ASPECTOS ECOLÓGICOS DE UN AVE MIGRATORIA NEÁRTICA-NEOTROPICAL DURANTE LA TEMPORADA NO REPRODUCTIVAEN LOS PASTIZALES DEL NORTE DE URUGUAY

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Foto de carátula: Paisaje de pastizal en los Campos del Norte de Uruguay.

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RESUMEN

Las aves de pastizal están declinando a nivel global y en Uruguay en particular, principalmente debido a la reducción y fragmentación de su ambiente. El Batitú (*Bartramia longicauda*), ave exclusiva de pastizal en el área reproductivaen Norte América y en la no reproductivaen Sudamérica, es un excelente modelo para aves migratorias de pastizal que realiza costosas migraciones de larga distancia. Congruentemente, la especie ha sido foco de diversos trabajos, aunque esencialmente durante el período de reproducción. No obstante, la ecología de la especie en los sitios de invernada es notablemente poco conocida, limitando su utilización como modelo general del ciclo migratorio. En este contexto, la presente tesis buscó avanzar en la comprensión de la ecología de la especie en este período. Específicamente, se estudiaron diversos aspectos de su historia de vida y estrategia de forrajeo en el período no reproductivo

Se cubrieron cuatro períodos no reproductivos(2008-2012), totalizando más de 500 registros de uso de ambiente, colecta de heces y monitoreo con radio-transmisor a 62 individuos. El perfil de uso de recursos tróficos del Batitú y su variabilidad temporal, indican que se trataría de una especie insectívora, con una estrategia generalista y oportunista que forrajea en pastizales. Los tres Ordenes de insectos: Coleoptera, Orthoptera e Hymenoptera dominaron la dieta con alta variabilidad en estos dos último ítems y posibles preferencias por algunas presas. Su estrategia de forrajeo es congruente con la necesidad de satisfacer sus demandas energéticas en el amplio rango de condiciones experimentadas dentro y entre migraciones.

La eficiencia de forrajeo y el riesgo de depredación del Batitú dependen de la estructura y altura de la vegetación, la cual es particularmente sensible a las opciones de manejo e intensidad de herbivoría. Los sitios de alimentación y refugio fueron congruentes con el tipo de alimento consumido por la especie, pero también con la necesidad de refugio prefiriendo ambientes con menos de 20 cm de altura pero con heterogeneidad espacial entre parches. La preferencia por este

mosaico de alturas de vegetación sustenta la hipótesis de una selección de ambientes, balanceando la presión de depredación con vegetación alta para refugio y la búsqueda de alimento con vegetación baja para una mejor detección de las presas.

Un componente central del balance energético en especies migratorios es su estrategia de muda de las plumas primarias de vuelo. La muda implica un compromiso energético importante, no tanto por su costo directo sino por la reducción de ingesta debido a una menor movilidad. Los individuos en muda presentan menor maniobrabilidad reduciendo su eficiencia de vuelo, lo cual además aumentael riesgo de depredación. El cambio de plumaje ocurrió al arribar al área de invernada completándose generalmente para finales de enero. La condición corporal mostró un descenso durante las primeras etapas del proceso de muda que posteriormente se revirtió sin detectarse diferencias significativas entre machos y hembras. Este patrón es congruente con la existencia de un compromiso energético durante el proceso de muda, frecuentemente invocado pero rara vez evaluado.

Esta tesis logra avanzar en la comprensión de la ecología de las especies migratorias. Los conocimientos generados se potencian por tratarse de una especie que ha sido estudiada en sus áreas de cría pero no así en el resto de su ciclo vital. Satisfacer las demandas energéticas en los ciclos de migración estaría asociado a estrategias de forrajeo amplias y oportunistas, la presencia de refugios en los períodos más vulnerables, como durante lamuda, y ambientes con alta disponibilidad de recursos para la recuperación post-migratoria, muda y preparación para la siguiente migración. El conjunto de estos estudios también sugiere que la conservación de especies migratorias no solo involucra la protección de sitios de parada, cría e invernada, sino también la estructura de los paisajes asociados a estos sitios.

CAPÍTULO 1. INTRODUCCIÓN GENERAL

INTRODUCCION GENERAL

Las aves migratorias

La distribución de los organismos depende de diversas variables ambientales e interacciones bióticas (Brown et al. 1995, Mysterud & Ims 1998, Harte et al. 2005). Los animales utilizan ambientes heterogéneos en diferentes escalas espaciales, desde el rango geográfico de cada especie hasta el área de acción de cada individuo (Aebischer et al. 1993, Mysterud and Ims 1998, Harte et al. 2005, Jedlikowski et al. 2016). La selección de hábitat involucra factores ecológicos y evolutivos relacionados tanto con el valor de supervivencia en cada sitio como con el mecanismo que utilizan para escogerlo (McArthur & Pianka 1966, Lima & Dell 1990, Lima & Bednekoff 1999). Para muchas aves, la supervivencia y el éxito reproductivo dependen de la elección del lugar donde nidificar (Krebs 2009). Sin embargo, para las especies de aves migratorias la supervivencia también depende de los lugares que escojan durante la migración y para pasar la temporada no reproductiva (Marra et al. 1998, Sillett & Holmes 2002, Newton 2008).

Las aves migratorias son capaces de explotar ambientes favorables durante períodos limitados del año, permitiéndoles acceder a nuevos recursos y disminuir la competencia inter específica por alimento y espacio (Root 1967, Berryman & Kindlmann 2008, Newton 2008). En el ciclo de vida de las aves migratorias existen tres procesos claves para poder realizar las migraciones: la navegación, la hiperfagia y la muda. Cada uno de estos procesos involucra capacidades fisiológicas únicas que determinan una fuerte selección y fidelidad por los sitios de alimentación, de reproducción y descanso (Newton 2008). Migrar tiene un alto costo energético y el desarrollo de esta estrategia involucra adaptaciones para garantizar el acceso a recursos y optimizar su utilización intra organismo (Huston 1998, Lindström 2007). Por estos motivos las aves migratorias dependen particularmente del acceso y utilización de hábitats con la cantidad de alimento necesaria para sus exigentes requerimientos energéticos (Buehler and Piersma 2008). Muchas especies de aves migratorias, ocupan hábitats parecidos durante la temporada reproductiva y la no reproductiva, con climas, estructura del hábitat y oferta de alimento similares (Warnock & Takekawa 1997, Vadász et al. 2008, Newton 2008). Estos rasgos de las aves migratorias las convierten en especies vulnerables a cambios ambientales naturales o de origen antrópico (Nott et al. 2002, Brennan & Kuvlesky 2005, Gordo 2007, O'Hara et al. 2007, Azpiroz et al. 2012a).

Para suplir la alta demanda energética de la migración las aves deben alimentarse en gran cantidad, incluso muy por encima de sus necesidades de mantenimiento en algunas etapas de su ciclo de vida, lo cual tiene costos fisiológicos (Biebach 1996, Berthold 1975). Antes de la migración, las aves aumentan hasta el doble de su masa corporal para acumular reservas (principalmente grasa) y poder volar largas distancias sin alimentarse (Piersma and Van Gils 2011). Además, los músculos pectorales (músculos de vuelo y músculos supracoracoides) aumentan de tamaño y el aparato digestivo (molleja, hígado e intestino) se atrofia de manera de disminuir el peso y el gasto energético de su mantenimiento (Norberg 1981, Piersma & Jukema 1990, Cavitt and Thomson 1997, Piersma 1998, Gunnarsson et al. 2010, Portugal et al. 2007, Piersma and Van Gils 2011) (Figura 1). La muda del plumaje y especialmente de las plumas primarias de vuelo también implica un costo energético y, en muchas especies, no se realiza durante los períodos de alta demanda energética como la reproducción y la migración (Murphy 1996). Sin embargo, la muda puede interactuar con los momentos de aumento de peso y la recuperación del tamaño normal de los órganos internos una vez que llegan a las áreas de descanso (Murphy 1996, Piersma & Lindström 1997). La muda es esencial para mantener la capacidad de vuelo y un buen desempeño durante la migración (Murphy 1996). En consecuencia, durante el período de muda de las plumas de vuelo (primarias y secundarias) los individuos tienen menor maniobrabilidad y por lo tanto se desplazan menos para no ser detectados por los depredadores, lo cual limita su acceso a los recursos con un consecuente detrimento de su condición corporal (Lima 1986, Panek and Majewski 1990, Portugal et al. 2007). En términos generales, el desarrollo de estrategias de administración de recurso eficientes suele involucrar compromisos con los riesgos de depredación y el menor desempeño comportamental de los individuos durante la muda (Lima 1986, Newton 1969, King and Murphy 1985, Panek and Majewski 1990, Chandler and Mulvihill 1992, Piersma 2003a, Portugal et al. 2007). El estudio de estas interacciones es esencial para la comprensión del ciclo anual de las aves migratorias y su manejo de las demandas energéticas de cada etapa del ciclo.

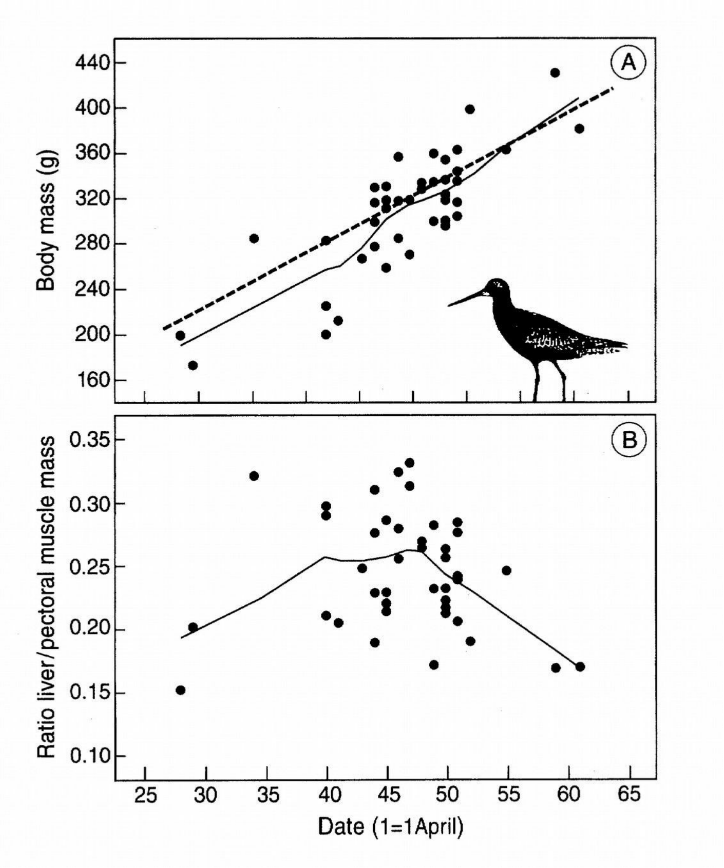


Figura 1. Aumento en la masa corporal (A) y la relación masa del hígado con masa de los músculos pectorales (B) de un macho adulto de Bar-tailed Godwits (*Limosa lapponica lapponica*) en Datch Wadden Sea, Netherlands. La línea punteada del gráfico (A) representa el promedio en el aumento de la masa de la población (regresión lineal) basado en el registro de 560 masas corporales (Piersma and Jukema 1990, Tabla 3). Gráfico extraído de Piersma (1998). Aquí se observa que las aves terminan la migración con los músculos pectorales muy desarrollados (B), pero a lo largo de su estadía la masa corporal (A) y la masa del hígado (B) van aumentando como respuesta a la ingesta de grandes cantidades de alimento mientras que los músculos de vuelo se reducen. Al final de la temporada deben prepararse nuevamente para migrar aumentando la masa muscular y reduciendo la masa de los órganos del aparato digestivo

Durante la migración, las poblaciones de aves pueden separarse por clases de edad o sexo (Nebel et al. 2002). La migración diferencial de sexos o clases etarias ha sido observada en muchas especies de playeros migratorias (Nebel et al. 2002, O'Hara et al. 2006). Existen varias hipótesis sobre este fenómeno en aves y otros vertebrados migratorios orientadas al efecto de las diferencias en tamaño corporal, dimorfismo sexual, diferencias en los requerimientos nutricionales, competencia y riesgo de depredación (Ketterson & Van Nolan 1982, Ardia & Bildstein 2001, Nebel & Ydenberg 2005). Las especies de playeros migratorios presentan una amplia variedad de estrategias de apareamiento, como son la promiscuidad sin barrera entre parejas, la monogamia con barrera entre parejas, la poligamia y la reproducción extra pareja (Reynolds and Székely 1997, Székely et al. 2006, Thomas et al. 2007). Dentro de esta variación también se incluye el cuidado parental y en qué medida cada sexo participa en la incubación y el cuidado de las crías (Gunnarsson et al. 2010, Tulp et al. 2009a, Székely et al. 2006, Thomas et al. 2007). En consecuencia, el almacenamiento de energía varía entre sexos, debido a demandas energéticas diferentes en la producción de gametos, estrategias reproductivas e inversión parental (Piersma et al. 2003b, Tulp et al. 2009b, Hayward and Gillooly 2011).

Muchos ambientes naturales de todo el mundo están siendo fragmentados rápidamente por las actividades humanas, lo cual genera que las poblaciones salvajes se vuelvan cada vez más pequeñas, restringidas en su distribución y aisladas unas de otras (Bender et al. 1998, Rockwood 2006). Particularmente, los ecosistemas de pastizal están siendo modificados a escala global debido a la agricultura, ganadería y forestación, las cuales continúan en aumento (Brennan & Kuvlesky 2005, Ribic et al. 2009, Isacch & Cardoni 2011, Azpiroz et al. 2012a, Codesio et al. 2013). En Norteamérica, muchas de las aves que utilizan el pastizal natural para su ciclo de vida están declinando debido a estos procesos de reducción y fragmentación de hábitat (Fritcher et al. 2004, Brennan & Kuvlesky 2005, Thomas et al. 2006, Ribic et al. 2009). Existen estudios que demuestran que el éxito reproductivo de las aves de pastizal depende de las características del mismo (altura, cobertura y diversidad) dado que las aves encuentran mayor refugio para sus nidos en pastizales heterogéneos tanto en su altura y cobertura como en su diversidad (Kentie et al. 2015, Sandercock et al. 2015). En este contexto, la comprensión de los patrones y mecanismos involucrados en la utilización del paisaje por aves migratorias es hoy esencial para entender el efecto de los cambios de hábitat, sus consecuencias para el funcionamiento de los ecosistemas y el desarrollo de medidas de manejo (Bender et al. 1998, Rockwood 2006).

Modelo de estudio: el Batitú *Bartramia longicauda* (Bechstein, 1812)

Distribución e historia de vida

Entre las especies de aves migratorias exclusivas de pastizal se encuentra el Batitú (*Bartramia longicauda*, Scolopacidae). Esta especie nidifica en Norteamérica y durante el invierno austral migra al sur de Sudamérica (Fig. 2) (Houston & Bowen 2001, Fritcher et al. 2004, Brennan & Kuvlesky 2005, Blanco & López-Lanús 2008, Ribic et al. 2009). En Sudamérica se encuentra principalmente en los pastizales del centro y norte de Argentina, sur de Brasil y Uruguay (Houston & Bowen 2001) (Figura 2). En Uruguay el Batitú se distribuye principalmente en el interior del país, siendo frecuentemente encontrado en la ecoregión de los Campos del Norte que incluye los departamentos de Paysandú, Salto, Tacuarembó, Rivera y Artigas (Blanco & López-Lanús 2008, Azpiroz and Blake 2009, Azpiroz et al. 2012a). Birdlife International y la Unión para la Conservación de la Naturaleza (2012) consideran al Batitú en la categoría de Preocupación Menor (Least Concern), sin embargo, ha sido catalogado como en peligro, amenazado o en situación crítica en varios estados en Norteamérica, debido principalmente a la degradación de su hábitat (Houston & Bowen 2001, Vickery et al. 2008).

En Norteamérica, se han estudiado algunas poblaciones de esta especie desde el punto de vista demográfico, reproductivo, genético, morfológico, depredación y selección de hábitat (Mong

& Sandercock 2007, Sandercock et al. 2008; 2015, Casey et al. 2009; 2011). El Batitú es una especie característica de pastizal con preferencia por los pastizales pastoreados aunque ocasionalmente también utiliza cultivos de alfalfa o similares (Houston & Bowen 2001, Blanco & López-Lanús 2008, Azpiroz & Blake 2009; 2016). La dieta del Batitú ha sido brevemente estudiada en Norteamérica, donde identificaron que estaba compuesta por langostas, escarabajos y otros pequeños artrópodo que son capturados utilizando la técnica de corridas y paradas mediante la detección visual de sus presas durante las horas de luz (Houston& Bowen 2001). Casey et al. (2011) encontraron que el Batitú tiene una de las tasas más altas, entre los Scolopácidos, de paternidad fuera de la pareja y observaron que las hembras emparentadas anidan de forma sincrónica y próxima entre sí, algo poco común entre las aves. Además, ambos padres cuidan los huevos pero, una vez nacidos los pichones, es el padre quién los cuida hasta que aprenden a volar (Houston & Bowen 2001, Casey et al. 2011). Consecuentemente, las reservas energéticas varían entre sexos debida a inversiones diferentes en la producción de los gametos, cortejo y el tiempo destinado al cuidado parental (Piersma et al. 2003b, Tulp et al. 2009a, Hayward & Gillooly 2011). A pesar de que esta especie se ha constituido en un modelo de estudio en Norteamérica, poco se sabe sobre su ecología en las áreas de invernada (Houston & Bowen 2001, Vickery et al. 2008).

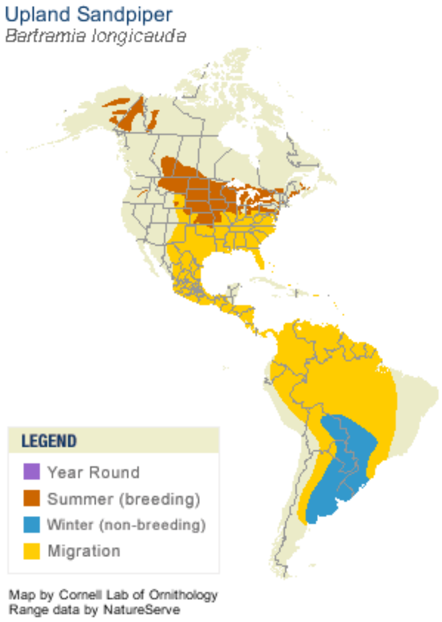


Figura 2. Mapa de distribución del Batitú (*Bartramia longicauda*). En amarillo se marca el área de utilizada durante la migración, en azul el área utilizada durante la temporada no reproductiva y en rojo el área de reproducción. Mapa extraído del Cornell Laboratory of Ornithology.

Morfología y taxonomía

El Batiú es un playero monotípico de tamaño mediano cuyos parientes más cercanos son los playeros del género *Numenius* spp. (Sibley & Monroe 1990, Vickery et al. 2008). Su largo promedio varía entre 280 y 320 mm (Hayman et al. 1986, Vickery et al. 2008). Se cree que las hembras de mas de 200 g se encuentran en período de gestación (Morrison et al. 2001, Vickery et al. 2008). La coloración de los adultos es marrón canela con pintas oscuras en la parte dorsal y blancuzca en la parte ventral (Houston & Bowen 2001). El cuello y el pecho presentan color canela claro con un estriado marrón oscuro que se extiende un poco hacia los lados (Houston & Bowen 2001). Su cabeza es pequeña y se continúa con un cuello delgado de largo medio; el pico es corto y las patas de largo medio, ambos de color amarillo (Figura 3, Houston & Bowen 2001).

