THE DIET OF UPLAND SANDPIPERS (BARTRAMIA LONGICAUDA) IN MANAGED FARMLAND IN THEIR NEOTROPICAL NON-BREEDING GROUNDS

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Resumen. – Dieta del Batitú (Bartramia longicauda) durante la temporada no reproductiva en los pastizales manejados de Sudamérica. – El Batitú es un ave playera migratoria que habita en pastizales tanto durante la temporada reproductiva como la no-reproductiva. Existen pocos estudios sobre su ecología trófica, los cuales indican que sería una especie insectívora. En este estudio, se describe la dieta del Batitú en términos de su composición y la variación temporal de su contenido, en pastizales del norte de Uruguay. Desde 2008 a 2012, fueron colectadas 67 heces en nueve diferentes lugares dentro de los Departamentos de Salto y Paysandú. La dieta estuvo compuesta principalmente por insectos (presentes en el 98% de las fecas) dentro de los Ordenes: Coleoptera (en 80% de las fecas), Orthoptera (79%) e Hymenoptera (48%). El consumo de Orthoptera e Hymenoptera fue variable entre años. En las heces también fueron encontrados restos de vegetales, que probablemente sean ítems ingeridos secundariamente, y pequeñas piedras que pueden ser utilizadas para el procesamiento de la comida en la molleja. Este estudio demuestra que la dieta del Batitú es generalista y sugiere que probablemente sea oportunista, dependiente de la disponibilidad de los recursos con un comportamiento flexible focalizado en las presas más abundantes.

Abstract. – The Upland Sandpiper (Bartramia longicauda) is a migratory shorebird that inhabits grasslands at the breeding and non-breeding grounds. The trophic ecology of the species is poorly known, but it is thought to be insectivorous. In this study, we describe the diet of the Upland Sandpiper and its temporal variation in grasslands of northern Uruguay. From 2008 to 2012, we collected 67 feces at nine different sites in the Departments of Salto and Paysandú. The diet consisted mainly of insects (present in 98% of the feces) belonging to three orders: Coleoptera (in 80% of feces), Orthoptera (79%), and Hymenoptera (48%). Consumption of Orthoptera and Hymenoptera varied among years. Plant remains and stones were also recorded in feces. Vegetation may have been consumed secondarily while stones could be used in food processing in the gizzard. Our study demonstrates that Upland Sandpipers are diet generalists and probably forage opportunistically, depending on resource availability and focusing on the most abundant prey items.

Key words: Bartramia longicauda, diet, fecal analysis, food preference, grasslands, insects, Nearctic migrant, Scolopacidae, Upland Sandpiper, Uruguay, wintering grounds.

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INTRODUCTION


The Upland Sandpiper (Bartramia longicauda) is a Nearctic long-distance migratory species, migrating twice a year ~ 14,000 km from breeding grounds in North America to non-breeding sites in southern South America (Houston & Bowen 2001, Blanco & López-Lanús 2008). Many aspects of its biology have been studied, including mating system, breeding success, population structure, habitat selection, distribution, and abundance (Houston & Bowen 2001, Mong & Sandercock 2007, Blanco & López-Lanús 2008; Casey et al. 2009, 2011; Azpiroz & Blake 2009, Sandercock et al. 2015). Diet studies at the breeding sites in North America yielded that sandpipers feed mainly on beetles and grasshoppers (Houston & Bowen 2001), and anecdotal information indicates that birds also feed on snails during migration (McAtee 1914, Hallinan 1924). As in many species of migratory birds, the non-breeding ecology is poorly known, and detailed information on diet is still lacking (Houston & Bowen 2001, Isacch et al. 2005, Blanco & López-Lanús 2008).

Native grasslands are the preferred habitat of Upland Sandpipers at both temperate breeding and non-breeding grounds, but they also occasionally use croplands (Houston & Bowen 2001, Blanco & López-Lanús 2008, Azpiroz et al. 2012). In Uruguay, the Upland Sandpiper is distributed throughout the country, but the highest numbers have been recorded in the past 20 years in the northern Departments of Artigas, Salto, and Paysandú, an area covered by extensive natural grasslands and managed for livestock production (Blanco & López-Lanús 2008, Alfaro in prep.).

