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Sex-specific patterns of fuelling and pre-breeding body moult of Little Stints *Calidris minuta* in South Africa

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The timing and duration of each stage of the life of a long-distance migrant bird are constrained by time and resources. If the parental roles of males and females differ, the timing of other life stages, such as moult or pre-migratory fuelling, may also differ between the sexes. Little is known about sexual differences for species with weak sexual dimorphism, but DNA-sexing enables fresh insights. The Little Stint *Calidris minuta* is a monomorphic long-distance migrant wader breeding in the Arctic tundra. Males compete for territories and perform elaborate aerial displays. Females produce two clutches a season. Each sex may be a bigamist and incubate one nest a season, each with a different partner. We expect that these differences in breeding behaviour entail different preparations for breeding by males and females, so we aimed to determine whether Little Stints showed any sex differences in their strategies for pre-breeding moult and pre-migratory fuelling at their non-breeding grounds in South Africa. We used body moult records, wing length and body mass of 241 DNA-sexed Little Stints that we caught and ringed between 27 January and 29 April in 2008–2018 at two neighbouring wetlands in North West Province, South Africa. For each individual we assessed the percentage of breeding plumage on its upperparts and took blood samples for DNA-sexing. We calculated an adjusted Body Moult Index and an adjusted Wing Coverts Moult Index, then used the Underhill–Zucchini moult model to estimate the start dates and the rate of body moult in males and females. We estimated the changes in the sex ratio of the local population during their stay in South Africa, and also estimated the timing and rate of pre-migratory fuelling and the potential flight ranges for males and females. The males started body moult on average on 7 February and the females on 12 February, but the sexes did not differ in their timing of wing covert moult, which started on average on 10 February. In January to mid-February, males constituted *c.* 57% of the population, but their proportion declined afterwards, indicating an earlier departure than females. We estimated that both sexes began pre-migratory fuelling on average on 15 March. The sexes did not differ in fuelling rate, but most females stayed at the non-breeding site longer than the males, and thus accumulated more fuel and had longer potential flight ranges. These patterns of moult and fuelling suggest sex differences in preparations for breeding. We suggest that the males depart from South Africa earlier but with smaller fuel loads than the females to establish breeding territories before the females arrive. We conclude that for each sex the observed trade-offs between fuelling and moult at the non-breeding grounds are precursors to different migration strategies, which in turn are adaptations for their different roles in reproductive behaviour.

Keywords: Afro-Palaearctic migrant, Charadriiformes, fat stores, feathers, moult pattern, phenology, Scolopacidae, wintering.

During the non-breeding season, most migrant birds undergo energy-costly moult and accumulate fat and proteins as energy stores for their migration

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north to the breeding grounds (Ginn & Melville 1983, Newton 2009, Remisiewicz 2011). Moult is a genetically determined process but is hormonally controlled, which enables birds to adjust the timing, duration and extent of their moult to environmental and biological conditions (Dawson 1994, 2006). Hence moult might buffer shifts in the timing of other life stages (Helm & Gwinner 2006, Conklin *et al.* 2013). Moult strategies differ between species depending on their size, breeding latitude and migration distance, and within a species between sex and age groups as well as different migratory populations (Newton 2009, Remisiewicz 2011). Migrant birds increase their food intake at non-breeding grounds and at migration stopover sites to accumulate energy stores required for long-distance flights (Berthold 1996, Vincze *et al.* 2019). Birds tend to avoid overlapping moult with other energy-costly activities unless food is abundant (Murphy & King 1992, Remisiewicz *et al.* 2019). Unfavourable conditions on the non-breeding grounds and time constraints posed by seasonal migration can lead to an overlap in moult and pre-migratory fuelling, which would result in trade-offs of energy allocation between these processes or even to delays (Piersma & Jukema 1993, Lindström *et al.* 1993, Conklin & Battley 2012). These trade-offs might differ for males and females because of their different roles in breeding and parental care.

The selection pressure on the males, which compete for territories and females, favours the early arrival of males at the breeding grounds (Kokko 1999, Kokko *et al.* 2006). In passerines, the greater the sexual size dimorphism in a species, the larger the protandry in spring arrival. However, protandry has been studied mostly in species with distinct differences between the sexes (Spottiswoode *et al.* 2006). We expect large differences between the sexes in waders, based on their often different involvement in parental care (Colwell 2010). These differences will shape the timing of post-breeding life-stages (Summers *et al.* 2004, Conklin & Battley 2012, Barshep *et al.* 2013). We set out to investigate whether for the Little Stint *Calidris minuta*, a long-distance migrant wader with different involvement of the sexes in reproduction but with small sexual size dimorphism, the sexes differed in the timing of non-breeding activities. Sex differences in the moult schedules of waders (Charadrii) tend to be small in species in which both males and females incubate and feed the young, such as seasonally monogamous Bar-tailed Godwits *Limosa lapponica* (Cramp & Simmons 1983, Conklin & Battley 2012), which are time-minimizing migrants in spring (van de Kam *et al.* 2004). In contrast, the differences are large in species in which the breeding roles of the males and females are asymmetrical, such as the polygynous and polyandrous Ruff *Calidris pugnax* (Jukema & Piersma 2000), in which only the females tend broods and usually migrate further than the males (Cramp & Simmons 1983, van de Kam *et al.* 2004). Other examples are the Curlew Sandpiper *Calidris ferruginea* (Barshep *et al.* 2013), a time-minimizing migrant, in which the males leave the breeding grounds soon after the eggs are laid and the females tend the brood, and the Purple Sandpiper *Calidris maritima* (Summers *et al.* 2004), another time-minimizing migrant, in which the females leave as soon as the chicks hatch and the males raise the young (Cramp & Simmons 1983, Tomkovich 1988). Moult studies have focused on species which use coastal habitats because inland waders tend to be dispersed and therefore difficult to catch (Remisiewicz 2011). Furthermore, sex differences have mostly been studied in strongly dimorphic species, but rarely in monomorphic species, which are difficult to sex without molecular methods (Battley *et al.* 2004). The moult schedules of males and females in species with dimorphic sexes have been relatively well described, but the fuelling patterns of the sexes in monomorphic species have received less attention (Jukema & Piersma 2000, Summers *et al.* 2004, Howell 2010, Conklin & Battley 2012, Barshep *et al.* 2013). Moult schedules might influence the fuelling rate in migrants (Remisiewicz *et al.* 2017, 2019), which is decisive for the timing of departure (Fusani *et al.*, 2009, Eikenaar *et al.* 2016) and migration strategy (Alerstam & Lindström 1990). That in turn would determine the timing of migration south and north in long-distance migrants. Knowledge of the relationship between the timing of moult and of fuelling, and the flexibility of these processes, facilitates wader conservation in the face of global climate changes and habitat loss.

