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Abstract.—Eastern populations of Semipalmated Sandpipers (*Calidris pusilla*) have declined severely in recent decades, particularly at wintering grounds in northern South America, where about 80% of the population was lost since the 1980s. This study investigates prey choice of Semipalmated Sandpipers at two sites in major wintering grounds on the coast of Maranhão, northeast Brazil. Prey availability estimated from intertidal sediment samples was compared with bird diet reconstructed from prey remains in droppings. Birds (flocks of 80-90 birds) fed almost exclusively on the polychaete *Laeonereis culveri* (present in all droppings at both sites; ≥ 97% of total setae found in droppings), the most abundant invertebrate in the intertidal sediments overall, but they avoided the smallest sizes despite abundance in sediments and avoided numerous other species. Setae from two other polychaetes were found in droppings (*Glycindes multidens*, 53% of droppings; *Hermondura tricuspis*, 47% of droppings), but these represented < 2% in average of all setae in droppings. The disproportional prevalence of a single prey species in the diet of sandpipers in this study is comparable to well-studied stopover areas. High dependence on a single staple prey at different sites in the migration route can make Semipalmated Sandpipers vulnerable to changes in prey abundance, which may partly explain declines observed at the flyway level. *Received 4 March 2019, accepted 14 April 2019.*

Key words.—foraging ecology, invertebrate prey, population declines, shorebirds, South America.

Strong evidence has been gathered over the last few decades showing that the eastern populations of Semipalmated Sandpipers (*Calidris pusilla*) are facing dramatic declines (Andres *et al.* 2012). Negative trends have been reported consistently at migration sites of eastern USA and Canada (reviewed by Gratto-Trevor *et al.* 2012a) and also in some breeding areas in arctic Canada (Jehl 2007; Smith *et al.* 2012), and population losses of ca. 80% since the 1980s were observed at key wintering areas of northern South America (Morrison *et al.* 2012). Sharp declines have also been observed in other shorebird species along the Atlantic Flyway, suggesting the existence of threats that are shared by different species (Morrison *et al.* 2001; Morrison *et al.* 2004; Bart *et al.* 2007; Watts and Truitt 2011). Although there are several factors that may have been contributing to the declines of shorebirds in the Atlantic Flyway, none seems to explain it in full (Morrison *et al.* 2004; Bart *et al.* 2007; Watts and Truitt 2011; Morrison *et al.* 2012). Environmental changes at the breeding grounds may seem a likely candidate to explain declines given the dramatic impacts of global warming in the Arctic. However, this hypothesis is not supported by data collected to date (Jehl 2007; Weiser *et al.* 2018). Therefore, it is likely that changes in environmental conditions at migratory stopovers and overwintering areas are driving the declines.

Recent tracking data showed that Semipalmated Sandpipers breeding in the eastern Arctic Canada overwinter in north-eastern South America, mainly Suriname, French Guiana and Brazil, and their main stopover sites are the James and Hudson Bays, the Bay of Fundy, Delaware Bay, and Gulf Coast of the USA (Brown *et al.* 2017). These patterns are supported by marked bird sightings, band recoveries, and patterns of bill length (Gratto-Trevor *et al.* 2012b). Among

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the stopover sites, Delaware Bay recorded major decreases in the availability of horseshoe crab (*Limulus polyphemus*) eggs owing to commercial fishing, which are a crucial food resource for Semipalmated Sandpipers and other shorebirds during their northbound migration to the Arctic (Mizrahi and Peters 2009). The horseshoe crab harvest was found to be the main cause of Red Knot (*Calidris canutus rufa*) population crash in the late 1990s and early 2000s (Baker *et al.* 2004; McGowan *et al.* 2011), and was at least partially related to the declines of the eastern populations of Semipalmated Sandpipers (Mizrahi *et al.* 2012). Several detrimental factors have also been pointed out to affect the eastern populations of Semipalmated Sandpipers at their wintering grounds, presumably the most important being hunting (Ottema and Spaans 2008), and changes in the intertidal sediment profiles (observed in Suriname and French Guiana; Morrison *et al.* 2012). However, the information on the wintering ecology of this species and other shorebirds in South America is extremely scarce, which greatly limits our understanding of the factors influencing their survival.

