

# Grasshopper (Orthoptera: Tettigoniidae) Species Composition and Size Across Latitude in Atlantic Coast Salt Marshes

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**Abstract** Although grasshoppers are common salt marsh herbivores, we know little about geographic variation in their species composition. We documented latitudinal variation in species composition of the tettigoniid grasshopper fauna of Atlantic Coast salt marshes. Tettigoniids ( $N=740$  adults) were collected from the *Spartina alterniflora* zone of 31 salt marsh sites across a latitudinal range of 13.19° (Florida to Maine), with an additional 52 individuals collected from the *Juncus roemerianus* zone of low-latitude marshes for comparative purposes. Eight species were collected, but some were common only at a few sites or rare throughout the entire collection range. The tettigoniid community was dominated by *Orchelimum fidicinium* at low latitudes and *Conocephalus spartinae* at high latitudes. Several factors might explain this shift, including changes in climate, plant phenology, and plant zonation patterns. *O. fidicinium* and *C. spartinae* increased in body size toward low latitudes. In laboratory feeding assays, *O. fidicinium* readily ate *S. alterniflora* and *J. roemerianus* leaves, *Orchelimum concinnum*, which is largely restricted to the *J. roemerianus* zone, ate only *J. roemerianus* leaves, and *Conocephalus* spp. ate neither, consistent with literature suggestions that they mainly consume seeds and flowers.

Geographic variation in species composition and body size of grasshoppers may help explain documented patterns of geographic variation in plant palatability and plant–herbivore interactions in Atlantic Coast salt marshes. Because it can be difficult to identify tettigoniids to species, we present a guide to aid future workers in identifying the tettigoniid species common in these marshes.

**Keywords** Biogeography · Latitude · Plant–herbivore interactions · Bergmann’s rule · Orthoptera · *Spartina alterniflora* · Salt marsh

## Introduction

Most ecological research is conducted at single sites, but ecologists are interested in generalizing their results as broadly as possible. Our ability to make broad generalizations is contingent upon an understanding of how abiotic and biotic conditions vary geographically and how this variation affects ecological processes.

Salt marshes along the Atlantic Coast of the USA are superficially similar from northern Florida through Maine (Pennings and Bertness 2001); however, there is extensive latitudinal variation in soil composition and salinity (Pennings and Bertness 1999; Craft 2007), plant phenology, morphology and productivity (Turner 1976; Seliskar et al. 2002), interactions between plant species (Bertness and Ewanchuk 2002; Pennings et al. 2003), plant–herbivore interactions (Pennings et al. 2001), and herbivore life history (Denno et al. 1996). Thus, extrapolating results from any one site requires an understanding of how both the abiotic and biotic conditions at that site compare with those at other sites.

In this paper, we focus on latitudinal variation in the composition of an important group of salt marsh herbivores,

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tettigoniid grasshoppers. Herbivore pressure on salt marsh plants appears to be stronger at lower latitudes (Pennings and Silliman 2005; Pennings unpublished data). This increased herbivore pressure may cause plants at low latitudes to develop stronger defenses against consumers (Siska et al. 2002), resulting in decreased palatability of plants with decreasing latitude (Pennings et al. 2001). It is likely that latitudinal variation in herbivore pressure is driven, at least in part, by geographic variation in grasshopper species composition (Pennings and Silliman 2005), but rigorous data to address this hypothesis are lacking.

Few data on grasshopper species composition exist for Atlantic Coast salt marshes, except for one study in North Carolina (Davis and Gray 1966). Although no comparative studies have been conducted across broad geographic regions, ecological studies in New England (Bertness et al. 1987; Bertness and Shumway 1992), Georgia (Smalley 1960), and Mississippi (Parsons and de la Cruz 1980) have focused on different tettigoniid grasshopper species (*Conocephalus spartinae* in New England, *Orchelimum fidicinium* in Georgia, and *O. concinnum* in Mississippi), which presumably were the most abundant grasshoppers at each site. Whether this reflects local site-to-site variation in species composition or a broader geographic pattern, however, is unclear. Nevertheless, based on these studies, the feeding ecology of different tettigoniid species appears to vary, with *C. spartinae* feeding primarily on flowers and seeds (Bertness et al. 1987; Bertness and Shumway 1992) and *Orchelimum* spp. feeding on leaves (Smalley 1960; Parson and de la Cruz 1980). This suggests that documenting patterns of grasshopper species composition across latitude would improve our understanding of biogeographic patterns in plant–insect interactions.

One obstacle to addressing these issues has been the difficulty in identifying tettigoniid grasshoppers to species. Although tettigoniids have been the subject of excellent taxonomic monographs (Rehn and Hebard 1915a, b, c), the species are morphologically quite similar and difficult for non-experts to identify to species. Therefore, in addition to documenting tettigoniid species composition and distribution in salt marshes along the Atlantic Coast of the USA, we provide a resource to facilitate tettigoniid species identification by future workers.