Little Stints are one of the smallest wader species breeding in the high-Arctic tundra (Tjørve *et al.* 2007). They are long-distance migrants to non-breeding grounds which span the Mediterranean coasts and throughout sub-Saharan Africa to South Africa in the south and southwest Asia in the east (del Hoyo *et al.* 1996). Individual birds are difficult to sex in the field; females are, on average, larger than males, but there is a large overlap in the range of their body measurements (Prater *et al.* 1977). Their mating system involves successive bigamy of both sexes, where the female lays a first clutch with a first male and then lays a second clutch with a different male. The first male incubates the first clutch and the female incubates the second; the second male incubates the clutch of his first female (Cramp & Simmons 1983). Behaviourally and physiologically, male and female Little Stints perform different activities during the breeding season. Males compete with each other to establish territories and use them for acrobatic and energy-sapping display flights (Underhill *et al.* 1993). The female (26.6 g) usually lays eight eggs in two clutches in quick succession (eggs average 6 g each (Cramp & Simmons 1983), *c.* 48 g in total). Considering the long distance of migration and this huge breeding effort, the female Little Stints are probably income breeders, which rely on the food supply at their breeding grounds to produce eggs, as do most Arctic waders (Drent & Daan 1980, Klaassen *et al.* 2001). The selective pressures on males and females on the breeding grounds differ greatly, with consequences for their biology, including while on migration and on the non-breeding grounds.

After arrival at the non-breeding grounds in sub-Saharan Africa in September–October (Chandler 2013), males and females undergo a complete post-breeding moult (Prater *et al.* 1977). In January–March they begin a partial pre-breeding moult of body feathers to attain a variable proportion of breeding plumage before departure to the breeding grounds in mid-March–April (Prater *et al.* 1977, Underhill 1997). Most first-year Little Stints leave the non-breeding grounds and attempt to breed, in contrast to many larger waders (Summers *et al.* 1995, Underhill 1997, Taylor & Navarro 1999, Underhill *et al.* 1999, Remisiewicz 2011). Previous moult studies on the biology of Little Stints have lumped males and females, and have not examined sex-related differences (Middlemiss 1961, Dean 1977). Studies of body moult, a part of the overall moult, have been impeded by a lack of appropriate statistical methods and have been mainly descriptive (Middlemiss 1961, Dean 1977, Zwarts *et al.* 1990, Ferns 2003) or have applied simple statistics (Battley *et al.* 2006, Meissner *et al.* 2012), and thus could not trace the detailed progress of the process.

We expected that the sex differences in Little Stints' mating and parenting duties would require different pre-breeding preparations. Our aim was to determine whether male and female Little Stints at a non-breeding ground in South Africa used different strategies for pre-migratory fuelling, departure timing and pre-breeding body moult to prepare for their northward migration.

METHODS

Data collection

We caught Little Stints at Barberspan and Leeupan (26°33′S, 25°36′E; North West Province, South Africa), adjoining pans which are a BirdLife-designated Important Bird Area and a Wetland of International Importance under the Ramsar Convention because of their significance as a stopover and final non-breeding destination for waterbirds, including Palaearctic migrants (Barnes 1998, Lipshutz *et al.* 2011, Remisiewicz & Avni 2011). Barberspan Bird Sanctuary is a 3118-ha provincial nature reserve centred on the shallow, alkaline and perennial Lake Barberspan fed by the Harts River (Cowan 1995). Unlike the hundreds of ephemeral local pans, Barberspan Lake does not dry up during droughts and is the only permanent waterbody in the surrounding area (Milstein 1975). Leeupan is a large but shallow hyper-alkaline pan; water levels change rapidly and it dries up in most years, creating favourable but unpredictable conditions for many waterbirds (Barnes 1998).

