An evaluation of lekking behavior in the fiddler crab *Uca* spp.

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**Abstract**

The reproductive behavior of *Uca* spp. has been extensively studied, especially the relationships between the dimorphically enlarged male claw and reproductive success. In contrast, little is known about the apparent congregations of adult males in marsh areas lacking vegetative cover where they engage in behaviors thought to attract mates. Similar congregations and displays in avian and mammalian species are termed ‘leks.’ In order to test the hypothesis that open-area assemblages of *Uca* spp. are functioning as leks, we examined the sex ratios, juvenile/adult ratios, and the percentage of time that adult males spend eliciting reproductive behaviors within open and vegetated areas of marsh habitats. Moreover, to evaluate whether differences in sediment-based food resources could explain open-area aggregations, we compared substratum organic content of open and vegetated areas of marsh habitats. Substrate was also examined to determine if grain size composition varied between open and vegetated areas and might preclude the construction of breeding burrows in vegetated areas of the marsh. Three species of *Uca* from four marsh habitats in biogeographically distinct regions of North America were sampled including Dauphin Island, Alabama, Hunting Island, South Carolina, Saxis, Virginia, and Wallops Island, Virginia. Comparisons of male/female and juvenile/adult ratio means indicated that greater numbers of adult males occurred in open areas of all marshes. In addition, adult males allocated significantly greater time to reproductive behaviors in open rather than in vegetatively covered areas across all biogeographic regions and among all species. Food levels (sediment organic content) in open areas were equal to or less than sediment organic contents in vegetated areas in marsh habitats at Dauphin Island and Hunting Island, the two marshes where the variable was examined. Similarly, substratum granulometry analysis revealed no significant differences between open and vegetatively covered areas of the marshes at Dauphin Island or Hunting Island that might influence choice of burrow location. Collectively, these observations support the hypothesis that lek behavior is an integral component of the reproductive repertoire in *Uca* spp. © 2000 Elsevier Science B.V. All rights reserved.

**Keywords:** Behavior; Crustacea; Lek; Reproduction; Substratum; *Uca* spp.; Biogeography

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1. Introduction

The reproductive behaviors of *Uca* spp. are diverse and complex (Crane, 1975; Christy, 1983; Christy and Salmon, 1984; Doherty, 1982; Greenspan, 1982; Murai et al., 1987; Salmon, 1967; Zucker, 1984). Males engage in elaborate waving displays with the single dimorphically enlarged cheliped, characteristic of the genus. Reproductively related above ground burrow structures and sound displays have also been reported (Christy, 1982; Greenspan, 1982; Zucker, 1981). Males sometimes congregate in open areas, defend burrows, and engage in waving displays. These open area assemblages have been well documented in many species of *Uca* (Crane, 1975; Croll, 1985; Greenspan, 1982; Hyatt, 1977; Zucker, 1981, 1984). Crane (1975) referred to these assemblages as ‘lek-like’ and Zucker (1981) referred to the open area aggregations as ‘communal displays.’

The evolutionary cost/benefit tradeoffs of lekking, as well as the reason for the occurrences of these breeding assemblages, have been studied at length in a variety of animals (Alexander, 1975; Beehler and Foster, 1988; Bradbury, 1981, 1985; Bradbury et al., 1986; Höglund and Alatalo, 1995; Stiles and Wolf, 1979; Thornhill and Alcock, 1983; Widemo and Owens, 1995). Female mate selection, in the absence of other resources influential to that selection such as food, water, or brooding sites, is considered a tenet of lek behavior. However, because mate choice is difficult to assess directly, it is often necessary to eliminate other factors that could be directing female choice. Furthermore, because the first lekking species identified were avian, subsequent additions to the list of species that exhibit lek behavior are compared to avian criteria. The genus *Uca* is generally excluded from classification as a lekking species because males defend burrows presumed to be a required resource for successful reproduction. However, Höglund and Alatalo (1995, p. 14) suggest that if female visitation to a breeding assemblage is not solely determined by the need for oviposition sites or feeding, then those assemblages should not be eliminated from consideration as a lek.