A pesar de que no existe evidencia de dos razas separadas, existe un descenso leve en el promedio de tamaño de las hembras a lo largo de su distribución en Norte América desde el oeste hacia el este (Hayman et al. 1986, Houston & Bowen 2001). Aparentemente, existirían tres poblaciones reproductivas aisladas con poco o nulo solapamiento (Vickery et al. 2008). Las poblaciones que reproducen al este de las Montañas Apalaches parecerían estar separadas de las poblaciones centrales en Ohio, Indiana e Illinois (USA) al oeste a través de las Grande Planicies de Alberta, Canadá (Vickery et al. 2008). Existe una población reproductiva separada en el centro de Alaska y Yukon en territorio Canadiense (Houston & Bowen 2001, Vickery et al. 2008, Miller et al. 2014). No está claro si las poblaciones de Washington y Oregon se dispersan hasta las poblaciones de las Grandes Planicies (Vickery et al. 2008). Recientemente fueron detectadas parejas reproductivas en Columbia Británica, Canadá (VandenDriessche et al. 1994).

Figura 3. Foto de un Batitú (*Bartramia longicauda*) posado en un poste de alambrado en los pastizales de los Campos del Norte en el Departamento de Salto, Uruguay. Foto: Luciano Liguori.

Hipótesis y objetivos

Hipótesis

1) El Batitú experimenta distintos escenarios ambientales dentro de los ciclos anuales de migración y entre migraciones. Para lograr suplir las demandas energéticas en estos escenarios cambiantes la especie desarrollaría una estrategia alimenticia generalista y oportunista dentro del rango de presas que su biología le permite explotar. La diversidad y composición de insectos de pastizal está determinada por la estructura del pastizal en relación a la altura y cobertura de la vegetación. Asimismo, estas variables están afectadas por el manejo del sistema (intensidad de pastoreo y mejoramiento del pastizal). La dieta del Batitú deberá seguir estas variaciones en la oferta de recursos entre años.

2) La estrategia de utilización de hábitat por el Batitú está orientada a maximizar la tasa de consumo y la detección de depredadores. Los pastizales bajos favorecen tanto el acceso a los insectos consumidos por el Batitú como la detección de depredadores, concentrándose la especie en estos ambientes cuando tiene buena capacidad de escape activo de la depredación.

3) Por otro lado, la vegetación alta ofrece protección pasiva contra los depredadores como zorros y aves rapaces. La agregación de individuos en zonas abiertas reduce el riesgo de depredación por un efecto de dilución y aumento en la eficiencia de detección de depredadores. Esto determinaría una asociación negativa entre el tamaño del grupo y la altura de la vegetación.

4) El proceso de muda reduce el desempeño de los individuos al limitar su movilidad. Esto se traduce en una menor eficiencia en la captura de presas y en la capacidad de escape activo a la depredación. Consecuentemente, durante el período de muda los individuos reducen su actividad disminuyendo así su demanda energética y probabilidad de ser detectados por depredadores. Esta reducción en la actividad se evidenciaría por una reducción en el área de acción de los individuos en muda. El costo energético de esta estrategia determinará una reducción de la condición corporal de los organismos durante el proceso de muda, la cual será posteriormente revertida y sobre compensada con miras a la siguiente migración.

5) Los diferentes requerimientos fisiológicos entre sexos determinan estrategias diferenciadas de migración en el Batitú. Los machos maximizan el tiempo de defensa de las crías mientras las hembras maximizan la mejora de su estado fisiológico. Esto afecta los tiempos asignados al cuidado parental versus migración, los recursos utilizados y los tiempos y lugares donde los obtienen. Las hembras, al liberarse del cuidado parental, pueden mejorar su condición corporal e iniciar la migración y llegar a las áreas no reproductivas antes que los machos. Por otro lado, al llegar antes inician la muda del plumaje antes y pueden encontrarse en mejor condición corporal antes que los machos hacia el final de la temporada.

Objetivo general:

Avanzar en la comprensión de los patrones de historia de vida y uso de ambiente del Batitú durante la temporada no reproductiva.

Objetivos específicos:

1) Determinar la estrategia de forrajeo del Batitú en base al perfil de utilización de presas y su variabilidad temporal.

2) Identificar las características del hábitat utilizado por la especie en relación a la altura y cobertura de la vegetación y la presencia de monocultivos.

3) Reportar la respuesta de agregación de individuos y su dependencia de el contexto ambiental.

4) Analizar las tendencias en la condición corporal a lo largo del período de invernada, entre sexos y en diferentes estados de la muda.

Aspectos Metodológicos

Sistema de estudio

El área escogida para esta tesis se encuentra en el centro-norte de Uruguay (31.50°–31.44°S and 56.51°–56.26°W), y abarca una superficie total de aproximadamente 1800 km^2 dentro de los Departamentos de Salto y Paysandú. El área de estudio está ubicada dentro de la ecoregión denominada Campos del Norte de Uruguay adyacente a la Cuchilla de Haedo e incluida en la región del Basalto que se caracteriza por una topografía levemente ondulada con suelos poco profundos y rocosos (Altesor et al. 2005, Lezama et al. 2006, Baeza et al. 2009, Azpiroz and Blake 2009, Azpiroz et al. 2012a). La ganadería es el uso principal que se hace de los suelos en esta región, incluyendo ovejas, vacas y caballos, por lo cual la mayor parte del territiorio es privado. En estos pastizales todavía existe una pequeña población de Venado de Campo (*Ozotoceros bezoarticus*) que junto con el ganado forman un mosaico de diferentes altura y configuración de la vegetación del lugar. Los Campos del Norte de Uruguay forman parte de los pastizales del sur de Sudamérica, una región que incluye: los pastizales del Río de la Plata, los pastizales altos del sur de Brasil y los pastizales del Chaco húmedo a lo largo del Río Paraguay en el sur de Paraguay y el norte de Argentina (Figura 4) (Lezama et al. 2011, Azpiroz et al. 2012a).

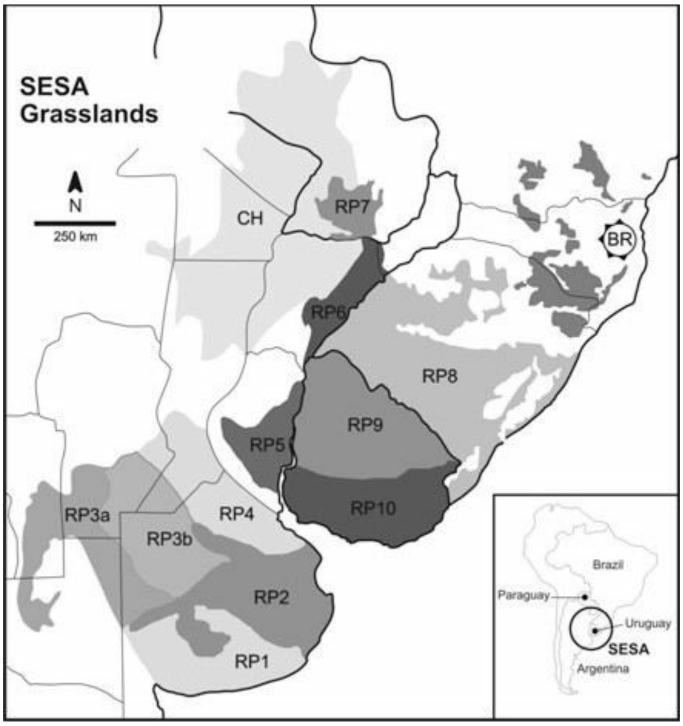


Figura 4. Mapa mostrando la región del los pastizales del sur de Sudamérica (SESA) en donde se encuentran los Campos del Norte de Uruguay (RP9). RP1: Pampa del sur, RP2: Pampa húmeda, RP3a: Pampa oeste interior, RP3b: Pampa chata interior, RP4: Pampa ondulada, RP5: Pampa mesopotámica, RP6: Campos del norte de Argentina, RP7: pastizales del sur de Paraguay, RP8: Campos del norte de Brasil, and RP10: Campos del sur, BR: pastizales altos de Brasil, CH: pastizales húmedos del Chaco. Imagen tomada de Azpiroz et al. (2012a).

La comunidad vegetal principal de los Campos del Norte de Uruguay está compuesta por pastizal nativo dentro de los que se incluyen *Piptochaetium montevidense*, *Botriochloa laguroides*, *Richardia humistrata*, *Wahlenbergia linarioides*, *Baccharis coridifolia, Andropogon lateralis, Panicum hians*, *Portulaca papulosa*, *Hordeum pusillum*, *Selaginella sellowii*, y *Paspalum dilatatum* (Lezama et al. 2006; 2011, Baeza et al. 2009). En la región también se observan pequeños parches de Eucaliptus (*Eucalyptus sp.*) plantados para dar refugio al ganado, bosques a lo largo de los ríos y arroyos, y una porción pequeña pero en aumento de campos cultivados con arroz, cebada, sorgo, trigo, girasol y soja (Baeza et al. 2009, Azpiroz et al. 2012a). En esta región de pastizales naturales habitan especies de vertebrados nativos que presentan problemas de conservación debido a la reducción y fragmentación de su hábitat como son la Loica Pampeana (*Sturnella defilippii*), el Ñandú (*Rhea americana*), el Venado de Campo y el Gato de Pajonal (*Leopardus braccatus*) entre otras (Azpiroz 2005, González & Martínez-Lanfranco 2010, Azpiroz et al. 2012b). Por esta razón la región ha sido catalogada como Área de importancia para las aves (UY007) con el nombre de “Campos del Tapado”, según Birdlife International (Important Bird Areas) (Aldabe et al. 2009).

Metodología de trabajo

Dieta

Existen diferentes métodos para el estudio de la dieta en aves: análisis de egagrópilas, contenido estomacal, regurgitados espontáneos o inducidos, análisis de las heces, observación directa, análisis de isótopos estables y código de barras del ADN (Rosenberg & Cooper 1990, Duffy & Jackson 1986, Valentini et al. 2009). En general todos estos métodos tienen sesgos asociados que tienden a sesgar la cantidad e identidad de las presas y especies consumidas (Duffy & Jackson 1986, Rosenberg & Cooper 1990). Dado que el análisis del contenido estomacal y los regurgitados espontáneos son técnicas invasivas que pueden producir la muerte del animal, el uso de las egagrópilas, heces, o la observación directa suelen ser más convenientes. Para el caso de las aves playeras de pastizal que no producen egagrópilas, como el Batitú, la técnica no invasiva más apropiada es el análisis de las heces o la observación directa.

Uno de los sesgos asociados al estudio de la dieta mediante el análisis de heces, es que las presas de gran tamaño pueden quedar sub-representadas con respecto a las de pequeño tamaño porque sus restos aparecen repartidos en más de una feca o porque la presa fue consumida parcialmente (Arim & Naya 2003). A su vez, heces de tamaño pequeño pueden contener menor cantidad de restos diagnósticos o carecer de ellos por lo tanto no deberían ser comparadas con el resto en términos de consumo de presas (Arim & Naya 2003). Por otro lado, presas de cuerpo blando, como los anélidos, puede quedar poco representadas o no ser detectadas debido a que los restos no digeridos que pueden aparecer en las heces son pocos y pequeños o no existen (Rosenberg & Cooper 1990, Duffy & Jackson 1986). Considerando los sesgos asociados, los estudios de dieta mediante la técnica de análisis de heces aportan valiosa información en cuanto al contenido de la dieta y proporcionan una estimación de la abundancia de cada ítem en la dieta.

Captura y marcaje

La captura de aves puede realizarse de diferentes formas dependiendo del tipo de aves que se quiera capturar y de sus hábitos de vida. La técnica clásica más utilizada es la de redes de niebla que es muy útil para capturar Passeriiformes en zonas de bosque, pero no tanto en ambientes abiertos (Bibby et al. 1998). Para capturar aves de pastizal que descansan en el suelo durante la noche como el Batitú y otros chorlos de pastizal, la técnica de encandilado con foco de luz es la más adecuada (Strum et al. 2010, Sandercock et al. 2015). Esta técnica consiste en encandilar a los individuos mientras descansan durante la noche y colocar una red circular sobre ellos.

Una vez capturado, cada individuo es marcado con un anillo metálico numerado y eventualmente con una combinación de anillos de plástico de colores en el caso que se quiera identificarlos luego con binoculares. Las recapturas visuales son difíciles en durante la temporada no reproductiva porque los individuos no se exiben como en la temporada reproductiva. Cuando se desea monitorear por un largo tiempo a los individuos capturados, también se les puede colocar un radio-transmisor de alta frecuencia (VHF), que es colocado sobre la espalda con un arnés elástico enganchado en las piernas y su tamaño depende del tamaño del ave con la que se esté trabajando. El método de retención del radio-transmisor que se utilizó en esta tesis ha sido testado en el Batitú, mostrando una alta eficiencia durante el tiempo que dura la batería del transmisor (~ 3 meses) (Mong and Sandercock 2007). A su vez, también fue testada la incidencia del radio-transmisor (Model PD-2, ~ 3,8 g, Holohil Ltd., Ontario, Canadá) sobre el comportamiento de los individuos demostrando que no interfiere en las actividades normales de alimentación, reproducción y migración (Mong and Sandercock 2007). Para localizar a los individuos marcados, se utilizan radio receptores portátiles (Modelo R2000, ATS, Isanti, MN).

Condición corporal

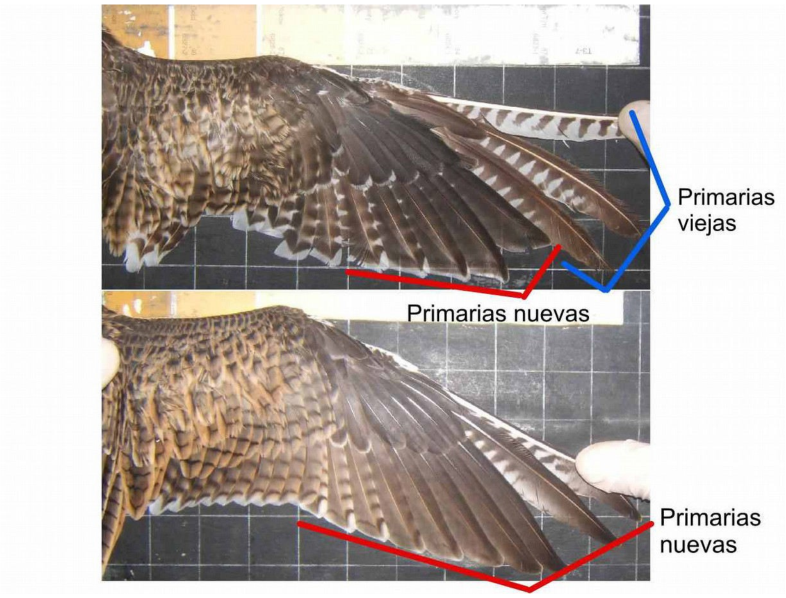
Existen una serie de medidas morfológicas y del estado fisiológico que pueden ser tomadas en las aves una vez capturadas. Las medidas morfológicas pueden ser las siguientes: largo de la cuerda del ala derecha, largo del pico-cabeza (desde la parte de atrás del cráneo hasta la punta del pico), largo del tarso derecho (desde la articulación con los dedos hasta el codo entre tarsos), largo de la cola (desde la rabadilla hasta la punta de la cola) y la masa entre otras. Como medidas del estado fisiológico se puede registrar la grasa subcutánea por transparencia y el estado de la muda de cada individuo.

La grasa subcutánea puede ser registrada visualmente observando dos regiones del cuerpo que no están cubiertas por plumas, la región entre la fúrcula y la región del parche reproductivo en el abdomen. Existen diferentes formas de contabilizar la cantidad de grasa, pero para este estudio se utilizó al técnica de Krementz et al. (1990) ya que se aplica bien para aves migratorias. El índice se registra de la siguiente manera: (0) = no existe grasa visible ni en la región de la fúrcula ni sobre el abdomen; (1) = se observa un poco de grasa en la región entre la fúrcula o en el abdomen pero ninguno de los dos está completo de grasa; (2) = la región de la fúrcula está cubierta de grasa pero no abultada y se observa un poco de grasa en el abdomen; (3) = la región de la fúrcula está completa de grasa y la región abdominal está casi completamente cubierta de grasa; (4) = tanto la zona de la fúrcula como la abdominal están completamente cubiertos de grasa y abultadas; y (5) = la grasa además se extiende alrededor del esternón.

Muda

El estado de muda de las plumas de vuelo puede ser medido por medio de la asignación de un puntaje a cada etapa del crecimiento de cada una de las 10 plumas primarias de una de las alas (ambas alas mudan simétricamente) de la siguiente forma (Newton 1966): (0) pluma vieja; (1) una pequeña punta apenas saliendo de la vaina ("pin feather"); (2) un cuarto de la pluma crecida; (3) entre un cuarto y la mitad de la pluma crecida; (4) entre la mitad y tres cuartos; (4.9–5) entre tres cuartos y la pluma completa, and (5) la pluma está completamente crecida y sin vaina en la base (Figura 5). Para el análisis estadístico la puntuación de cada pluma puede ser convertida en un índice de muda según las siguientes proporciones: un puntaje igual a 0 = 0, 1 = 0.125, 2 = 0.375, 3 = 0.625, 4 = 0.875 y 5 = 1.000 (Underhill & Summers 1993, Underhill & Joubert 1995). Este proceso de conversión tiene el propósito de lograr linealidad a lo largo del tiempo del proceso de la muda (Summers 1980). El índice de muda es la suma de las proporciones de las 10 plumas primarias, siendo un índice del estado de la muda de cada individuo al momento de la captura (Newton and Rothery 2009). Para el estudio del proceso de muda es conveniente el seguimiento de la plumas primarias porque el reemplazo de las plumas se extiende a lo largo de casi todo el período de la muda de todo el cuerpo y es generalmente tomado como una referencia del proceso general de muda (Jenni & Winkler 1994).

Figura 5. Ala del Batitú mostrando arriba, un individuo en proceso de muda de las plumas de vuelo y abajo un individuo con todas las plumas del ala nuevas. La muda de las plumas primarias ocurre desde adentro hacia afuera como se observa en la foto de arriba.



Sexado

Para conocer el sexo de las especies de aves que no presentan dimorfismo sexual, como el Batitú, se puede extraer una muestra de sangre y realizar un análisis genético. En las aves, las hembras son el sexo heterogamético (WZ) y los machos el homogamético (ZZ), por lo tanto un microsatélite de un locus en el cromosoma W sirve como marcador de las hembras (McDonald & Potts 1997). Para el sexado del Batitú se amplificaron, mediante PCR (Primers 2550F/2718R, Casey et al. 2011), los genes CHD1 que están presente en los cromosomas sexuales de las aves W y Z. Los machos son así identificados en un gel de electroforesis en donde se observa una sola banda (de CHD1Z) mientras que las hembras presentan dos bandas (de CHD1W y CHD1Z) (Figura 6).

