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DIGGING MECHANISMS AND SUBSTRATE PREFERENCES OF SHOVEL NOSED LOBSTERS, *IBACUS PERONII* (DECAPODA: SCYLLARIDAE)

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A B S T R A C T

Digging is a distinct form of locomotion that poses different mechanical problems than other locomotor modes that are commonly used by crustaceans, e.g., walking, swimming. I examined the mechanisms of digging by shovel nosed lobsters (*Ibacus peronii*), which spend most of the day underneath sand. *Ibacus peronii* were videotaped while digging. *Ibacus peronii* use a “wedge” strategy to submerge into sand. An individual penetrates the sand with the walking legs, then extends the abdomen to push sand backwards, then flexes the abdomen while pushing backward with the legs, which slowly drives the body into the sand. This basic sequence repeats for several minutes. Digging often ends with a short series of tailflips. Digging by “wedging” is substantially different from previously described mechanisms in more specialized digging species. When presented with a choice of substrates, *I. peronii* preferred to dig in sand over shell grit, but individuals showed no preference for different types of sand.

INTRODUCTION

Crustaceans have many means of locomotion. These include walking, both underwater (Ayers, 2004; Clarac, 2002) and on land (Sleinis and Silvey, 1980); punting (Martinez et al., 1998), and; swimming, by swimmeret beating (Davis, 1969; Mulloney, 2003; Paul and Mulloney, 1986; Stein, 1971; Tschuluun et al., 2001), or tailflipping (Cooke and Macmillan, 1985; Kramer and Krasne, 1984), or uropod beating (Paul, 1971). Many crustaceans locomote by digging, i.e., movement through a substrate, but digging is a poorly understood form of locomotion. Examples of digging crustaceans include sand crabs (Dugan et al., 2000; Faulkes and Paul, 1997a, 1997b, 1998; Trueman, 1970), brachyuran crabs (Skinner and Hill, 1987), and scyllarid lobsters (Faulkes, 2004; Jones, 1988, 1993). Digging is not to be confused with burrowing, although the two terms have been conflated. Burrowing is the excavation of a permanent or semi-permanent structure, i.e., a burrow; examples of burrowers include crayfish (Correia and Ferreira, 1995; Hasiotis et al., 1998) and thalassinidean mud shrimp (Bird and Poore, 1999; Kinoshita, 2002; Shimoda and Tamaki, 2004).

There is currently no general framework for making predictions about digging behaviour. Digging poses substantially different problems for an organism than other forms of locomotion. First, loads are heavier and resistances are greater than either air or water. Second, most crustaceans dig in sand, which is a granular material. The physics of granular materials are complex, such that granular materials have substantially different properties than media like air or water (Jaeger et al., 1996). For example, granular materials can switch between having solid-like properties and liquid-like properties. The ability of sand to become more fluid when stirred is thixotropy (Cubit, 1969; Mewis, 1979). Thixotropy is critical to understanding digging; for example, the large-scale thixotropic properties of beaches explains much of the distribution of the sand crab species *Emerita analoga* (Cubit, 1969).

Scyllarid lobsters seem unlikely diggers at first glance, given that digging species such as sand crabs have robust legs (Faulkes and Paul, 1997b) whereas scyllarids have slender legs. Indeed, digging is not universal among scyllarids: *Scyllarides latus* and *S. nodifer* do not dig (Barshaw et al., 2003; Barshaw and Spanier, 1994; Ogren, 1997), even under extreme predation (Barshaw et al., 2003), but instead seek refuge in shelters and reef crevices (Barshaw and Spanier, 1994; Ogren, 1977; Spanier and Almog-Shtayer, 1992). Nevertheless, species in at least two scyllarid genera, *Thenus* and *Ibacus*, do dig (Faulkes, 2004; Jones, 1988, 1993). Digging is thought to be a predator-avoidance mechanism (Faulkes, 2004; Jones, 1988) that may have led to the loss of rapid escape tailflips in the genus *Ibacus* (Faulkes, 2004). The radically different morphology of scyllarid lobsters compared to sand crabs suggests that they have different solutions to the biomechanical problem posed by locomotion through wet sand. Informal anecdotes suggest that scyllarids’ flat, broad antennae are used for digging, leading to one of the common names for scyllarids, “shovel nosed lobsters.” A brief description of *Thenus* species in an unpublished doctoral thesis (Jones, 1988) indicates that *Thenus* species do not use their antennae to dig, but it is not clear if other scyllarid genera, such as *Ibacus*, dig in the same fashion as *Thenus* species.