## Materials and Methods

### Study Sites and Collections

We collected tettigoniid grasshoppers from the *Spartina alterniflora* zone of 31 salt marsh sites along the Atlantic Coast of the USA from Florida to Maine across a latitudinal

range of 13.19° (Table 1). Our sampling focused on the *S. alterniflora* zone because this is the largest vegetation zone in many Atlantic Coast salt marshes and occurs at all latitudes. We collected an average of 24 (range 1 to 59) adult tettigoniids from each site, for a total of 740 individuals. We visited most sites once or twice in the summer of each of 3 years (2004–2006). In addition, we made a few collections ( $N=99$  of the 740) in May, September, and October to confirm that species composition did not vary seasonally (it did not), and a small number ( $N=24$  of the 740) of specimens were collected in October of 2003. Collecting methods were consistent across sites, although the time spent collecting was greater at sites where grasshopper density was low. Because our interest was in the relative abundance of different grasshopper species, we did not document absolute densities (numbers per square meter). We collected only adult tettigoniids, avoiding juvenile tettigoniids, which were difficult to identify to species, as well as individuals from other grasshopper families (i.e., Acrididae), which were rare in the *S. alterniflora* zone. We collected tettigoniids using a combination of sweep netting, targeted netting, and hand collection. In addition, we collected tettigoniids ( $N=52$ ) from the *Juncus roemerianus* zone of four low-latitude salt marsh sites for comparative purposes (three sites in GA and one in SC) on one date per site in either 2005 or 2006. The *Juncus* zones at these sites were dominated by *J. roemerianus*, with small amounts of *Batis maritima*, *Borrichia frutescens*, *Distichlis spicata*, or *S. alterniflora*.

### Identification of Tettigoniid Species

We classified tettigoniids to species following Rehn and Hebard (1915a, b, c) and by comparing our specimens to those in the collection of the Entomology and Nematology Department, University of Florida, Gainesville. The eight tettigoniid species that we found in Atlantic Coast *S. alterniflora* salt marshes can be distinguished based on body size, wing length, coloration, and morphology of genitalia (cerci in males and ovipositors in females). Tettigoniids were observed under a dissecting microscope and measured with electronic calipers (Fig. 1). Body size was measured as the length of the grasshopper, excluding the cerci or ovipositor, from the tip of the head to the end of the abdomen. Measurements of body size, however, are affected by the posture of the preserved grasshopper. A more reliable indicator of size is the length of the hind tibia, which was measured from the joint between the tibia and femur to the joint between the tibia and tarsus. We focused on tibia length for our analyses, but analyses of body length produced similar results. Wing length was measured from the abutment of the pronotum and wing to the distal end of the wing. Each cercus was measured from the abutment with the

**Table 1** Study sites for tettigoniid collections

Site name	State	Latitude	Number collected ( <i>Spartina alterniflora</i> zone)	Number collected ( <i>Juncus roemerianus</i> zone)
Guana River	FL	30.01	51	
Amelia Island	FL	30.40	26	
Dean Creek	GA	31.23	45	9
Visitor Center	GA	31.27	59	9
Hunt Camp	GA	31.28	21	24
North End	GA	31.30	29	
Eulonia	GA	31.32	24	
Fenwick Island	SC	32.32	27	
Lighthouse Road	SC	33.19	30	
Third Boundary	SC	33.21	20	10
Goat Island	SC	33.22	20	
Zeke's Island	NC	33.57	20	
Center for Marine Studies	NC	34.08	15	
Bodie Island	NC	35.53	1	
Cattlett Island	VA	37.17	39	
Box Tree Road	VA	37.23	25	
Red Bank	VA	37.26	17	
Stockton	MD	38.02	18	
St. Jone's	DE	39.05	19	
Cousteau	NJ	39.33	19	
Cottrell Marsh	CT	41.20	5	
Bluff Point	CT	41.21	20	
Waquoit Bay	MA	41.34	22	
Nag Creek	RI	41.37	24	
Providence Point	RI	41.39	8	
100 Acre	RI	41.45	21	
Great Neck	MA	42.42	24	
Nelson Island	MA	42.44	25	
Great Bay	NH	43.02	20	
Harbor Road	ME	43.19	26	
Little River	ME	43.20	20	
Total			740	52

The number of tettigoniids collected from each site is indicated separately for the *S. alterniflora* and the *J. roemerianus* zones

abdomen to its distal tip. Each ovipositor was measured from its ventral abuttal with the abdomen to its distal end.

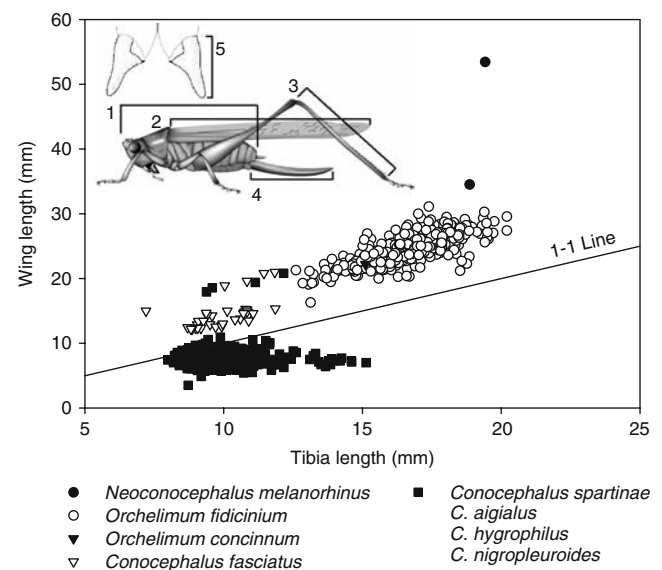
### Tettigoniid Feeding Preferences

To gain additional insight into the abundance of different tettigoniid species in different vegetation zones, we conducted feeding assays with *O. fidicinium*, *O. concinnum*, *C. spartinae*, *C. aigialus*, and *C. nigropleuroides* adults, offering them *S. alterniflora* or *J. roemerianus*. Insects and vegetation used in the assays were collected from salt marshes in Georgia. Feeding assays were conducted in the laboratory during June and July of 2006. Individual feeding

