factors, one of which is its habitat. Male blue crabs, *Callinectes sapidus*, have a courtship display in which they elevate their body by standing high on their legs, open their chelae and paddle their swimming legs. This courtship display is not reported in other swimming (portunid) crabs and is rarely expressed in laboratory experiments on male blue crabs. In this study, we characterised this display, which we call 'courtship stationary paddling', and distinguished it from other types of paddling. To explain the species specificity of courtship stationary paddling, we hypothesised that this behaviour is an adaptation to low visibility and abundant refuges in the habitat of blue crabs, and that this behaviour enhances chemical signalling when females are relatively inaccessible to males. We used particle imaging velocimetry to visualise water currents generated during courtship stationary paddling, showing that it created water currents directed away from the male and towards the female, thus enhancing chemical signalling. We also showed that males did not perform courtship stationary paddling when females were freely walking such that males could quickly contact and cradle carry them. Rather, males typically performed courtship stationary paddling only when females were inaccessible to them. These results indicate that courtship stationary paddling is a context-dependent behaviour, occurring only when females are not accessible to males, and suggesting that it evolved as an adaptation to life in habitats with many refuges and low visibility.

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Key words: habitat-dependent signalling, courtship display, chemical communication, chemoreception, pheromone, sexual behaviour, portunid, blue crab, *Callinectes sapidus*.

INTRODUCTION

Courtship signals

Many species have evolved to communicate sexual information using courtship signals, including visual displays, songs and pheromones. Female choice can affect the evolution of courtship signals. For example, males may send more signals to choosy females and females may select males based on the quality and quantity of those signals (Andersson, 1994). Another factor that can influence the evolution of courtship signals is the nature of the species' habitat. For example, species that breed in darkness tend to use vocal signals more than visual signals to attract mates (Ryan, 1990). Characteristics of the habitat may affect features of the courtship signals in ways that facilitate communication in that habitat. For example, acoustic signals of species living in bushes, such as bird songs and advertisement calls by bladder grasshoppers, are adapted to enhance signal transmission in their native habitat (Slabbekoorn and Smith, 2002; Couldridge and van Staaden, 2004).

Courtship display of male blue crabs

Male blue crabs *Callinectes sapidus* Rathbun produce a distinctive courtship display behaviour when they smell a pubertal female. A pheromone, which is currently not chemically characterised but is present in the pubertal female's urine, is detected by sensors in the aesthetasc sensilla on the antennules of males (Gleeson, 1980; Gleeson, 1982; Gleeson, 1991). Some components of this courtship

display of blue crabs are also part of the display of most other portunid crabs, including spreading their chelae and extending their walking legs to elevate the body high off the bottom (Ryan, 1966; Fielder and Eales, 1972; Berrill and Arsenault, 1982). An additional component of the male courtship display, unique to *C. sapidus* and one other portunid crab, the lesser blue crab *Callinectes similis*, is paddling of its swimming legs, or fifth pereopods (Teytaud, 1971; Gleeson, 1991; Wood and Derby, 1995) (M.K., personal observation).

Courtship paddling by male blue crabs has been described in several studies (Teytaud, 1971; Gleeson, 1980; Gleeson, 1991; Wood and Derby, 1995; Jivoff and Hines, 1998; Bushmann, 1999). The definition of paddling display that we use in this paper follows Teytaud's original definition, with some modifications. According to our definition, courtship paddling involves raising the swimming legs vertically over the carapace, turning them so that the flat side of the paddle blade faces anteriorly to push water forward and then moving them from side to side (Movies 1A and B in supplementary material). This paddling is always preceded by and combined with a chelae spread, and the body is always highly elevated. In addition to the side-to-side movement, the blade moves from outside to inside and backward to forward to make a circular motion. In this movement, the left and right paddles are 180 degrees out of phase, as described by Wood and Derby (Wood and Derby, 1995). Our observations show that when performing courtship paddling, crabs

do not move or walk. When the male walks between bouts of courtship paddling, he changes the type of paddling in order to keep his balance. The paddling during walking differs from courtship paddling in that in paddling during walking, the two legs do not move in tight synchrony (whereas in courtship paddling, the paddles move in antiphase synchrony), the paddles are positioned more laterally (compared to a more medial-dorsal position during stationary courtship paddling) and the paddle blade faces are held in a sideward or downward position (rather than the flat side of the blade facing anteriorly in courtship stationary paddling) (Movie 2 in supplementary material). Thus we call the courtship paddling behaviour 'courtship stationary paddling' to distinguish it from the other types of paddling.