Given that many scyllarids dig, their ecology and distribution may be influenced not only by the availability of sand, but by the type of sand as well. In laboratory settings, *Thenus indicus* prefers mud, whereas *Thenus orientalis* prefers coarse sand (Jones, 1988), a pattern that is also generally reflected in catches from trawls (Jones, 1993). It is known that *Ibacus* species live in sandy environments (Stewart and Kennelly, 1998), but whether individuals have more specific preferences for particular types of sand is not known. Species of *Ibacus* are sold commercially as seafood (Stewart, 2003; Stewart and Kennelly, 1998, 2000), so knowledge of whether these

species prefer particular types of sand, or whether all sand is preferred equally, may be useful for fisheries.

MATERIALS AND METHODS

Live *Ibacus peronii* Leach, 1815 (known locally as “Balmain bugs” or “bugs”) were bought from a local commercial seafood supplier (Briary’s Seafood Connection, Queen Victoria Market, Melbourne) and housed in the University of Melbourne’s seawater system. They were provided with sand to dig in, and fed a diet of squid.

Animals were videotaped using standard, commercially available VHS cameras and videotape machines (PAL format) while freely behaving in an aquarium in which the bottom was covered by a thick layer of fine sand (average diameter ~0.3 mm). The VHS camera imprinted a time code (hours: minutes: seconds) on the tape during recording. The videotapes were later converted to digital video disks (DVDs; NTSC format). Durations of behaviour were measured to the nearest second using the time code imprinted on the video image at the time of recording.

To test substrate preferences, *I. peronii* were placed in a tank (1.0 m long × 0.6 m deep × 0.6 m high) in which each half was covered 100 mm deep with a different material. Four individuals were placed in the tank at once, with two on each side of the aquarium, and then left for 2 hours, or until all were dug into the sand. Three substrates were used: fine sand (average diameter ~0.3 mm), coarse sand (average diameter ~1 mm), and shell grit (mollusc shell fragments; average diameter ~5 mm). Individuals were presented with the choice of shell grit versus coarse sand, and coarse sand versus fine sand. Behaviour of animals digging in coarse sand or shell grit was similar to that of individuals digging into fine sand.

RESULTS

A brief description of the normal posture and locomotion of *I. peronii* is helpful to place digging behaviour in context. Decapod crustaceans have five pairs of legs (pereopods), numbered from 1 to 5, starting with anterior legs. In many decapod crustaceans, legs 1 are enlarged claws, but all legs in *I. peronii* are similar in size and shape. *Ibacus peronii* walks using legs 3–5 (Johnston and Yellowlees, 1998) in a standard alternating tripod gait (Wilson, 1966). *Ibacus peronii* normally hold the tailfan curled underneath the abdomen by flexing the joints between the fifth and sixth abdominal segments, and the sixth abdominal segment and the telson. The more anterior abdominal segments tend to be held straight.