trials lasted 4 days, with each replicate beginning on the day that each individual insect was collected. Individual tettigoniids were housed in 1,000-ml glass jars and offered a single undamaged leaf of either *S. alterniflora* or *J. roemerianus*. The basal end of the leaf was inserted into a small bottle filled with water, which kept the leaf hydrated and erect in the jar. The amount of plant material consumed was noted each morning and evening. For *S. alterniflora*, consumption was recorded as area (mm<sup>2</sup>) of damage. For *J. roemerianus*, consumption was recorded as the length (mm) of the cylindrical leaf that was damaged. Leaves were replaced whenever feeding damage was noted and on the morning of the third day regardless of feeding damage. Consumption by each tettigoniid was recorded as cumulative plant consumption over the 4 days. Data were analyzed using the Kruskal–Wallis non-parametric analysis of variance.

### Latitudinal Variation in Body Size

To examine latitudinal variation in body size of tettigoniids, we pooled them by sex from adjacent sites to give “pooled sites” with sample sizes of 1–34 (average of 8) females and 1–20 (average of 7) males per site. We calculated the



**Fig. 1** Tettigoniid wing length as a function of body size (tibia length). A total of 656 individuals are represented, including *N. melanorhinus* ( $N=2$ ), *O. fidicinium* ( $N=372$ ), *O. concinnum* ( $N=1$ ), *C. fasciatus* ( $N=36$ ), and four other *Conocephalus* species ( $N=245$ ): *C. aigialus* ( $N=1$ ), *C. hygrophilus* ( $N=23$ ), *C. nigropleuroides* ( $N=9$ ), and *C. spartinae* ( $N=212$ ). Only tettigoniids with at least one leg are included. Individuals below the 1–1 line have wings shorter than their tibiae; conversely, individuals above the 1–1 line have wings that are longer than their tibiae (and that extend past their abdomens). All *Conocephalus* individuals (other than *C. fasciatus*) above the 1–1 line are *C. spartinae* ( $N=13$ ). Inset shows all morphological measurements made: 1 body length, 2 wing length, 3 tibia length, 4 ovipositor length, 5 cercus length

average latitude for each of these pooled sites. The grouping of sites differed among species depending on abundance at different sites. For each pooled site for each species, we calculated average tibia length for each sex and examined variation in tibia length due to sex and latitude using analysis of covariance (ANCOVA).

## Results

Our collections from the *Spartina alterniflora* zone contained eight tettigoniid species: *Neoconocephalus melanorhinus* (Rehn and Hebard;  $N=2$ ), *Orchelimum fidicinium* (Rehn and Hebard;  $N=424$ ), *Orchelimum concinnum* (Scudder;  $N=1$ ), *Conocephalus fasciatus* (De Geer;  $N=37$ ), *Conocephalus spartinae* (Fox;  $N=234$ ), *Conocephalus hygrophilus* (Rehn and Hebard;  $N=31$ ), *Conocephalus nigropleuroides* (Fox;  $N=10$ ), and *Conocephalus aigialus* (Rehn and Hebard;  $N=1$ ).

### Identification of Tettigoniid Species

Although all three of these tettigoniid genera have received excellent taxonomic treatments (Rehn and Hebard 1915a, b, c), identification to species can be very difficult even for the specialist. Fortunately, because only a fraction of the species from each genus commonly occurs in Atlantic Coast salt marshes, adults of the species likely to be encountered by salt marsh scientists can be confidently distinguished based on size, wing length, coloration, and morphology of the cerci and ovipositor (Figs. 2 and 3; color photographs of the species and