In this study we investigated prey choice of Semipalmated Sandpipers at the coast of Maranhão in northeast Brazil, which is among the most important wintering areas for this species, particularly the declining populations of the Atlantic Flyway (Morrison *et al.* 2012; Brown *et al.* 2017). The diet and prey availability was studied at two areas, one of them included in a Western Hemisphere Shorebird Reserve Network (WHSRN) site of Hemispheric Importance, the Reentrâncias Maranhenses. The winter foraging ecology of this species, particularly for eastern populations, is virtually unknown (but see Kober and Bairlein 2006a,b; Kober and Bairlein 2009), but this knowledge is crucial to understanding the causes of the population declines.

METHODS

Study Area

We studied the prey selection of Semipalmated Sandpipers at two sites along the coast of Maranhão, the first close to the city of Alcântara (2° 24′ 54″ S, 44° 24′ 21″ W)

and the second close to the city of São Luís (2° 33′ 11″ S, 44° 21′ 25″ W). The coast of Maranhão and Pará form the world's largest area of contiguous mangrove, covering more than 7,000 km^2 (Nascimento *et al.* 2013). This coast is highly dynamic with large sediment discharges from the Amazon and other smaller rivers, which are deposited and shaped by coastal currents and macro-tides reaching 8 m of amplitude (González-Gorbeña *et al.* 2015). The climate is tropical humid with most of the annual precipitation (ca. 2,200 mm) occurring between February and May, and the dry season extending from August to November (INMET 2018). Mangroves are dominated by *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa* (Menezes *et al.* 2008). Human population in this region mostly lives under a subsistence economy that relies on the extraction of mangrove products and small-scale fisheries, with the harvesting of the mangrove crab (*Ucides cordatus*) being the main income source (Glaser 2003).

Field Sampling

The two study sites were sediment banks of muddy sand adjacent to areas of mangrove forest. These sites were chosen due to their high density of Semipalmated Sandpipers feeding during the low tide. At both sites, flocks of 80 to 90 birds were observed feeding as the sediments became exposed during the receding tide. Thirty minutes after the area became totally exposed, we collected 108 droppings (from each site) in areas that were intensely used by Semipalmated Sandpipers, and not visited by other shorebird species of similar size. In both sites, birds concentrated in an area of 0.5 to 1 ha, and fed by pecking and probing. After the collection of droppings, we collected thirty sediment cores (78.5 cm^2, 30 cm deep) uniformly distributed throughout the feeding area. The top 5 cm of the sediment cores were separated and sieved through a 0.5 mm mesh, while the remaining sediment was broken in small pieces by hand to search for large polychaetes and bivalves. The sediment cores were grouped in batches of three to facilitate sieving and the storage of invertebrates, resulting in 10 samples per site for analysis. Sampling was conducted on 4 February 2016 in the Alcântara site and on 4 April 2016 in the São Luís site.

Laboratory Analysis

Invertebrates extracted from sediment samples were identified to the lowest possible taxonomic level and measured, and a reference collection of diagnostic structures resistant to bird digestion (polychaete setae and mandibles, shells of bivalves and gastropods, and exoskeletons of crustaceans and insects) was built to facilitate the identification of prey in the droppings. In addition, we built a relationship between the mandible size and the total length of the polychaete *Laeonereis culveri*, which allowed us to estimate the sizes consumed by Semipalmated Sandpipers. The relationship was built from 60 animals ranging from 3 to 32 mm, and was expressed by the following equation ($R^2 = 0.8$):

$$Total\ Length = 85.3*Mandible\ Length - 10.3$$

Droppings were observed with a stereomicroscope to search for prey remains. Each dropping was homog-

enized in an Eppendorf tube with 1.5 ml of water, and a subsample of two drops collected with a 3-ml pipette was spread on a microscope slide and examined under a microscope at 400x magnification to search for polychaete setae. Mandibles of the polychaete *L. culveri* were measured using a reticule eyepiece adapted to the stereomicroscope. Comparisons of mandible size between sites and between dropping and sediment samples were made using a two-sample t-test (independent, two-tailed, α = 0.05).

