Article

Body condition and feather molt of a migratory shorebird during the non-breeding season

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Migratory shorebirds have some of the 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 energetically 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 seasons (2008–2012). Sex was determined by genetic analyses of blood samples taken at capture. Molt 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 (body condition) showed a U-shaped relationship with the day of the season, indicating that birds arrived at non-breeding grounds in relatively good condition. 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 distance, 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 (Berthold 1975, Biebach 1996). The upland sandpiper *Bartramia longicauda* is a long-distance migratory shorebird that breeds in North America and winters in southern South America (Fig. 1) (Houston and Bowen 2001). 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 and Bowen 2001, Blanco and López-Lanús 2008, Casey et al. 2011, Alfaro et al. 2015, Sandercock et al. 2015). Upland Sandpipers use inland grasslands for reproduction and feeding but during migration they may use coastal areas (Houston and Bowen 2001, Blanco and López-Lanús 2008, Azpiroz et al. 2012, Sandercock et al. 2015). The diet includes small terrestrial arthropods such as grasshoppers and ground beetles, but they can also feed on snails during migration (McAtee 1914, Houston and 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 or feather molt during the non-breeding season have been conducted.
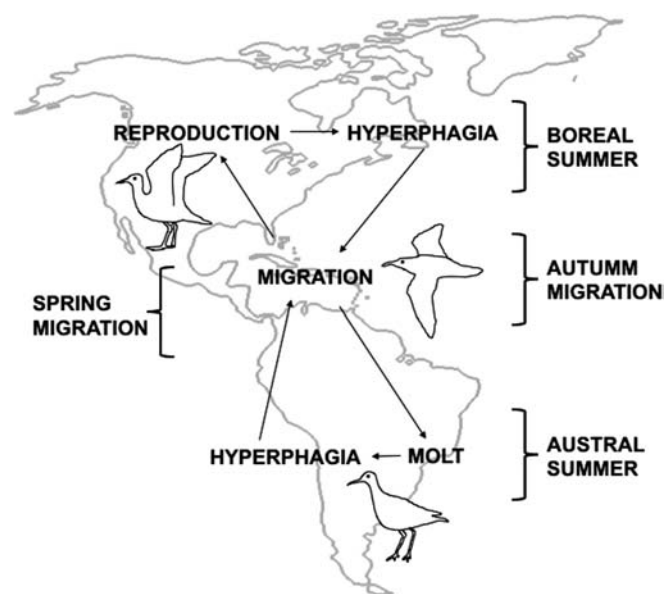

Figure 1. Diagram showing the different phases of the annual cycle of upland sandpipers.

Body mass of birds can be labile, due to fat metabolism 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 costs during energy-costly activities such as reproduction, migration, and feather molt (Norberg 1981, Cavitt and Thompson 1997, Portugal et al. 2007, Gunnarsson et al. 2010, 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. Furthermore, effects can carry-over because different periods of the annual cycle are linked and ecological conditions experienced by individuals at one season can influence their performance at another (Newton 2008). Body mass maintained by non-breeding birds could also be affected by risk of predation, because maintaining low body mass during the period of molt compensates for potential reductions in flight performance during replacement of rectrices and remiges (Newton 1969, King and Murphy 1985, Lima 1986, Panek and Majewski 1990, Chandler and Mulvihill 1992, Piersma et al. 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 (Bachman and Widemo 1999, Székely et al. 2006, Thomas et al. 2007, Tulp et al. 2009a, Gunnarsson et al. 2010). In upland sandpipers and other monogamous shorebirds, males guard their mates during pre-laying, incubation is shared by both sexes, but females depart after the eggs hatch and leave males to care for the chicks until they fledge (Whitfield and Brade 1991, Tomkovich and Soloviev 1996, Houston and Bowen 2001, Casey et al. 2011). Consequently, energy budgets differ between the sexes because of different energy demands in courtship displays, gamete production, 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, but there is scarce information on sex differences during 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 hypothesized that sexual differences in reproduction between male and female 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 hypothesized 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 which had not or recently started the process of molt might be in poor body condition compared to individuals that had 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. 2). Our study area is part of the Northern Campos ecoregion of Uruguay, close to the Haedo Ridge and included in the Basaltic region (Lezama et al. 2006, 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 of native grasses including *Piptochaetium montevidense*, *Botriochloa laguroides*, *Richardia humistrata*, *Wahlenbergia linarioides*, *Baccharis coridifolia*, *Panicum hians*, *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 (31.4642°S, 56.2329°W), Valdéz Ranch (31.4808°S, 56.3430°W), Wilson Ranch (31.5302°S, 56.5316°W), and Ramos Ranch (31.5238°S, 56.3049°W).