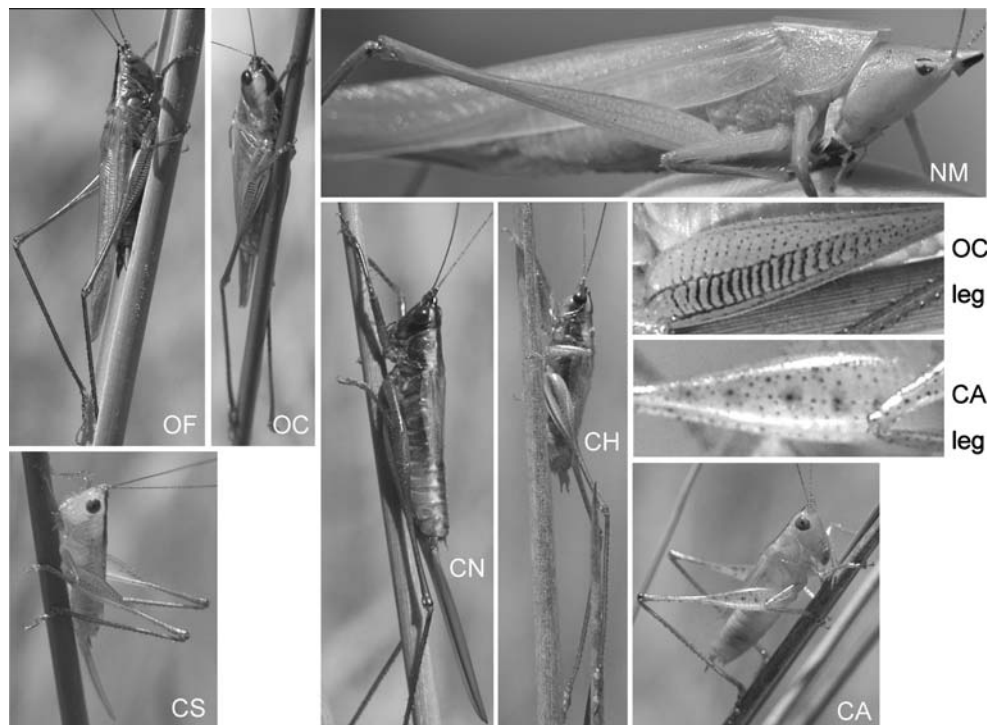
genitalia can be found at <[http://gce-lter.marsci.uga.edu/public/app/all\\_species\\_lists.asp](http://gce-lter.marsci.uga.edu/public/app/all_species_lists.asp)>).

**Body Size** Size is the least reliable characteristic for species identification, but can allow cursory identification of the three genera. Although body size varies with latitude (see below), when comparing individuals collected from any given latitude, *Orchelimum* spp. are about 50% larger than *Conocephalus* spp., and *N. melanorhinus* is about 25% larger than *Orchelimum* spp. Body size is not a reliable character for distinguishing species within a genus.

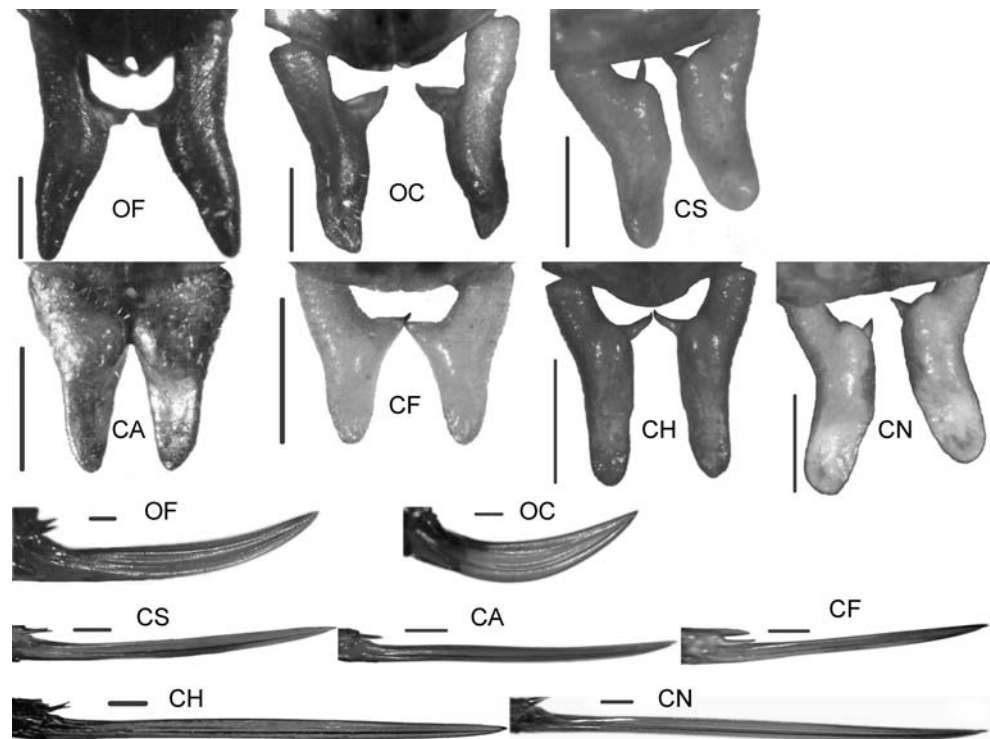
**Wing Length** Wings of *N. melanorhinus* always extend well past the abdomen in adults, and wings of both *Orchelimum* species are always longer than the abdomen in adults, extending up to or beyond the caudal femora (Rehn and Hebard 1915b). Wings of *Conocephalus* species usually extend near the tip of the abdomen in adults, but this varies both between and within species (Rehn and Hebard 1915c). Wings of *C. fasciatus* extend past the abdomen. Wings of *C. spartinae*, *C. nigropleuroides*, and *C. aigialus* usually extend near the end of the abdomen, but some individuals have long wings that extend past the tip of the abdomen (we collected a few long-winged individuals of *C. spartinae*, but none of *C. nigropleuroides* or *C. aigialus*). The wings of *C. hygrophilus* extend near the tip of the abdomen (Figs. 1 and 2).