Courtship stationary paddling probably delivers a multimodal signal to females. A visual signal is indicated by the observation of Teytaud (Teytaud, 1971) that sexually receptive female crabs respond to a model of male crabs in a stationary posture (Teytaud, 1971). Blue crabs can distinguish blue from other colours (Burse, 1984), suggesting that the chelae spread may be a visual display. The paddling component of the display makes a characteristic and conspicuous visual stimulus and thus it might contribute as a visual courtship signal, but this has not been tested. In addition to a visual signalling component, the courtship display may create chemical and mechanical signals to the female. During paddling, the volume of water pumped out of the gill chambers increases (Gleeson, 1991) and paddling generates a strong current projected forward from the male (Wood and Derby, 1995; Jivoff and Hines, 1998) (M.K., personal observation). This water flow may be a significant communication signal by indicating physical proximity of the male to the female and by transporting chemical information to the female (Gleeson, 1991; Jivoff and Hines, 1998). Male blue crabs release a chemical signal that attracts females (Gleeson, 1991). Thus, courtship stationary paddling potentially contains visual, chemical and mechanical signals.

Although described by many researchers, courtship paddling is not commonly observed in male crabs in the laboratory, even to stimulation with female pheromone. For example, Wood and Derby (Wood and Derby, 1995) used eye ligation instead of stimulation by female odour as a more reliable releaser of courtship paddling. In addition, the courtship display, including paddling, is not an essential prelude to successful precopulatory pair bonding (Teytaud, 1971; Gleeson, 1991; Jivoff and Hines, 1998; Bushmann, 1999). Male-male competition is one factor that increases the frequency of courtship display, and this has been demonstrated in blue crabs (Jivoff and Hines, 1998). Levels of sexual conflict can also increase courtship behaviour (Parker, 1979). In general, when females are more selective, less responsive, or more unwilling to mate, males are likely to use their signals more frequently, at higher intensity or for longer durations (Murai and Backwell, 2005). However, blue crab males do more paddling to less choosy, late premoult females (Jivoff and Hines, 1998). This suggests that courtship stationary paddling has not evolved mainly through female choice, since if females choose males based on the display, males should display more to early premoult females.

Courtship paddling behaviour has been reported only in *Callinectes sapidus*, although *Callinectes similis* also produces it (M. K., personal observations). Other swimming portunid crabs have paddles but do not use courtship paddling. A possible explanation for why only *C. sapidus* and *C. similis* males show paddling display is that it may be an adaptation to their habitat. Blue crabs live in *Spartina* marshes where the water is turbid. Premoult females have low mobility and are susceptible to predators. According to this

scenario, premoult females may hide in *Spartina* patches or in the substrate to avoid predators, and release sex pheromone from these shelters. Males might be able to detect the pheromone but be unable to locate or contact the females because they are inaccessible. Males would then have to attract the females from their refuge, and courtship stationary paddling would contribute to this by enhancing information transfer. According to this hypothesis, we made two predictions: (1) courtship stationary paddling creates powerful water currents directed towards the female, and (2) males produce more paddling when they detect the presence of a female but cannot access her.

As a test of this hypothesis, we created a physical barrier between male and female crabs and examined its effect on the incidence of courtship stationary paddling. We also visualised the water flow generated by the courtship paddling behaviour using particle imaging velocimetry, the first effort to visualise and quantify the water currents generated by courtship paddling.

MATERIALS AND METHODS

Animal collection and maintenance

Male and female blue crabs (*Callinectes sapidus*) were collected, using cage traps, from the waters near St Augustine, Florida. Animals were held in aquaria equipped with flow-through natural sea water at an ambient temperature of 28°C. All experiments were performed at The Whitney Marine Laboratory, University of Florida, St. Augustine, Florida. All male crabs were mature, intermoult, and with a carapace width of 10.5–12.0 cm. All females were obtained from the soft shell crab industry in Florida. Female crabs were in their reproductive phase: pubertal and in late stage premoult ('red' or D4). Moult stage was determined by testing morphological changes on the dactyl of their swimming legs (Smith and Chang, 2007). Males were fed shrimp and the late premoult females did not eat.

Caging experiment

The same pair of male and female was used in both the accessible and inaccessible conditions as described below, in random order. Twelve male–female sets were used under both conditions, so we used a paired test, the non-parametric sign test, to statistically analyse the data.

