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Claw-pinching force of sand fiddler crabs in relation to activity and the lunar cycle

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ABSTRACT

Male sand fiddler crabs, *Uca pugilator* (Ocypodidae), possess a single enlarged claw that is used in ritualized contests over breeding burrows. Ability to close the claw forcefully, which increases with claw size and stoutness, may promote success in contests. As the density of males at breeding burrows changes across the lunar cycle, the frequency of contests may also change and affect the advantage associated with a powerful claw. At an Atlantic coast salt water marsh in northern Florida, we investigated claw size, claw stoutness, and pinching force with daily samples of foraging and courting males made across three lunar cycles. Foraging and courting males constituted the vast majority of surface-active males. Foraging males occurred in dense aggregations, droves, on moist, low-elevation sediments. Courting males, recognized by claw-waving displays, were at burrows in dry, high-elevation sediments where they fed relatively little. On average, courting males had greater claw-closing force than droving males but claw length and stoutness did not vary by activity. Claw-closing force, claw length, and claw stoutness of courting males were greatest on and near the days of new or full moons, when the densities of courting males peaked. No temporal patterns were observed for droving males. Mark/recapture of males revealed that claw power declined during courtship and increased while droving. Moreover, males switched from droving to courting as claw power increased and switched from courting to droving as claw power decreased. In the laboratory, the claw-closing force of unfed males decreased over time but rebounded quickly after males were given food. We suggest that males cycle between activities in response to strength and condition. However, it appears that males with larger, stouter claws are more likely to court at new and full moons, when the number of mating-receptive females peaks.

1. Introduction

Sexual selection on males can favor the evolution of weapons used in contests that determine mating success (Kelly, 2008). Within a species, the size of energetically costly weapons may reveal male condition during growth (Cotton et al., 2004; Knell et al., 1999; Lailvaux et al., 2005). However, the ultimate expression of male quality may be the ability to execute dynamic tasks with weapons which exposes the association between morphology and physiology (Arnold, 1983; Irschick et al., 2007). As there is a physiological cost to mating competition between males (Berglund et al., 1996), changes in physiological status will introduce variation in the relationship between weapon size and performance (Irschick and Le Galliard, 2008; Lappin and Husak, 2005). Thus, performance may change within individuals as a function of recent experience and fluctuating environmental conditions. Changes in performance may underlie important activity decisions. For instance, opting to feed may promote physiological recovery, while opting to engage in courtship may erode physiological condition.

Male fiddler crabs have a single enlarged sexually-selected claw that can be used as an intra- or intersexual signal and as a weapon (Crane, 1975; Levinton and Judge, 1993). The mass of the claw may exceed 1/2 the mass of the rest of the body (McLain et al., 2003). In many species, males use the claw in ritualized contests for breeding burrows (Crane, 1975). Contests frequently escalate from initial displays of claw size to fierce pinching with pushing, pulling, and lifting maneuvers that occur while opponents' claws are inter-locked (e.g., Pratt et al., 2003). Escalated contests favor males with larger (Jennions and Backwell, 1996; Morrell et al., 2005) and stouter claws (Reaney et al., 2008; McLain et al., 2010; Callander et al., 2012). Thus, closing force is greater among males both winning contests (Lailvaux et al., 2009) and possessing burrows that females prefer (McLain et al., 2010). Across the lunar cycle, the density of breeding males varies (Pratt et al., 2005) as does claw size (Pratt and McLain, 2002).

In this study of the sand fiddler crab, *Uca pugilator* Bosc (Brachyura: Ocipodidae), we compare claw closing (pinching) force among large males as a function of activity over three lunar cycles in northeastern

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Florida. We focus on two activities, droving and courting, and relate switching between activities to changes in claw-closing force.

Droving is foraging in a dense aggregation, the drove (Crane, 1975). The food of sand fiddler crabs consists of organic matter, especially benthic algae, in the upper layer of sediment (Robertson et al., 1980). Males scoop moist sediment with a minor cheliped that is the bilateral partner to the claw. At our study site in northeast Florida, droves are typically male-biased aggregations that consist of hundreds to tens of thousands of crabs, usually within one to a few body widths of another crab (McLain et al., 2005). Droves occur on moistened sand flats and near the waterline of tidal creek banks. Wet sediment is a necessary for feeding (see Miller, 1961; Reinsel and Rittschof, 1995). Droves move as food content of the sediment patches becomes exhausted (Reinsel and Rittschof, 1995; Reinsel, 2004). While droving, sand fiddler crab males are not aggressive toward one another and do not court females. Droving is not observed in many fiddler crab species but is a common activity of sand fiddler crabs in coastal salt marshes of the southeastern U.S. (Crane, 1975).

During the daytime of the breeding season, which extends from late March through September in northeast Florida, most sand fiddler crab males who are not droving engage in breeding-related activities at defended burrows. The most obvious of these is waving the claw in a circular arc to attract females (Salmon and Atsaides, 1968; Pope, 2000). Females prefer burrows that are in more elevated, drier marsh sediments (Christy, 1983) where food and feeding opportunities are limited (Christy and Salmon, 1984; McLain and Pratt, 2010; Allen and Levinton, 2014).