Digging by *I. peronii* is similar to *Thenus* species (Jones, 1988). One of the indications that an individual *I. peronii* is liable to begin digging is that all the legs are inserted into the sand, which is similar to foraging behaviour (Johnston and Yellowlees, 1998). The posterior legs are inserted into the sand up to approximately the merus-carpus joint. In some cases, the legs are then withdrawn and the animal continues walking, presumably searching for another location in which to dig. After the legs have been inserted into the sand at the start of a digging sequence, the abdomen flexes at all joints. The abdomen is pressed down so that the tailfan contacts the sand; the pleon is then extended, pushing the sand backwards. As the pleon becomes more submerged, the resistance of the sand to abdominal extension causes the anterior end of the carapace to pivot up slightly. The legs remain submerged in sand for the first few pleonal extensions and flexions.

Initially, digging consists of: (1) pleonal extension and; (2) pleonal flexion. As individuals descend into sand, the behaviour becomes a slightly more complex sequence of four elements: (1) pleonal extension; (2) repositioning the legs during pleonal extension; (3) pleonal flexion, and; (4) pausing before the next pleonal extension.

The movement of the legs occurs in the middle of the digging sequence. In the first few cycles to involve leg movement, sometimes only the most anterior legs (first pair alone, or first and second pairs alone) are repositioned. The repositioning of the legs begins one to two seconds after the beginning of pleonal extension. The legs are lifted out of the sand in a metachronal wave that begins with the anterior legs. The legs are then repositioned, with the tips placed more posterior than previously. The legs apparently brace the body and cause little movement of the sand, in contrast to the active shovelling of sand by the legs of sand crabs (Faulkes and Paul, 1997b, 1998).

The initial cycles of extension and flexion have a period of a few seconds (mean ± SD of first three cycles = 5.8 ± 3.7 s, n = 7). The period substantially slows as individuals dig (mean ± SD of last three cycles = 24.5 ± 7.9 s, n = 8). This increase in pleonal period is not simply due to the increased resistance of the sand, which would be predicted to increase the duration of pleonal extension and flexion. Although the durations of extension and flexion do increase slightly during digging, they are much less variable than the length of a pause between the end of flexion and the onset of extension, when there is no visible movement of the body. This pause is the main factor increasing cycle period.

Ibacus peronii are slow diggers, requiring several minutes to submerge into sand. The average duration of digging sequences was 276.3 ± 68.9 s (mean ± SD; n = 9), requiring an average of 17.00 ± 3.11 cycles (mean ± SD; n = 7) of pleonal extension and flexion to complete. In five of nine individuals, digging ended with a short series of tailflips, which caused a small avalanche of sand that had piled at the rear of the carapace to run down the front of the carapace. This usually resulted in the animal being completely covered in sand, and not at all visible from above it. It appeared that a few sand grains rolling down around the eyestalks triggered tailflipping. These tailflips are not, however, examples of specialized escape responses, because *I. peronii* lacks the giant neurons associated with escape (Faulkes, 2004).

Ibacus peronii prefer sand to gravel. Of 34 animals presented with a choice of coarse sand and shell grit, 26 dug into sand (76.5%) compared to five dug in shell grit (14.7%). Three individuals (8.3%) did not dig in the time given. Of the 31 individuals that dug, the frequency of animals digging in sand is significantly greater than the 50% expected by chance ($\chi^2 = 14.23$, d.f. = 1, $P < 0.01$). *Ibacus peronii* do not discriminate between sand types within the ranges of particle sizes tested, however. In the second test (n = 35), 20 individuals (57.1%) dug into fine sand compared to 13 individuals (37.1%) digging in coarse sand. Two individuals (5.8%) did not dig in the time allotted. Of the 33 to dig in, there was no statistically significant difference between substrates chosen ($\chi^2 = 1.48$, d.f. = 1, $P = 0.22$).

DISCUSSION

Ibacus peronii use their legs and tail to dig into the sand. Despite the common name of “shovel nosed lobster,” *I. peronii* do not dig into sand face-first with their “noses,” i.e., antennae. Instead of functioning in digging, the flattened

antennae of *I. peronii* help to direct swimming trajectories (Jacklyn and Ritz, 1986), and presumably have sensory abilities comparable to other decapod crustacean antennae.