Inaccessible female condition: male behaviour toward females in a cage

This experiment was performed in a 122×63×76 cm fibreglass aquarium equipped with flow-through natural sea water with a water depth of 40 cm and a salinity of 35 p.p.t. A second 50×25×20 cm plastic aquarium was used, which had a plastic mesh lid on the 50×25 cm face. Within this smaller aquarium, a late stage premoult female was added and the entire aquarium was placed within one end of the larger aquarium, with the mesh side facing the spacious end of the larger aquarium (Movie 3 in supplementary material). A male crab was then introduced into the large aquarium, allowing the male to see and smell but not touch or grab the female. The male crab was videotaped for 30 min or until he performed full courtship display with courtship stationary paddling.

Accessible female condition: male behaviour toward uncaged, walking females

This experimental setup was similar to the 'inaccessible female condition' except that the female was not in a cage and so could walk freely in the aquarium. Thus the male could easily access, touch and grab the female. The male and a female were introduced

into the aquarium at opposing ends, and the male was videotaped for 30 min or until the male and female formed a precopulatory pair.

Visualisation of male-generated water currents using particle imaging velocimetry

Particle imaging velocimetry (PIV) was used to examine the water currents generated by male crabs performing courtship stationary paddling. Data were collected from a single male crab with a carapace width of 11.5 cm. The male was placed in a 60×30×40 cm aquarium containing natural seawater with no flow, and stimulated to produce courtship paddling by the addition of 100 µl of premoult female urine. *Artemia* eggs (40 ml dry volume) with a mean diameter of 200 µm, were added to the water and used as neutrally buoyant tracer particles. A 30 cm wide×2 mm thick laser sheet was generated using an array of three 7 mW laser diodes with a light emission at 670 nm (World Star Tech, Toronto, ON, Canada; UH5-7G-670). Attached to each laser was a 30° cylindrical beam expander to create the 2 mm thick light sheet. The lasers were aligned horizontally along a plane and attached to an adjustable ring stand so that the location of the laser sheet could be adjusted vertically above the crab. The movement of particles was videotaped from an angle of 90° to the plane of the laser using a Sony Handycam DCR-DVD203. Video frames were divided into a series of jpg image files with a framing rate of 30 Hz and image resolution of 720×480 pixels. Images were processed using MatPIV 1.6.1 software written for Matlab® (Sveen, 2004) from a PIV method developed by Cowen and Monismith (Cowen and Monismith, 1997). This software divided each image frame into an array of ‘interrogation sub-windows’ and calculated the most probable displacements of particles in successive pairs of frames using cross-correlation analysis. The final output from the calculations produced a horizontal and vertical velocity estimate for each 8×8 pixel sub-window, giving 89×59 velocity measurements every image pair. For most experiments, individual paddling behaviour was recorded for 5 s (150 images), during which time all the images were processed and averaged to obtain mean velocity magnitude and direction.

RESULTS

Caging experiment

The following behaviours by males were observed as courtship-related behaviour in our experiments.

Chelae spread. Crab lifts and fully extends the chelae laterally, with the chelae closed (Movie 3 in supplementary material).

High on legs. Crab extends its legs and stands high (Movie 1B, Movie 3 in supplementary material).

Paddles up. Crab holds its fifth pereopods (swimming legs) laterally behind the body with the swimming legs’ paddle blades (dactylus) up (Movie 3 in supplementary material).

Courtship stationary paddling. Crab holds its swimming legs high above its dorsal carapace and waves them side to side. The flat surface of each dactylus faces forward. In addition to the side-to-side movement, the paddle moves from outside to inside as it moves from backward to forward to make a circular motion. The phase of circular motion of the left and right paddles is 180° out-of-phase, as described by Wood and Derby (Wood and Derby, 1995). When a crab performs this behaviour, it does not walk or move backward or forward, and it always performs the chelae spread and high on legs behaviours (Movies 1A, 1B in supplementary material).

Cage touch. Male crab walks to the cage containing the female and touches the mesh of the cage with a part of his body (Movie 4 in supplementary material).