Contests and waving displays and concomitant exposure to heat and water stress erode the physiological condition of courting males (Genoni, 1985; Yamaguchi, 2001a; Kim and Choe, 2003; Matsumasa and Murai, 2005; Kim et al., 2008; Allen and Levinton, 2014). Moreover, claws impose energy stresses that increase with crab size (Allen and Levinton, 2007). As courtship in the sand fiddler crab is largely sustained on internal energy stores (Christy and Salmon, 1984), courting males will eventually need to opt out of courtship in order to replenish energy stores and regain good physiological condition (Kim et al., 2008).

The sand fiddler crab is especially suited to the investigation of the relationship between activity and condition, as revealed in claw pinching performance, because most surface-active males during the daytime of the breeding season are engaged in either droving or courtship. These activities, which are expected to have opposite effects on male condition, are easily visually distinguished and occur in different microhabitats.

At any given point in the lunar cycle at sites such as ours, some male sand fiddler crabs attempt to breed while others drove (Pratt et al., 2005). Nevertheless, burrow defense, waving, copulation, and release of eggs are predominately synchronized with the lunar cycle (Christy, 1983; Salmon and Hyatt, 1983; Thurman, 2004). Thus, the density of courting males peaks during the few days around new and full moons (Pratt et al., 2005). We conducted the present study across three entire lunar cycles to capture variation in male condition, revealed in claw-closing force, and to expose interactions between condition and activity.

Several predictions follow if (1) courtship erodes physiological condition, (2) foraging restores condition, and (3) physiological condition is reflected in claw-closing force. First, claw-closing force will be higher for breeding than droving males. This is because we expect males to opt for courtship when their condition is good and to opt for foraging when their condition is poor. Also, we expect that males in better condition will be better able to acquire and defend breeding burrows. Second, among courting males, claw-closing force will be higher when the density of courting males is higher. This is because competition for burrows, which favors stronger males (Lailvaux et al., 2009), is expected to be more intense at times when more males opt to court. Both predictions assume that males switch between foraging and courting. We investigate activity switching through the recapture of marked males.

2. Methods

2.1. Field site and collection

The study was conducted in Crescent Beach, Florida in a *Spartina alterniflora* Loisel salt marsh that drains into an estuary, the Matanzas River. The site experiences semi-diurnal tides (see Thurman, 2004). Crabs were collected during the daytime at low tide from six sand mounds within tidal channels in the marsh. Collections were not made from the same mound on consecutive days to permit habitat recovery and to reduce the odds of resampling the same males. Most mounds were connected to channel banks at low tide which resulted in the exchange of crabs. We targeted larger individuals for collection to reduce variance in claw-closing force attributable to body and claw size. We identified courting males as those males waving their claw at burrows. Consequently, we use waving male (or waver) synonymously with courting male.

Collections of waving and droving males were made every day in 2011 from 30 June to 30 July (= lunar set 1), in 2013 from 8 July to 7 August (= lunar set 2), and in 2014 from 27 July to 26 August (= lunar set 3). Each lunar set extended from 15 days before to 15 days after a full moon. Thus, each lunar set included a new moon before and after the full moon. On each date, 10–30 waving and 10–30 droving males were collected. Crabs were measured and tested for claw-closing force in the field, then returned to the site of collection.

The density of courting males was estimated each day at the site of collection by counting the total number of males waving within two 1-m^2 quadrats that were watched for 15 min. Also, we counted the number of females that approached and entered burrows of quadrat males during a 10-minute observation period. Entering burrows is an activity that characterizes mate-seeking females in a number of fiddler crab species (e.g., Christy, 1983; Backwell and Passmore, 1996; deRivera, 2005).

2.2. Measurements

Measurements, repeatable to 0.05 mm, were made with digital dial calipers to permit determination of body size (carapace width) and claw size and stoutness. Carapace width was measured across the antero-lateral angles. Two measurements were made on each claw. These were the length of the propodus, a common index of claw size, and the length of manus. The propodus consists of the palm-like manus that contains the claw closer muscle and the fixed, thumb-like pollex. The length of the pollex was determined by subtracting the length of the manus from the length of the propodus. During claw pinching, the dactyl, an articulating finger-like projection off of the manus, is moved toward the pollex by the contraction of the closer muscle.

We scored the development of teeth and tubercles on the pollex and the dactyl. For each, development was scored from 0 (none) to 3 (maximum expression) (McLain and Pratt, 2011). Teeth focus the claw-closing force (Dennenmoser and Christy, 2013) while tubercles reduce slippage during pinching in contests (Crane, 1975). Scoring of tooth and tubercle development along with claw measurements permits the calculation of a claw stoutness index, (2 + sum of dactyl and pollex tooth and tubercle scores) · (manus length) / (carapace width · pollex length) (McLain and Pratt, 2011).

2.3. Claw-closing force

Claw-closing force (henceforth, closing force) was determined with a “bite” force meter consisting of parallel bite plates of steel bonded to aluminum arms, and adjustable fulcrum, a force sensor, cable, and charge amplifier (Fig. 1; McLain et al., 2010). Each crab was held by the carapace so that the pollex contacted the underside of the lower plate while the dactyl contacted the topside of the upper plate. Pinching