Diversity of grassland insects is often correlated with the structure and composition of their habitat, intensity of grazing or agricultural activities, and with climatic conditions, such as temperature and precipitation (Gilbert & Raworth 1996, Schaffers et al. 2008, Medan et al. 2011, Peri et al. 2013, Srygley 2014, Jonas et al. 2015). Spatial and temporal variation in resource availability may affect the diet of Upland Sandpipers, and may be linked to their ability to track variation in resource traits and abundance. We hypothesize that as a consequence of living in a changing environment with variable resources, and being a migratory species with high energy requirements, Upland Sandpipers have a generalist diet, showing variation in the items consumed through time. Our objectives were both to describe prey items composition, and to analyze temporal diet variation in non-breeding areas of northern Uruguay.

METHODS

Study area. Our study area was located in north-central Uruguay (31°50′–31°44′S and 56°51′–56°26′W), covering a total area of ~ 2900 km² inside Salto and Paysandú Departments (Fig. 1). The Northern Campos ecoregion of Uruguay is close to the Haedo Ridge and included in the Basaltic region, which is characterized by a slightly rolling topography,
and rocky and shallow soils (Altesor et al. 2005, Lezama et al. 2006, Baeza et al. 2009, Azpiroz & Blake 2009, Azpiroz et al. 2012). Livestock grazing is the main agricultural use throughout this region, including sheep, cattle, and horses which, together with the native pampas deer (Ozotoceros bezoarticus), create a mosaic of different grass structure. Vegetation is mainly composed by native grasses like Piptochaetium montevidense, Botriochloa laguroides, Richardia humistrata, Wahlenbergia linarioides, Baccharis coridifolia, Panicum bians, Stipa charaxana, Aristida venusta, A. uruguayensis, and Paspalum dilatatum (Lezama et al. 2006, Baeza et al. 2009). The region also includes occasional stands of introduced Eucalyptus trees planted for shade and wood products, native forests along creeks and rivers, and a small but increasing portion of agricultural fields used for cultivation of grain crops, including rice, barley, sorghum, wheat, sunflower, and soy beans (Baeza et al. 2009, Azpiroz et al. 2012). The sites, where fecal samples of sandpipers were collected, corresponded to farms used for livestock grazing and all have similar communities of native grasses.

**Diet analysis.** The field study was based on the analysis of feces (Duffy & Jackson 1986, Rosenberg & Cooper 1990), which were obtained during four spring and summer seasons starting mid-November and ending in late February, from 2008–2009 to 2011–2012. Fecal samples were collected opportunistically at nine sites throughout the study area and throughout each season (Fig. 1). No repeated feces were collected from the same individual, or group of individuals, at the same time. Collection of feces was done by observing sandpipers from a distance with binoculars (10x50) until birds defecated. Samples were collected in the field, stored in dry paper bags,
and later processed in the laboratory. A stereomicroscope (20x) was used to separate and identify the heads, jaws, and other insects remains found in each sample. Prey identification was completed using insects collected in the field, identification guides (Arnett et al. 2002, Henry 2009, Bentancourt & Scatoni 2010), and assistance from entomologists at the Universidad de la República, Montevideo, Uruguay.

Any method of diet inference is biased to some degree, and analyses of feces are no exception. Potential biases associated with this technique include feces identification, variation in the digestibility of different prey items, underrepresentation of soft prey species, and challenges with identification of prey remains (Duffy & Jackson 1986, Rosenberg & Cooper 1990). However, this technique is also a relatively easy and non-invasive way of studying the diet of wild birds (Duffy & Jackson 1986, Rosenberg & Cooper 1990). By collecting fresh feces from known individuals and sampling insects at Upland Sandpipers’ feeding grounds to aid prey identification, two of the main biases were minimized. To evaluate the power of detecting prey items of our sample survey we used the following equation: $\beta = 1 - (1 - F)^n$, where $\beta$ is the probability of prey item detection, $F$ (frequency of occurrence) is the number of feces in which the item was found, and $n$ is the sample size (Arim & Naya 2003, Trites & Joy 2005).

For each item, the frequency of occurrence ($F$) was calculated (see above) (Duffy & Jackson 1986). Temporal variation in occurrence was analyzed using a Canonical Correspondence Analysis comparing frequencies of occurrence between years. Estimation of maximum prey size was done using insects collected in the field and values reported in the literature (Schatz & Wcislo 1999, Arnett 2000, Arnett et al. 2002, Henry 2009, Bentancourt & Scatoni 2010, Soares et al. 2010, Aisenberg et al. 2011).