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 tried to make all captures at the beginning of the season each year because birds are molting and easier to catch. 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, 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
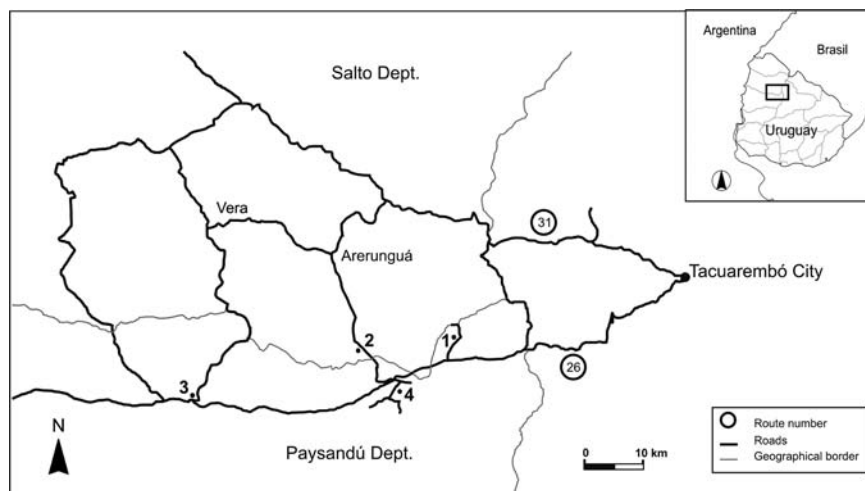

Figure 2. Map of the study area in the Northern Campos of Uruguay, showing four ranches (numbers) where upland sandpipers were captured during four austral summers of November to February, 2008 to 2012. Locations for each bird captured are in Supplementary material Appendix 1 Table A1.

1.0 mm. We also recorded body mass to nearest 1.0 g with a Pesola spring balance, and molt scores as follow.

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 and Summers 1993, Underhill and 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). Molt 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 and Winkler 1994). Primaries are also the wing feathers with the largest effect on flight performance (Swaddle and Witter 1997).

To determine how long the birds stayed in the study area after capture, we 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). This radio transmitter was previously tested on upland sandpipers and had effective radio retention and high seasonal survival independently of sex (Mong and Sandercock 2007). 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

Body condition was estimated as the residuals from the linear relationship of body mass with body size, measured as tarsus length (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 for 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, accounting for the effect of individual size on body mass. The remaining variation in body mass is independent of body size and may be interpreted as body condition. When body size is incorporated as a covariate, the other associations of the multiple regressions capture the effect of other variables controlled by body size (Neter et al. 1990). Thus, the other variables are related with the residuals of the body mass-tarsus length relationship without statistical problems of working with residuals (Freckleton 2002). 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 at the end of the season.

Independent variables for testing predictions of our hypotheses included molt, sex, fat, day (since the first to the last day of capture), a quadratic function for day of season, study season and ranches. Variables with non significant coefficients were removed from the model, using contrasting models and AIC criteria. Interactions between sex and body size, molt, day, and season were evaluated. Partial residuals were plotted to visualize the relationships with every single variable after removing the effects of all independent variables (following White et al. 2012, Ziegler et al. 2016). Last, in a separate analysis, the distribution of individuals' timing of molt and stay time in the study area was contrasted between sexes with a two sample Kolmogorov–Smirnov test. The distribution of dates at which molt was finished and the distribution of how many days that birds stayed in the study area after capture were used for these contrasts respectively. All statistical analyses were conducted using base functions of the R software (<www.r-project.org>).