We caught 222 Little Stints at Barberspan in 2008–2016 and 2018, and 19 in 2017 at a shallow wetland next to Leeupan (26°30’6.40"S, 25°36’34.83"E) between 27 January and 29 April before their departure to the breeding grounds. We used mist-nets at night and walk-in traps by day (Busse & Meissner 2015), depending on water levels and the activity of the Little Stints. We ringed all individuals and aged them as full-grown because immatures from the previous breeding season are indistinguishable from adults after they moult into adult plumage (Prater *et al.* 1977). One observer (M.R.) took all morphological measurements of each bird, including wing length on the flattened and straightened wing (Evans 1986), measured to 1 mm with a ruler, and body mass with an electronic scale to 1 or 0.1 g. We recorded body moult by assessing the percentage of coverage by new, breeding plumage, assessing feathers in six plumage tracts, three on the body (head, scapulars, back and mantle (excluding rump; hereafter 'back')) and three on the wings (lesser, median and greater coverts) (Fig. S1). We used eight categories to score each tract (Meissner *et al.* 2012): 0% for all old feathers, 1% for birds with single new feathers, four categories on a 20%-interval scale, 99% for almost complete breeding plumage and 100% for all new feathers. We also assessed the percentage of feathers in pin (Page 1974) in six plumage tracts: head, neck, back, scapulars, coverts and belly, and checked whether a bird seemingly in full breeding plumage had finished body moult. Only two observers (M.R. and A.M.), who had calibrated their scoring with each other, scored the plumage. From each individual we took a blood sample and preserved it in 96% ethanol for DNA-sexing (Niemc *et al.* 2018). For the analyses we combined the data of all birds from 2008–2018 at both locations; samples used in each analysis differed slightly depending on the set of measurements available for the included birds (Table 1).

Analysis of sex ratios during the pre-migratory period

To identify the trend in the proportion of sexes at the site over subsequent pentades of the pre-migratory period, we applied generalized additive models (GAMs) (Hastie & Tibshirani 1990, Wood 2017a), using the package mgcv 1.8-22 (Wood 2017b) in R 3.3.3 (R Foundation for Statistical Computing 2017). To test whether the proportion of sexes changed over time we used generalized linear models (GLMs) for data with binomial distribution (Crawley 2007). We tested the goodness-of-fit (GOF) of these models using the Hosmer–Lemeshow test, in which a significant *P*-value indicates poor fit (Hosmer & Lemeshow 1989).

Analysis of pre-breeding moult

We analysed moult records of Little Stints caught between 27 January and 29 April in 2008–2018. To analyse sex differences in the progress of pre-breeding body moult we used the method of Meissner *et al.* (2012), but modified it to be able to apply the Underhill–Zucchini moult model to the moult scores obtained (Underhill & Zucchini 1988, Underhill *et al.* 1990). The recorded moult scores for the three tracts on the body were transformed to a scale of 0–1: 0% = 0, 1–20% = 0.1, 21–40% = 0.3, 41–60% = 0.5, 61–80% = 0.7, 81–99% = 0.9, 100% = 1. The sum of the three values, doubling the value for back its relative area was about twice the size of other tracts, was defined as the Body Moult Index (BMI, range 0–4). The sum of the values for the lesser, median and greater coverts of the upper wing were defined as the Wing Covert Moult Index (WCMI, range 0–3). We developed separate indices for the body and the wing coverts because a preliminary analysis of each of the six plumage tracts showed that the wing coverts differed in moult pattern from the body; a similar approach was used by Meissner *et al.* (2012). We rescaled these indices into the range 0 (no breeding plumage) to 1 (full breeding plumage) to use the Underhill–Zucchini moult model (Underhill & Zucchini 1988, Underhill *et al.* 1990, Erni *et al.* 2013). We counted the date of capture as days since 1 January. We used Data Type 5, which assumes that birds that have not started to moult and those in moult are available for capture on each sampling occasion (Underhill *et al.* 1990). However, we considered that an unknown fraction of the Little Stints might depart from the study area on migration before or just after completing moult. We considered that the decision to depart could be governed either by reaching a certain fuel load or by a date in the

Table 1. Numbers of DNA-sexed male and female Little Stints caught in January–April 2008–2018 at Barberspan and Leeupan, North West Province, South Africa, and numbers of males and females for which moult scores, wing lengths, body mass and the calculated adjusted body mass (aBM) were recorded.

		Body moult status		Wing length (mm)		Body mass (g)		aBM (g)	
Sex	DNA-sexed	Pre-moult	In moult	*n*	Mean (sd)	*n*	Mean (sd)	*n*	Mean (sd)
Females	128	23	101	107	102.2 (±2.05)	121	24.39 (±3.934)	104	23.78 (±4.176)
Males	113	28	81	97	98.5 (±2.00)	109	21.87 (±2.863)	97	23.03 (±2.693)
Total	241	51	182	204	100.4 (±2.75)	230	23.19 (±3.683)	201	23.12 (±4.538)

Mean values and sd for the measurements are provided.

season. In either situation, we devised a strategy for compensating, at least partially, for the inconsistency with the assumption by increasing the weighting in our analysis of birds which were caught in moult after the general departure had started. We estimated two parameters of moult for males and females – the mean start date and its standard deviation. Most Little Stints continue their moult after leaving South Africa, with possible temporary suspensions during migration, as do other waders (Piersma & Jukema 1993), so drawing conclusions about the duration and the end of moult was unjustified in these conditions. The weighting strategy we used was driven by data analysis and is developed in the Results. To check whether sex affected the timing of Little Stint prebreeding body moult, we compared models which used sex as a covariate affecting parameters of moult (mean start date, standard deviation of start date) in various combinations with a model with no covariates (Table S1), using Akaike's information criterion (AIC) (Burnham & Anderson 1998), as in Remisiewicz *et al.* (2014). For all moult analyses we used the package moult 2.0.0 (Erni *et al.* 2013) in R 3.3.3 (R Foundation for Statistical Computing 2017).