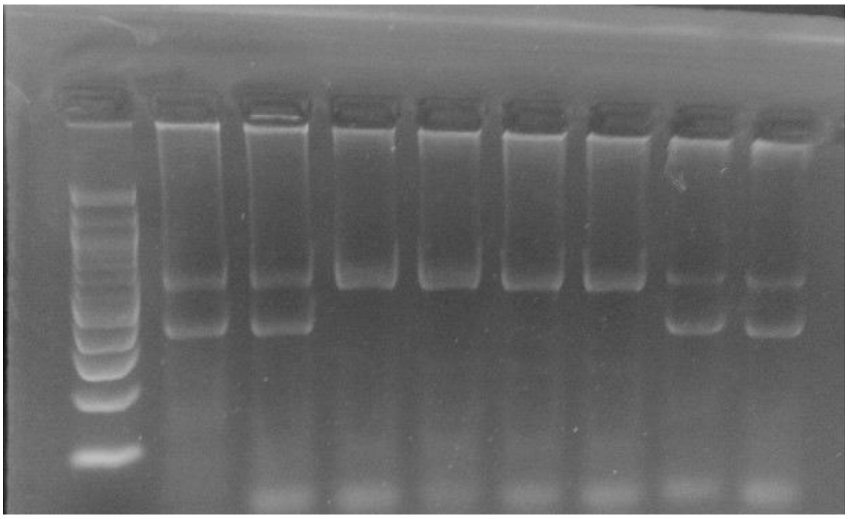


Figura 6. Fotografía del gel mostrando parte de los resultados del sexado molecular del Batitú. En el gel se pueden ver cuatro hembras (dos bandas al costado izquierdo y derecho) y cuatro machos (una banda, como se observa en las líneas centrales). La columna de la izquierda representa la escala de referencia.

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CAPITULO 2. THE DIET OF UPLAND SANDPIPERS (*Bartramia longicauda*) IN MANAGED FARMLAND IN THEIR NEOTROPICAL NON-BREEDING GROUNDS.

DIETA DEL BATITÚ (*Bartramia longicauda*) EN PASTIZALES MANEJADOS DE SU ÁREA NO REPRODUCTIVA EN EL NEOTRÓPICO.

Foto: Matilde Alfaro

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

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RUNNING HEAD: DIET OF UPLAND SANDPIPERS IN URUGUAY.

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.

INTRODUCTION

Survival of migratory birds depends mainly on resource abundance and availability, climatic conditions, predation pressure, habitat availability and intra- and inter-specific competition (Huston 1998, Skagen 2006, Newton 2008). Food acquisition, in particular, is essential during migration, and long distance movements of migratory birds would not be possible without deposition of extensive fat stores (Huston 1998, Lindström 2007, Covino & Holberton 2011). The rate of foraging, energy acquisition during fuel deposition, and composition of avian food sources are therefore key components in the understanding of bird migration (McNamara *et al.* 1994, Lindström 2007, Newton 2008).

The Upland Sandpiper (*Bartramia longicauda*) is a Nearctic Neotropical 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, Blanco & López-Lanús 2008, Casey et al. 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 & Lopez-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 km^2 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 hians*, *Stipa charruana*, *Aristida venustula*, *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.

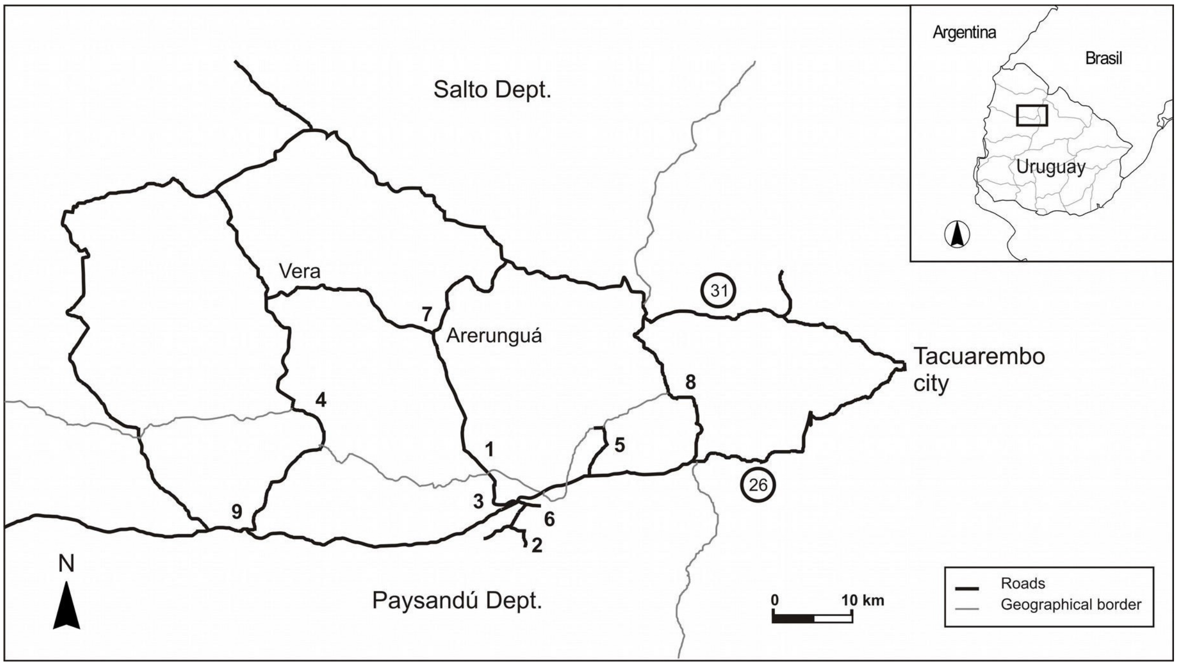

FIG. 1. Map of Uruguay showing the Northern Campos ecoregion and the borders of Salto, Paysandú, and Tacuarembó Departments. Numbers indicate the field sites where feces of Upland Sandpipers were collected: 1 = Valdéz, 2 = Ramos, 3 = Cilindro, 4 = Venados, 5 = Sarandí, 6 = Cabrera, 7 = Arerunguá, 8 = Haedo, and 9 = Wilson.

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: $\beta = 1 - (1 - \mathrm{F})^{n}$, where β 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 norther Uruguay: Arerunguá (N = 1), Cabrera (N = 6), Cilindro (N = 10), Haedo (N = 2), Ramos (N = 6), Sarandí (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, elytrae, 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 unidentified 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 27 mm, grasshoppers being the largest prey items (Table 1).

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 (the white-fringed beetle, *Naupactus* sp.) appeared in the center of the graph because this insect was consumed homogeneously throughout the four seasons (Fig. 2). Plant rests found in the diet included remains of grass leaves and whole seeds and were always together with arthropods. Seeds were identified as grasses (Poaceae). Stones found in feces were ~ 3 mm diameter and varied in number from 4 to 10 per feces.

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.

ITEMS		FREQUENCY OF OCCURRENCE				MPZ (mm)	SOURCE
		2008–2009	2009–2010	2010–2011	2012–2013		
		N = 16	N = 11	N = 13	N = 27		
INSECTA	unidentified	0.19	0.08	0.38	0.08		
Orthoptera	unidentified	0.06		0.08	0.24		
Acrididae	unidentified	0.31	0.23	0.69	0.16		
	Borellia bruneri	0.75	0.85	0.31	0.16	23	This study
	Dichroplus elongatus	0.06				27	Bentancur & Scatoni 2010
	Dichroplus pratensis	0.25	0.08			27	Bentancur & Scatoni 2010
	Ronderosia sp.	0.25	0.78	0.15	0.2	27	Bentancur & Scatoni 2010
TOTAL		0.94	1	0.85	0.56		
Coleoptera	unidentified	0.06		0.46	0.16		
Curculionidae	unidentified				0.12		
	Naupactus sp.	0.63	0.69	0.46	0.6	14	Arnett et al. 2002
Carabidae	unidentified			0.08	0.08		
Tenebrionidae	unidentified			0.08	0.28		
TOTAL		0.75	0.77	0.77	0.88		
Himenoptera	unidentified				0.08		
Formicidae	unidentified			0.23	0.19		
	Camponotus sp.		0.27	0.54	0.59	13	Arnett 2000
	Acromyrmex sp.				0.04	10	Soares et al. 2010
	Ectatomma sp.			0.23	0.07	9	Schatz & Wcislo 1999
TOTAL			0.27	0.69	0.8		
Isoptera							
Termitidae	unidentified			0.15	0,2	10	Arnett 2000
TOTAL				0.15	0.2		
Hemiptera	unidentified				0.04		
Cydnidae	unidentified				0.04	20	Henry 2009
TOTAL					0.04		
ARACNIDA							
Araneae	unidentified				0.08	25	Aisenberg et al. 2011
TOTAL					0.08		

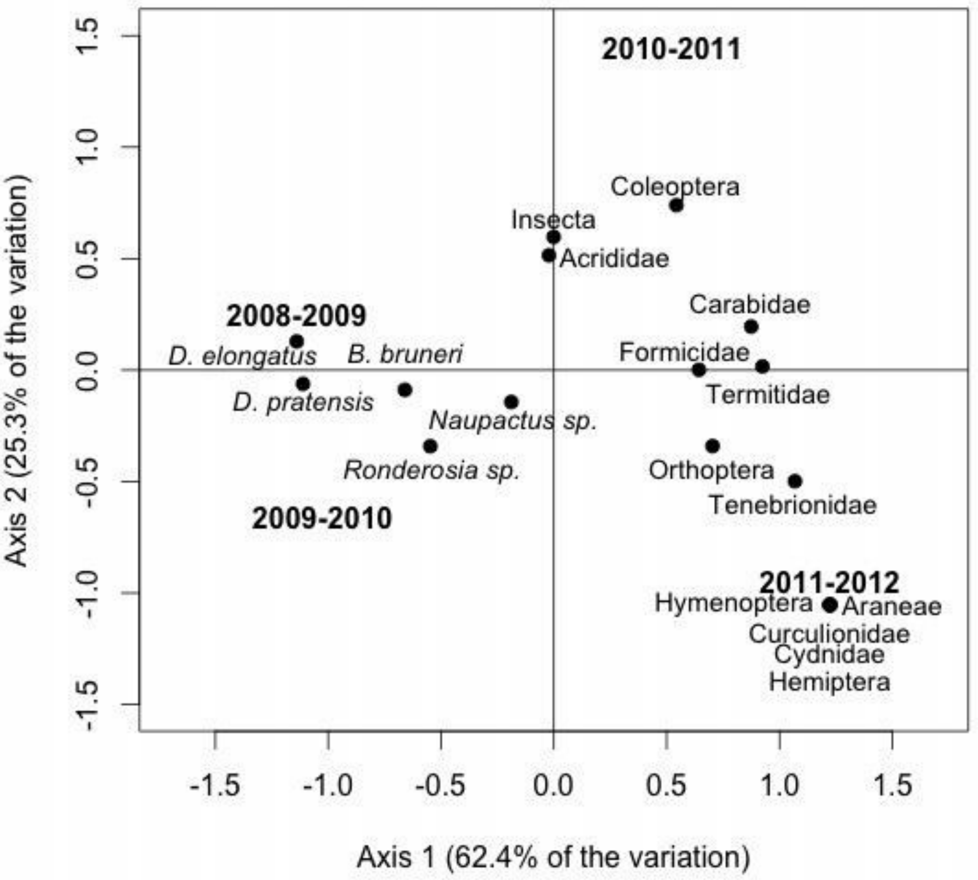

FIG. 2. First two components (Axis 1 and Axis 2) of a Canonical Correspondence Analysis showing temporal variation of food items in the diet of Upland Sandpipers in Uruguay, 2008–2012.

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).

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 suggests 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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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

Survival of migratory birds depends mainly on resource abundance and availability, climatic conditions, predation pressure, habitat availability and intra- and inter-specific competition (Huston 1998, Skagen 2006, Newton 2008). Food acquisition, in particular, is essential during migration, and long distance movements of migratory birds would not be possible without deposition of extensive fat stores (Huston 1998, Lindström 2007, Covino & Holberton 2011). The rate of foraging, energy acquisition during fuel deposition, and composition of avian food sources are therefore key components in the understanding of bird migration (McNamara *et al.* 1994, Lindström 2007, Newton 2008).

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 & Lopez-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 km^2 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,

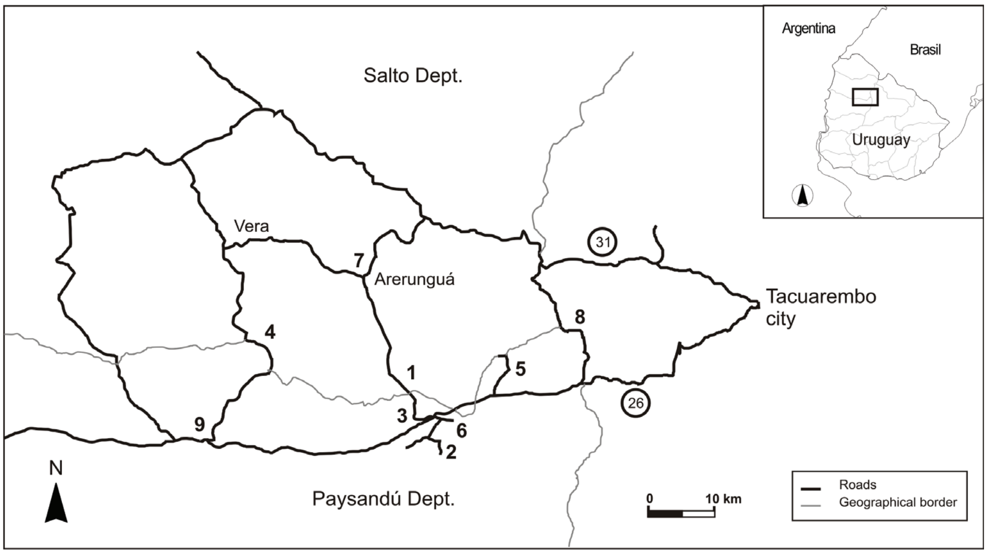

FIG. 1. Map of Uruguay showing the Northern Campos ecoregion and the borders of Salto, Paysandú, and Tacuarembó Departments. Numbers indicate the field sites where feces of Upland Sandpipers were collected: 1 = Valdéz, 2 = Ramos, 3 = Cilindro, 4 = Venados, 5 = Sarandí, 6 = Cabrera, 7 = Arerunguá, 8 = Haedo, and 9 = Wilson.

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 hians*, *Stipa charruana*, *Aristida venustula*, *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 β 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 norther Uruguay: Arerunguá (N = 1), Cabrera (N = 6), Cilindro (N = 10), Haedo (N = 2), Ramos (N = 6), Sarandí (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, elytrae, 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 unidentified 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.

ITEMS		FREQUENCY OF OCCURRENCE				MPZ (mm)	SOURCE
		2008–2009 N = 16	2009–2010 N = 11	2010–2011 N = 13	2012–2013 N = 27		
INSECTA	unidentified	0.19	0.08	0.38	0.08		
Orthoptera	unidentified	0.06		0.08	0.24		
Acrididae	unidentified	0.31	0.23	0.69	0.16		
	Borellia bruneri	0.75	0.85	0.31	0.16	23	This study
	Dichroplus elongatus	0.06				27	Bentancur & Scatoni 2010
	Dichroplus pratensis	0.25	0.08			27	Bentancur & Scatoni 2010
	Ronderosia sp.	0.25	0.78	0.15	0.2	27	Bentancur & Scatoni 2010
TOTAL		0.94	1	0.85	0.56		
Coleoptera	unidentified	0.06		0.46	0.16		
Curculionidae	unidentified				0.12		
	Naupactus sp.				0.6	14	Arnett *et al.* 2002
Carabidae	unidentified	0.63	0.69	0.46	0.08		
Tenebrionidae	unidentified			0.08	0.28		
TOTAL				0.08	0.88		
Himenoptera	unidentified	0.75	0.77	0.77	0.08		
Formicidae	unidentified				0.19		
	Camponotus sp.			0.23	0.59	13	Arnett 2000
	Acromyrmex sp.		0.27	0.54	0.04	10	Soares *et al.* 2010
	Ectatomma sp.				0.07	9	Schatz & Wcislo 1999
TOTAL				0.23	0.8		
Isoptera			0.27	0.69			
Termitidae	unidentified				0,2	10	Arnett 2000
TOTAL				0.15	0.2		
Hemiptera	unidentified			0.15	0.04		
Cydnidae	unidentified				0.04	20	Henry 2009
TOTAL					0.04		
ARACNIDA							
Araneae	unidentified				0.08	25	Aisenberg *et al.* 2011
TOTAL					0.08		

27 mm, grasshoppers being the largest prey items (Table 1).

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

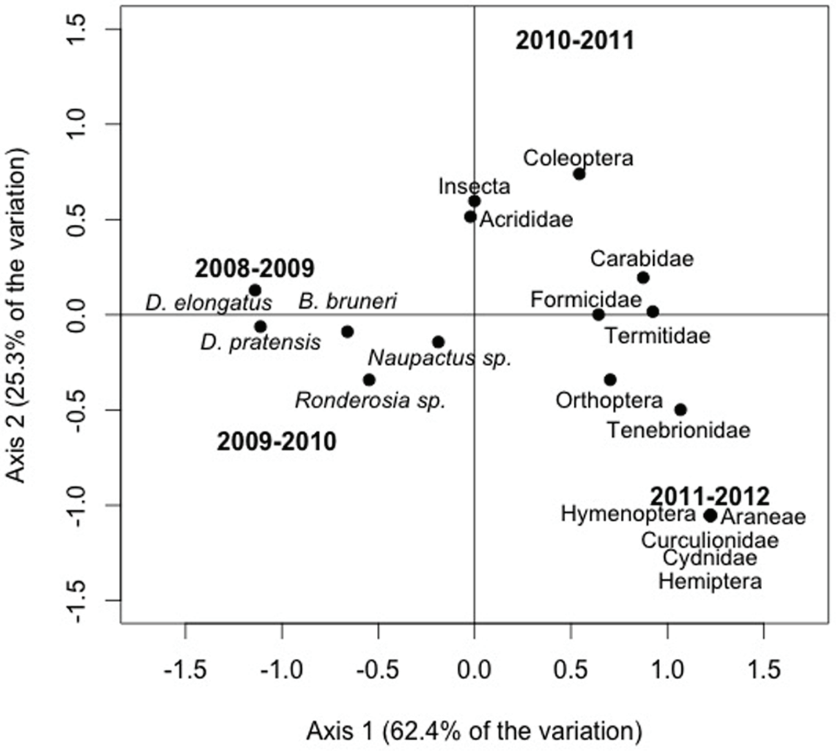

FIG. 2. First two components (Axis 1 and Axis 2) of a Canonical Correspondence Analysis showing temporal variation of food items in the diet of Upland Sandpipers in Northern Campos, Uruguay, 2008–2012.

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).

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 suggests 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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CAPÍTULO 3. FACTORS AFFECTING SPACE USE OF UPLAND SANDPIPERS AT NON-BREEDING GROUNDS

FACTORES QUE AFECTAN EL USO DEL ESPACIO POR EL BATITÚ EN LAS ÁREAS NO REPRODUCTIVAS.