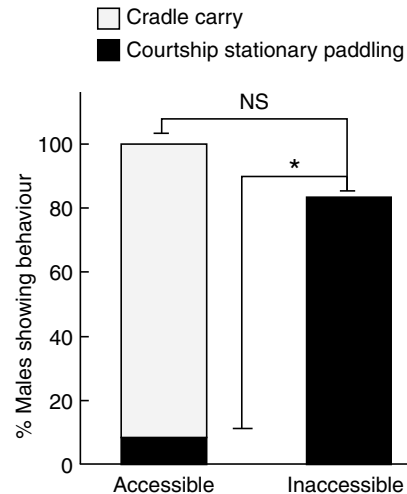


Fig. 1. Stacked column of courtship-related behaviours shown by males in the presence of an accessible female and in the presence of an inaccessible female. Twelve male–female pairings were used, and each animal was used in both the accessible and inaccessible conditions. The number of animals showing courtship stationary paddling was significantly different between the accessible and inaccessible conditions (* $P<0.01$, Sign test). There was no significant difference in total courtship behaviour (Cradle carry + Courtship paddling) between the accessible and inaccessible conditions (NS, not significant $P=0.48$, Sign test).

Cage pinch. Male crab walks to the cage and pinches the mesh to a degree sufficient to break the plastic material of the mesh (Movie 5 in supplementary material).

Cradle carry. Male crab moves his chelae inward from an extended position to physically enclose a female between them and position the female beneath him such that both crabs face in the same direction (Movie 6 in supplementary material).

Males in the presence of either accessible or inaccessible females showed courtship-related behaviours. However, the type of courtship-related behaviours under these two conditions differed. In the presence of accessible females, most male crabs (11 of 12) showed ‘cradle carry behaviour’ whereas only one male showed ‘courtship stationary paddling’ (Fig. 1). Males initiated cradle carry behaviour 1.2 ± 0.9 min (mean \pm s.d., with a range of 0.3–2.9 min) after initiation of the experiment. The single male that showed courtship stationary paddling initiated it after 2.2 min, it lasted for 2 s, and was immediately followed by cradle carry behaviour.

When in the presence of inaccessible females, males showed ‘chelae spread’ while walking ‘high on legs’. Most males approached the caged female before the courtship stationary paddling: this was true for 8 of the 10 crabs that paddled (Fig. 2). Males first ‘cage touched’ after 5.2 ± 5.8 min, $N=8$. Of these crabs, 7 ‘cage pinched’ after 7.9 ± 5.1 min, $N=5$. Most males (10 of 12) showed ‘courtship stationary paddling’, which was initiated 12.0 ± 8.2 min, $N=10$ (range of 3.6–30 min) after the start of the experiment. The other two animals showed no courtship-related behaviours.

In the presence of either accessible or inaccessible females, males showed courtship-related behaviours, and there was no significant difference in this number (10 of 12 in inaccessible condition, 12 of 12 in accessible condition: Sign test, $Z=0.70$, $P=0.48$). But males produced significantly more courtship stationary paddling in the inaccessible condition compared with accessible (10 males in inaccessible condition, 1 male in the accessible condition: Sign test, $Z=2.67$, $P=0.008$).

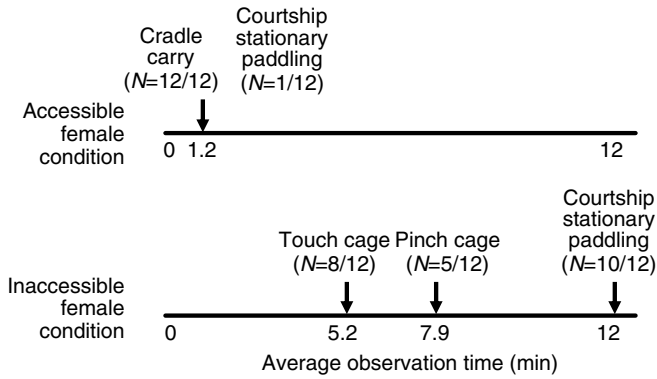


Fig. 2. Time course of behaviours produced by a male crab in the presence of an accessible female (above the time line) or in the presence of an inaccessible female (below the time line). N =the number of males that performed the given behaviour out of the number of males tested. The time line represents the average time (min) from the start of observation.

Flow visualisation experiment

Male crabs that were not performing the courtship stationary paddling produced a 'gill current' (Atema, 1986). This current originating from the gill chamber was directed upward, with a dominant flow direction 10° from vertical (Fig. 3A). The maximum velocity generated during this upward current was 0.6 cm s^{-1} . Once a male began courtship stationary paddling, a forward-directed current was created that changed both the direction and magnitude of the water flow. The paddling motion produced water currents by propelling water masses originating from above and behind its body, through the gill current, and then outwards in front of its body, parallel to the aquarium floor (Fig. 3B,C). Averaged over 150 images (lasting 5 s), the mean velocity was measured to be 3.1 cm s^{-1} for flow generated from the paddling behaviour, with peak instantaneous velocities up to 17 cm s^{-1} near the paddles, indicating intense paddling behaviour in the presence of a caged female. Not only was the maximum velocity of the flow more than five times greater, but a much larger volumetric flow was generated compared to that of the gill current alone.