RESULTS

Polychaetes dominated the invertebrate community at both of our study sites, with *L. culveri* and *Isolda pulchella* being by far the most abundant species (Table 1). Densities of *L. culveri* were similar at both study sites, while *I. pulchella* was denser at the Alcântara site (Table 1). Setae of *L. culveri* occurred in all droppings collected at both sites and represented an average 97% and 99% of the total setae found in droppings in Alcântara and São Luís sites, respectively (Table 1). Setae from two other polychaetes, *Glycindes multidens* and *Hermondura tricuspis*, were found in 53% and 47% of droppings, respectively. However, setae of these species represented less than 2% in average of all setae in droppings (Table 1). Although these other two polychaete species were preyed upon frequently at both sites, their densities in sediments within the superficial 5 cm were lower than those of other polychaete species that were not found in droppings (Table 1).

Individuals of *L. culveri* consumed by Semipalmated Sandpipers were slightly smaller at São Luís than at Alcântara (São Luís diet: $\bar{x}$ = 13.0 mm ± 0.5 SE; Alcântara diet: $\bar{x}$ = 13.8 mm ± 0.5 SE; t = -3.1, df = 1310.2, P = 0.002; Fig. 1), and those con-

Table 1. Densities of invertebrates available in intertidal sediments of two study sites and corresponding prey found in Semipalmated Sandpiper (*Calidris pusilla*) droppings. Ten sediment core samples and 108 bird dropping samples were examined from each site.

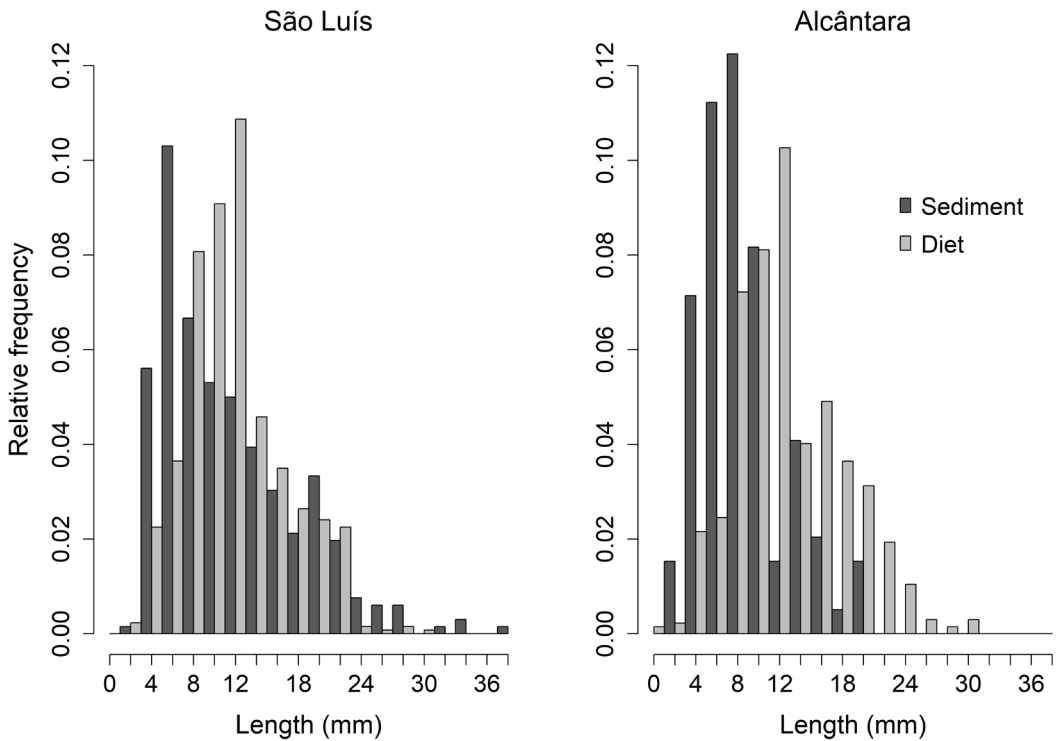| Species	Density (individuals m⁻²) in sediment (mean ± SE)		Percentage of setae found in droppings (mean ± SE)	
	Alcântara	São Luís	Alcântara	São Luís
Polychaeta				
Laeonereis culveri	2987.9 ± 514.1	3539.6 ± 916.7	97.3 ± 0.5	99.2 ± 0.2
Glycindes multidens	4.2 ± 4.2	25.5 ± 9.4	1.6 ± 0.3	0.3 ± 0.1
Hermondura tricuspis	4.2 ± 4.2	21.2 ± 21.2	1.2 ± 0.2	0.6 ± 0.2
Isolda pulchella	4031.9 ± 697.2	127.3 ± 91.0	—	—
Scoletoma tretaura	106.1 ± 53.8	59.4 ± 19.2	—	—
Polidora sp.	46.7 ± 25.7	—	—	—
Hemipodia californiensis	—	29.7 ± 11.0	—	—
Leitoscoloplos sp.	—	25.5 ± 25.5	—	—
Sigambra grubei	4.2 ± 4.2	17.0 ± 9.4	—	—
Gastropoda	—	—	—	—
Heleobia australis	—	80.6 ± 40.7	—	—
Bivalvia	—	—	—	—
Telina versicolor	—	25.5 ± 6.9	—	—
Phacoides pectinatus	—	4.2 ± 4.2	—	—
Amphipoda	—	—	—	—
Monocorophium acherusicum	93.4 ± 44.2	4.2 ± 4.2	—	—
Nematoda	84.9 ± 33.5	—	—	—
Oligochaeta	—	8.5 ± 5.7	—	—
Cumacea	—	50.9 ± 15.2	—	—
Insecta	—	—	—	—
Ceratopogonidae	123.1 ± 60.8	—	—	—
Chironomidae	63.7 ± 25.5	—	—	—