**Color** Color can be useful in classifying adult tettigoniids to species (Fig. 2), although to a lesser extent than

**Fig. 2** Adults of seven tettigoniid species collected from the *S. alterniflora* zone in Atlantic Coast salt marshes. OF, *O. fidicinium*; OC, *O. concinnum* (note cephalic stripe); NM, *N. melanorhinus* (note pigmented cone); CS, *C. spartinae*; CN, *C. nigropleuroides* (note black head); CH, *C. hygrophilus*; CA, *C. aigialus*. Note distinguishing leg coloration of *C. aigialus* vs leg coloration of other tettigoniid species (in this case, *O. concinnum*). Color photographs of these species can be found at this URL: <[http://gce-lter.marsci.uga.edu/public/app/all\\_species\\_lists.asp](http://gce-lter.marsci.uga.edu/public/app/all_species_lists.asp)>



**Fig. 3** Male cerci (*top*) and female ovipositors (*bottom*) in seven tettigoniid species. *OF*, *O. fidicinium*; *OC*, *O. concinnum*; *CS*, *C. spartinae*; *CA*, *C. aigialus*; *CF*, *C. fasciatus*; *CH*, *C. hygrophilus*; *CN*, *C. nigropleuroides*. Photographs are not to the same exact scale. Scale bars represent 1 mm. Range of cercus lengths (mm): *OF*, 1.40–3.28; *OC*, 1.00–2.06; *CA*, 1.70; *CF*, 1.17–1.53; *CH*, 1.20–2.20; *CN*, 1.60–2.20. Range of ovipositor lengths (mm): *OF*, 9.10–15.06; *OC*, 8.20; *CS*, 7.00–11.94; *CF*, 6.28–7.92; *CH*, 10.56–15.77; *CN*, 13.90–16.80. Color photographs of the reproductive anatomy for these species can be found at the following URL: [http://gce-lter.marsci.uga.edu/public/app/all\\_species\\_lists.asp](http://gce-lter.marsci.uga.edu/public/app/all_species_lists.asp)



anatomical features (Rehn and Hebard 1915b, c), especially if specimens have been preserved in alcohol. *O. fidicinium* is green or brown. The distinguishing feature of *O. concinnum* is its vertical facial stripe. Its body is variegated, with areas of green, yellow, purple, and brown. *C. fasciatus* is green, with a black stripe from its fastigium to the end of its abdomen. *C. spartinae* is green with an orange abdomen, while *C. hygrophilus* can be either uniformly green or dark brown on its head and sides, light brown on its back and legs, and dark orange on its abdomen. *C. nigropleuroides* has a strikingly unique coloration, with a black head, orange abdomen, and green legs. It is important to note the color of *C. nigropleuroides* when it is alive because it can be difficult to distinguish from other *Conocephalus* species based on anatomy alone. *C. aigialus* is superficially similar to *C. spartinae* (green with an orange abdomen), but in contrast to the linear color patterns on the femora of the other tettigoniids, femora of this species are green, with mottled orange. *N. melanorhinus* is light green and is distinguished by black coloration of half or all of the ventral surface of the cone at the tip of its head (Rehn and Hebard 1915a).

**Cercus Morphology** The cerci of *Orchelimum* spp. are easily distinguishable from those of *Conocephalus* spp. (Fig. 3). *Orchelimum* spp. cerci are about 50% larger and pointed at their distal ends compared to *Conocephalus* spp. cerci, which are smaller and relatively blunt at their distal ends (Rehn and Hebard 1915b, c).

The cerci of *O. fidicinium* are long, and each comes to a narrow point at the distal end, with an upward curving tooth. The cerci of *O. concinnum* are slightly shorter than those of *O. fidicinium*; each cercus is comparatively blunt at the distal end with a tooth that extends perpendicularly. The cerci of *C. fasciatus* are short relative to other *Conocephalus* species, and each cercus has a tooth that extends perpendicularly with a unique blackened tip. Each cercus of *C. spartinae* has an extended medial swelling in the shape of a rectangle. The distal end often diverges from the medial swelling at an angle extending laterally. The cerci of *C. nigropleuroides* are very similar to those of *C. spartinae*. Rehn and Hebard (1915c) state that the cerci of *C. spartinae* are slightly shorter, with smooth outlines, whereas the cerci of *C. nigropleuroides* are longer with irregular outlines, but we found these details difficult to consistently observe. The cercus of *C. hygrophilus* is streamlined from the distal end to the portion proximal to the abdomen until disruption by a bulbous swelling, which can partially obscure the tooth when viewed from above. The cercus of *C. aigialus* is shaped like an inverted triangle, coming to a tapered and flattened point at the distal end, with a large bulbous swelling near the tooth.

**Ovipositor Morphology** Rehn and Hebard (1915b, c) state that ovipositor morphology is not helpful in identifying species because many species have similar ovipositors that display considerable intraspecific variation. As a last resort, female tettigoniids can be classified by association with males found at the same site (T. J. Walker, personal communication).

Given the limited number of species found in Atlantic Coast salt marshes, however, ovipositor length and shape are helpful in distinguishing among some species (Fig. 3), especially if used in combination with other characters.