Fotos: Luciano Liguori

FACTORS AFFECTING SPACE USE OF UPLAND SANDPIPERS AT NON-BREEDING GROUNDS

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RUNNING HEAD: SPACE USE OF NON-BREEDING UPLAND SANDPIPERS

ABSTRACT. Migratory birds select patches of habitat during migration and in the breeding and non-breeding seasons. In grassland species, patch selection is determined by features of vegetation that are probably associated with food resources or predation risk. Our field study focuses on habitat preference and space use of a long distance migratory bird, the Upland Sandpiper (*Bartramia longicauda*), during the non-breeding season within Northern Campos of Uruguay. We evaluated patterns of space use with the hypothesis that local conditions of food availability and predation risk in grasslands managed by different grazing activities and agriculture determine bird preferences for different vegetation conditions and social interactions in flock size. Our field study was conducted in an extensive area of private grasslands managed mainly for livestock production. During four non-breeding seasons, we recorded 544 observations of birds in the field, and we captured and monitored 62 birds. Upland Sandpipers mainly preferred native grasslands associated with shallow and rocky soils, and intermediate vegetation cover for feeding. At a patch scale, sandpipers used low to intermediate levels of vegetation height and cover in native grasslands, but we foundno relationship between habitat use and flock size. The vegetation configuration of disturbed pastures could offer open spaces that are good for prey detectability with spread stands for protection. Low to moderate livestock production provides habitats of different vegetation height and cover in large areas and allows the co-existence of species with different habitat requirements. The amount of suitable habitat at managed grasslands and levels of fragmentation are important determinants of the distribution and abundance of populations of grassland birds, and should be managed considering habitat preferences of grassland birds. Our research contributes new information for the conservation of migratory species of grassland birds and for the creation of protected areas at non-breeding sites in South America.

Keywords: group size, habitat preference, migratory bird, vegetation height.

INTRODUCTION

Habitat preferences and space use are important features for describing a species' biological requirements, ecological interactions, and for setting priorities for conservation areas (Rosenzweig 1981, Masse et al. 2014, Leclerc et al. 2016). Animals use heterogeneous environments at different spatial scales, from the species' geographic range to individual's home range (Aebischer et al. 1993, Mysterud and Ims 1998, Jedlikowski et al. 2016). Consequently, a complete understanding of habitat use should consider the evaluation of patterns and processes at multiple spatial scales (Johnson 1980, Mysterud and Ims 1998). On the other hand, human activities related to land use such as agriculture, afforestation and livestock grazing are producing large changes on many features of landscape structure (Brennan and Kuvlesky 2005, Baldi and Paruelo 2008, Ribic et al. 2009, Isacch and Cardoni 2011, Azpiroz et al. 2012). Land-use and land-cover change likely impact migratory species that use suitable features of the landscape to orient during migration and to find specific sites during migration and at breeding and non-breeding grounds (Huston 1998, Lindström 2007).

Migratory birds use a variety of geographic areas during migration, selecting stopover sites and stationary areas for reproduction or feeding periods depending on local environmental conditions and an individual's energetic demands (Huston 1998, Lindström 2007). During patch selection, birds typically respond to food resources and predation risk, by engaging in behaviors that balance the benefits of feeding with the cost of predation risk (McArthur and Pianka 1966, Lima and Dell 1990, Lima and Bednekoff 1999). The spatial distribution of individuals within a site may depend on the distribution of the food abundance and predation risk which also vary spatially or temporally, and depend on structural characteristics of suitable habitats (Pomeroy 2006, Masse et al. 2014, Jedlikowski et al. 2016). Further, resource availability, competition and predation, could also determine the space use at smaller spatial scales such as the home range or microhabitat selection (Rosenzweig 1991, Aebischer et al. 1993, Lima 1993, Bayer et al. 2010, Beerens et al. 2015).

Migratory birds use high feeding rates to acquire the energy reserves for migration while avoiding their predators (Huston 1998, Lindström 2007). To achieve high feeding rates, most species of migratory birds increase flock size as an anti-predator behavior to increase the probability of predator detection and reduce the probability of being attacked if detected (Myers 1980, Cresswell 1994, Lima 1995, Barbosa 1997, Whitfield 2003, Pomeroy 2006). The many-eyes hypothesis states that as group size increase, in socially foraging animals, there are progressively more eyes scanning the environment for predators (Lima 1995, Olson et al. 2015). Therefore, individuals foragers can allocate more time to feeding as group size increases (Lima and Dell 1990, Lima 1995). For social animals, changes in risk due to changes in group size have been widely reported (Quenette 1990, Hunter and Skinner 1998, Lima and Bednekoff 1999, Burger et al. 2000). Predation risk could also have large variation over short time periods, and the risk allocation hypothesis states that optimal antipredator behavior in a given situation depends on the temporal and spatial context in which risk varies (Myers 1980, Lima and Bednekoff 1999). In this sense, depending on time and spatial structure, animals can opt to be solitary or join a group, and use the protection of the habitat or not (Lima 1990, Burger et al. 2000, Kullberg and Lafrenz 2007)

Our field study focuses on habitat preference and space use of a long distance migratory bird, the Upland Sandpiper (*Bartramia longicauda*), during the non-breeding season at northern grasslands of Uruguay. Previous efforts have mapped the distribution of birds at the non-breeding grounds (White 1988, Blanco & López-Lanús 2008). Upland Sandpiper feeding strategies consist of an active search of the ground with visual prey detection and a run-and-peck behavior similar to plovers (Charadriidae) (Houston & Bowen 2001, Alfaro et al. 2015). At breeding grounds habitat preferences are related to foraging mode, birds using sites with shortvegetation height for feeding

(Dechant et al 1999, Fritcher et al. 2004, Powell 2006, Sandercock et al. 2015, Ahlering and Merkord 2016). Forage in grazed sites with short grass probably allow sandpipers easier movement and more efficient prey detection in open habitats (Sandercock et al. 2015). On the other hand, vegetation height and density may offer protection to sandpipers while feeding but could also reduce prey and predator detection (Metcalfe 1984,Colwell and Dodd1995)At non-breeding grounds, community surveys suggested that the Upland Sandpipers could be associated with intermediate values of vegetation patchiness in grazed grasslands (Azpiroz et al. 2012, Azpiroz and Blake 2016). Habitat use and selection of Upland Sandpipers at non-breeding grounds remain poorly understood. The Northern Campos of Uruguay exhibits a mosaic of different vegetation height and density determined by soil characteristics, livestock grazing, and agricultural activities (Lezama et al. 2006; 2011, Baeza et al. 2009; 2011). Understanding habitat requirements is particularly important considering the large changes in landcover that have taken place at the non-breeding areas (Isacch and Cardoni 2011, Azpiroz and Blake 2016).

Most native grasslands have been modified by agriculture, afforestation and cattle grazing (Tilman et al. 2001, Ramankutty and Foley 1999, Baldi and Paruelo 2008). Many of these anthropogenic landscapes can change fast, making configurations of the landscape different from that of native grasslands grazed by native herbivores with changes in the abundance and persistence of local plant and animal populations (Fahrig and Merriam 1994, Galetto et al. 2007, Baldi and Paruelo 2008). In our field project, we evaluated the habitat preferences and space use of Upland Sandpipers at non-breeding grounds and consider the possible consequences of human activities on the spatial ecology of sandpipers. Within this context, we investigated associations between species occurrence and flock size with the vegetation height and cover, which are determined by soil characteristics, and the changing cattle and agriculture activities. Thus, we attempt to contribute to the understanding of the connection between land use and the ecology of migratory birds. Considering the specific mechanisms for this connection, we hypothesized that local conditions related to food availability and predation risk likely determine bird preferences for different vegetation height and cover and flock size. Consequently, short vegetation grasslands and isolated foraging would be the preferred strategy if acquisition of food resources is the only limiting factor. However, tall vegetation and large flocks may be selected if predation risk becomes important. If space use results in a tradeoff between food detection and predation risk, then birds are predicted to use grasslands with intermediate levels of vegetation height and cover, which offers open space for prey detectability but also some cover for protection.

METHODS

Study System

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 ~ 1,800 km^2 inside Salto and Paysandú Departments (Figure 1). The area is part of the Northern Campos ecoregion of Uruguay, close to the Haedo Ridge and included in the Basaltic region, which is characterized by slightly rolling topography with rocky and shallow soils (Altesor et al. 2005, Lezama et al. 2006, Baeza et al. 2009, Azpiroz and 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. The vegetative community is mainly composed by native grasses including *Piptochaetium montevidense*, *Botriochloa laguroides*, *Richardia humistrata*, *Wahlenbergia linarioides*, *Baccharis coridifolia*, *Andropogon lateralis*, *Panicum hians*, *Portulaca papulosa*, *Hordeum pusillum*, *Selaginella sellowii*, and *Paspalum dilatatum* (Lezama et al. 2006; 2011, 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 grains and other crops, including rice, barley, sorghum, wheat, sunflower, and soybeans (Baeza et al. 2009, Azpiroz et al. 2012).

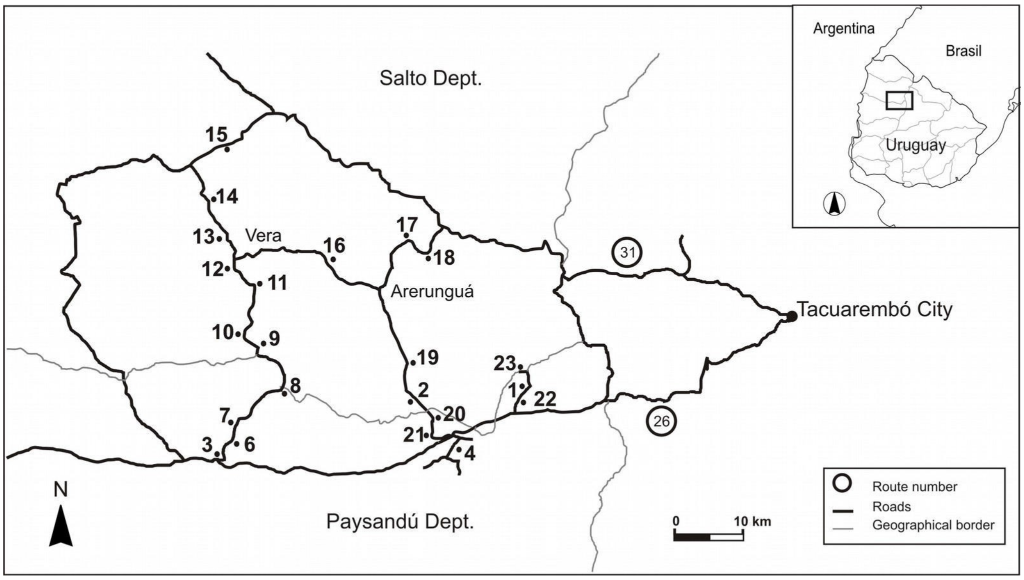

Figure 1. Map of the study area in the Northern Campos, showing sites (numbers) where Upland Sandpipers were recorded. Descriptions of each site are in Table S1 of Supplemental Material.

The Upland Sandpiper is a migratory species of shorebird that uses native grasslands and occasionally croplands at both the breeding and non-breeding grounds (Houston & Bowen 2001, Blanco & Lopez-Lanús 2008, Azpiroz et al. 2012). Their diet includes grasshoppers, ground beetles, and other small arthropods that are captured with a run-stop-search mode of foraging (Houston & Bowen 2001, Alfaro et al. 2015). In Uruguay, Upland Sandpipers are distributed at inland sites throughout the country, but they are more frequently observed in the Northern Campos ecoregion (Blanco & López-Lanús 2008, Azpiroz and Blake 2009, Azpiroz et al. 2012). There is no information about predators of Upland Sandpipers in South America, but at breeding areas in North America foxes, mesocarnivores and raptors have been reported as predators of eggs, chicks and adults (Houston & Bowen 2001, Sandercock et al. 2015). Possible diurnal predators observed at our study areas in Uruguay included foxes (*Cerdocyon thous* and *Lycalopex gymnocercus*), Swainson´s Hawk (*Buteo swainsoni*), White-tailed Hawk (*Geranoaetus albicaudatus*), Savanna Hawk (*Buteogallus meridionalis*), Crested Caracara (*Caracara plancus*), Long-winged Harrier (*Circus* *buffoni*), Cinereous Harrier (*C. cinereus*), Aplomado Falcon (*Falco femoralis*) and Black-chested Buzzard-Eagle (*Geranoaetus melanoleucus*). Other grassland shorebirds regularly observed in our study area during the austral summer included the American Golden-Plover (*Pluvialis dominica*) and the Buff-breasted Sandpiper (*Tryngites subruficollis*) (Azpiroz and Blake 2009, Azpiroz et al. 2012, Alfaro et al. 2015).

Habitat Preferences and Space Use

Our field study was conducted during four austral spring and summer seasons between mid-November to late February from 2008 to 2012. We collected non-breeding records of Upland Sandpipers at different spatial scales within the Northern Campos with the aim to analyze habitat preference in relation to habitat availability and microhabitat use at sightings. At a regional level, we recorded 23 opportunistic sightings of Upland Sandpipers while driving on rural ranch roads exploring for sites for a focal population study (Figure 1, Supplemental Material Table S1). Depending on the presence of birds, logistics of access, and by land owner permission, we selected four ranches to capture, radio-mark and monitor sandpipers during the non-breeding season: Sarandi Ranch, Valdéz Ranch, Wilson Ranch, and Ramos Ranch (Figure 1). All ranches corresponded to farms used for livestock grazing and all had similar communities of native grasses. At each location of radio-marked birds or opportunistic sighting records, we collected information about individual microhabitat selection and aggregation in order to test our space-use hypothesis.

We measured habitat preferences from the presence of birds observed at different vegetation units in relation to proportion of vegetation available at three spatial scales: i) the regional scale, which was limited by the whole set of individual sightings observed, ii) the four ranches used for focal population studies, which represented internal heterogeneity of the study area (e.g., land use, vegetation cover) and were limited by the set of individuals captured at our focal sites, and iii) within individual's home ranges of radio-tagged birds. We used a vegetation map of the Basaltic region to measure the different types of vegetation available in our study area at three spatial scales (Baeza et al. 2011). The habitat map was based on a previous characterization of vegetative communities (Lezama et al. 2006, 2011), and a recent vegetation map (Baeza et al. 2009). To analyze Upland Sandpiper habitat preferences in the Northern Campos, we plotted points in the vegetation map of the Basaltic region using the Program QGIS (Open Source Geographical Information System) (Quantum GIS Development Team 2015).

According to Baeza et al. (2011), native grasslands covered 91% of the 2.8 million hectares in the Northern Campos ecoregion. The authors categorized native grasslands into two main strata: B1 (36%) and B2 (56%). The rest of the area consisted of agriculture (5%), planted forest (1%), native forest (2%), and water (0.1%) (Baeza et al. 2011). The B1 strata included open grasslands with short vegetation cover on shallow soils: the meso-xerophytic grasslands and the lithophytic steppes over rocky outcrops. The meso-xerophytic grasslands have a low herbaceous layer (5-10 cm) of grasses and forbs, and a height strata (~ 30 cm) dominated by erect grasses and the shrub *Braccharis coridifolia.* The lithophytic steppes are mainly one low stratum (5-10 cm) dominated by a spike moss, *Selaginella sellowii* (Baeza et al. 2009). In contrast, the B2 strata included dense meso-hydrophytic grasslands with high vegetation cover on deep soils. The meso-hydrophytic grasslands have one low stratum of prostrate grasses (< 5 cm) and a taller canopy of erect grasses (≥ 30 cm) (Baeza et al. 2009, M. Alfaro, pers. obs.).

To determine the local limits of individual home ranges, vegetation height and cover used and flocking behavior, we captured and monitored birds at each of four ranches. Birds were captured at roosting sites during the night using high-powered spotlights and a long-handled dip net. We individually marked sandpipers with a numbered metal band and a unique combination of colored leg bands. We also marked all birds with small 3.8 g VHF radio transmitters attached to the back with an elastic leg-loop harness (model PD-2, Holohil Systems, Carp, ON), a method known to have effective radio retention and high seasonal survival on Upland Sandpipers (Mong and

Sandercock 2007). We used portable radio receivers (R2000, ATS, Isanti, MN) to relocate and approach radio-tagged birds on foot every one to seven days. At each sighting, we recorded the number of birds seen with the marked bird (group size), the UTM coordinates, the vegetation height and the percentage of vegetation cover of shorter and higher stratum. We also record all these measurements at the 23 opportunistic sightings recorded during roadside surveys at a regional scale.

An adult Upland Sandpiper standing upright is ~ 30 cm tall (M. Alfaro, pers. obs.), so we separated vegetation height at each sighting in two strata, grasses shorter or higher than 30 cm. We measured vegetation height of the shorter and higher strata to the nearest centimeter, taking two measurements at each strata, the highest and shorter in grasses higher than 30 cm (high strata) and the highest and shortest in grasses shorter than 30 cm (short strata). Percentage of each strata was determined within a radius of 20 m from the sighting.

Statistical Analyses

At each spatial scale, we estimated the area occupied by the different land covers within the individuals' minimum convex polygon (MCP) determined locations of radio-marked birds. Program QGIS was used for all calculations (Aebischer et al. 1993). We grouped vegetation strata in five categories as follow: B1 and B2 (native grasslands cf. Baeza et al. 2011), AG (agricultural lands), F (forested patches of exotic trees for cattle refuge) and O (others, native forest and water). Preference for each vegetation unit was evaluated contrasting the observed use of different land cover classes with their availability with a *G*-test (Sokal and Rohlf 1995). Specifically, the *G*-test compared the observed numbers of individuals using each land covers with the expected counts if individuals are distributed along land covers proportional to its availability (Sokal and Rohlf 1995). Results are expressed as the $\log_{10}$ of the ratio between observed and expected frequency of landcover use. The log-ratio is expected to be zero if birds use the strata in the same proportion that it is available, positive if land use is higher than available, and negative if a strata is avoided We used the mean and the standard deviation to expressed results of individual's MCP size.

For the analysis of habitat use at each sighting, we calculated the mean vegetation height of the site and then, using the coverage, the mean weighted vegetation height with the following equation: [(hsts x covsts)+ (hsth x covsth)] / 100, where *hsts* and *covsts* are the mean vegetation height and percentage of vegetation cover of the shortest strata (grasses shorter than 30 cm), and *hsth* and *covsth* are the mean vegetation height and the percentage of vegetation cover of the highest strata (grasses higher than 30 cm). To explore the vegetation height-cover most frequently used, we calculated the frequency of occurrence as the number of times birds were observed at intervals of one mean weighted vegetation height. The mean weighted vegetation height is a measure of habitat heterogeneity in wich low numbers means mostly of short grass, height numbers mostly tall grass and intermediate numbers means different intermediate levels of heterogeneity.