Results

Captures of upland sandpipers were conducted during the austral summer of north-west Uruguay, between 19 November to 25 January with some variation each year depending on the day of first and last capture (Supplementary material Appendix 1 Table A1). Genetic analyses showed an even sex ratio (Supplementary material 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 (Supplementary material Appendix 1 Table A1 and Fig. A1). Molt index varied between 5 to 10 (mean 9.24 ± 1.12) (Supplementary material Appendix 1 Table A1 and Fig. A2).

A multivariate model with significant parameters was identified. Model validation showed residuals were normally distributed and no signs of violation of homogeneity and independence (Supplementary material Appendix 1 Fig. A3). Distribution of residuals showed a significant association between body mass and tarsus length (Fig. 3A). 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 $=143.8 \pm 13.2$ g, mean tarsus length $=49.9 \pm 2.7$ mm, $n=34$) being 7.7% heavier and 4.1% larger in tarsus length than males (mean mass $=133.1 \pm 10.5$ g, mean tarsus $=47.9 \pm 2.6$ mm, $n=28$) (Fig. 3A). Body condition showed a U-shaped
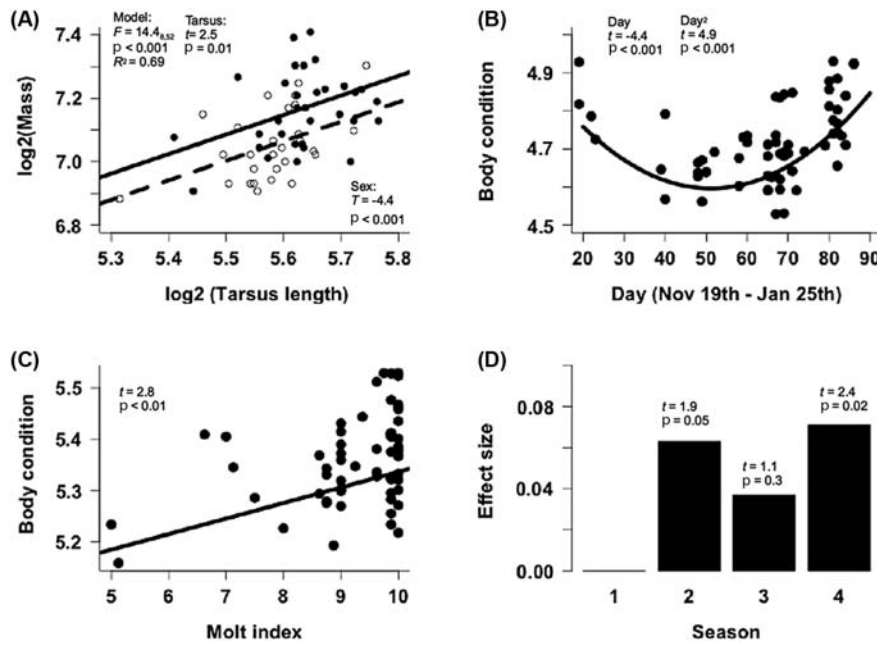
Figure 3. Results of a multiple regression model relating body mass to tarsus length by sex (A), and body condition to day of the season (B), molt index (C) and season of the field study (D). Parameters of the model are given on each panel of the figure. In panel (A) females (black dots and solid line) and males (white dots and dashed line). In panel (D) the analyses compare every season to the first season as a reference because it presented the lowest body condition during the study period. Independent variables in all plots are partial residuals corrected to have the same range of values as the original observations.

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. 3B). An improved body condition was observed among birds with advanced feather molt (Fig. 3C). Last, a significant season effect was detected, showing that individuals in our last field season were in better body condition comparing to the first season (2011–2012) (Fig. 3D). No significant difference in the distribution of molt period between sexes was detected with a Kolmogorov–Smirnov test (D = 0.42, p = 0.37, Fig. 4). Although individuals depart from the study area differentially (Supplementary material Appendix 2 Table A2, Fig. A4), we found no significant differences between males and females in the distribution of how long (in days) birds stayed in the study area (D = 0.28, p = 0.2, Fig. 5).