The ovipositor of *O. fidicinium* is relatively long with a weak upward sigmoidal curve (Rehn and Hebard 1915b). The ovipositor of *O. concinnum* is relatively short with a robust upward curve. The ovipositor of *C. fasciatus* shows the beginnings of a weak sigmoidal curve at its base, proximal to the abdomen, but thereafter is straight. The ovipositor of *C. spartinae* is relatively short, with a slight upward curve. The ovipositor of *C. nigropleuroides* is extremely long and straight. The ovipositor of *C. hygrophilus* is similar to that of *C. nigropleuroides*, but tends to be shorter than the body, whereas the ovipositor of *C. nigropleuroides* tends to be longer than the body. The ovipositor of *C. aigialus* is long and straight, with a small but distinct hump at the proximal end.

#### Variation in Tettigoniid Species Composition

*O. fidicinium* and *C. spartinae* dominated the tettigoniid fauna of the *S. alterniflora* zone of Atlantic Coast salt marshes, comprising 89% of the total individuals collected (57 and 32% of the total, respectively; see Fig. 4). In addition, *O. concinnum* and *C. fasciatus* could be locally

abundant, comprising more than 50% of the individuals at one and three sites, respectively. The four remaining species were never abundant at any site.

*Orchelimum* spp. and *Conocephalus* spp. showed a striking pattern of latitudinal turnover in relative abundance (Fig. 4). *Orchelimum* species, mostly *O. fidicinium*, dominated the *S. alterniflora* zone of low-latitude salt marshes, while *Conocephalus* species, mostly *C. spartinae*, dominated in high-latitude marshes. A precipitous switch in the relative abundances of these taxa occurred at about 37° of latitude.

Comparative sampling in the *J. roemerianus* zone at four low-latitude sites (between 31.23 and 33.21° of latitude, from GA to SC; see Table 1) yielded only *O. concinnum* ( $N=29$ ), *C. spartinae* ( $N=15$ ), *C. aigialus* ( $N=7$ ), and *C. nigropleuroides* ( $N=1$ ). *O. concinnum* was most abundant overall, although *C. aigialus* and *C. spartinae* were locally abundant at particular sites (data not shown). Although a few individuals of *O. fidicinium* and *N. melanorhinus* were visually observed in the *Juncus* zone of low-latitude marshes, both were absent from these collections, as were *C. fasciatus* and *C. hygrophilus*.

#### Tettigoniid Feeding Preferences

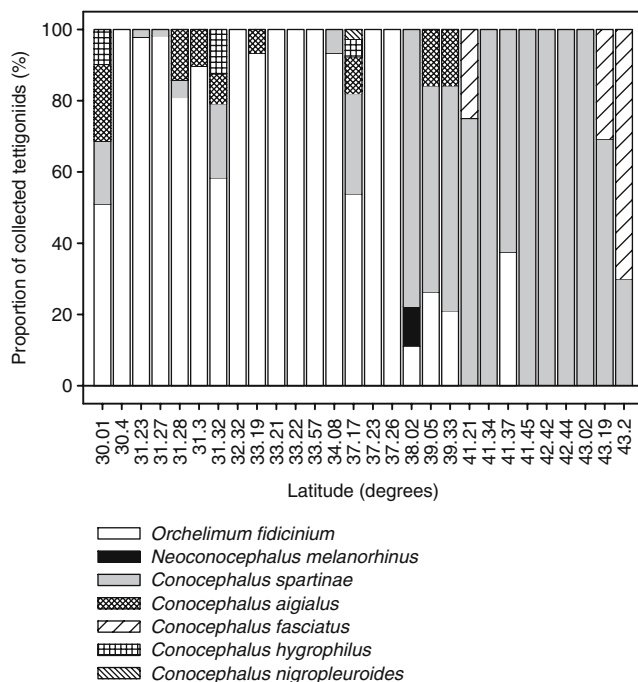
*O. fidicinium* consumed large amounts of *S. alterniflora* [ $635.6 \pm 93.3$  (SE)  $\text{mm}^2$ ], but *O. concinnum*, *C. spartinae*, *C. aigialus*, and *C. nigropleuroides* almost completely ignored this plant (maximum consumption of  $1.4 \pm 1.1$   $\text{mm}^2$ ;  $F_{4,60}=79.0$ ,  $P<0.0001$ ). *O. fidicinium* and *O. concinnum* consumed more *J. roemerianus* ( $54.5 \pm 9.9$  and  $123.2 \pm 46.5$   $\text{mm}$ , respectively) than did *C. spartinae* and *C. nigropleuroides* species, which completely ignored this plant ( $F_{3,35}=49.6$ ,  $P<0.0001$ ).