The first prediction of our hypothesis suggests a negative linear relationship between the frequency of occurrence and the vegetation height-cover (mean weighted vegetation height), when the foraging is not limited by the predation risk. A second prediction suggests a positive linear relationship between the frequency of occurrence and the vegetation height-cover, but a negative linear relationship between the group size and the vegetation height-cover because of reduced predation risk in tall and dense vegetation. A third prediction, considering a possible tradeoff between foraging and predation risk, predicts a quadratic relationship between the frequency of occurrence and the vegetation height-cover. We tested the alternative predictions using generalized linear models (GLM) linked to Poisson distribution because our response variable was count data (Zuur et al. 2009). Frequency of occurrence and group size were treated as the response variables, and vegetation height and its quadratic value were the explanatory variables. The addition of a quadratic term allowed detection of nonlinear relationships predicted by our working hypothesis. Linear or quadratic models were selected as candidate models based on minimum values of Akaike's

Information criterion corrected for small sample size (AICc, Zuur et al. 2009). All models and statistical analysis were performed using base functions and the vegan package of R software (www.r-project.org/).

RESULTS

During 2008 to 2012, we recorded a total of 544 sightings (120, 186, 72 and 166 at each season respectively) of radio-tagged birds and occasional sightings of Upland Sandpipers feeding or resting in the study area in the Northern Campos (Basaltic Region) of Uruguay. At four capture sites, we radio-marked a total of 62 individuals, 15 birds in the 2008-2009 season, 20 in 2009-2010, 9 in 2010-2011 and 18 in 2011-2012 (see Supplemental Material Table S2). Number of sightings per individual varied between 1 to 18 records. Marked individuals were monitored during all the season except in two cases in which the VHF radio failed (individual 30257) or if the harness failed and the bird dropped the radio (individual 30243).

Habitat Preference at Three Spatial Scales

Estimation of the MCP was conducted at each of the three spatial scales: regional, ranches and individual home ranges, and the proportion of vegetation available was calculated at each scale (Tables S3 and S4 of Supplemental Material). The ratio of vegetation available and used in the regional scale showed that sandpipers used more B1 strata (meso-xerophytic grasslands and lithophytic steppes with low vegetation cover) than expected by the proportion available, but less B2 (meso-hydrophytic grasslands with dense vegetation cover), AG (agricultural lands) and F (forested sites) than expected, and not other (O) vegetation unit (Figure 2). Results of the *G*-test showed that proportion of vegetative strata used at the regional scale ($n = 544$ sightings) were statistically different from the proportion of vegetation available ($n = 97,864$ pixels), birds used more B1 grasslands than expected by availability ($G = 43.9$, df = 4, $P < 0.001$) (Figure 2). Availability of vegetation units at a regional scale versus used inside each ranch showed significant differences, with birds using more B1 grasslands at all ranches, except at Valdez where birds used the B2 and AG strata more than expected (Figure 3). However, when comparing availability of vegetation units versus used at the spatial scale of ranches, none showed statistical differences except Ramos and Valdez ranches where birds use more B1 grasslands than expected: Sarandí (G = 7.3, df = 4, P = 0.12), Wilson (G = 7.8, df = 4, P = 0.09), Valdez (G = 9.4, df = 4, P = 0.05), Ramos (G = 11.3, df = 4, P < 0.05) (significant level ≤ 0.05).

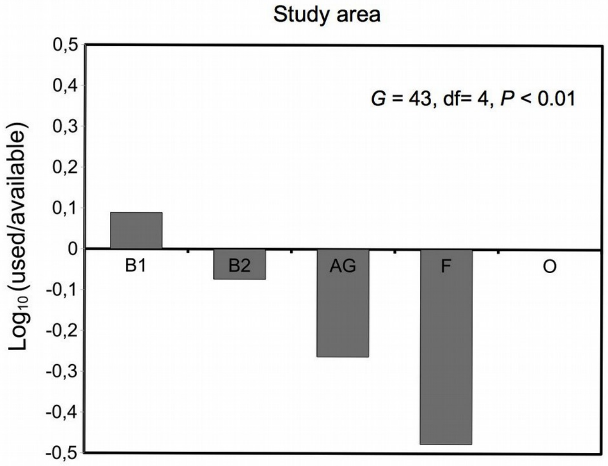

Figure 2. Proportions of vegetation used vs available ($\log_{10}$(used/available)) at a regional scale in the Northern Campos, Uruguay. Strata included:B1: meso-xerophytic grasslands and the lithophytic steppes, B2: meso-hydrophytic grasslands, AG: agricultural lands with cultivated crops, F: forested sites and O: others. Results of the G test comparing vegetation used and available are show inside each graph.

Of 62 sandpipers captured, we estimated MCP from birds with 15 or more visual resightings, to ensure accurate home range size estimates (Seaman et al. 1999, Singer et al. 2015): one at Sarandi, six at Valdez and two at Ramos (Supplemental Material Table S4). The area MCP for individual Upland Sandpipers during the non-breeding season were relatively small, and ranged between 38.6 ha to 149.8 ha (mean = 90.7 ± 39.6, n = 9). When comparing habitat availability at these three ranches versus use inside the nine individual's MCP, three individuals (two at Valdez and one at Ramos) showed significant differences, using more B1 grasslands than expected (Supplemental Material Table S5). The other three individuals at Valdez ranch showed no significant differences between proportions of habitat that wereavailable vs. used, using more B2 grasslands (Supplemental Material Table S5).

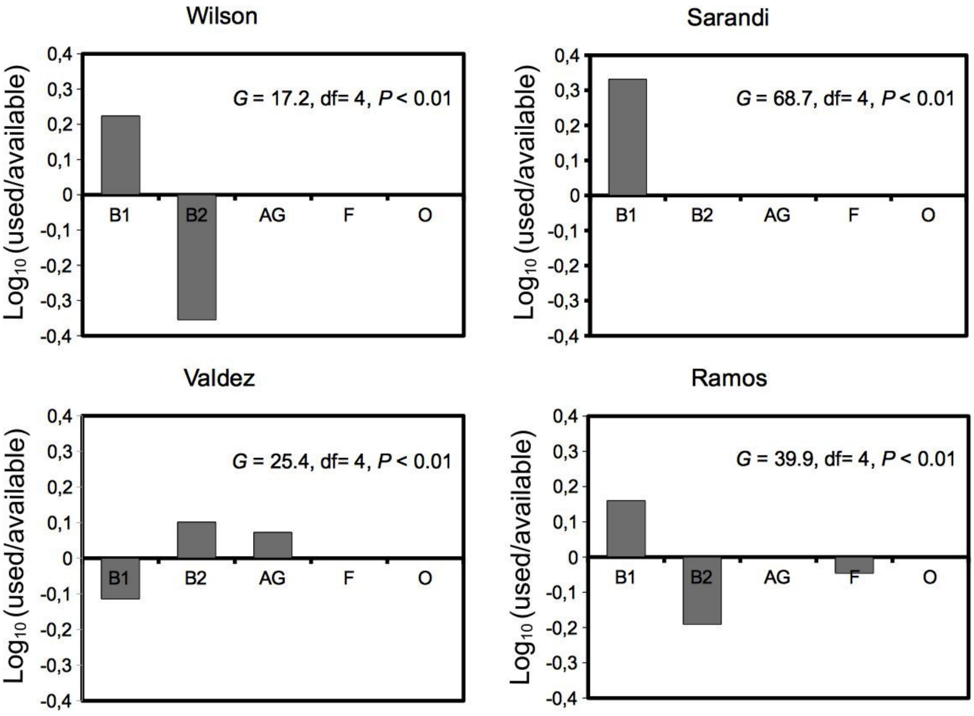

Figure 3. Proportion of habitat strata used at each ranch vs available ($\log_{10}$(used/available)) at the regional scale in the Northern Campos, Uruguay. B1: meso-xerophytic grasslands and the lithophytic steppes, B2: meso-hydrophytic grasslands, AG: agricultural lands, F: forested sites and O: others. Results of the G test comparing vegetation used and available are show inside each graph.

Spatial Usage at Individual Sightings

Vegetation height used by the Upland Sandpipers at each sighting varied between 3 to 150 cm (*n* = 328), but the most frequently used heights (48% of the records) were between 10 to 20 cm in mean weighted vegetation height (Figure 4), which represent a mean vegetation height varying between

6.5 to 50 cm and a coverage varying between 50 to 90% of the short strata and 10 to 50% of the high strata. The used percent of vegetation cover of the high strata varied between 0 to 100 (*n* = 338), with 2% of individuals observed using grasslands with less than 10% of high strata, 94% between 10 to 50%, and 4% between 60 to 100%. Our results indicated birds mainly used low to intermediate vegetation cover. At Ramos ranch, we occasionally observed sandpipers roosting in the shade of a group ofeucalyptus trees. This behavior was recorded twice during midday when temperatures were around 40 °C. At Valdez ranch, some birds were observed using artificial grasslands (sorghum and ray-grass). We also observed that in 27% of the cases birds were alone, 62% were in small groups (2 to 20) and 8% of records were larger flocks of >20 birds (*n* = 544) (Figure 5).

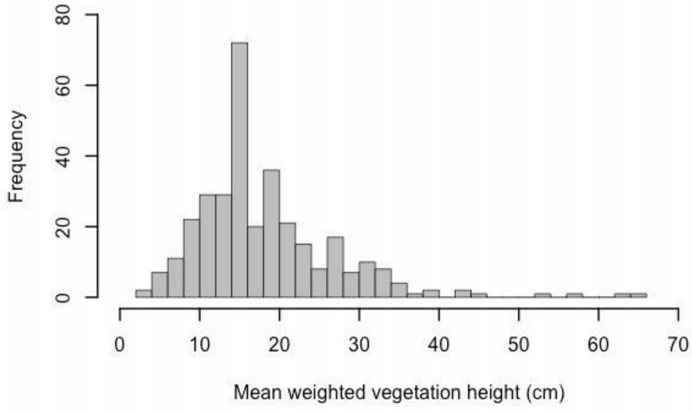

Figure 4. Frequency distribution of the vegetation height used by Upland Sandpipers in the Northern Campos, Uruguay (*n* = 328 observations).

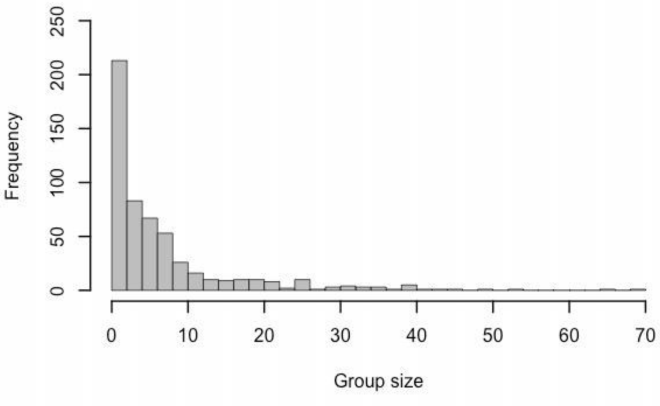

Figure 5. Frequency distribution of Upland Sandpiper's group size in the Northern Campos, Uruguay (*n* = 544 observations).

The generalized linear model for occurrences ofUpland Sandpipers in Uruguay included vegetation height-cover in a quadratic relationship, and outperformed the linear model as an alternative (ΔAIC= 2123; Fig. 6). The quadratic model accounted for 42% of the variation in sandpiper occurrence (Fig. 6). Our results suggest that birds frequently used grasslands with intermediate levels of vegetation height-cover. We found no relationship between group size and the vegetation height-cover (pseudo R^2= 0.01).

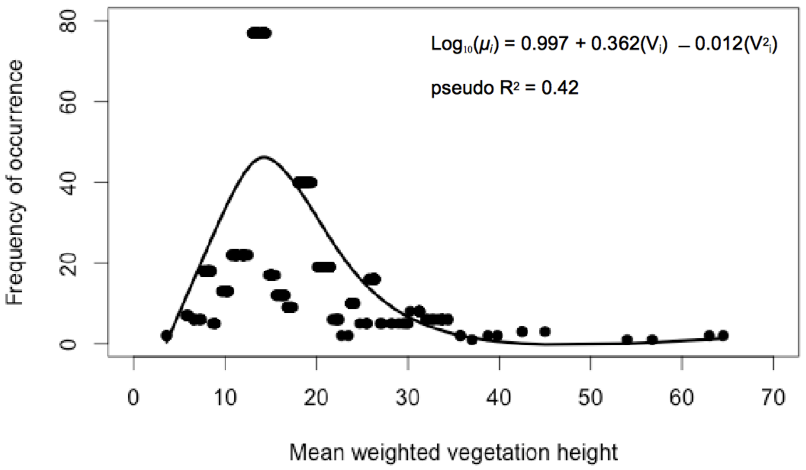

Figure 6. Effects of vegetation height and cover on the occurrence of Upland Sandpipers living in managed grasslands of the Northern Campos of Uruguay. V is the mean weighted vegetation height and μ_i is the mean of the frequency of occurrence.

DISCUSSION

Our field study investigated the habitat preferences of Upland Sandpipers at non-breeding sites in the Northern Campos of Uruguay and the possible mechanisms involved in patch selection for feeding. The managed grasslands of the Northern Campos offers a heterogeneous matrix of different vegetation configurations including agriculture and cattle with different grazing intensities (Lezama et al. 2006; 2011, Baeza et al. 2009; 2011). Within this habitat matrix and at three different spatial scales, birds mainly prefer native grasslands associated with shallow and rocky soils and low to intermediate vegetation cover (B1 grasslands). At a patch scale, sandpipers also used low to intermediate levels of vegetation height and cover. The prefered type of vegetation structure is available in native grasslands managed with moderate livestock production (Azpiroz et al. 2012, Azpiroz and Blake 2016). Such vegetation configuration could offers open spaces good for prey detectability and spread stands for protection. Our results support the assumption of a tradeoff between the needs of feeding and the cost of predation risk (McArthur and Pianka 1966, Lima and Dell 1990, Lima and Bednekoff 1999). Upland Sandpiper home ranges were variable in size, but we could not obtein the minimum number of locations (>20) needed for a Kernel estimates of home range size (Seaman et al. 1999, Singer et al. 2015). Estimates of home range area based on MCP are generally biased high compared to Kernel methods (Seaman et al. 1999, Singer et al. 2015). Nevertheless, at breeding sites in Kansas, Upland Sandpiper home ranges estimated with kernel methods were about 10 times larger (ca. 8.4 km^2) than our estimates of range size for non-breeding birds in Uruguay (Sandercock et al. 2015), possibly indicating that space requirements were small and food resources were more abundant at non-breeding sites.

Animals are able to detect and respond to temporal variation in the risk of predation, which determines their antipredator decisions like flocking or using vegetation cover for protection, as stated in the risk allocation hypothesis (Lima and Bednekoff 1999). At breeding sites, Upland Sandpipers have large area requirements and use habitat with short vegetation for feeding, but build their ground nests in sites with tall vegetation for concealment(Ailes 1980, Ailes and Toepfer 1977, Bowen and Kruse 1993, Vickery et al. 1994, Klemek 2008, Garvey et al. 2013, Sandercock et al. 2015). Diet studies of Upland Sandpipers at non-breeding ground indicated they feed mainly on aboveground adult insects like grasshoppers, beetles and ants that can be easily detected in heterogeneous vegetation heights (Alfaro et al. 2015). However, American Golden Plovers, Buff-breasted Sandpiper and other grassland shorebirds that feed on insect larvae also need sites with homogeneous short vegetation (grass height < 10 cm) to detect their prey (Isacch et al. 2005b, Isacch and Cardoni 2011). We found no evidence of predation mortality of Upland Sandpipers at non-breeding grounds (unpubl. data), but we conducted our study during daylight when raptors are potential predators. Spread stands of tall vegetation may provide refuge from raptor and other predators that rely mainly on visual cues (Lima 1990, Kullberg and Lafrenz 2007), but birds could probably also use their cryptic plumage instead of flocking for protection. We occasionally found birds roosting in the shade of trees or fence poles, a behavior also been reported at breeding sites (Young and Thompson 2014). Use of shade was related to a selection of a cooler microclimate during the hottest hours of day, and is unlikely to be related to an antipredator behavior if trees potentially provide cover for raptor attacks.

Cattle management provides habitats of different vegetation height and cover in large areas and allow the co-existence of species with different habitat requirements (Fuhlendorf et al. 2006, Codesio et al. 2013, Ahlering and Merkord 2016, Azpiroz and Blake 2016). The spatial heterogeneity of vegetation structure generated by different practices of grazing can increase the species richness of grassland bird communities (Isacch et al. 2005a, Isacch and Cardoni 2011, Ahlering and Merkord 2016). The low to intermediate levels of vegetation height and cover preferred by Upland Sandpipers are available in grasslands managed with extensive systems of livestock production where animals graze in large paddocks year-round, that are commonly applied in Uruguay (Baeza et al. 2009, MGAP 2015). Upland Sandpipers also preferred extensive areas of native grasslands, a condition actually found in the Northern Campos but scarce in other grasslands of the region (Baeza et al. 2011, Azpiroz et al. 2012, Azpiroz and Blake 2016). Upland Sandpipers required less cover than resident species of birds, such as Pampas Meadowlark (*Sturnella defillippi*), the Hudson's Canastero (*Asthenes hudsoni*) and the Black-and-white Monjita (*Xolmis* *dominicanus*) that use grasslands with dense cover of tall grass for nesting (Azpiroz et al. 2012, Azpiroz and Blake 2016). On the other hand, American Golden Plovers and Buff-breasted Sandpipers, also used homogeneous short grass in areas of high levels of cattle grazing (Isacch and Cardoni 2011), or patches of lithophytic steppes in the Northern Campos (M. Alfaro, pers. obs.). Thus, Upland Sandpiper have habitat requirements that support the importance of grazing-created heterogeneity in native grasslands for the conservation of bird biodiversity (Isacch and Cardoni 2011, Azpiroz and Blake 2016).

Knowledge of the ecology of grassland birds is increasing, but additional studies are needed to improve our understanding about factors affecting bird´s decisions in terms of habitat use and preference. Studies in North America found the elevation of the site and soil depth are important determinants of habitat preferences for Upland Sandpipers (Dechant et al. 1999, Fritcher et al. 2004, Sandercock et al. 2015, Ahlering & Merkord 2016). We did not evaluate elevation because our field sites showed little topographic variation, but soil depth is related with vegetation composition. Future studies could examine elevation, soil depth and vegetation composition to determine how these variables are related. In relation to protection from predators and the use of vegetation cover and flocking, studies of anti-predator behavior which measures the time expended in vigilance, the escape strategy and food abundance in relation to the size of the group, the vegetation height and cover and interactions with cryptic coloration and feather molt in the anti-predator behavior are needed. For example, at non-breeding grounds in Argentina, Buff-breasted Sandpipers defend their feeding territories but aggregate into small flocks when a predator approaches (Myers 1980).