The purpose of this study was to determine if lek behavior is a part of the reproductive repertoire of selected *Uca* species within marshes across biogeographic regions ranging from the Atlantic to the Gulf Coasts of North America. To test the hypothesis that lek behavior is part of the *Uca* behavioral repertoire, we tested three lek requirements: (1) male aggregation, (2) male reproductive behavior, and (3) female visitation. Male/female and juvenile/adult ratios in open and vegetated areas and between populations within marshes were examined to determine if males are aggregating in open areas as compared to vegetated areas. Behavioral time budgets were used to test whether males engage in reproductive behaviors preferentially in open areas when compared to vegetatively covered areas within and across biogeographic regions and species. To test for the presence of other resources attractive to females, two environmental parameters were examined: substratum organic content and substratum granulometry. The organic content of the surface substratum provides an indicator of food availability. Higher organic content in open areas would provide an alternate reason for female visitation to sites with no vegetation. Similarly, substratum grain size composition provides an indicator of substratum suitability for breeding burrow construction. Therefore, differences in substratum granulometry could limit where males construct breeding burrows and consequently affect female selection.
2. Methods

Studies were conducted during the months of June, July, and August between 1994 and 1999 at Dauphin Island, Alabama (30°20.5′N, 88°7.5′W), Hunting Island, South Carolina (32°22.5′N, 80°27.5′W), Saxis, Virginia (37°55.5′N, 75°42.3′W), and Wallops Island, Virginia (37°53.0′N, 75°26.5′W). Three species of fiddler crabs were investigated: *Uca minax* (LeConte, 1855) at the Saxis site, *U. longisignalis* (Salmon and Atsaiðes, 1968) at Dauphin Island, and *U. pugnax* (Smith, 1870) at Saxis, Wallops Island and Hunting Island.

In order to determine male/female and juvenile/adult ratios, vegetative sites within each marsh were sampled. One hundred and twenty to 140 quadrats were established using flags to mark perpendicular transect lines. Each quadrat measured 30 m². Eighteen to 23 sampling sites per marsh were selected by random number generation and collections of crabs were made at the intersections of quadrat boundaries. Similar collections of crabs were also made at randomly selected open areas throughout the marshes (*n* = 1–10 open areas/marsh). Quantitative crab collections at all sampling sites were made using a 1-m square wood box with sides 20 cm in height (modified from Teal, 1958; Wolf et al., 1975). A stainless steel border extended 12 cm from the bottom of each side. The box was driven into the substratum by launching the box forward and allowing it to fall onto the marsh. The skirts of the box were then forced completely into the substratum to prevent subterranean escape of crabs. Juvenile crabs (carapace < 5 mm) inside the box were captured, counted, and released. All fiddler crabs, on or below the substrate, with a carapace width greater than 5 mm were sexed, measured (carapace width), counted, identified to species, and released. Male/female and juvenile/adult ratios were calculated for both open and vegetated sites within the four marshes. Because the data were heteroscedastic, they were rank transformed before analysis. A non-parametric mixed model two-factor ANOVA (Potvin and Roff, 1993; Zar, 1999), using fixed (vegetation type) and random (marsh location) factors, was used to examine male/female ratios. Because juveniles were never found in the open areas, a Kruskal–Wallis analysis (Potvin and Roff, 1993; Zar, 1999) was used to clarify differences in juvenile/adult ratios in vegetated sites between the sampled marshes. When significant interactions were identified, Tukey’s HSD post-hoc test for simultaneous pair-wise mean comparison was used to identify lower level differences. Higher male/female ratios in open or vegetated sites would indicate male aggregation, while differences in juvenile/adult ratios would further illustrate community differences.

Observations of discrete reproductive and non-reproductive behaviors (Table 1) were conducted at open and vegetatively covered marsh sites (modified from Caravello and Cameron, 1987; Greenspan, 1982; Hyatt, 1977; Zucker, 1984). Behavioral data was obtained by observing one or two males at each site for 1 h. The time spent by individual males in each behavioral category was recorded and the fraction of the total time calculated. Only males with a propodus greater than 20 mm in length were included in the observation. To reduce the influence of tidal and climate patterns, observations were alternated between open and vegetatively covered sites located within 5 m of each other. Observations were conducted at low tide and timed to occur within 1 week of the spring tide. Following each observational period, the observed individuals were captured, measured, and removed from the site. As in the male/female ratio analysis, a
non-parametric mixed model two-factor ANOVA (Potvin and Roff, 1993; Zar, 1999) was used to identify significant interactions between fixed (vegetation type) and random factors (marsh location). A greater mean percent time devoted to reproductive display and associated behaviors in open areas would provide evidence of display site selection by male crabs.