#### Latitudinal Variation in Body Size

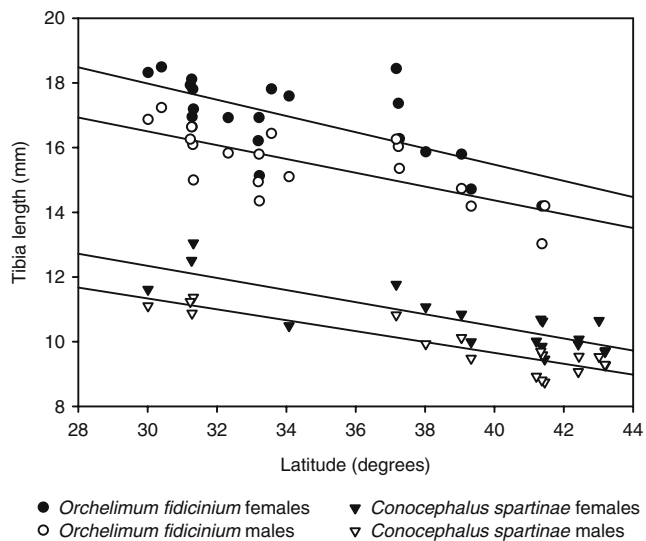
For both *O. fidicinium* and *C. spartinae*, body size (tibia length) decreased with increasing latitude (Fig. 5), and females were larger than males. Similar analyses are not reported for the six other tettigoniid species because they occurred at relatively few sites; however, data for *C. hygrophilus* (the species found at the next highest number of sites) strongly suggested that the same patterns held for this species. Identical conclusions were reached with analyses of body length instead of tibia length (not shown).

#### Discussion

Because the tettigoniid species collected from the *S. alterniflora* zone of Atlantic Coast salt marshes likely



**Fig. 4** Relative abundance of adults of eight tettigoniid species collected from the *S. alterniflora* zone at 31 sites along a latitudinal gradient. Sample size ranged from 15 to 59 individuals per site (average 26 individuals per site; three sites with sample sizes of fewer than ten individuals were omitted from this figure)



**Fig. 5** Body size (tibia length) of adult *O. fidicinium* and *C. spartinae* males and females as a function of latitude. For *O. fidicinium*,  $N=20$  sites (total of 196 females and 176 males nested within sites); for *C. spartinae*,  $N=18$  sites (total of 109 females and 103 males nested within sites). For both species, body size differed among sexes and across latitude (ANCOVA,  $P<0.0001$  for both effects for both species)

differ ecologically, we provide a guide to help salt marsh ecologists identify them. We then discuss likely reasons for and implications of the dramatic geographical turnover in species composition and geographic patterns in body size.

Distinguishing among the 15–19 tettigoniid species in each genus can be a difficult task even for trained taxonomists (we obtained incorrect identifications of multiple individuals sent to two museums). Fortunately, only a subset of the species in each genus is common in Atlantic Coast salt marshes. These species can, with a little study, be readily identified based on size, wing length, coloration, and morphology of the cerci and ovipositor, as described in detail in “Results”. Because color fades in preserved specimens, especially those preserved in alcohol, it is helpful to observe the coloration of live insects. This is particularly important for *C. nigropleuroides*, which is difficult to distinguish from *C. spartinae* (males have similar cerci) and *C. hygrophilus* (females have similar ovipositors) except by color. Although anatomical features can suffice to differentiate these tettigoniid species, their distinctive songs can also be useful in identification (Walker 1964). In most cases, ecologists can begin to identify their species by assuming that *C. spartinae* will dominate high-latitude collections and *O. fidicinium* low-latitude collections, but this is not always the case, as some other species may be abundant at particular sites (Fig. 4).

Correct identification of salt marsh tettigoniids is likely to be important for understanding their ecological impacts. Studies with high-latitude tettigoniid assemblages, likely

dominated by *C. spartinae*, have concluded that they feed mostly on seeds and flowers, and thus, influence plant communities by impacting sexual reproduction more than somatic growth (Bertness et al. 1987; Bertness and Shumway 1992). In contrast, studies with low-latitude tettigoniid assemblages, likely dominated by *O. fidicinium* (Georgia *S. alterniflora* zone) and *O. concinnum* (Mississippi *J. roemerianus* zone), have focused on consumption of leaves (Smalley 1960; Parsons and de la Cruz 1980). These patterns were confirmed in our laboratory feeding assays using southern *S. alterniflora* and *J. roemerianus*. Some studies on the northeast coast, however, have found that *Conocephalus* spp. eat plant leaves, with increased consumption in fertilized plots (R. Goeriz, personal communication). In addition, like most tettigoniids, these species are omnivorous (J. Jimenez and S.C. Pennings, unpublished data; R. Goeriz, personal communication), and it is likely that they differ in the proportion and species composition of arthropods in their diet. Thus, correctly identifying the species composition of the tettigoniid fauna at any particular site is likely to be vital to a proper understanding of their ecological interactions. In particular, it would be productive for future studies to explore differences in trophic interactions among the several *Conocephalus* species.

There are several possible explanations for the dramatic turnover in species composition from *O. fidicinium* to *Conocephalus* at about 37° of latitude in Virginia. Because *O. fidicinium* and *C. spartinae* dominated the collections, a very similar pattern would occur if only these two species were considered. First, it is possible that the precipitous decrease of overwintering *S. alterniflora* at about the same latitude (Turner 1976) contributes to the observed decline of *O. fidicinium* populations. As *S. alterniflora* appears to compose much of the diet of *O. fidicinium* (Smalley 1960), the seasonal disappearance of *S. alterniflora* at high latitudes might restrict *O. fidicinium* to lower latitudes where its food source is more readily available.

A second possible explanation is that the decline of both *S. alterniflora* and *O. fidicinium* might reflect parallel but independent responses to temperature. For example, low temperatures might both kill overwintering grasshopper eggs and damage leaves of *S. alterniflora*. This hypothesis assumes that *Conocephalus* species can tolerate cold temperatures that *O. fidicinium* cannot. The physiological and life history adaptations that might explain such differences in climatic tolerance are currently unknown.