By examining the dynamics of how animals use the habitat, we can begin to understand the individual demands that influence animal behavior and fitness (Rosenzweig 1991, Morris 2003, Gaillard et al. 2010). Similarly, our study attempted to advance on the mechanisms by connecting land use and its ongoing changes, with space use of migratory species. Migratory birds often have high site fidelity to local sites chosen for feeding or breeding within and across years (Smith and Houghton 1984, Huston 1998, Lindström 2007, Isacch and Martínez 2003). Sites chosen by migratory birds should be managed considering their requirements. The spatial heterogeneity of vegetation structure generated by different practices of livestock grazing in native grasslands have created the habitat characteristics preferred by the Upland Sandpiper during the non-breeding season. However, most managed grasslands have not been developed to promote heterogeneity and provide habitat for co-existing species with different habitat requirements; in contrast, the conversion of grasslands to croplands has resulted in loss of habitat for many grassland birds (Brennan and Kuvlesky 2005, Ribic et al. 2009, Isacch and Cardoni 2011, Azpiroz et al. 2012, Codesido et al. 2013). Loss of habitat could have severe consequences on the survival of migratory species like the Upland Sandpiper, and other migratory and endangered species dependent on grassland ecosystems. The Northern Campos ecoregion still maintains extended areas of native grasslands managed by different levels of livestock productivity, but no protected areas exist in the region and, during the years we worked there, we saw an increase in crop production. Ongoing research about habitat preferences of grassland birds in the campos of Uruguay and northern Argentina are important tools for governmental decisions over managed grasslands and for the creation of protected areas.

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Ethics statement: Research was conducted under federal and state wildlife permits issued in USA and national wildlife permits issued in Uruguay. Research protocols were approved by the Comisión Honoraria de Experimentación Animal at Universidad de la República del Uruguay, Montevideo, Uruguay (Exp. N° 241000-001186-12).

Author contributions: M. Alfaro, B. K. Sandercock and M. Arim conceived the idea, formulated questions and hypothesis, wrote the paper, developed and designed the methods; M. Alfaro, B. K. Sandercock and L. Liguori collected the data and conducted the research; and M. Alfaro, M. Arim and M. Berazategui analyzed the data.

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SUPPLEMENTAL MATERIAL

Tables S1. List of the 23 sites along the Northern Campos of Uruguay where records of Upland Sandpipers were collected. The first four sites correspond to the ranches where sandpipers were captured. *n* records = number of records at each site taken at different days of the season.

Point	**Location**	**Coordinates**	***n* records**	**Year**
1	Sarandi Ranch	31.4642ºS, 56.2329ºW	45	2008-2009
2	Valdéz Ranch	31.4808ºS, 56.3430ºW	232	2008-2012
3	Wilson Ranch	31.5302ºS, 56.5316ºW	41	2008-2009
4	Ramos Ranch	31.5238ºS, 56.3049ºW	187	2009-2012
6	5.5 km NE of Route 26	31.5142ºS, 56.5147ºW	2	2008, 2011
7	6.5 km NE of Route 26	31.5043ºS, 56.5140ºW	4	2008-2009
8	19 km NE of Route 26	31.4724ºS, 56.4630º W	1	2008
9	16.5 km N of Cerrillada	31.4513ºS, 56.4730º W	2	2008
10	8 km N of Cerrillada	31.4221ºS, 56.4936ºW	3	2009,2011
11	Cerrillada	31.3859ºS, 56.4931ºW	7	2009,2011
12	5 km SW of Vera	31.3721ºS, 56.5059ºW	3	2008-2009
13	8 km NW of Vera	31.3450ºS, 56.5157ºW	1	2009
14	12 km NW of Vera	31.3250ºS, 56.5344ºW	1	2009
15	8.7 km SW of Paso del Potrero	31.2822ºS, 56.5447ºW	1	2011
16	10 km NW of Arerungua	31.3727ºS, 56.4219ºW	1	2011
17	7 km SW of Route 31	31.3706ºS, 56.3410ºW	1	2011
18	4 km SW of Route 31	31.3630ºS, 56.3247ºW	4	2009, 2011
19	10 km S of Arerungua	31.4447ºS, 56.3509ºW	2	2009
20	5 km N of Route 26	31.4954ºS, 56.3242ºW	10	2008-2012
21	2.2 km N of Route 26	31.5115º S, 56.3214ºW	2	2011-2012
22	3.8 km N of Route 26	31.4758ºS, 56.2338ºW	1	2009
23	11 km N of Route 26	31.4450ºS, 56.2323ºW	1	2011

Tables S2. Individuals Upland Sandpipercaptured (*n* = 62) at the four ranches in the Northern Campos of Uruguay. Date = capture date. N records = number of locations where the bird was relocated by telemetry during the season.

Band number	**Date**	**Site**	***n* records**		**Band number**	**Date**	**Site**	***n* records**
30238	12/18/2008	Wilson	6		**30281**	1/09/2010	Ramos	8
30237	12/19/2008	Wilson	7		**30282**	1/10/2010	Ramos	2
30239	1/04/2009	Wilson	14		**30283**	1/10/2010	Ramos	7
30240	1/04/2009	Wilson	5		**30286**	1/11/2010	Ramos	9
30241	1/04/2009	Wilson	4		**30287**	12/30/2010	Valdez	9
30242	1/06/2009	Sarandi	5		**30288**	12/30/2010	Ramos	9
30243	1/07/2009	Sarandi	6		**30289**	1/04/2011	Valdez	14
30244	1/07/2009	Sarandi	15		**30290**	1/04/2011	Valdez	4
30245	1/07/2009	Sarandi	13		**30291**	1/05/2011	Ramos	14
30246	1/09/2009	Sarandi	4		**30292**	1/06/2011	Valdez	4
30248	1/21/2009	Valdez	2		**30293**	1/06/2011	Valdez	12
30249	1/21/2009	Valdez	15		**30294**	1/06/2011	Valdez	3
30250	1/22/2009	Valdez	2		**30295**	1/13/2011	Ramos	10
30256	1/23/2009	Valdez	6		**30296**	12/20/2011	Ramos	13
30257	1/23/2009	Valdez	1		**30297**	12/22/2011	Ramos	12
30267	11/19/2009	Valdez	18		**30298**	12/28/2011	Valdez	12
30268	11/19/2009	Valdez	16		**30299**	12/28/2011	Valdez	6
30284	11/22/2009	Valdez	6		**30300**	12/29/2011	Valdez	7
30285	11/23/2009	Valdez	18		**52201**	1/18/2012	Ramos	6
30269	12/09/2009	Valdez	15		**52202**	1/19/2012	Valdez	8
30270	12/10/2009	Valdez	11		**52203**	1/19/2012	Valdez	12
30271	12/10/2009	Valdez	16		**52204**	1/19/2012	Valdez	2
30272	12/18/2009	Valdez	5		**52205**	1/20/2012	Ramos	6
30273	12/18/2009	Valdez	7		**52206**	1/20/2012	Ramos	2
30274	12/19/2009	Valdez	6		**52207**	1/20/2012	Ramos	11
30275	1/06/2010	Ramos	13		**52208**	1/21/2012	Valdez	5
30276	1/07/2010	Ramos	12		**52209**	1/21/2012	Valdez	2
30277	1/08/2010	Ramos	6		**52210**	1/21/2012	Valdez	1
30278	1/08/2010	Ramos	4		**52211**	1/22/2012	Ramos	11
30279	1/08/2010	Ramos	2		**52212**	1/25/2012	Ramos	15
30280	1/08/2010	Ramos	9		**52213**	1/25/2012	Ramos	1

Tables S3. Proportion of vegetation available and the estimations of MCP for the study area, at four ranches (Sarandi, Valdéz, Ramos and Wilson) in the Northern Campos, Uruguay. MCP: is the minimum convex polygon in hectares. B1: are meso-xerophytic grasslands and lithophytic steppes, B2: are meso-hydrophytic grasslands, AG: agricultural lands and, F: forested sites, *n*: is the number of pixels in the map (1 pixel = 30 x 30 m).

		Vegetation available (%)					
SITE	**MCP (ha)**	**B1**	**B2**	**AG**	**F**	**Others**	***n***
Study area	165569	46.6	49.8	1.1	0.6	1.9	97864
Sarandi	1360.6	92.2	7.7	0	0	0.1	15134
Valdez	942.2	29.2	67.6	2.3	0.3	0.6	10473
Ramos	513.2	57.1	41.4	0.3	0.5	0.7	5710
Wilson	749.8	57.5	42.1	0	0.3	0.1	8339

Tables S4. Proportion of vegetation available inside the MPC nine birds with more than 15 records. MCP: is the minimum convex polygon in hectares. B1: are meso-xerophytic grasslands and lithophytic steppes, B2: are meso-hydrophytic grasslands, AG: agricultural lands, F: forested sites, *n*: is the number of pixels in the map (1 pixel = 30 x 30 m) and Id: is the band number of individuals.

			Vegetation available (%)					
SITE	**Id**	**MCP (ha)**	**B1**	**B2**	**AG**	**F**	**Others**	***n***
Sarandi	30244	149.8	91.9	8.1	0	0	0	1615
Valdéz	30249	62.8	24.3	75.4	0.3	0	0	692
Valdéz	30267	38.6	14.9	84.2	0.9	0	0	443
Valdéz	30268	139.8	26.2	73.7	0.1	0	0	1558
Valdéz	30269	109.5	29.7	70.3	0	0	0	1210
Valdéz	30271	66.2	23.1	76.9	0	0	0	733
Valdéz	30285	118.3	21.3	78.5	0.2	0	0	1320
Ramos	52212	56.7	86.2	13.8	0	0	0	622
Ramos	52213	74.8	40.7	59.3	0	0	0	850

Tables S5. Results of the *G*-test of goodness of fit comparing vegetation available at ranches Sarandi, Valdez and Ramos with vegetation used by the nine individuals (significant level < 0.05).

Available vs used	*G*	**df**	***P*** ≤
Sarandi-30244	2.5	4	0.056
Valdez-30249	0.13	4	0.47
Valdez-30267	6.4	4	**0.02**
Valdez-30268	0.9	4	0.6
Valdez-30269	1.9	4	0.4
Valdez-30271	1.9	4	0.4
Valdez-30285	4.8	4	**0.04**
Ramos-52212	16.8	4	**0.002**
Ramos-52213	1.2	4	0.874

CAPÍTULO 4. BODY CONDITION AND FEATHER MOLT OF A MIGRATORY SHOREBIRD DURING THE NON-BREEDING SEASON.

CONDICIÓN CORPORAL Y MUDA DEL PLUMAJE EN UN AVE MIGRATORIA DURANTE LA TEMPORADA NO REPRODUCTIVA.

Fotos: Luciano Liguori

BODY CONDITION AND FEAHER MOLTOF A MIGRATORY SHOREBIRD DURING THE NON-BREEDING SEASON

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RUNNING HEAD: BODY CONDITION OF A MIGRATORY SHOREBIRD

Abstract. Migratory shorebirds have some ofthe highest fat loads among birds, especially species which migrate long distances. The Upland Sandpiper (*Bartramia longicauda*) makes long-distance migrations twice a year, but variation in body condition or timing of feather molt during the non-breeding season has not been studied. Molt is an important part of the annual cycle of migratory birds because feather condition determines flight performance during migration and long-distance movements are energy costly. However, variation in body condition during molt has been poorly studied. The objective of our field study was to examine the timing and patterns of feather molt of a long distance migratory shorebird during the non-breeding season and test for relationships with body size, fat depots, mass, and sex. Field work was conducted at four ranches in the Northern Campos of Uruguay (Paysandú and Salto Departments). We captured and marked 62 sandpipers in a 2-month period (Nov-Jan) during four non-breeding season (2008-2012). Sex was determined by genetic analyses of blood samples taken at capture. Molt and fat was measured in captured birds using rank scores based on published standards. Body mass and tarsus length measurements showed female-biased sexual size dimorphism with males smaller than females. Size-corrected body mass showed a U-shaped relationship with the day of the season, indicating that birds arrived to non-breeding grounds in relatively good condition. Fat scores showed a significant relationship with size-corrected body mass but did not explain much of the variation. Arriving in good body condition at non-breeding grounds is probably important because of the energetic demands due to physiological adjustments after migration and the costs of feather molt.

Keywords: body mass, migration, molt, tarsus length, temporal variation.

Introduction

Long-distance migratory birds perform energetically demanding movements, traveling through unfamiliar landscapes, balancing conflicting demands between fuel acquisition and predator avoidance, and coping with unfavorable weather conditions (Piersma 1987, Piersma et al. 1990). To achieve the energy requirements for migration, birds exploit available resources during periods of high productivity (Buehler and Piersma 2008). However, to gain these benefits, individuals require a complete change in physiology as they alternate between different phases of their annual cycle (Piersma and Lindström 1997, Piersma 1998, Wingfield 2005). Migratory birds can reduce the mass of digestive organs not required for flight such as the gizzard and intestine to increase potential flight, but then recover the organs when feeding at breeding or non-breeding grounds (Piersma and Lindström 1997, Dekinga et al. 2001, Piersma 2002).

Migratory shorebirds have some of the highest fat loads among birds, especially species which migrate long distances (Biebach 1996, Berthold 1975). The Upland Sandpiper (*Bartramia longicauda*) is a long-distance migratory shorebird that breeds in North America and winters in southern South America (Houston & Bowen 2001, Blanco & Lopez-Lanús 2008). Some aspects of its biology have been studied, including mating system, breeding success, population structure, habitat selection, home range, distribution and diet at breeding and non-breeding grounds (Houston & Bowen 2001, Blanco & López-Lanús 2008, Casey et al. 2011, Azpiroz & Blake 2009, Sandercock et al. 2015, Alfaro et al. 2015). Upland Sandpipers use inland grasslands for reproduction and feeding but during migration they may use coastal areas (Houston & Bowen 2001, Blanco & Lopez-Lanús 2008, Azpiroz et al. 2012, Sandercock et al. 2015). The diet includes small terrestial arthropods such as grasshoppers and ground beetles, but they can also feed on snails during migration (McAtee 1914, Hallinan 1924, Houston & Bowen 2001, Alfaro et al. 2015). The Upland Sandpiper makes costly long-distance migrations twice a year, but no studies on variation in body mass variations or feather molt during the non-breeding season have been conducted.

Body mass of birds can be labile, due to fat expenditure or mass reduction of internal organs such as the gizzard, liver or gut. Reductions in body mass are an important strategy to improve agility and to reduce maintenance cost during energy-costly activities such as reproduction, migration, and feather molt (Norberg 1981, Cavitt and Thomson 1997, Gunnarsson et al. 2010, Portugal et al. 2007, Piersma and Van Gils 2011). Feather molt is costly in terms of energy expenditure and, in many species, molt is avoided during periods of high energy demand such as reproduction and migration (Murphy 1996). Consequently, in many migratory species, timing and energetics of molt interact with mass gain and recovery of internal organs before or after arrival at the non-breeding grounds (Murphy 1996). The study of these interactions is essential for the understanding of the annual cycle of migratory birds. Body mass maintained by non-breeding birds could also be affected by risk of predation, because mainteining low body mass during the period of molt compensates for potential reductions in flight performance during replacement of rectrices and remiges (Lima 1986, Newton 1969, King and Murphy 1985, Panek and Majewski 1990, Chandler and Mulvihill 1992, Piersma 2003a, Portugal et al. 2007).

Shorebirds show a broad variety of mating strategies (Reynolds and Székely 1997, Székely et al. 2006, Thomas et al. 2007). Mating strategies affect duration of parental care and the extent that each sex participates in incubation or brood rearing (Székely et al. 2006, Thomas et al. 2007, Tulp et al. 2009a, Gunnarsson et al. 2010). In Upland Sandpipers and other monogamous shorebirds, incubation is shared but females depart after the eggs hatch and leave males to care for the chicks until they fledge (Tomkovich and Soloviev 1996, Whitfield and Brade 1991, Houston & Bowen 2001, Casey et al. 2011). Consequently, energy budgets differ between the sexes because of different energy demands in gamete production, courtship displays, and time allocation for parental care (Piersma et al. 2003b, Tulp et al. 2009a, Hayward and Gillooly 2011). Sexual differences in reproductive effort during the breeding season could also impact individual energy budgets during the non-breeding season. Sexual differences in timing of migration have been reported for many species of migratory birds where females depart first from breeding grounds on autumn migration (protogyny), but males depart first from non-breeding grounds (protandry) on spring migration (Morbey and Ydenberg 2001, Mills 2005, Kokko et al. 2006). Sex differences are expected in species where males have a reproductive advantage when arriving first at breeding grounds and females desert parental care after eggs hatch (Morbey and Ydenberg 2001, Mills 2005, Kokko et al. 2006). Sexual differences in diet or habitat use could also determine patterns of body condition between males and females at non-breeding grounds. However, variation in body condition at non-breeding grounds has not been studied for the Upland Sandpiper, and more importantly, is poorly known for migratory bird species in general.

We hypothesize that sexual differences in reproduction between male and females Upland Sandpipers will affect the seasonal timing of hyperphagia, migration, and feather molt. While males with successful nests remain to attend young at breeding grounds, females can feed to improve their physiological state before migration and can start migration and arrive at non-breeding grounds before males. Consequently, we predicted that females might be in better body condition than males during the non-breeding season. We also hypothesize that gains in body mass among Upland Sandpipers after arrival at non-breeding grounds is limited by the process of flight feather molt because of energetic costs and potential reductions in the time spent foraging due to predation risk. We predicted that individuals who had not or recently started the process of molt are might be in poor body condition compared to individuals that have molted most or all of their primary feathers. The objective of our field study was to analyze the temporal variation of the body condition of Upland Sandpipers during the non-breeding season and to test for relationships between condition and sex, fat and the stages of flight feather molt.

Methods

Study area

Non-breeding Upland Sandpipers were captured at four ranches located in north-central Uruguay in the departments of Salto and Paysandú (Fig. 1). The area is part of the Northern Campos ecoregion of Uruguay, close to the Haedo Ridge and included in the Basaltic region (Altesor et al. 2005, Lezama et al. 2006, Azpiroz and Blake 2009, Baeza et al. 2009, Azpiroz et al. 2012). Livestock grazing is the main agricultural use throughout this region and at the four ranches selected. The vegetative community is mainly composed by native grasses including *Piptochaetium montevidense*, *Botriochloa laguroides*, *Richardia humistrata*, *Wahlenbergia linarioides*, *Baccharis coridifolia, Panicum hians*, *Andropogon lateralis*, *Portulaca papulosa*, *Hordeum pusillum*, *Selaginella sellowii*, and *Paspalum dilatatum* (Lezama et al. 2006; 2011, Baeza et al. 2009). The four ranches were selected based on the presence of birds, logistics of access, and by owner permission, and included: Sarandi Ranch (31.4642ºS, 56.2329ºW), Valdéz Ranch (31.4808ºS, 56.3430ºW), Wilson Ranch (31.5302ºS, 56.5316ºW), and Ramos Ranch (31.5238ºS, 56.3049ºW).

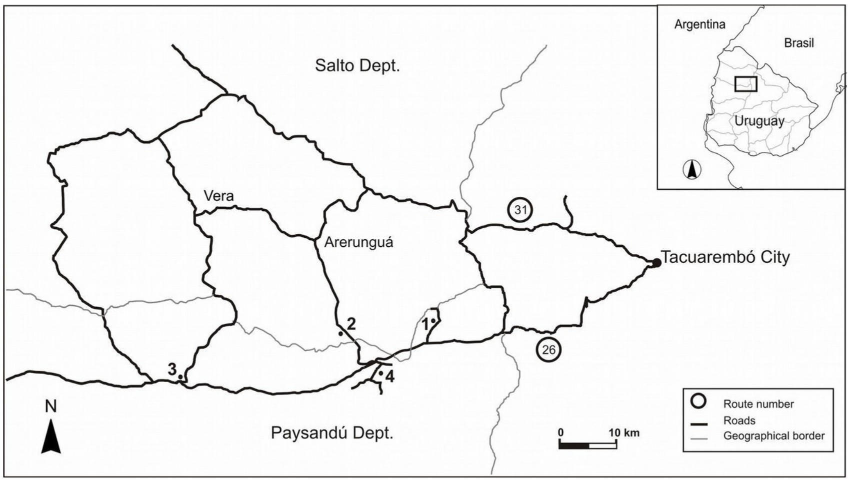

Fig. 1. Map of the study area in the Northern Campos of Uruguay, showing four ranches (numbers) where Upland Sandpipers were captured during four austral summers of November to February, 2008 to 2012. Locations for each bird captured are in Supplemental material Table S1.