**RESULTS**

A total of 67 feces, containing 21 prey types, were collected during the four seasons: 2008–2009 ($N = 16$), 2009–2010 ($N = 11$), 2010–2011 ($N = 13$), and 2011–2012 ($N = 27$), at nine different sites in northern Uruguay: Arerunguá ($N = 1$), Cabrera ($N = 6$), Cilindro ($N = 10$), Haedo ($N = 2$), Ramos ($N = 6$), Sarandi ($N = 6$), Valdez ($N = 27$), Venados ($N = 1$), and Wilson ($N = 6$). With 67 feces and 21 different prey items detected, the probability of detecting prey with more than a 10% of incidence in the diet was higher than 0.99. Similarly, for the year with the smallest sample size ($N = 11$), the detection probability for items with more than 10% of occurrence in the diet was higher than 0.68. These threshold values represent an acceptable power of prey-item detection. The main feces contents included insect remains (100%), stones (15%), plant remains (10%), and spiders (1.3%). Insect remains included heads, jaws, elytra, antennae, legs, wings, and forelegs. Plant remains were represented by seeds and leaves.

The diet of non-breeding Upland Sandpipers was composed mainly of insect/arthropod species in the orders Coleoptera (80% of the feces collected contained at least one Coleoptera insect remain), Orthoptera (79%), Hymenoptera (48%), Isoptera (10%), Hemiptera (0.03%), and Araneae (0.03%). A total of 16% of feces also included unidentifiable insects (Table 1). Proportion of Coleoptera (beetles) was nearly constant among years (~ 0.75–0.85), while Orthoptera (mainly grasshoppers) decreased (1.0 to 0.56) and Hymenoptera (ants) increased (0 to 0.80) during the four-year study period (Table 1). Main identified prey species included: *Borellia bruneri* (Orthoptera, Acrididae), *Naupactus* sp. (Coleoptera, Curculionidae), and *Camponotus* sp. (Hymenoptera, Formicidae) (Table 1). Maximum prey body size was estimated to be
TABLE 1. List of prey items (Insecta and Arachnida) found in Upland Sandpiper feces collected at different sites in the Northern Campos, Uruguay. Table shows the frequency of occurrence (number of feces in which the item was found/total number of feces) per year and the estimated maximum prey size (MPZ) taken from the literature and this study.