Because fiddler crabs are detritivores and their mouth parts glean organic material from the substratum (Caravello and Cameron, 1987; Crane, 1975; Miller, 1961; Weissburg, 1993), substratum organic content provides a measure of food availability (Caravello and Cameron, 1987; Miller, 1961; Montague, 1980; Weissburg, 1993; Zimmer-Faust, 1987). To test if differential food resources provide an alternate reason for female visitation, replicate sediment samples were collected from both habitats. Because crab feeding could affect organic content, samples were collected as the water receded from the marsh following high tide. Substratum samples were removed from the top 1-mm of the marsh sediment surface and frozen for return to the laboratory. In the laboratory, sediment samples were lyophilized, weighed, and then ashed at 400°C for 5 h. The ashed sediments were reweighed and percent organic content calculated. Similar to the male/female ratio analysis above, a mixed model two-factor ANOVA (Potvin and Roff, 1993; Zar, 1999), utilizing the same factors, was used to delineate differences in organic content in the sampled marshes at Dauphin Island and Hunting Island. A Kruskal–Wallis test was used to detect differences in the substratum organic content of vegetated areas across the four biogeographic regions (marshes). When indicated, Tukey’s HSD post-hoc test for simultaneous pair-wise mean comparison was used to identify lower level differences. If present, a higher organic content in open areas would provide an alternate reason for female visitation to these potential lek arenas.

Because substratum grain size composition has been linked to burrow stability and reproductive success (Christy, 1982, 1995), the ashed sediments were examined by direct observation using an optical reticule. Grains were divided into four categories: (I) \( x < 10 \ \mu m \); (II) \( 10 \ \mu m < x < 50 \ \mu m \); (III) \( 50 \ \mu m < x < 100 \ \mu m \); (IV) \( 100 < x < 200 \ \mu m \).
μm (x = grain size). The numbers of grains per square millimeter in each category were counted and the percent comprising each size fraction determined. A non-parametric mixed model two-factor ANOVA (Potvin and Roff, 1993; Zar, 1999) was used to determine if significant differences existed in the granulometry of open and vegetated areas in the marshes at Dauphin Island and Hunting Island. Correspondingly, a Kruskal–Wallis test (Potvin and Roff, 1993; Zar, 1999) was used to detect differences across the four biogeographic regions. Differences in granulometry between open and vegetated sites could indicate a differential capacity of the substratum to support breeding burrow construction and provide an alternate reason for male aggregation in open areas.

3. Results

Significant (P < 0.05) differences in mean male/female ratios were detected when sub-populations of crabs in open areas were compared to those in vegetated areas within marshes at Dauphin Island, Hunting Island, and Wallops Island (F = 24.9, df = 1). In all cases, male/female ratios were 3 to 4 times greater in open areas compared to vegetated sites (Table 2). The marsh at Saxis was excluded from analysis because only one suitable open area was available for observation.

Mean juvenile/adult ratios in vegetated areas within marshes at Dauphin Island, Hunting Island, and Wallops Island were greater than 2.16 while the same sub-populations in open areas had no juveniles. Significant (P < 0.05, F = 4.03, df = 2) differences in mean juvenile/adult ratios occurring in vegetated areas were detected between biogeographic regions and species. Further analysis using the Tukey method indicated that the Wallops Island marsh had particularly high densities of juveniles