Field methods

Our field study was conducted during four austral spring and summer seasons between mid-November to late February from 2008 to 2012. We searched for roosting sandpipers at night using high-powered spotlights, and captured birds with a long-handled dip net. We individually marked sandpipers with a numbered metal band, a unique combination of colored leg bands, and collected a 200 µL blood sample from the brachial wing vein. We extracted DNA from the blood samples with DNeasy kits (Qiagen Inc., Valencia, CA) and sexed all birds with molecular markers for the CHD gene (primers P2/P8 or 2550F/2718R, Casey et al. 2011). At first capture of each individual, the following measurements were recorded: left wing chord, bill–head length (from the rear of the skull to the tip of the bill), right tarsus (bending the foot at the toes and the intertarsial joint and measured as the distance between the extreme bending points), all to nearest 1.0 mm. We also recorded body mass to nearest 1.0 g with a Pesola spring balance, and fat and molt scores as follow.

Fat scores were recorded in six categories after Krementz et al. (1990): (0) = no visible trace of fat in either furcular region or over the abdomen; (1) = a trace of fat in the interclavicular fossa or abdomen but neither completely lined; (2) = interclavicular fossa lined, but not bulging, and little fat on the abdomen; (3) = fat filling interclavicular fossa, some fat on abdomen but not full; (4) = interclavicuar fossa and abdomen completely filled and bulging; and (5) = interclavicular fossa and abdomen full, with fat extending across the apex of the sternum. Molt in the flight feathers was recorded by allocating a rank score to each of ten primary feathers, according to its state of growth (Newton 1966): (0) old; (1) pin-brush stage; (2) brush to one-quarter grown; (3) one-quarter to one-half grown; (4) one-half to three-quarters grown; (4.9–5) three-quarters to fully grown, and (5) feathers that were fully grown and no longer sheathed at the base. Molt scores for each feather were then converted into molt indices as proportions: molt score 0 = 0, 1 = 0.125, 2 = 0.375, 3 = 0.625, 4 = 0.875, and 5 = 1.000 (Underhill & Summers 1993, Underhill & Joubert 1995), a process which aimed to achieve linearity through time of molt progression (Summers 1980). The total molt score was taken as the sum of the scores of all the primaries in the right wing, which gave an index of stage of molt in each bird at the time of capture (Newton and Rothery 2009). Scores were bounded from zero (no feathers replaced) to 10 (all primary feathers replaced). We choose primary feathers to study the process of feather molt because feather replacement extends over almost the entire molt period and is usually taken as a reference for the process of molt in other feather tracts (Jenni & Winkler 1994). Primaries are also the feathers with the largest effect on flight performance (Swaddle and Witter 1997).

To determine how long the birds stay in the study area after capture we also marked all of birds with small 3.8 g VHF radio transmitters attached to the back with an elastic leg-loop harness (model PD-2, Holohil Systems, Carp, ON). We used portable radio receivers (R2000, ATS, Isanti, MN) to relocate radio-marked birds 2-3 times per week over the 4-month non-breeding season of November to February.

Data analysis

Size-corrected body mass was estimated as the residuals from the linear relationship of body mass with body size, measured as tarsus length (Reist 1985, Jakob et al. 1996, Peig and Green 2009). An individual with a positive residual was considered to be in better body condition than an individual with a negative residual (Jakob et al. 1996, Schulte-Hostedde et al. 2001). The reference of body size was tarsus length because the linear measurement has a strong correlation with body mass after both variables were log transformed, and tarsus has been associated with structural size (Rising and Somers 1989). We used base 2 log transformations to improve connection with the original scale.

All predictions from our hypotheses were evaluated with a multiple regression analysis. The response variable of the model was body mass. Tarsus length was included as an independent variable. With incorporation of tarsus length in the multiple regression the variation in body mass associated with body size (tarsus length) was incorporated in the model, and the remaining variation, after controlling for by individual size, was interpreted as body condition. Our approach is similar to use of body mass-tarsus length residuals as an index of body condition withoutthe problem of an inflated number of degree of freedom and biases in parameter estimation when size residuals are used as an independent variable (see Freckleton 2002). Independent variables for testing predictions of our hypotheses included molt, sex, fat, day (since the first to the last capturing day), day quadratic value, and study season. Interactions between sex and body size, molt, day, and season were evaluated. Partial residuals were plotted to visualize the relationship with every single variable after removing the effects of all independent variables multiplied by the proper coefficients of the multiple regression (White et al. 2012, Ziegler et al. 2016). Last, in a separate analysis, the distribution of timing of molt between sexes was contrasted with a two sample Kolmogorov-Smirnov test. The distribution of dates at which molt was finished was used for this contrast. All statistical analyses were conducted using base functions of the R software (www.r-project.org).

Results

Captures of Upland Sandpipers were conducted between November 19th to January 25th. A total of 62 individuals were captured and monitored: 15 birds in 2008-2009, 20 in 2009-2010, 9 in 2010-2011, and 18 in 2011-2012. Genetic analyses showed an even sex ratio: 34 birds were females and 28 males; 9 females and 6 males in first season, 11 females and 9 males in second season, 5 females and 4 males in third season, and 9 females and 9 males in the fourth season (Appendix 1, Table A1). The mean ± standard deviation of all measurements taken from the 62 individuals were: wing 162.5 ± 10.83 mm, bill-head length 61.9 ± 1.85 mm, tarsus length 29.5 ± 1.53 mm, and body mass 139 ± 13.12 g. We observed fat scores of 0 (N = 36), 1 (N = 14), 2 (N = 7) and 3 (N = 5). The average body mass of Upland Sandpipers that were assigned 0 fat scores was 137 ± 11.6 g, for 1 scores 136 ± 9.9 g, for 2 scores 143 ± 16.4 g and for 3 scores 157.6 ± 13.5 g. Molt index varied between 5 to 10 (mean = 9.26 ± 1.11, N = 62) (Appendix 1, Table A1). One individual (band number 52211) was not considered in the analyses because the bird was emaciated at capture and had a poor body condition index by the end of the season.

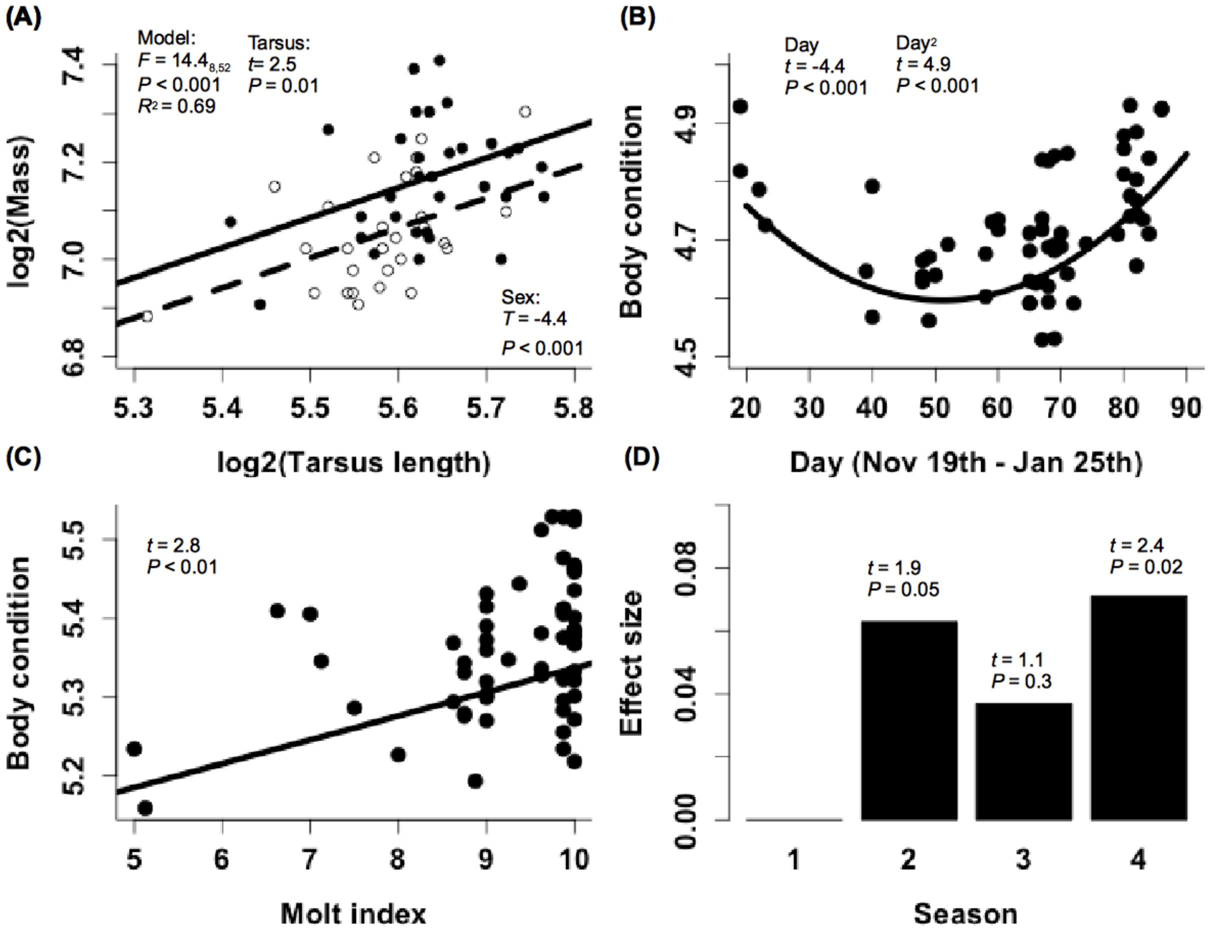

Fig. 2. Results of a multiple regression model relating body mass to tarsus length by sex (A), and body condition to day of the season (B), molt index (C) and season of the field study (D). Parameters of the model are given on each panel of the figure. In panel (D) the analysis compares every season from the first season used as reference because it presented the lower body condition during the study period.

A multivariate model with three significant parameters was identified. A significant association between body mass and tarsus length was detected (Fig. 2A). None of the independent variables showed a significant interaction with sex, indicating that body condition varied in the same way for both females and males. A significant sex effect was detected in body size, with females (mean mass = 143.8 ± 13.2 g, mean tarsus length = 49.9 ± 2.7 mm, N = 34) being 7.7 % heavier and 4.1 % largert in tarsus length than males (mean mass = 133.1 ± 10.5 g, mean tarsus = 47.9 ± 2.6 mm, N = 28) (Fig. 2A). The residuals of body mass and tarsus length showed a significant relationship with fat scores (F = 5.991, $p < 0.05$), but we decided not to include them into the model because fat scores explained only 10% of the variation. Body condition showed a U-shaped seasonal trend during the non-breeding season indicating a relative large decline after arrival at the non-breeding grounds in Uruguay (~ one month) and a progressive recovery until departure on spring migration (Fig. 2B). An improved body condition was observed among birds with advanced feather molt (Fig. 2C). Last, a significant effect of season was detected, showing that individuals were in better body condition during our last field season (2011-2012) (Fig. 2D). No significant difference in the distribution of molt period between sexes was detected with Kolmogorov-Smirnov test (D = 0.42, *P* = 0.37, Fig. 3).

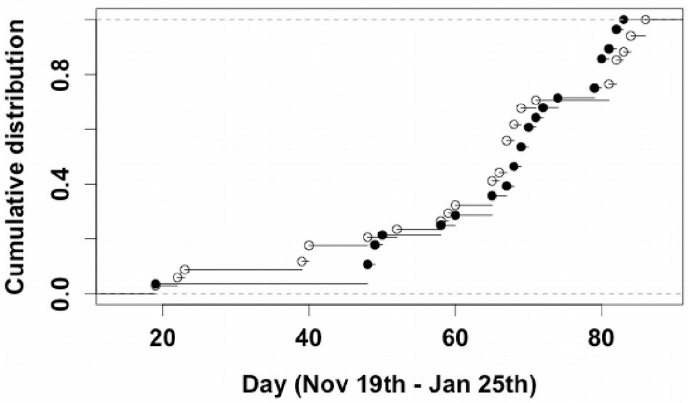

Fig. 3. Result of a Kolmogorov-Smirnov test showing no significant differences in the cumulative distribution of the wing molt schedule between males (black dots) and females (white dots) versus day of the non-breeding season (day 1 =

November 19th). Scores of zero indicate all primary feathers are old whereas scores of 1 indicate that molt is completed and all primary feathers have been replaced. Parameters of the test are shown in the figure.

Discussion

Our field project resulted in three major results. First, Upland Sandpipers arrived at non-breeding grounds in relative good body condition but during the process of molt, birds balanced the risk of predation versus the risk of starvation with a reduction of body mass. Our results are congruent with past studies of other migratory shorebirds in relation to the physiological costs of molt (Murphy 1996, Piersma et al. 2003b, Portugal et al. 2007, Buehler and Piersma 2008, Piersma and Van Gils 2011). The assumption that birds complete migration with extra energy reserves has been previously reported for sandpipers when arriving at the breeding grounds (Farmer and Wiens 1999, Skagen 2006, Krapu et al 2006, Tulp et al. 2009b), but here we show that this phenomena occurs among sandpipers at non-breeding grounds as well. Second, Upland Sandpiper energy budgets and time allocation for parental care differ between sexes during the breeding season (Houston & Bowen 2001, Casey et al. 2011), but we found no significant differences in body condition, fat and molt schedule between males and females during the non-breeding season. Last, with the development of a multiple regression model integrating all variables affecting body condition during the non-breeding season, we also established that females are larger than males and there was a slight inter-seasonal variation in body condition independent of sex.

Use of a single model had statistical and biological advantages for which all our former predictions could be evaluated. On statistical grounds, no biases or false positives are expected due to the performance of several tests with the same database or the use of residuals in further analysis without properly accounting for the loss of degrees of freedom (Freckleton 2002). In this sense, the widespread use of log(mass)-log(length) residuals as index of body condition fails to properly account for the use of the same data with different tests. When body size is incorporated as a covariate, the other associations of the multiple regression capture the effect of other variables controlled by body size (Netet et al. 1997). Thus, the other variables are related with the residuals of the body mass-tarsus length relationship without statistical problems of working with residuals. On biological grounds, both significant and non-significant associations provides relevant clues about the study system.

Inter-seasonal variation in the body condition of Upland Sandpipers could be related to annual variation in climatic conditions or food resources that we reported in our previous study (Alfaro et al. 2015). Future studies of the energetic content of shorebird prey are needed to test for potential trophic links between food quality and individual performance. A U-shaped trend in body condition along the non-breeding season indicates that individuals are losing body condition at the beginning of the season with a progressive recovery until departure. We expected birds to recover body condition after molt but were surprised to find that birds retained body reserves at arrival. In many migratory birds studied, individuals often to arrive at breeding areas with residual body reserves not totally used on the journey; which could be a strategy for the initial costs of reproductive activities and adjustment of internal organs during the transition from migration to breeding condition (Sandberg 1996, Fransson & Jakobsson 1998, Farmer and Wiens 1999, Skagen 2006, Krapu *et al.* 2006, Tulp et al. 2009a). However, past studies have not considered extra energy reserves upon arrival at non-breeding grounds. A negative effect of molt on body condition has also been observed in other shorebird species (Piersma et al. 2003b, Portugal et al. 2007, Buehler and Piersma 2008, Piersma and Van Gils 2011). This phenomena has been attributed to the energetic costs of molt, and other indirect costs such as less time dedicated to foraging because an increased predation risk (Murphy 1996, Piersma et al. 2003b, Portugal et al. 2007, Buehler and Piersma 2008, Piersma and Van Gils 2011). In this sense, arrive at non-breeding grounds with extra body reserves can be explained as a strategy for coping with the initial direct and indirect costs of feather molt and probably to post-migration internal organ mass adjustment.

Our study does not provide evidence for any sex differences in the molt and migration strategies of Upland Sandpipers. On the basis of previous studies on sex differences during reproduction (Reynolds and Székely 1997, Székely et al. 2006, Thomas et al. 2007), it was expected that some differences in seasonal timing associated to migration should be observed, but that was not the case. Our results support the idea of an energetic balance between males and females during reproduction, with males expending energy during courtship displays, incubation and brood care, and females expending energy during egg production and incubation (Tulp et al. 2009a, Jamieson 2012). The only trait that showed sex size dimorphism in Upland Sandpipers was body mass, with smaller differences in components of body size. In some shorebirds, including Upland Sandpipers, males display acrobatically during courtship flights (Jehl and Murray 1986, Houston & Bowen 2001). Maneuverability decreases with body size (Biebach 1996), so that in acrobatic shorebirds it is predicted that males should be small relative to females (Székely et al. 2004; 2006).

Understanding the biology of migration involve a synthetic analysis of events during both the breeding and non-breeding periods. In general, the attention is biased to the reproductive season and the different strategies displayed by males and females (Reynolds and Székely 1997, Székely et al. 2006, Thomas et al. 2007, Buehler and Piersma 2008, Tulp et al. 2009a, Jamieson 2012). Our study contributes to a more general understanding of migration by investigating individual behavior at non-breeding areas. The lack of significant sex differences in migration and molt schedules allowed us to speculate about the energetic balance of adults during reproduction. We also report evidence of female-biased sexual size dimorphism in Upland Sandpipers, which was consistent with predictions about courtship displays and body size in males. Hypotheses about the energetic cost of feather molt were also supported in our study. The discovery that Upland Sandpipers arrive at non-breeding grounds with energy reserves, is a behavior not yet reported in shorebirds but is important for understanding of the energetic demands in migratory birds. Studies that follow individuals, making repeated measurements of body mass and body size during the non-breeding season, could be conducted to evaluate individual variation in the patterns of body condition observed in our study.