<table>
<thead>
<tr>
<th>ITEMS</th>
<th>FREQUENCY OF OCCURRENCE</th>
<th>MPZ (mm)</th>
<th>SOURCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>INSECTA</td>
<td>N = 16</td>
<td>N = 11</td>
<td>N = 13</td>
</tr>
<tr>
<td>Orthoptera</td>
<td>N = 16</td>
<td>N = 11</td>
<td>N = 13</td>
</tr>
<tr>
<td>Acrididae</td>
<td>N = 16</td>
<td>N = 11</td>
<td>N = 13</td>
</tr>
<tr>
<td>Borellia bruneri</td>
<td>0.19</td>
<td>0.08</td>
<td>0.38</td>
</tr>
<tr>
<td>Dichroplus elongatus</td>
<td>0.06</td>
<td>0.23</td>
<td>0.69</td>
</tr>
<tr>
<td>Dichroplus pratensis</td>
<td>0.75</td>
<td>0.85</td>
<td>0.31</td>
</tr>
<tr>
<td>Ronderosia sp.</td>
<td>0.25</td>
<td>0.08</td>
<td>0.15</td>
</tr>
<tr>
<td>TOTAL</td>
<td>0.94</td>
<td>1</td>
<td>0.85</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>N = 16</td>
<td>N = 11</td>
<td>N = 13</td>
</tr>
<tr>
<td>Curculionidae</td>
<td>N = 16</td>
<td>N = 11</td>
<td>N = 13</td>
</tr>
<tr>
<td>Camponotus sp.</td>
<td>0.63</td>
<td>0.69</td>
<td>0.46</td>
</tr>
<tr>
<td>Formicidae</td>
<td>N = 16</td>
<td>N = 11</td>
<td>N = 13</td>
</tr>
<tr>
<td>Camponotus sp.</td>
<td>0.75</td>
<td>0.77</td>
<td>0.77</td>
</tr>
<tr>
<td>Acromyrmex sp.</td>
<td>0.27</td>
<td>0.54</td>
<td>0.04</td>
</tr>
<tr>
<td>Ectatomma sp.</td>
<td>0.07</td>
<td>0.23</td>
<td>0.59</td>
</tr>
<tr>
<td>TOTAL</td>
<td>0.86</td>
<td>0.23</td>
<td>0.8</td>
</tr>
<tr>
<td>Hemiptera</td>
<td>N = 16</td>
<td>N = 11</td>
<td>N = 13</td>
</tr>
<tr>
<td>Formicidae</td>
<td>N = 16</td>
<td>N = 11</td>
<td>N = 13</td>
</tr>
<tr>
<td>Camponotus sp.</td>
<td>0.15</td>
<td>0.2</td>
<td>0.04</td>
</tr>
<tr>
<td>Acromyrmex sp.</td>
<td>0.15</td>
<td>0.2</td>
<td>0.04</td>
</tr>
<tr>
<td>TOTAL</td>
<td>0.15</td>
<td>0.2</td>
<td>0.04</td>
</tr>
<tr>
<td>Araneae</td>
<td>N = 16</td>
<td>N = 11</td>
<td>N = 13</td>
</tr>
<tr>
<td>TOTAL</td>
<td>0.08</td>
<td>0.08</td>
<td>0.08</td>
</tr>
</tbody>
</table>
Correspondence analysis showed considerable annual variation in the diet of Upland Sandpipers (Fig. 2). The first two axes of the analysis represented 87.7% of the total variation observed in the data (axis 1: 62.4%, eigenvalue = 0.353, axis 2: 25.3%, eigenvalue = 0.143) (Fig. 2). Axis 1 separated seasons 2008–2009 and 2009–2010 from season 2011–2012. The separation was associated with the addition of new prey items (Araneae, Hemiptera, Hymenoptera, Curculionidae, Cydnidae, and Tenebrionidae) during 2011–2012 and a decrease in Acrididae (grasshoppers) (Fig. 2). Axis 2 separated the third season, 2010–2011, from the last season, 2011–2012. The separation was associated with the presence of many undetermined Coleoptera and grasshoppers in the third season and again the incorporation of many new prey items in the last season (Fig. 2). One of the most abundant and frequent species of insects eaten (white-fringed beetle, Naupactus sp.) appeared in the center of the graph because this insect was consumed homogeneously throughout the four seasons (Fig. 2).

**DISCUSSION**

We found that the non-breeding diet of Upland Sandpipers in Uruguay is composed of a diversity of small invertebrates with body sizes < 27 mm (Table 1). Insects, particularly grasshoppers, beetles and ants from a limited set of species, comprised the bulk of the diet. Due to the low occurrence of plant remains, we consider that these items probably represent secondary or accidental ingestion while capturing insects. Temporal variation in food consumption also supports our hypothesis that this migratory bird is a diet generalist. This study was performed during four years, within the same environment and during the same period of the sandpiper's annual life cycle. Although we have no information about prey availability, variations in the items consumed between seasons suggest that Upland Sandpipers are probably opportunistic foragers, responding to variations in prey availability.

Changes in mean annual temperature and precipitation among years, or modifications of the grass communities due to livestock and agriculture, can cause variation in composition and abundance of many species of insects (Gilbert & Raworth 1996, Schaffers et al. 2008, Medan et al. 2011, Peri et al. 2013, Srygley 2014, Jonas et al. 2015). In the first two seasons of our study, Upland Sandpipers fed mainly on grasshoppers, at times when this prey item was particularly abundant. The drop in the presence of grasshopper species during the last two seasons was compensated by an increase in the intake of a variety of species of Coleoptera and Hymenoptera, especially ants. Other important species found in the diet included white-fringed beetles, a species considered pest in agricultural lands and grasslands (Caballero 1972, Zehnder 1997, Lanteri et al. 2002, Lanteri et al. 2013). The white-fringed beetle is the only prey that was frequently observed in the diet in all four years studied.