Discussion

Our field project results 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, Krapu et al. 2006, Skagen 2006, Tulp et al. 2009b), but here we show that this phenomena also occurs among sandpipers at non-breeding grounds. Second, upland sandpiper energy budgets and time allocation for parental care differ between sexes during the breeding season (Houston and Bowen 2001, Casey et al. 2011), but we found no significant differences in body condition, molt schedule and departure day from the study area between males and females during the non-breeding
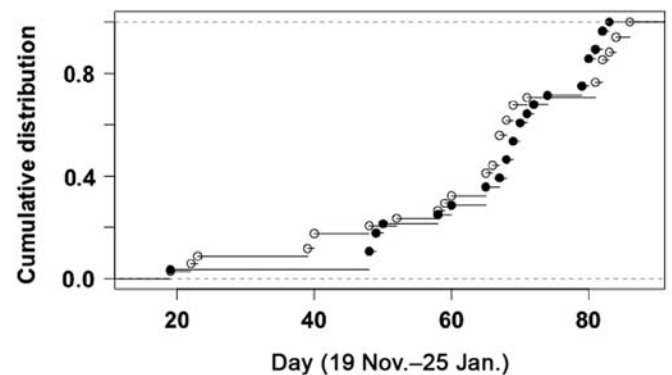

Figure 4. Result of a Kolmogorov–Smirnov test showing no significant difference in the cumulative distributions of the wing molt schedules between males (black dots) and females (white dots) during the non-breeding season (day 1 = 19 Nov.). Parameters of the test are D = 0.42, p = 0.37.
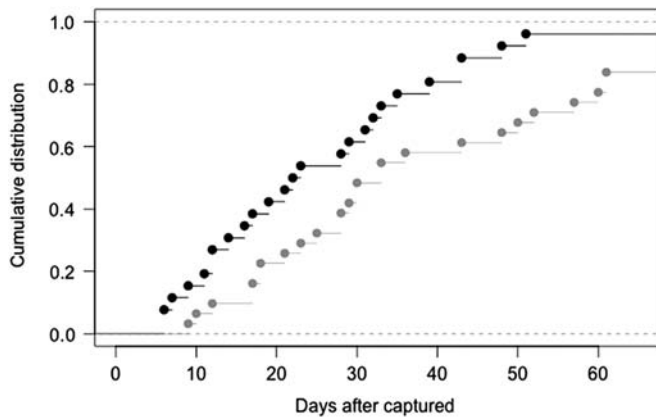
Figure 5. Result of a Kolmogorov–Smirnov test showing no significant difference in the cumulative distributions of how long males (black dots) and females (gray dots) stayed in the study area. Parameters of the test are D = 0.28, p = 0.2.

season. Last, with development of a multiple regression model integrating all variables available in this study that affected 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. On biological grounds, in our approach both significant and non-significant associations provided 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) and potential interactions with physiological plasticity, predation or competition. 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 during 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, individuals often 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 and Moore 1996, Fransson and Jakobsson 1998, Farmer and Wiens 1999, Krapu et al. 2006, Skagen 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 phenomenon has been attributed to the energetic costs of molt, and other indirect costs such as less time dedicated to foraging because of 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, arrival 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 of 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). We reported sexual size dimorphism in upland sandpipers. In some shorebirds, including upland sandpipers, males display acrobatically during courtship flights (Jehl and Murray 1986, Houston and Bowen 2001, Székely et al. 2006). Maneuverability decreases with body size (Biebach 1996), so that in acrobatic shorebirds like the painted snipe *Rostratula benghalensis* (Jehl and Murray 1986) the sex that displays for courtship (in this example the female) is smaller (Székely et al. 2004, 2006). But, in nonagile shorebirds and especially species with polygyny and lek-mating reproductive strategies like the ruff *Philomachus pugnax* (Bachman and Widemo 1999), body mass is important for fighting and males are larger than 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, 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 acrobatic shorebirds. 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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