<table>
<thead>
<tr>
<th></th>
<th>Dauphin Island</th>
<th>Hunting Island</th>
<th>Saxis</th>
<th>Wallops Island</th>
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</thead>
<tbody>
<tr>
<td>Open areas</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uca pugnax</td>
<td>–</td>
<td>4.5±1.5</td>
<td>–</td>
<td>4.9±0.6</td>
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<tr>
<td></td>
<td>(n = 10)</td>
<td>(n = 5)</td>
<td></td>
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<tr>
<td>Uca longistignalis</td>
<td>2.5, 5.5</td>
<td>–</td>
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<tr>
<td></td>
<td>(n = 2)</td>
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<tr>
<td>Uca minax</td>
<td>–</td>
<td>–</td>
<td>4.3±</td>
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<td>(n = 1)</td>
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<tr>
<td>Vegetated</td>
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<tr>
<td>marsh</td>
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<tr>
<td>Uca pugnax</td>
<td>–</td>
<td>1.3±0.2</td>
<td>1.1±0.2</td>
<td>2.0±0.3</td>
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<td>(n = 46)</td>
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<tr>
<td>Uca longistignalis</td>
<td>1.5±0.0</td>
<td>–</td>
<td>–</td>
<td></td>
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<tr>
<td></td>
<td>(n = 53)</td>
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<tr>
<td>Uca minax</td>
<td>–</td>
<td>–</td>
<td>1.1±0.2</td>
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<td>(n = 22)</td>
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* Shown are the means±1 S.E. (n = number of independent 1-m² quadrats sampled).
† Species not present.
Table 3
Juvenile/adult ratios of *Uca* spp. in open and vegetated areas of marshes at Dauphin Island, Alabama, Hunting Island, South Carolina, Saxis, Virginia, and Wallops Island, Virginia

<table>
<thead>
<tr>
<th></th>
<th>Dauphin Island</th>
<th>Hunting Island</th>
<th>Saxis</th>
<th>Wallops Island</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open areas</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><em>Uca pugnax</em></td>
<td>–</td>
<td>NJ</td>
<td>–</td>
<td>NJ</td>
</tr>
<tr>
<td><em>Uca longisignalis</em></td>
<td>NJ</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><em>Uca minax</em></td>
<td>–</td>
<td>–</td>
<td>NJ</td>
<td>–</td>
</tr>
<tr>
<td>Vegetated marsh</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Uca pugnax</em></td>
<td>–</td>
<td>3.1±0.9</td>
<td>NJ</td>
<td>7.8±2.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(<em>n</em> = 45)</td>
<td></td>
<td>(<em>n</em> = 50)</td>
</tr>
<tr>
<td><em>Uca longisignalis</em></td>
<td>2.2±0.04</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>(<em>n</em> = 32)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Uca minax</em></td>
<td>–</td>
<td>–</td>
<td>NJ</td>
<td>–</td>
</tr>
</tbody>
</table>

* Both the vegetated marsh habitat and specific open areas where large males aggregate are shown. Shown are the means ±1 S.E. NJ, No juveniles.

(P < 0.05, Table 3) when compared to the marsh at Wallops Island. The marsh at Saxis was excluded from analysis because no juveniles were encountered in any sampled open or vegetated area (Table 3).

Examination of open and vegetated areas within all four marshes indicated significant (P < 0.05, *F* = 116.2, df = 1) differences in the mean percent time devoted to reproductive behavior (Fig. 1). In all marshes, adult male fiddler crabs in open areas devoted a greater percentage of their time to reproductive behaviors than adult male crabs in vegetated areas. In contrast, there were no significant differences in the mean time...
Table 4
Mean percent time±1 S.E. of selected reproductive behaviors exhibited by adult *Uca* male crabs in open marsh areas

<table>
<thead>
<tr>
<th></th>
<th>Burrow Maintenance (mean % time)</th>
<th>Burrow Defense (mean % time)</th>
<th>Claw Waving (mean % time)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dauphin Island (n = 10)</td>
<td>1±0.7</td>
<td>3±0.7</td>
<td>33±6.0</td>
</tr>
<tr>
<td>Hunting Island (n = 10)</td>
<td>3±1.7</td>
<td>4±1.2</td>
<td>34±6.7</td>
</tr>
<tr>
<td>Saxis (n = 5)</td>
<td>5±2.7</td>
<td>0±0.3</td>
<td>55±14</td>
</tr>
<tr>
<td>Wallops Island (n = 8)</td>
<td>7±4.3</td>
<td>1±0.4</td>
<td>4±2.0</td>
</tr>
</tbody>
</table>

† Means are derived from pooled observations of individuals representing three species in four marshes: Dauphin Island, AL (*Uca longisignalis*), Hunting Island, SC (*Uca pugnax*), Saxis, VA (*Uca minax*), and Wallops Island, VA (*Uca pugnax*). The mean percent times are based on 1-h observational blocks.

allocated to reproductive behaviors between the four marshes (P > 0.05, F = 1.6, df = 3) or between (P > 0.05, F = 2.2, df = 3) fixed (vegetation type) and random (marsh location) effects (Table 4).