Grasshopper species, like *B. bruneri*, can be abundant in native grasslands of Uruguay during summer, when they cause considerable reduction of the grass cover (Martínez Crosa & Zerbino 2008, Bentancourt & Scatoni 2010). However, damages caused by these species occur in years where favorable environmental conditions generate higher population levels (Schaffers et al. 2008, Martínez Crosa & Zerbino 2008, Bentancourt & Scatoni 2010, Medan et al. 2011, Jonas et al. 2015). Low levels of soil moisture and high temperatures are optimal conditions for grasshopper reproduction (Martínez Crosa & Zerbino 2008, Srygley 2014, Jonas et al. 2015). Indeed, from mid-2007 to 2009, levels of precipitation...
in Uruguay were lower than normal, producing one of the most severe droughts ever recorded (Paruelo et al. 2009). The climatic conditions produced an increase in populations of grasshoppers in all the country during summer 2008–2009 (MGAP 2009). This increase probably explains the high consumption of grasshoppers during the first two years.

The diet of Upland Sandpipers in the non-breeding grounds was mainly composed of insects, which is consistent with data from breeding areas (McAtee 1914, Houston & Bowen 2001). A study on the diet of similar migratory species, American Golden Plover (Pluvialis dominica) and Buff-breasted Sandpiper (Tryngites subruficollis), that also use grazed grasslands during the non-breeding season in the Pampas region, showed similar dietary preferences (Isacch et al. 2005). In both species, as in Upland Sandpipers, beetles and other coleopterans were the main prey items consumed, although earthworms, beetle larvae, seeds, and plant remains were also well represented in the diet (Isacch et al. 2005). In contrast to Upland Sandpipers, the consumption of grasshoppers was low in both species (Isacch et al. 2005). We also report the presence of small pieces of rocks ingested by Upland Sandpipers during the four years. The ingestion of small rocks is used by many species of birds to help physically break down food and to aid digestion (Whelan & Schmidt 2007).

![Diagram](image-url)  
**FIG. 2.** First two components (Axis 1 and Axis 2) of a Canonical Correspondence Analysis showing temporal variation of food items in the diet of Upland Sandpipers in Northern Campos, Uruguay, 2008–2012.
There is some evidence that Upland Sandpipers have different food preferences, mainly snails, during migration (Hallinan 1924). It is common for migratory species to change feeding habits during migration because long distance movements imply high energy requirements, intense competition at stopover sites, and the need to adapt to different environments and climate conditions with changing resources (Covino & Holberton 2011, Newton 2008, Lindström 2007, Huston 1998). Certain items, like worms and snails, can be underrepresented or missed when analyzing diet using feces (Duffy & Jackson 1986, Rosenberg & Cooper 1990). However, during four seasons and a total of ~70 hours of direct observation, the consumption of mollusks or annelids was not observed in our field study. Further analyses using stomach contents, direct observations, or stable isotopes throughout their entire distribution range would complement diet studies based on fecal analysis. Furthermore, the number of feces collected and the richness of items in feces should be large enough in order to reduce the amount of variability that is attributable to sampling error (Arim & Naya 2003, Trites & Joy 2005). Without other methods used we believe that the high number of prey items detected (21) in an acceptable sample size (67 feces) should be adequate to describe the diet of the Upland Sandpipers in the study area.

The variation observed in the diet of the Upland Sandpiper in managed farmland in Uruguay shows dietary flexibility; sandpipers consume a variety of different prey items with different body sizes and ecological adaptations (e.g., beetles, grasshoppers, colonial ants and termites). Grasshoppers were the largest-bodied items found in the diet, with each individual providing large amounts of food (Bell 1990). In contrast, sandpipers would need to consume larger numbers of ants or termites, the smallest prey items in our sample, to obtain similar energy input (Bell 1990, Cooper & Whiters 2004). These different prey attributes suggest that Upland Sandpipers have a flexible foraging behavior, feeding in areas where certain items are most abundant and having different hunting strategies for different prey; a behavior that could be crucial to deal with the different environments experienced during their life cycle. Future studies, that relate food-intake rate with the amount and rate of fat deposition, could assess the importance of foraging flexibility during the migration of Upland Sandpipers. In addition, there may be segregation in the use of space and resources among Upland Sandpipers and other grassland birds, such as American Golden Plovers or Buff-breasted Sandpipers, since flocks of the latter two species were occasionally observed feeding in places near to those of sandpipers. Hence, future studies should focus on their spatial-temporal patterns in the non-breeding grounds to formally test this idea.

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