Figure 1. Size frequency distribution of *Laeonereis culveri* found in intertidal sediments of the two study sites and in the droppings of Semipalmated Sandpipers (*Calidris pusilla*). Sample sizes were 98 and 330 animals measured from sediment samples for Alcântara and São Luís, respectively, and 672 and 644 mandibles measured from droppings for Alcântara and São Luís, respectively, from which animal sizes were estimated.

sumed were significantly larger at both sites than those available in the sediments (São Luís sediment: $\bar{x}$ = 10.8 mm ± 0.6 SE, t = 5.4, df = 504.2, P < 0.001; Alcântara sediment: $\bar{x}$ = 7.8 mm ± 0.8 SE, t = 13. 5, df = 149.3, P < 0.001; Fig. 1).

DISCUSSION

Semipalmated Sandpipers fed almost exclusively on the polychaete *L. culveri* at two sites sampled in our study. *Laeonereis culveri* was the most abundant species in the sediments of those sites with densities of ca. 3,000 individuals m⁻². In addition, we found that birds avoided feeding on the smallest *L. culveri* available in the sediments. We also found remains of two other polychaete species (*G. multidens* and *H. tricuspis*) in the droppings from both study sites, which were both in low densities in the sediments. These patterns were highly consistent at both study

sites suggesting that they may be an accurate representation of the foraging conditions of Semipalmated Sandpipers wintering on the coast of Maranhão, which includes the Reentrâncias Maranhenses WHSRN site of Hemispheric Importance.

The visual identification of prey remains in droppings may provide a biased picture of shorebird diet (Verkuil 1997). In particular, it is limited to estimate the relative importance of different prey when they have different sorts of indigestible structures, and it omits soft body prey. Since we found only polychaetes in droppings and all were identified by setae using the same method, we are confident that the relative importance of different prey was well depicted. In addition, we found no soft-bodied invertebrates in our sediment samples and are therefore confident that no prey larger than 0.5 mm were missing in our diet results. However, we cannot exclude that Semipalmated Sandpipers fed upon prey smaller than 0.5 mm in

our study area. In fact, these birds were described recently to feed upon ostracods and biofilm (MacDonald *et al.* 2012; Quinn and Hamilton 2012; Gerwing *et al.* 2016). However, if feeding upon these items, the birds would have exhibited skimming behaviour (Kuwae *et al.* 2008; MacDonald *et al.* 2012; Quinn and Hamilton 2012), which we never observed.