Comparison of substratum organic content between open and vegetated areas within the two marshes examined indicated significant (P < 0.05, F = 16.1, df = 1) differences in substratum organic content at both Dauphin Island and Hunting Island (Fig. 2). In both marshes the mean percent organic content was less in open areas (Dauphin Island = 15.4; Hunting Island = 5.5) than in vegetated areas (Dauphin Island = 18.9; Hunting Island = 12.8). Conversely, there were no significant (P > 0.05, F = 0.7, df = 1) interactions between fixed (vegetation type) and random (marsh location) factors within

Fig. 2. Mean±1 S.E. percent organic content of the surface substratum collected in open and vegetated sites at Dauphin Island, Alabama (open, n = 16; vegetated, n = 52) and Hunting Island, South Carolina (open, n = 25; vegetated, n = 23).
the same marshes. When vegetated site substratum organic content was compared across the four biogeographic regions, a significant ($H = 120.9$, df = 3) difference was detected. Further analysis using the Tukey method indicated that only the Dauphin Island and Wallops Island marshes had similar substratum organic content (Fig. 3).

Granulometric analysis of substratum from open and vegetated areas of Dauphin Island and Hunting Island indicated no significant ($P > 0.05$, $F = 0.0$, df = 1) differences in the mean percent of any grain size category at either marsh (Fig. 4). Similarly, there were no significant ($P > 0.05$) interactions between the two marshes ($F = 9.3$, df = 1) or between the marshes and the type vegetation ($F = 0.1$, df = 1). Examination of substratum in all sampled biogeographic areas revealed no significant ($P > 0.05$, $H = 2.0$, df = 3) differences in the mean percent of grains in any size category (Fig. 5).

4. Discussion

Lek behavior has been reported in amphibians, birds, insects, fish, and mammals (Höglund and Alatalo, 1995). Grier and Burke (1992) define a lek as “a communal display aggregation of males each defending a small area in which it displays, to which females are attracted”. This general definition of a lek, while accurate, encompasses a variety of behaviors and types of lekking locations. Other researchers have extended criteria that are more rigorous. Bradbury (1985) lists four: (1) there is no male parental care, (2) males occur on territories that are spatially clustered, (3) the territories contain
no resources that influence female attraction or mate choice, and (4) females have the freedom to choose mates within the cluster of male territories. Similar requirements have been tenured by Smith (1986) and Krebs and Davies (1993). In contrast, Höglund and Alatalo (1995) define a lek as an “aggregated male display that females attend primarily for the purpose of fertilization”. This concise definition focuses on the evolutionary function of mating aggregations rather than required tenets. Similarly, Alexander (1975) indicates that it is the aggregation or activity of the organisms, and not the arena in which the activity takes place that is important in defining a lek.

While male–female ratios in vegetated areas of marshes differed across biogeographical regions and between species in the marshes sampled, comparisons between open and
Fig. 5. Mean ± 1 S.E. percent substratum grain size as a fraction of the total number of grains present. Grains were divided into four size categories: (I) $x < 10 \, \mu m$; (II) $10 \, \mu m < x < 50 \, \mu m$; (III) $50 \, \mu m < x < 100 \, \mu m$; (IV) $100 \, \mu m < x < 200 \, \mu m$ ($x =$ grain size). No grains $> 200 \, \mu m$ were encountered in any of the samples. Substrate was randomly sampled from vegetated sites at Dauphin Island, Alabama ($n = 49$), Hunting Island, South Carolina ($n = 32$), Saxis, Virginia ($n = 59$), and Wallops Island, Virginia ($n = 59$).

vegetatively covered areas within each marsh indicated higher male to female ratios in all open areas. Similarly, open areas were consistently devoid of juveniles, while juveniles were found in most vegetated areas. These findings provide the first empirical evidence that adult male aggregations do in fact occur within open marsh areas, an observation that is reinforced by the fact that we observed this pattern across biogeographically distinct marshes and among three different species. This aggregatory adult male behavior conforms to one of the most characteristic prerequisites for lekking (Alexander, 1975). While the scarcity of juveniles in open areas may be related to the scarcity of protective vegetative cover or intraspecific adult male aggression, it accentuates the difference in community structure when the two cover types are compared.