Estimation of pre-migratory fuelling

Little Stints show a small degree of sexual size dimorphism (Cramp & Simmons 1983, Niemc *et al.* 2018), so to compare the progress of fuelling between males and females we calculated an adjusted body mass (aBM) to correct for size differences between the sexes (Summers *et al.* 1992). Of the various morphometrics we examined, males and females differed most significantly in wing length (Prater *et al.* 1977, Niemc *et al.* 2018), and therefore we used it for body mass adjustment, following Summers *et al.* (1992). We calculated the least squares linear regression equation between the natural logarithm of body mass (lnBM, in g) and wing length (lnWL, in mm). We used the slope coefficient (β) from this regression equation to estimate an aBM, as done by Summers *et al.* (1992), using the equation:

$$\mathrm{aBM} = \mathrm{BM} \times \frac{\mathrm{meanWL}^{\beta}}{\mathrm{WL}^{\beta}}$$

where meanWL is mean wing length for all Little Stints that were caught, and WL and BM are the wing length and body mass of the bird the adjustment is being made for. This strategy removes the additional variability caused by birds of different sizes because masses were adjusted to that of a Little Stint with an average mean wing length. To model seasonal changes in body mass during the pre-migratory period we applied a locally weighted regression smoother (Summers *et al.* 1985; R code in Remisiewicz *et al.* 2017) and used quantile regression (Kirkman *et al.* 2013, Remisiewicz *et al.* 2019) with a smoothing parameter of 25 days (R package quantreg; Koenker 2017). Light and heavy birds were present at the study site in the prebreeding season, so we used only the upper quartile of the heaviest birds when deriving the trend in body mass through time to ensure we analysed only individuals which were fuelling (Remisiewicz *et al.* 2019). We then calculated daily increments of the smoothed body mass curve to find the starting date of pre-migratory fuelling, defined as the first date on which the daily increase was larger than 0.1 g. We divided the fuelling period into two sections: period 1, when both sexes were present at the study site, and period 2, after the males had begun departing and mostly females remained at the site. We compared the mean rates of fuelling between male and female Little Stints in period 1, and for the females from the end of period 1 to the end of 2, using a pairwise permutation test with 1000 permutations (Manly 2007).

Estimation of potential flight ranges

To investigate sexual differences in Little Stint migration strategies, we compared their potential flight ranges using the equation given by Davidson (1984):

$$R = 95.447 \times \mathrm{S} \times (a\mathrm{BM}^{0.302} - a\mathrm{LBM}^{0.302}),$$

where S is flight speed (km/h), aBM is adjusted body mass (g) and aLBM is the adjusted mean lean body mass (g), common for both sexes. We used a flight speed of 75 km/h, suggested by Summers and Waltner (1979). To calculate aLBM, we averaged the smallest 10% of the adjusted body masses of males and females combined ($n = 23$). We computed individual fuel loads by subtracting lean body mass from the adjusted body mass (Remisiewicz *et al.* 2014). For each sex separately we calculated the mean potential flight ranges for 20% of the heaviest males and females. The distributions of fuel loads and flight ranges departed from normal, so we used the *U*-test to compare the sexes. All statistical analyses and specialized R packages were run in R 3.3.3 (R Foundation for Statistical Computing 2017).

RESULTS

Differences in sex ratio and pre-breeding body moult of males and females

Of the 241 Little Stints we caught, DNA sexing showed that 128 were females and 113 males. In January to mid-February, males constituted 57% of the captured birds (Fig. 1), which did not differ significantly from a 50:50 sex ratio (Chi-square test with Yates' correction: $\chi^2 = 0.15$, $P = 0.70$). From mid-March the numbers of Little Stints and the proportion of males at the study area decreased (Fig. 1, GLM: day = –0.0178, se = 0.0059, $Z = -3.02$, $P = 0.0025$, Hosmer–Lemeshow GOF: $P = 0.11$), although a few males were still present at the site until the end of April (Fig. 1). Most of the birds we caught had a Body Moult Index (aBMI) and a Wing Covert Moult Index (aWCMI) between 0 and 0.2, with fewer birds (43.7% for aBMI, 33.9% for aWCMI) having a moult index higher than 0.2, independent of date (Fig. S2). Therefore, we assumed that the decision to depart was primarily governed by the bird reaching a stage of moult rather than by the date in the season. To compensate for this effect, we increased by four the weighting of indices for birds with a Moult Index > 0.2: $n = 94$ for aBMI and $n = 79$ for aWCMI. After multiplying by four, the numbers of birds with moult indices > 0.2 in each 0.1-wide class approximately matched the numbers of birds with a Moult Index < 0.2 (Fig. S3), so the data met the requirements of the Underhill–Zucchini moult model. Different numbers of individuals had aBMI and aWCMI > 0.2, and hence after the four-fold weighting increase for these birds the sample sizes analysed for these indices differed (Figs 2, 3 and S3, Table 2). Although some birds appeared to have moulted completely into breeding plumage because all the new feathers were of the breeding type, they still had a few feathers in pin, meaning that moult was still in progress. We considered the possibility that we had overestimated the moult indices for these birds, so we rescaled all their moult indices to a maximum of 0.8 to compensate for this effect. By the time of their departure from South Africa, Little Stints had moulted 50–80% body and wing coverts (Figs 2 and 3). For aBMI the best-fitted