Digging in a species like *I. peronii*, which is able to both walk and dig, may be used as a proxy ancestral behaviour for species like sand crabs, which cannot walk and are obligate diggers (Faulkes and Paul, 1997a, 1997b, 1998). Presumably, there was a point in sand crab evolution where sand crabs were able to dig and walk, but no extant anomuran is known that performs both behaviours. Like *I. peronii*, sand crabs also use their legs and tail to dig backwards (Faulkes and Paul, 1997a, 1997b; Trueman, 1970), but the similarities end there. *Ibacus peronii* are slow diggers, taking an average of over four minutes to submerge into the sand, compared to less than two minutes for *Thenus* species (Jones, 1988) and seconds for sand crabs (Dugan et al., 2000). The sharp difference in speed between scyllarid lobsters and sand crabs is related to the differences in digging mechanisms. *Ibacus peronii* do not create a thixotropic effect (except, perhaps, at the very end of a dig when they tailflip), instead slowly inserting themselves into the sand. Sand crabs take advantage of thixotropy by liquefying the sand using high frequency movements of either the pleon (in abuneids) or uropods (in hippids), plus shovelling with their robust legs (Faulkes and Paul, 1997a, 1997b, 1998). The legs of *I. peronii* are slender, whereas the legs of sand crabs are robust. Robust legs seem advantageous for digging, but *I. peronii* may have relatively fine legs because their legs are used to prey on molluscs. *Ibacus peronii* pry apart bivalve shells with their legs, then insert the sharp dactyls to cut the clam's adductor muscles, which allow the lobster to open the shell easily (Johnston and Yellowlees, 1998).

Scyllarid digging is correlated with the loss of rapid escape tailflips and associated giant interneurons in *Ibacus peronii* (Faulkes, 2004). Escape tailflips are an example of an antipredator mechanism, i.e., a mechanism for increasing survival once an individual is detected (Barshaw et al., 2003). It is conceivable that rapid digging could serve as an antipredator mechanism, but given how slow digging by *I. peronii* is, digging is better characterised as a predator-avoidance mechanism; i.e., a mechanism that seeks to minimize detection by predators (Barshaw et al., 2003). Thus, scyllarid digging is not a simple substitute for escape tailflipping, and a more substantial shift in defensive tactics occurred in the transition from the dorsoventrally elongated body plan of clawed lobsters and spiny lobsters to the dorsoventrally flattened body plan of scyllarids (Barshaw et al., 2003).

Digging mechanisms in crustaceans (or other hard bodied aquatic organisms) might be placed into three basic categories: wedges, shovels, and fans. Wedge-like mechanisms are characterized by low speed movements, and the majority of work is accomplished through leverage. This is the primary digging mechanism used by *I. peronii*. Shovel-like mechanisms have higher speeds and frequencies than wedges, and function by moving sand by presenting a wide surface to the sand as it moves, and perhaps causing a moderate thixotropic effect. Examples of shovel-like mechanisms include legs 2–4 of sand crabs (Faulkes and Paul, 1997b, 1998). Fan-like mechanisms may be small, are

characterized by higher speeds and frequencies than wedges or shovels, and function by creating thixotropic effect: liquefying the sand to allow penetration of limbs and/or the body. The abdomen or uropods in sand crabs are best characterised as fans (Faulkes and Paul, 1997a). These proposed categories are presented to provide a framework for discussing biomechanics of digging. These categories may be more rigorously defined by future research, or entirely new mechanisms may be added to the three suggested here.

Within the range of substrates tested here, *I. peronii* preferred fine sand substrates over coarse ones. That *I. peronii* could dig in shell grit shows the difference in selection was not due to any physical inability to penetrate coarse substrates. It is also not the case that the finer the substrate the better: individuals did not pick fine sand significantly more often than medium sand. Preference for very fine sediments, e.g., mud, remains to be tested, however.

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