Höglund and Alatalo (1995) argue that because male crabs defend breeding burrows used by females for egg incubation, Uca spp. should not be considered a lekking genus. However, this implies that it is the location of the breeding burrows that causes Uca spp. to form breeding assemblages. If burrow availability and position are what causes Uca spp. to form breeding aggregations in open marsh areas, then breeding burrows which are constructed only by males in some and by both sexes in other Uca spp. (Christy, 1983, 1994, 1995; Christy and Salmon, 1984; Murai et al., 1987), should be confined to
open areas. In fact, burrow sites, although aggregated in some locations, are dispersed throughout the marshes, including vegetated areas of all marshes sampled in our study (mean±1 S.D. burrows/vegetated m² = 9.3±10.2 (Dauphin Is.; n = 54), 38.8±46.3 (Hunting Is.; n = 23), 8.6±12.1 (Saxis; n = 40), 5.9±13.1 (Wallops Is.; n = 40)). Whether these burrows are suitable as breeding burrows is unknown at present. However, physical characteristics of the substratum, ground water level, and granulometry, appear to contribute to the design and positioning of the breeding burrows in Uca spp. (Christy, 1982, 1983; Christy and Salmon, 1984; Montague, 1980). Sediment granulometry in all marshes sampled showed little variation between open and vegetated areas or across biogeographic regions. This indicates that sediment granulometry is equally conducive to breeding burrow construction in both open and vegetative areas (Bertness, 1985; Christy, 1982, 1983; Christy and Salmon, 1984).

Although males of the genus Uca display to females while defending burrows (Crane, 1975; Doherty, 1982; Greenspan, 1982; Zucker, 1981, 1984), female access to similar burrows in other areas of the marsh have not been shown to be under male control (Crane, 1975; Doherty, 1982; Greenspan, 1982; Murai et al., 1987, 1996; Zucker, 1981, 1984). In the marshes we sampled, levels of food resources (% sediment organics) in open areas were always similar to or less than levels in vegetated areas. Therefore, adult males do not appear to be aggregating in open areas to defend food resources.

A more likely resource to be defended by males in open areas is mating burrows (Crane, 1975; Doherty, 1982; Greenspan, 1982; Zucker, 1981, 1984). If such burrows represent a secure location for females to mate with males who have demonstrated their fitness by displaying, maintaining and defending a given mating burrow, then fitness should be enhanced in males best able to maintain and defend a burrow. Leks essentially provide a testing ground for males to display their fitness (Krebs and Davies, 1993). For example, bower birds construct a ‘bower’ in an open area. The bower is made of twigs and, in some species, is ornamented with colorful pieces of flowers, feathers, or leaves (Krebs and Davies, 1993). Male birds display and mate with females in these open arenas. Presumably, the bower provides an indication of male fitness and a safe place to mate (Krebs and Davies, 1993). Females of Uca spp. also appear to be selective when searching for mates (Crane, 1975; Christy, 1982, 1983; Hyatt, 1977, 1984; Zucker, 1984) and, it seems plausible, considering the variety of reproductive systems employed by Uca spp. (Crane, 1975; Christy and Schober, 1994; Doherty, 1982; Greenspan, 1982; Murai et al., 1987; Zucker, 1981; 1984) that female mate choice based on male traits, rather than or in addition to choice of a breeding site, is why females visit male aggregations in open areas of marshes.

While aggregations of Uca spp. in open areas are likely to be subject to increased predation pressure, open unobstructed areas facilitate visual components of mating rituals including cheliped waving (Christy, 1995; Crane, 1975; Sturmbauer et al., 1996). Open areas may also provide requisite physical space for the ritualized male–male combat that is characteristic of the genus (Crane, 1975). Collectively, our observations indicate that adult males aggregate in open areas for the purpose of displaying to females. Subsequent female mate choice associated with selection of a suitable male and breeding burrow, are consistent with lekking behavior in Uca spp.
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