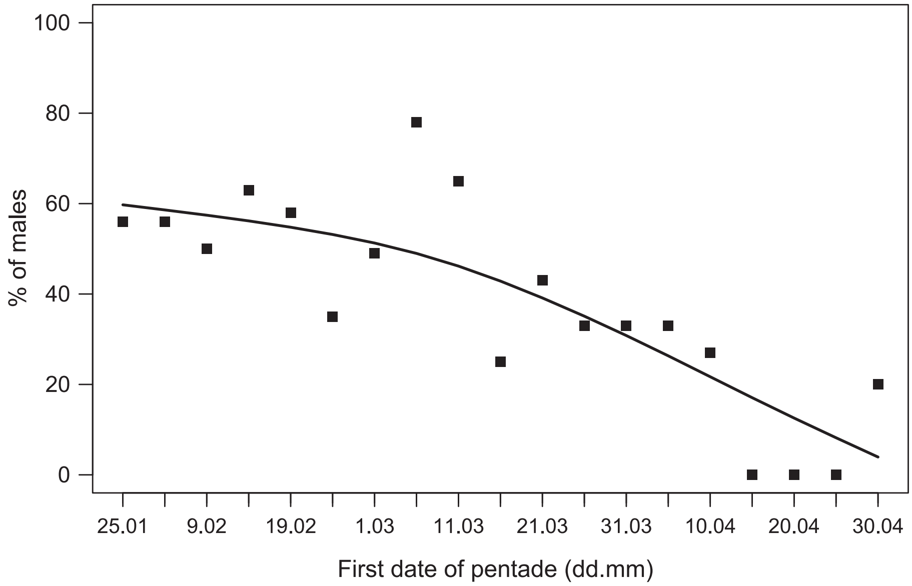

Figure 1. Changes in the proportion of male ($n = 113$) and female ($n = 128$) Little Stints caught in subsequent pentades of the pre-migratory period (January–April) in 2008–2018 at Barberspan and Leeupan. Black squares = percentage of males among the birds caught in the pentade. Continuous line = the trend in the proportion of males over time modelled by a general additive model (GAM), $R^2 = 0.657$; the significance of the effect of time: $P = 0.00096$.

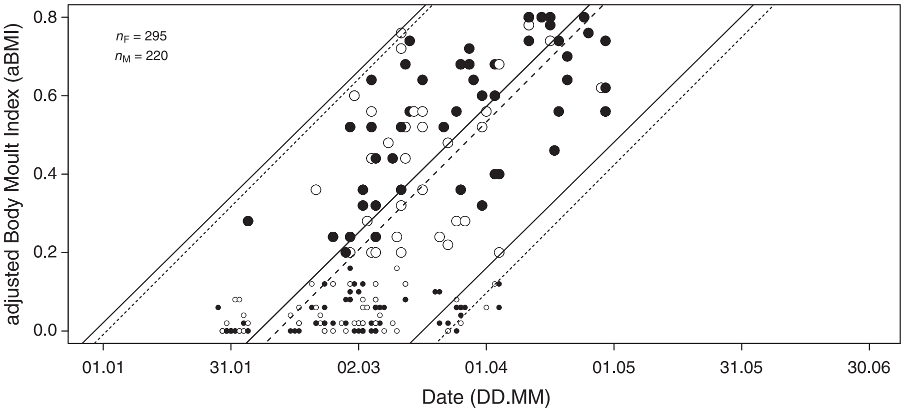

Figure 2. Progress of upper body moult of Little Stints caught in January–April 2008–2018 at Barberspan and Leeupan. Black circles = females, open circles = males, thick lines = mean course of moult, thin lines = 95% Prediction Interval (continuous lines = females, dashed lines = males); n_F = sample size of females, n_M = sample size of males. Large points = birds whose weighting was increased by four for the analysis (Moult Index > 0.2).

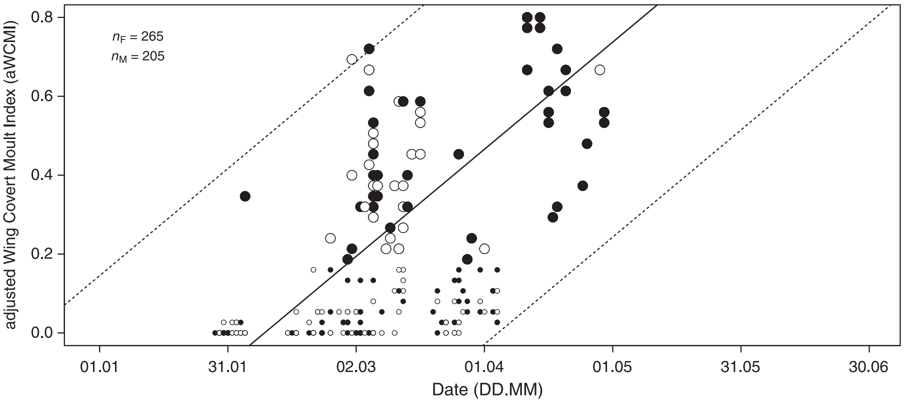

Figure 3. Progress of wing covert moult of Little Stints caught in January–April 2008–2018 at Barberspan and Leeupan. Black circles = females, open circles = males, thick line = mean course of moult, dashed line = 95% Prediction Interval; n_F = sample size of females, n_M = sample size of males. Large points = birds whose weighting was increased by four for the analysis (Moult Index > 0.2).

model was the one where the mean start date of moult differed between the males and the females, and the standard deviation and duration did not differ between the sexes (Model 1 in Tables S1 and Table 2, Fig. 2). For aWCMI the best-fitted model was the one in which the moult parameters for both sexes did not differ (Model 1 in Table S1). The estimates of moult timing shifted by 3–10 days, depending on which weighting factor we applied (Table S2).