DISCUSSION

Portunid crabs use sex pheromones and visual signals to communicate reproductive status (Ryan, 1966; Gleeson, 1991; Hardege et al., 2002). This includes a courtship display by males towards a sexually receptive pubertal female crab (Ryan, 1966; Fielder and Eales, 1972; Berrill and Arsenaault, 1982; Gleeson, 1991; Hardege et al., 2002). However, only the blue crab *Callinectes sapidus* (Teytaud, 1971; Gleeson, 1991; Wood and Derby, 1995; Jivoff and Hines, 1998) and the lesser blue crab *Callinectes similis* (M.K., personal observation) are known to have paddling as one component of the male display, in which they rhythmically wave their swimming legs. Our experiments give insights to why this is so.

Function of the paddling: generation of forward water current that facilitates bidirectional sexual communication

Our quantitative results with particle imaging velocimetry reveal that the water current generated by courtship stationary paddling redirects water away from the male toward the female at a mean velocity of 3.1 cm s^{-1} (Fig. 3). This water current could deliver both hydrodynamic and chemical information from males to females, and this signalling is probably the main function of the courtship

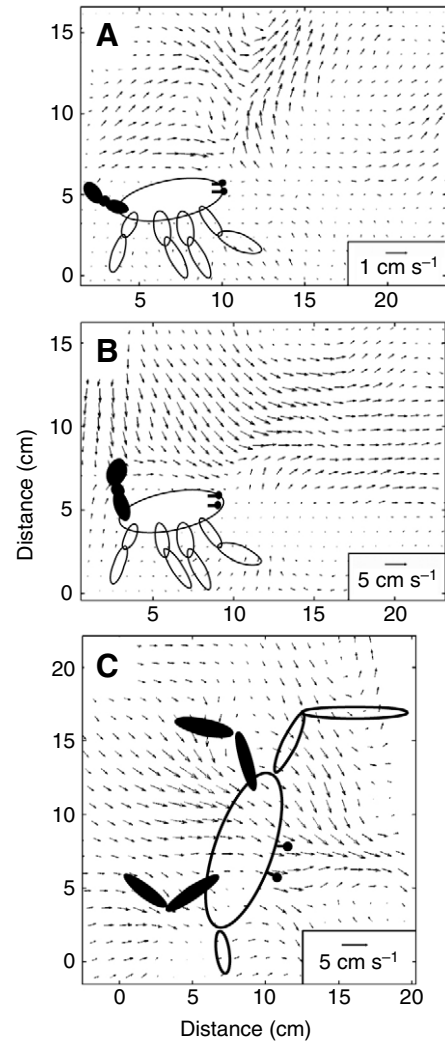


Fig. 3. Particle imaging velocimetry images of currents generated by a male crab, with and without courtship stationary paddling. (A) Side view of the crab when it is not performing courtship stationary paddling. The gill current generates flow upwards toward the water surface. (B) Side view of the crab performing courtship stationary paddling, which generates a forward current. (C) View from above of the crab performing courtship stationary paddling, which generates a forward current. The mean velocity for current generated by the paddling was 3.1 cm s^{-1} .

stationary paddling. The speed of the water current might be even faster than that described in our laboratory experiment, because crabs can perform higher frequency paddling than that measured in this experiment, even in the same laboratory conditions as used in this experiment (M.K. and M.A.R., personal observation). The effective distance that water is transported due to paddling is an important factor in evaluating the function of this behaviour. Our PIV experiment was performed using a crab with a carapace width of 11.5 cm in a $30 \times 40 \text{ cm}$ plane space. Because the size of the aquarium limits the distance of the water flow, using either a larger aquarium or larger males would likely yield currents of greater velocity that could deliver the chemical stimulus to a greater distance away from the male than was possible in our experiment.

Although pheromone release is less frequently reported for males compared to females, male blue crabs release a pheromone that attracts pubertal females (Gleeson, 1991). Male pheromones are also

known in other decapod crustaceans (Sato and Goshima, 2007). We speculate that bidirectional communication involving sex pheromones from both sexes is more common in crustacean species than is currently known.