The disproportional relevance of a single food item (*L. culveri*) in the diet of Semipalmated Sandpipers in our study area is comparable to that in the Bay of Fundy during the southbound migration, where birds feed almost exclusively on the amphipod *Corophium volutator* (Hicklin and Smith 1984). Likewise, during the northbound migration in Delaware Bay, Semipalmated Sandpipers join other shorebird species to feed upon highly abundant horseshoe crab eggs (Tsipoura and Burger 1999). In these three cases (including our study), the food chosen stands out by their exceptional abundance, with densities of thousands of food items per square meter, while alternative prey were considerably less abundant (Hicklin and Smith 1984; Peer *et al.* 1986; Mizrahi and Peters 2009). However, while these birds may seem food-specialized in each of these sites, they change their main prey among sites, suggesting they are opportunistic rather than selective predators. This is in agreement with the wide variety of prey that has been described for the species across their overall distribution and annual cycle (Skagen and Oman 1996), and is supported also by recent findings in the Bay of Fundy showing that birds change to alternative prey when *C. volutator* becomes less abundant (MacDonald *et al.* 2012; Quinn and Hamilton 2012; Gerwing *et al.* 2016).

Nevertheless, some patterns of prey selection emerged in our results. Birds clearly rejected small *L. culveri* despite their abundance in the sediments, coinciding with a similar pattern in the Bay of Fundy, where birds do not feed upon small *C. volutator* despite their high abundance (Peer *et al.* 1986). Interestingly, in both cases, the size threshold to reject prey was 4 mm, suggesting that this corresponds to a limit of prof-

itability, as has been shown in many other shorebird species (van de Kam *et al.* 2004). In addition, we found that Semipalmated Sandpipers preyed upon the polychaetes *G. multidens* and *H. tricuspis*, although they were rare in the top 5 cm of the sediments. These species were generally larger than *L. culveri*, thus their preference as food may be related to a high profitability. However, it is also possible that we underestimated the availability of these polychaetes, as large polychaetes may retract to lower layers of the sediment during sampling, becoming absent in the top 5 cm samples. In fact, we have found *G. multidens* in the bottom part of the sediment cores when we search for large invertebrates by hand, although we did not quantify their density.

Overall patterns of food choice of eastern populations of Semipalmated Sandpipers suggest that they are flexible to some extent to cope with changes in the abundance of their food, but they might be vulnerable to dramatic changes in the abundance of their main prey because alternative prey may not sustain their feeding needs. This was clearly the case at Delaware Bay where there was no alternative food for sandpiper species to compensate the dramatic reduction of horseshoe crab egg abundance in the late 1990s and early 2000s, which caused major bird population declines (reviewed by Mizrahi and Peters 2009).

Although there are no diet studies of Semipalmated Sandpipers in the wintering areas where large population declines were observed (Suriname, French Guiana and Guyana; Morrison *et al.* 2012), the very high abundance of the tanaid crustacean *Halmyrapseudes spaansiand* (densities up to 73,000 individuals m^{-2}) and its similar behaviour to *C. volutator* (Jourde *et al.* 2017) suggests that this species could be the staple prey of Semipalmated Sandpipers in these areas. While there are two studies that report densities of tanaid crustaceans of similar magnitude in the 1980s and the 1990s in some habitats of these areas (Swennen *et al.* 1982; Clavier 1999), it is difficult to evaluate from the published data how much change occurred in the extent of the habitat for these ani-

mals. Important habitat changes were observed by Morrison *et al.* (2012), suggesting that mudflats might have been significantly eroded since the 1980s, and this might have impacted tanaid crustaceans that are abundant in very soft mudflats (Swennen *et al.* 1982).

Our study not only brings additional information of feeding conditions of eastern populations of Semipalmated Sandpipers in their wintering grounds, but also highlights how limited our knowledge is on this topic. Additional efforts must be conducted both to address the lack of information on the foraging ecology of these populations in their wintering grounds and to integrate this with knowledge already gathered in their main stopover areas. Such a framework is fundamental for identifying what is causing the declines of the eastern populations of Semipalmated Sandpipers.

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