Sex differences in pre-migratory fuelling and potential flight ranges

Males had on average 3.7 mm longer wings than females ($t_{202} = -12.95$, $P < 0.001$, Table 1). Thus, we calculated adjusted body mass (aBM) using the slope coefficient β from the regression equation:

$$\ln \mathrm{BM} = -6.90 + 2.18 \times \mathrm{InWL}.$$

($F_{1,199} = 37.3$, $P < 0.001$, $R^2 = 0.15$) and the mean wing length (meanWL) of 100.4 mm, calculated for both sexes combined.

Little Stints of both sexes began fuelling about a month after the start of their pre-breeding moult. The sexes did not differ in the rate of fuelling (Table 3) but females stayed longer at the non-breeding site and thus the heaviest 20% of females on average accumulated 3.5 g, 18% of the adjusted lean body mass (aLBM), more fuel than the heaviest males (Table 3, Fig. 4). After mid-

Table 2. Parameters of pre-breeding moult estimated from adjusted Body Moult Index (aBMI) and adjusted Wing Covert Moult Index (aWCMI) for full-grown Little Stints caught in January–April 2008–2018 at Barberspan and Leeupan, according to the best models (Table S1).

	Moult parameters		
Moult index/Sex	*n* (n_{adjusted})	Mean start date (se)	sd of start date in days (se)
aBMI			
Females	124 (295)	7 February (±2.7)	20 (±5.0)
Males	109 (220)	12 February (±2.8)	20 (±6.2)
aWCMI			
Females + Males	233 (470)	10 February (±2.7)	28 (±7.3)

n_{adjusted} = sample sizes after increasing by four the weighting of those with aBMI > 0.2 or aWMI > 0.2, respectively, in the analysis (see Results).

April the females' fuelling rate increased by 95% in comparison with the earlier period (Table 3, Fig. 4). The estimated flight range, based on aLBM of 19.5 g common for both sexes, was *c.* 700 km longer for females (Table 4).

DISCUSSION

The selection pressure on males, which compete for territories and for females, favours the early arrival of males at the breeding grounds (Kokko 1999, Kokko *et al.* 2006). The greater the sexual dimorphism in a species in plumage and size, the greater the protandry, as shown in passerines, hirundinides and bee-eaters, but this phenomenon has rarely been studied in monomorphic species because they are difficult to sex in the field (Spottiswoode *et al.* 2006, Briedis *et al.* 2019). In waders, with their variety of mating and parental care patterns (Székély *et al.* 2006), asymmetrical involvement in reproduction might shape sex differences in their next life-stages more than sexual dimorphism (Summers *et al.* 2004, Conklin & Battley 2012, Barshep *et al.* 2013). Thus, we expected some differences in the timing of the non-breeding stages, such as moult and pre-migratory fuelling, in a wader with little sexual dimorphism but with different roles in parental care, such as the Little Stint. The timings of migration, moult and fuelling are similar for both sexes of species in which both parents incubate and care for the young, such as Bar-tailed Godwit, but species with asymmetrical parental care tend to show more pronounced sexual differences, as in Ruff, Curlew Sandpiper and Purple Sandpiper (Cramp & Simmons 1983, Jukema & Piersma 2000, Summers *et al.* 2004, van de Kam *et al.* 2004, Conklin & Battley 2012, Barshep *et al.* 2013). Despite the lack of distinctive sexual dimorphism in size or plumage in Little Stints, we found sex differences in the timing of migration, moult and fuelling. These differences are presumed to be related to migration strategies which vary between the sexes, and which are likely to be linked to their mating strategies and different breeding roles. Our results showed that the progress of moult and fuelling was similar in male and female Little Stints and that both sexes were able to moult into breeding plumage and to fuel simultaneously during the pre-migratory period (Figs 2–4). However, males began their departure from the southern non-breeding grounds to the northern hemisphere breeding grounds a few weeks earlier than the females (Fig. 1) and therefore the heaviest males

Table 3. Estimated fuelling periods and rates for male and female Little Stints caught in January–April 2008–2018 at Barberspan and Leeupan in two periods: period 1 – common fuelling period for both males and females; period 2 – period when mostly females stayed at the site after the departure of males.

Sex/fuelling period	Duration of fuelling (days)	Fuelling period	Mean fuelling rate (sd) (g/day)	Comparison of fuelling rates
Period 1				
Males	34	15 Mar–17 Apr	0.25 (±0.25)	*P* = 0.352
Females			0.20 (±0.15)	
Females				
Period 1	34	15 Mar–17 Apr	0.20 (±0.15)	***P* = 0.001**
Period 2	13	18 Apr–30 Apr	0.39 (±0.28)	

Fuelling rates were compared between the sexes, and between the two periods for females, using pairwise permutation tests. Significant *P*-values are presented in bold type.