Third, variation in body size across latitude might also provide an explanation for the rarity of *O. fidicinium* at high latitudes. Tettigoniids decrease in size with increasing latitude (see below). If a particular body size range is optimal for a particular species, given its autecology, individual *O. fidicinium* at high latitudes may be too small to reproduce or survive well, leading to smaller population

sizes. In contrast, *Conocephalus* species are about 50% smaller than *O. fidicinium* at the same latitude, and so may be able to prosper at high latitudes despite selective pressures for small size.

Fourth, and finally, reduced zonation of vegetation in northern marshes could also contribute to the observed species turnover. Plants in salt marshes are arranged in more or less monospecific zones across an elevational gradient (Chapman 1975). At high latitudes on the Atlantic Coast of the USA, salt marshes are relatively small, and plant zones are therefore highly compressed (Teal 1986). In contrast, low-latitude marshes are more expansive, and vegetation zones are broader (Wiegert and Freeman 1990). If *Conocephalus* species prefer other vegetation zones more than the *S. alterniflora* zone (see below), they would be more likely to wander into the *S. alterniflora* zone as transients at high latitudes, where the vegetation zones are compressed, than at low latitudes where the vegetation zones are expansive.

Whatever the reason for the variation in species composition across latitude, this variation likely has implications for marsh trophic ecology. As *Conocephalus* species mostly eat seeds and insect prey, whereas *O. fidicinium* feeds readily on leaves of *S. alterniflora*, the different feeding preferences of these different tettigoniid species may contribute to a gradient in consumer pressure along the Atlantic Coast, with greater herbivore pressure at lower latitudes (Pennings and Silliman 2005). If so, this could help select for the lower palatability of *S. alterniflora* leaves at low vs high latitudes (Pennings et al. 2001).

Although tettigoniid collections from the *J. roemerianus* zone consisted of relatively few individuals, they were distinctive enough to help explain some of the patterns observed in the more extensive collections from the *S. alterniflora* zone. The data suggest that components of the diet of *C. spartinae* can be found in both zones. Other species were more specialized in their habitat use. *O. fidicinium* appears to be limited to the *S. alterniflora* zone. Given that *O. concinnum* was found much more frequently in the *Juncus* than the *Spartina* zone, it appears to be a specialist herbivore on *J. roemerianus* (Parsons and de la Cruz 1980), along with *C. aigialus*. These two tettigoniid species appear to be transient visitors to the *S. alterniflora* zone. It is possible that differences in feeding preferences among tettigoniid species are reinforced by competition or intraguild predation (Wason, unpublished data), but experimental tests of these possibilities are lacking. The remaining four species were not collected often enough to make definitive statements about their habitat use. Further studies should examine the tettigoniid composition of high-elevation marsh zones, dominated by *J. roemerianus* at low latitudes and *J. gerardii* and *S. patens* at high latitudes, to more definitively determine the geographic distributions of species

that are not common in the *S. alterniflora* zone or that use multiple vegetation zones.

It has long been anecdotally noted that many species of tettigoniids decrease in size with increasing latitude (Rehn and Hebard 1915a, b, c), in agreement with the “Converse to Bergmann’s Rule” (Masaki 1967, 1978; Masaki and Walker 1987; Mousseau 1997). Our results provide quantitative data to rigorously support these observations for *O. fidicinium* and *C. spartinae* (Fig. 5). We also documented that females of these species are larger than males, which appears to be a general pattern in tettigoniids (Rehn and Hebard 1915a, b, c) and many other insect species, likely because female egg production is limited by body size.

The generality and causes of latitudinal variation in body size are widely debated in the literature (Partridge and Coyne 1997; Van Voorhies 1997; Walters and Hassall 2006) and are outside the scope of this paper. Our interest here is in relating these body size patterns to latitudinal turnover in species composition and latitudinal variation in herbivore pressure. First, as we noted above, selection for small body sizes at high latitudes may contribute to the turnover in species composition from the large-bodied *O. fidicinium* at low latitudes to the small-bodied *C. spartinae* at high latitudes. Second, because as a general rule feeding rates increase with body size (Peters 1983), larger tettigoniid body size at low latitudes is likely to lead to greater herbivore pressure even if herbivore species and density are constant. Data suggest, however, that grasshoppers occur in higher abundance at low latitudes (Pennings, unpublished data). Thus, latitudinal variation in herbivore body size may contribute to observed gradients in herbivore pressure (Pennings and Silliman 2005) and plant resistance to herbivores (Pennings et al. 2001) at low latitudes.

In summary, we found striking differences in the tettigoniid community of the *S. alterniflora* zone at low and high latitudes. Low-latitude sites were dominated by *O. fidicinium* and high-latitude sites by *C. spartinae*. Six other tettigoniid species were present. At least two species were likely transients from the *J. roemerianus* zone or other habitats, but others were occasionally locally abundant. The two most common species increased in body size at low latitudes. Feeding preferences varied among tettigoniid species. Latitudinal variation in tettigoniid species composition and body size likely contributes to latitudinal patterns in marsh community structure and plant palatability.

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