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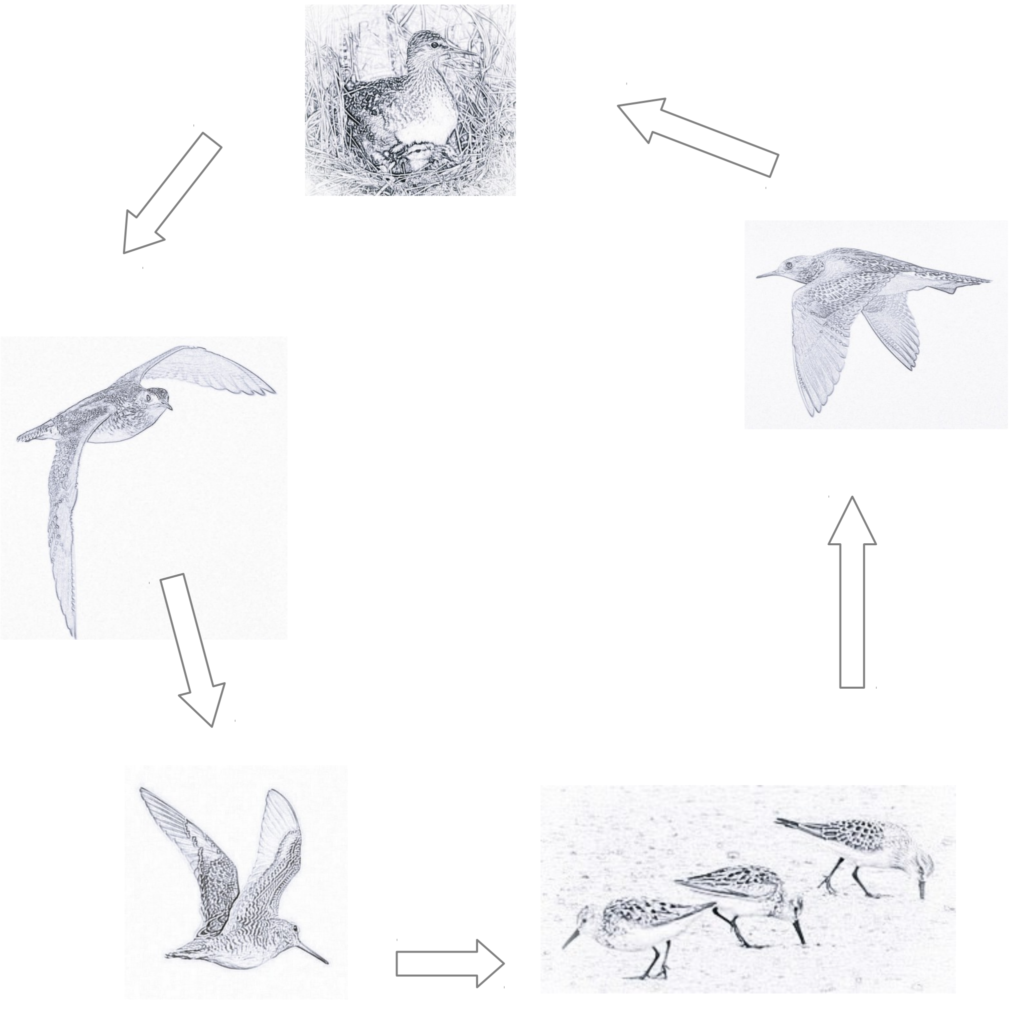
APPENDIX 1

Table A1. Measurements recorded for 62 Upland Sandpipers captured at four different ranches located in the Northern Campos of Uruguay, 2008 to 2012.

Band N^0	Date	Season	Sex	Mass (g)	Tarsus (mm)	Wing (mm)	Head (mm)	Fat scores	Molt index for right wing
30238	12/18/08	1	F	136	48.4	171	60.6	0	10
30237	12/19/08	1	M	122	49	147	60.3	1	10
30239	01/04/09	1	F	129	47.6	162	61.9	0	9
30240	01/04/09	1	M	126	48.1	164	60.3	0	9.625
30241	01/04/09	1	F	133	49.2	168	79.6	0	9.875
30242	01/06/09	1	F	149	50.5	175	65.7	0	10
30243	01/07/09	1	F	133	49.6	154	63.3	0	8.75
30244	01/07/09	1	M	122	46.6	152	62.4	1	9.875
30245	01/07/09	1	M	131	50.3	148	61.7	0	8.75
30246	01/09/09	1	M	130	47.9	161	59.3	0	9.25
30248	01/21/09	1	F	151	52.2	158	60.5	1	9
30249	01/21/09	1	F	148	49.3	162	62.7	0	9.875
30250	01/22/09	1	M	123	47.8	157	60.8	0	5.125
30256	01/23/09	1	F	149	52.9	180	64.2	2	10
30257	01/23/09	1	F	160	50.4	179	62.6	0	10
30267	11/19/09	2	M	148	49.2	179	64.4	3	7
30268	11/19/09	2	F	146	54.3	170	64.5	0	5
30284	11/22/09	2	F	152	48.6	170	62.1	0	10
30285	11/23/09	2	F	144	49.8	177	61.7	3	9
30269	12/09/09	2	F	132	49.7	177	62	0	7.5
30270	12/10/09	2	F	135	42.5	164	57.7	0	6.625
30271	12/10/09	2	F	120	43.5	177	62.1	0	8
30272	12/18/09	2	M	126	46.8	153	59.4	0	9
30273	12/18/09	2	M	130	50.4	166	59.8	0	10
30274	12/19/09	2	M	118	39.8	162	60.7	0	8.625
30275	01/06/10	2	F	158	49.7	163	63.7	0	9.75
30276	01/07/10	2	F	158	49.2	170	63.2	0	10
30277	01/08/10	2	M	142	44	165	65	0	9.875
30278	01/08/10	2	F	136	47.1	155	61.4	0	8.75
30279	01/08/10	2	F	128	49.3	163	58.6	0	10
30280	01/08/10	2	M	134	49.5	160	62.1	0	10
30281	01/09/10	2	M	130	45.1	155	63.1	0	9.625
30282	01/10/10	2	M	122	45.4	143	60	0	8.75
30283	01/10/10	2	F	154	45.9	165	63.7	0	9.625
30286	01/11/10	2	M	122	46.8	159	60.8	0	9.875
30287	12/30/10	3	F	150	53.3	157	60.9	0	9.375
30288	12/10/10	3	M	137	52.8	--	65.1	0	9
30289	01/04/11	3	F	140	50.1	165	62.8	0	9
30290	01/04/11	3	M	130	46.6	161	63.4	1	9
30291	01/05/11	3	F	140	52.8	160	64.1	1	9.875
30292	01/06/11	3	F	132	47.1	148	62	1	9
30293	01/06/11	3	F	128	52.6	161	61.5	1	8.875
30294	01/06/11	3	M	136	49.4	161	62.1	1	9.875

30295	01/13/11	3	M	132	48.4	150	59.1	2	9.625
30296	12/20/11	4	M	128	48.6	159	61.7	0	9.875
30297	12/22/11	4	F	140	54.4	170	60.9	0	7.125
30298	12/28/11	4	M	120	47	139	59.8	2	8.625
30299	12/28/11	4	F	140	48.2	165	60.3	2	9.875
30300	12/29/11	4	F	144	49.3	169	62.9	1	9
52201	01/18/12	4	M	134	47.9	162	59.9	2	10
52202	01/19/12	4	M	152	49.4	153	64.7	3	9.875
52203	01/19/12	4	M	148	47.6	166	60.7	1	10
52204	01/19/12	4	M	145	49.2	170	63.7	1	9.875
52205	01/20/12	4	F	170	50.1	176	64.5	3	10
52206	01/20/12	4	M	138	45.9	158	64.6	1	10
52207	01/20/12	4	F	150	51	171	64.2	0	10
52208	01/21/12	4	M	144	48.8	165	62.3	0	10
52209	01/21/12	4	F	142	51.9	162	60.5	1	9.875
52210	01/21/12	4	M	158	53.6	172	63.9	2	10
52211	01/22/12	4	F	122	49.3	168	59.7	1	10
52212	01/25/12	4	F	168	49.1	172	60.7	2	10
52213	01/25/12	4	F	174	53.9	168	60.4	3	10

CAPÍTULO 5. DISCUSIÓN GENERAL



DISCUSIÓN GENERAL

Esta tesis ha aportado a la comprensión del ciclo de vida de un ave migratoria, su dieta, estrategia de forrajeo, preferencia de hábitat, ritmo de muda y condición corporal a lo largo de la temporada no reproductiva. Además esta tesis demuestra el período no reproductivo es igualmente exigente en cuanto a consumo de energía que el período reproductivo, dado por los costos directos e indirectos de mudar el plumaje. Este tipo de información es muy poco conocida no solo para el Batitú sino para otras especies de aves migratorias de larga distancia también exclusivas de pastizal. Incluso si consideramos especies que han sido foco de estudios en la región como el Chorlo Pampa *Pluvialis dominica* o el Playero Canela *Tryngites subruficollis* (Lanctot et al. 2002, Isacch & Martínez 2003a; 2003b, Isacch et al. 2005, Strum et al. 2010). También se ha contribuido a una comprensión más integral del funcionamiento de los ecosistemas de pastizal. Estos sistemas han sido sustituidos principalmente por el avance de la agricultura, la ganadería y la forestación (Hannah et al. 2005, Baldi & Paruelo 2008, Altesor 2011). Comprender el efecto del manejo del pastizal sobre las especies que lo habitan sirve para la aplicación de medidas de conservación adecuadas, bien sustentadas en el conocimiento del sistema y las especies que lo habitan (Brennan and Kuvlesky 2005, Ribic et al. 2009, Isacch and Cardoni 2011, Azpiroz et al. 2012, Codesido et al. 2013). En este sentido, debe destacarse que las especies presa del Batitú incluyen herbívoros, polinizadores y consumidores de ambos. El efecto de este consumo sobre la composición y funcionamiento de la productividad primaria es desconocido. No obstante, las altas demandas energéticas de las aves y las relativamente altas densidades que alcanzan en la zona (M. Alfaro, observ. pers.), sugieren que estos organismos estarían teniendo un papel central en estos ecosistemas.

Los estudios de dieta aportan información básica para la comprensión de las interacciones tróficas entre las especies y para determinar características fisiológicas, ecológicas y de requerimientos energéticos de los individuos. Los resultados de esta tesis demostraron que la dieta del Batitú en sus áreas no reproductivas estuvo principalmente compuesta por insectos incluyendo insectos peste de la agricultura al igual que en las áreas reproductivas (McAtee 1914, Houston & Bowen 2001). Otras especies migratorias que habitan el pastizal durante la temporada no reproductiva (Chorlo Pampa y Playero Canela) también consumen principalmente insectos (Isacch et al. 2005). Existe evidencia de que el Batitú tiene diferentes preferencias alimenticias en los sitios de parada durante la migración, consumiendo principalmente moluscos (Hallinan 1924). Es común en las aves migratorias cambiar de hábitos alimenticios durante la migración debido a las altas demandas energéticas del vuelo prolongado, la intensa competencia en los sitios de parada, y la necesidad de adaptarse a ambientes y condiciones climáticas diferentes y con recursos cambiantes (Covino & Holberton 2011, Newton 2008, Lindström 2007, Huston 1998). Uno de los sesgos de estimar la dieta con los restos encontrados en las heces es que algunas presas, como gusanos, caracoles o arácnidos, pueden quedar poco representados o no ser detectados (Duffy & Jackson 1986, Rosenberg & Cooper 1990). A pesar de que en este estudio se realizó observación directa durante la colecta de las heces, estudios futuros que analicen contenido estomacal, mayor cantidad de horas de observación mientras se están alimentado o el análisis de ADN en heces (DNA barcoding) podrían identificar nuevos ítems o sugerir una mayor incidencia de presas ya identificadas. De todas maneras, con un alto número de ítems detectados y un número de muestras aceptable, los resultados obtenidos fueron suficientes como para describir la dieta del Batitú durante la temporada no reproductiva en Uruguay. La variabilidad de tipos y tamaños de artrópodos terrestres consumidos por el Batitú demostró que tiene un comportamiento alimenticio flexible, lo cual es congruente con la variabilidad de los ambientes utilizados durante su ciclo de vida.

En esta tesis también se investigó la preferencia y el uso del hábitat del Batitú en los Campos del Norte de Uruguay. En los pastizales del norte existe un mosaico de ambientes con diferentes intensidades de pastoreo en pasturas nativas y mejoradas, y diferentes cultivos (arroz, soja, sorgo, avena y trigo) (Lezama et al. 2006; 2011, Baeza et al. 2009; 2011). En esta matriz y a tres diferentes escalas espaciales, el Batitú prefirió principalmente los pastizales nativos asociados a suelos poco profundos y rocosos con baja o intermedia cobertura vegetal. A escala de parche utilizó niveles bajos a intermedios de altura y cobertura de vegetación pero no se encontró relación entre el tamaño del grupo y la altura-cobertura de la vegetación. El tipo de estructura de la vegetación preferida por el Batitú generalmente se encuentra disponible en pastizales pastoreados con intensidades intermedias de producción ganadera (Azpiroz et al. 2012, Azpiroz and Blake 2016). Este tipo de configuración vegetal puede ofrecer espacios abiertos buenos para la detección de las presas, en especies como el Batitú que busca sus presas visualmente entre la vegetación, y arbustos esparcidos buenos para camuflarse y ser detectados por depredadores (aves rapaces y mamíferos) . Estos resultados son congruentes con la hipótesis de un balance entre la necesidad de encontrar el alimento y el costo de ser depredado (McArthur and Pianka 1966, Lima and Dell 1990, Lima and Bednekoff 1999).

A pesar de que el conocimiento sobre las aves de pastizal se ha incrementado en los últimos años, todavía son necesarios más estudios de comportamiento alimenticio con el fin de comprender qué hay detrás de las decisiones de los individuos sobre el uso y la preferencia del hábitat. También son necesarios estudios sobre el comportamiento anti-depredador en donde se mida el tiempo utilizado en vigilancia, la estrategia de escape y la oferta de alimento en relación al tamaño de grupo. Por último, debe considerarse cómo la coloración críptica del Batitú y el estado del plumaje afectan las decisiones en cuanto la altura y cobertura de los lugares donde se alimentan.

Los resultados de esta tesis contribuyen al conocimiento sobre los mecanismos que conectan el uso del territorio por los seres humanos con el uso del espacio por las especies migratorias de pastizal. Los sitios escogidos por las aves migratorias para descansar y alimentarse deberían ser manejados considerando sus requerimientos. La heterogeneidad espacial en la estructura de la vegetación generada por las diferentes prácticas de las ganadería en los pastizales naturales ofrecen el hábitat preferido por el Batitú y otras especies de aves migratorias y residentes que dependen del pastizal para alimentarse y reproducirse. Sin embargo, la mayoría de los pastizales manejados no fueron desarrollados para promover la heterogeneidad espacial de la vegetación, por el contrario la conversión de los pastizales en cultivos y pasturas ha resultado en pérdida de hábitat para muchas aves de pastizal (Brennan and Kuvlesky 2005, Ribic et al. 2009, Isacch and Cardoni 2011, Azpiroz et al. 2012, Codesido et al. 2013). Esta pérdida de hábitat puede tener consecuencias severas en la supervivencia de muchas especies como el Batitú y otras que se encuentran amenazadas. La región de los Campos del Norte de Uruguay aún mantiene grandes extensiones de pastizal natural manejado con diferentes niveles de producción ganadera, pero dentro de la región no existen áreas protegidas y durante los cuatro años de trabajo de campo de esta tesis se pudo observar un gran aumento en la producción de granos, donde se sustituyó el pastizal natural por monocultivos. El conocimiento generado sobre uso y preferencia de hábitat de las aves que habitan la región de los pastizales del sur de Sudamérica debería ser utilizado al momento de tomar decisiones sobre el tipo de manejo que se hace de los pastizales naturales con el fin de conservar la biodiversidad y para la creación de áreas protegidas. Existen programas de agricultura sustentable que involucran la asociación con los dueños de los campos con el fin de fomentar la conservación de las especies.

En esta tesis se observó que el Batitú llega a las áreas de invernada con una condición corporal relativamente buena. Sin embargo, durante el proceso de muda del plumaje se observó una reducción de su masa corporal. Terminar la migración con energía extra ya había sido reportado en aves playeras al llegar a las áreas de reproducción pero no cuando llegan a las áreas de invernada (Farmer and Wiens 1999, Skagen 2006, Krapu et al 2006, Tulp et al. 2009). Llegar a las áreas de reproducción en buena condición corporal puede servir para lidiar con los ajustes de los órganos internos luego de la migración y para lidiar con los costos iniciales de la reproducción (Sandberg 1996, Fransson & Jakobsson 1998, Farmer and Wiens 1999, Skagen 2006, Krapu et al. 2006, Tulp et al. 2009). Por otro lado, ha sido observado un efecto negativo en la condición corporal de las aves migratorias durante el proceso de muda y esto ha sido atribuido al costo energético de la muda y a una serie de costos indirectos relacionados dedicar menor tiempo a alimentarse por tener un mayor riesgo de ser depredado a causa de una menor agilidad de vuelo (Murphy 1996, Piersma et al. 2003, Portugal et al. 2007, Buehler and Piersma 2008, Piersma and Van Gils 2011). En este sentido, el hecho de llegar a las áreas no reproductivas con energía extra puede ser explicado como una estrategia para lidiar con el costo directo de la muda y con el costo indirecto de una menor movilidad y de ajustes en la masa de órganos internos.

En este estudio también se documenta que no existe ninguna diferencia en el calendario de muda o en las estrategias de migración entre sexos. En cambio, estos resultados apoyan la idea de un balance energético entre machos y hembras en los costos de la reproducción, con los machos gastando energía en los despliegues de cortejo, incubación de los huevos y cuidados de los pichones, y las hembras gastando energía durante la producción de los huevos y la incubación (Tulp et al. 2009, Jamieson 2012). La única diferencia observada entre machos y hembras fue en su tamaño corporal, siendo los machos más pequeños que las hembras. En general en chorlos y playeros, incluyendo al Batitú, los machos realizan despliegues de cortejos acrobáticos haciendo saltos y elevando las alas (Jehl and Murray 1986, Houston & Bowen 2001). La agilidad decrece con el tamaño del cuerpo por lo tanto, en especies en que los machos realizan despliegues de cortejo acrobáticos es predecible que deban ser más pequeños que las hembras (Biebach 1996, Székely et al. 2004; 2006). Estudios futuros que realicen un seguimiento individual, con mediciones repetidas de la masa corporal y la grasa subcutánea a lo largo de la temporada, servirán para evaluar patrones de variación individual de la condición corporal.

La comprensión del fenómeno de la migración involucra un análisis profundo de los eventos que ocurren en las áreas de reproducción, en las no-reproductivas y en los efectos sobre el cruce de estaciónes. Sin embargo, la atención ha estado principalmente enfocada en el período reproductivo (Reynolds and Székely 1997, Székely et al. 2006, Thomas et al. 2007, Buehler and Piersma 2008, Tulp et al. 2009, Jamieson 2012). Esta tesis contribuye a una comprensión más general de la migración investigando diversos aspectos ecológicos de un ave migratoria durante la temporada no-reproductiva. Asimismo, se ha generado una masa de conocimiento básico sobre la historia de vida del Batitú que motiva a poner el foco de futuros estudios en aspectos concretos de la biología de especie y el ecosistema de pastizal. Los conocimientos generados se potencian por tratarse de una especie que ha sido estudiada en sus áreas de cría pero no así en el resto de su ciclo vital. El éxito de los ciclos de migración energéticamente exigentes probablemente depende de estrategias de forrajeo amplias y oportunistas, la presencia de refugios en los períodos más vulnerables como la muda de las plumas de vuelo y ambientes adecuados para la recuperación de recursos luego de la migración y el período de cambio de plumaje. Los estudios realizados en esta tesis también sugieren que para la conservación de especies migratorias no solo basta con generar áreas protegidas a lo largo de su distribución, sino del manejo que se haga del pastizal en los lugares donde habitan.

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