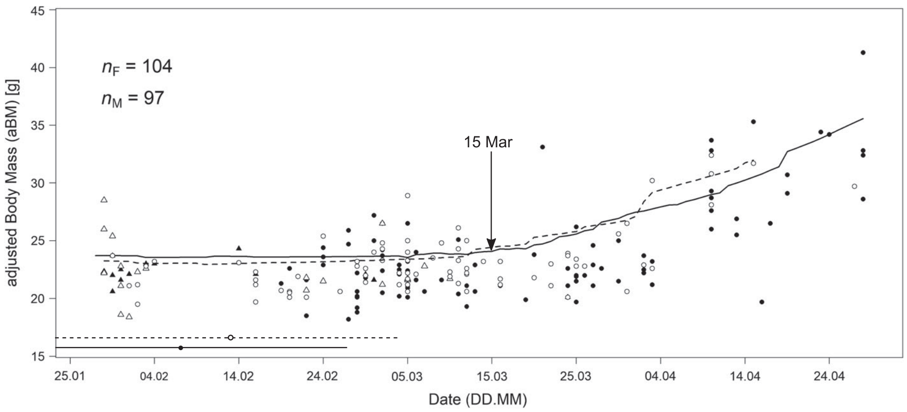

Figure 4. Adjusted body mass in relation to the date of capture for male (open circles) and female (black circles) Little Stints. Lines show body mass trend (locally weighted quantile regression) of the 75th percentile of body mass; arrow and date show the beginning of fuelling, indicated by daily increments of body mass >0.1 g. Triangles = pre-moult birds; circles = moulting birds. Horizontal lines and markers above the *x*-axis = mean dates and sd of the body moult start (Table 2) for females (black circles, solid lines) and males (open circles, dashed lines).

carried fuel loads 18% lighter than the heaviest females and were less advanced in body moult (Fig. 2). We will discuss these findings in the context of potential trade-offs between moult and fuelling in the sexes which might have carry-over effects on their subsequent migration strategy and performance at the breeding grounds.

Moult and fuelling consume energy, and thus one process might compromise the other (Newton 2009) and conducting both activities simultaneously entails trade-offs in the allocation of resources between these processes (Morton & Welton 1973, Lindström *et al.* 1993). Moult requires a fast turnover of body proteins and a large expenditure of energy on the production of feathers and on thermoregulation because of reduced insulation (Ginn & Melville 1983, Rohwer & Rohwer 2013). In contrast, fuelling involves the storage of energy in deposits of fat and protein as fuel to power migration (Jenni-Eiermann & Jenni 1996). In migrant birds, moulting, especially of large flight feathers, and fuelling tend to be separated in time so that the energy expense of these activities does not overlap (Newton 2009, Remisiewicz 2011). Our results, however, suggest that Little Stints are capable of moulting and fuelling simultaneously in habitats with abundant food, such as Lake Barberspan (Remisiewicz & Avni 2011, Cumming *et al.* 2013). Partial pre-breeding moult involves the replacement of small body feathers, which requires less energy than growing large feathers and therefore might facilitate this overlap. Little Stints which leave South Africa with incomplete breeding plumage might continue replacing body feathers during migration, as do many other waders, such as Temminck's Stints *Calidris temminckii* (Lislevand 2017) and Common Snipes *Gallinago gallinago* (Podlaszczuk *et al.* 2017), for which moulting flight feathers during migration does not induce a stress response (Włodarczyk *et al.* 2018). Alternatively, Little Stints might suspend body moult during migration and resume it at stopovers on route to the breeding grounds, as do Bar-tailed Godwits (Piersma & Jukema 1993).

Those Little Stints which were least advanced in body moult late in the season (Figs 2 and 3) are most likely to be immatures. They arrive at the non-breeding grounds about 3–4 weeks later than the adults (Urban *et al.* 1986; present authors' unpubl. data) and therefore their primary moult is delayed by about 3 weeks (Pearson 1984). Body moult might be delayed by the same time. From January until departure, Little Stints cannot be aged by plumage or morphometrics (Prater *et al.* 1977), and thus we were unable to confirm whether the late moulters were immatures. Immature Little Stints are unusual among Palaearctic migrant waders because most migrate back to the breeding grounds with the adults and do not spend an austral winter in southern Africa (Summers *et al.* 1995, Underhill 1997, Taylor & Navarro 1999, Underhill *et al.* 1999). Therefore, the departure date imposes the same time constraint on the immatures as on adults. However, the first-year birds might be

Table 4. Estimated fuel loads and flight ranges according to Davidson's (1984) formula of the heaviest 20% of male and female Little Stints caught in January–April 2008–2018 at Barberspan and Leeupan. Mean fuel loads and potential flight ranges differed between the sexes (*U*-test: $P = 0.001$).

	Fuel load (g)			Flight range estimates (km)			
Sex	Mean (sd)	Min.	Max.	Mean (sd)	Min.	Max.	*n*
Females	11.20 (±3.90)	6.8	21.9	2538 (±745.1)	1645	4464	21
Males	7.70 (±2.60)	4.6	13.0	1823 (±540.2)	1166	2915	20

delayed further on route because they are less experienced in foraging and choosing stopover sites with abundant food, which might lead to their slower migration with lower fuel loads and later arrival at breeding areas than adults (Hockey *et al.* 1998).