When does a male paddle?: when females are inaccessible

Our results show that a male crab produced courtship stationary paddling only when there was a barrier between him and the female (Figs 1 and 2). When the female was caged behind a barrier, a male first walked up to the cage toward the female and attempted to break the barrier by ripping the mesh of the cage or the cage itself, and only after attempting to move beyond the barrier for some time did the male finally begin courtship stationary paddling. These results indicate that courtship stationary paddling is not the behaviour of first choice for a male attempting to form a precopulatory pair. This conspicuous and active courtship stationary paddling is a vigorous behaviour that makes the male more obvious to predators, and thus is likely to be energetically costly and to increase the risk of being attacked by a predator, as is the case for many other courtship display behaviours (Andersson, 1994). This explains why courtship stationary paddling is not common in male crabs in the laboratory, i.e. males should not perform courtship stationary paddling unless they encounter a barrier preventing access to females.

Why do they paddle?: adaptation to their habitat

Our results are consistent with a habitat adaptation hypothesis for the evolution of this courtship display. According to this idea, reproductive females, either in the premolt pubertal stage or the immediate postmolt mature stage, are vulnerable to predators. Sea turtles, sharks, rays, alligators, birds and fish are predators of blue crabs (Hines, 2007). Their habitat – *Spartina* marshes and shallow water with seagrass beds – provides ample protective shelter in the grass and mud, as well as murky water. Indeed, premolt crabs are typically captured by fishermen in the Chesapeake Bay by dredging seagrass beds (Hines, 2007). These seagrass refuges may allow females to avoid predators, and they also act as barriers to males seeking females based on their odour. Males may be able to get close to the pheromone-releasing female but may not be able to access the female to initiate precopulatory guarding. When a male locates the female using its chemical and visual senses but cannot access her, the male may initiate courtship stationary paddling to deliver his pheromone to inform the female of his location. Upon sensing his pheromone, the female may leave her refuge to form a precopulatory pair with the male. This hypothesis is consistent with the fact that late premolt females are prone to form precopulatory pairs (Jivoff and Hines, 1998) (and others). The habitat adaptation hypothesis explains why only blue crabs and lesser blue crabs show courtship stationary paddling but portunid species that inhabit open ocean habitats do not. However, this hypothesis does not explain why for species living in similar habitats with many refuges and low visibility that result in inaccessible premolt females, the males do not show stationary paddling. We speculate that other portunid species that live in a habitat similar to blue crabs and lesser blue crabs may also perform courtship stationary paddling.

Discrimination of courtship stationary paddling from the other forms of paddling

Walking forward while performing courtship paddling should be difficult because paddling produces a forward current that generates a backward directed force. In our experiments, males performing stationary paddling slipped backward because of this

backward directed force (Movie 7 in supplementary material). Male crabs are reported to show falling back display (Teytaud, 1971) and/or jumping back behaviour (Jivoff and Hines, 1998) combined with paddling display. We observed such falling back behaviour in our experiments (Movie 8 in supplementary material) but interpret it to result from the backward directed force generated by paddling. Jivoff and Hines (Jivoff and Hines, 1998) reported that the rate of the paddle waving varies but often increases as the displaying crab moves closer to another crab. Paddling is typically combined with approach and chelae spread. Paddling while moving forward was observed in our experiments; however, during moving forward, males stopped stationary paddling for a short period or changed the type of paddling (Movie 9 in supplementary material). Paddling during forward walking can thus be distinguished from courtship stationary paddling. Jivoff and Hines (Jivoff and Hines, 1998) described that courtship paddling is typically combined with approach. This is not consistent with our observations. One possible explanation is experimental differences. In our experiments, crabs were in an aquarium with a flat and smooth bottom with almost no substrate, and crabs may not have had secure enough footing to make courtship stationary paddling during forward walking without slipping and falling back. Another possibility is that courtship stationary paddling was not distinguished from the other type of paddling in Jivoff and Hines (Jivoff and Hines, 1998).

Role of gill currents in courtship display

In American lobsters and crayfish, the gill current moves water forward and away from the signaler, sending urine toward the opposite sex or opponent (Atema, 1986; Breithaupt and Eger, 2002). In our experiments on blue crabs, the gill current projected upward and did not make a large contribution to the forward-directed current. This can be one of the reasons why blue crabs need courtship stationary paddling. However, many kinds of water flow can be generated by fan organs, as reported in crayfish (Breithaupt, 2001). It is possible that male blue crabs change the direction of gill current when they start paddling.

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