Our results suggest sex differences in the premigratory fuelling of Little Stints in South Africa. A proportion of the females stayed longer at the non-breeding site and accumulated fuel loads about 18% heavier than the males (Table 4). Thus, they probably required fewer stopovers on route (Nilsson *et al.* 2013). We observed the last females at Barberspan on 28 April (Fig. 3). The heaviest females would have been able to fly to the Nile Valley in a non-stop flight using the fuel they had accumulated (Table 4), although these estimates should be treated cautiously. The breeding season in Siberia, about 12 000 km away, begins in June (Hildén 1983, Cramp & Simmons 1983). Thus, these females would have about a month to arrive in time for nesting, and large fuel stores would facilitate their fast movement. Male Little Stints depart from the non-breeding grounds in South Africa with, on average, less advanced breeding dress and lower fuel loads than females, which suggests that initially at least they undertake short non-stop flights (Figs 2 and 3, Table 4). The departure fuel loads of males would enable the first flight to reach the Limpopo River valley, the Rift Valley lakes or the Indian Ocean coast in Mozambique (Table 4). Their early start to migration would provide the males time for refuelling on route. The selection pressure on males, which compete for territories and females, favours the early arrival of males at the breeding grounds (Kokko 1999, Kokko *et al.* 2006). This would explain their early departure from South Africa. Little Stints of both sexes arrive at the breeding grounds in June with an average fat store of 1.6 g (Tulp *et al.* 2009), reserves which might be used as a backup in case of adverse weather and delays in snowmelt (Tulp *et al.* 2002, Tulp & Schekkerman 2006). Producing two clutches of four eggs each by the females, about 1.7 times their body weight, from late June to early July (Hildén 1983, Kania & Chylarecki 1992, Tomkovich & Soloviev 1994, del Hoyo *et al.* 1996) requires greater energy reserves. Most Arctic waders are income breeders which use the local food supply at the breeding grounds to produce eggs (Drent & Daan 1980, Klaassen *et al.* 2001, Hobson & Jehl 2010). Considering their small fuel stores on arrival in Siberia (Tulp *et al.* 2002, Tulp & Schekkerman 2006), we suggest the deficit in the females' reserves shows that these Little Stints are income breeders, which would require them to supplement with local food before egglaying. We cannot exclude that female Little Stints might use some endogenous lipid and protein supply to produce the early laid eggs, as in Ruddy Turnstones *Arenaria interpres* breeding in the High Arctic (Morrison & Hobson 2004), but these nutrients would come from stopover sites closer to the breeding grounds. We suggest that it is the difference in fuel loads between the males and the females on their departure from South Africa that determines their sex-differential migration strategies, considering the *c.* 12 000 km they cross between South Africa and Siberia, rather than the sex differences in their energy capital upon their arrival at the breeding grounds.

The coasts and lakes of the Rift Valley in Kenya, Lake Uromiyeh in Iran and the Caspian region support large flocks of Little Stints on migration in April–May (Pearson 1987, Delany *et al.* 2009). Little Stints of both sexes probably use the stopover sites to continue their body moult, as do Bar-tailed Godwits (Piersma & Jukema 1993), and to accumulate energy stores to complete their migration and initiate breeding. Little Stints are capable of raising one clutch per adult, rather than the normal one clutch per pair.

The earlier the males establish their territories and the earlier the females lay the first clutch, the more likely the males will be able to father the second clutch, and the females will be able to raise it successfully (Hildén 1983, Tulp & Schekkerman 2006). Furthermore, early arrival probably enables males to occupy better territories than those arriving later and decreases the chance of extra-pair paternity in their first clutch (Kokko 1999, Kokko *et al.* 2006). Thus, the selection pressures differ between the sexes, favouring early arrival of the males and later arrival of the females, which would correspond to the differences in the migration strategy of the sexes we described.

The males depart South Africa with smaller fuel loads, but earlier than the females, which leave with more reserves. We expect that the males thus use an energy-minimizing migration strategy to reach the breeding grounds before the females, and that females use a time-minimizing strategy, at least for the first stages of their journey north. Our results correspond with the findings that the main determinants of sex differences in arrival time at the breeding grounds in migrants are their different departure timings from Africa and migration duration (Briedis *et al.* 2019). We suggest that sex differences in the timing of pre-migratory fuelling, and departure, as we showed in Little Stints, contribute to their sex-differential migration to their northern-latitude breeding grounds.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Plumage tracts of Little Stints for which we assessed the percentage of new feathers.

Figure S2. Distribution of values of adjusted Body Moult Index (aBMI, top) and adjusted Wing Covert Moult Index (aWCMI, bottom) of male and female Little Stints caught during the pre-migratory period (January–April) in 2008–2018 at Barberspan and Leeupan (NW Province, South Africa).

Table S1. Moult models used to determine the effect of sex on moult parameters using adjusted Body Moult Index (aBMI) and adjusted Wing Covert Moult Index (aWCMI) of full-grown Little Stints caught in January–April 2008–2018 at Barberspan and Leeupan.

Table S2. Parameters of pre-breeding moult estimated from adjusted Body Moult Index (aBMI) and adjusted Wing Coverts Moult Index (aWCMI) for full-grown Little Stints caught in January–April 2008–2018 at Barberspan and Leeupan, depending on the weighting factor (1 to 4) applied to increase the numbers of birds with aBMI > 0.2 and aWM > 0.2 in the analysis.