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Great Snipes in sub-Saharan Africa: seasonal patterns of abundance, moult and body mass in relation to age and sex

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Great Snipes *Gallinago media* spend about eight months per year in sub-Saharan Africa, but most aspects of their non-breeding ecology are poorly known. We analysed the seasonal pattern of appearance, flight feather moult (primaries and secondaries), and body mass in relation to age and sex, based on 3,247 birds collected by hunters in 1990–2000 in Benin, Gabon, Cameroon and the Democratic Republic of Congo. Adult males arrived in Africa from mid-August with a suspended flight feather moult. Adult females on average arrived somewhat later, and were about one month behind in the progress of flight feather moult. The adults of both sexes resumed moult immediately upon arrival. Flight feather moult was generally completed by the end of November in males, and end of December in females. Juvenile Great Snipes arrived later than adults and did not moult their flight feathers. The temporal pattern of occurrence at the different study sites suggests a general relocation of snipes from West Africa to Central Africa in October–December. Body masses did not differ between age groups and were generally low from August to February (155–170 g in males and 165–185 g in females). Males apparently departed northwards from late March to late April, and the females about two weeks later. Prior to departure, body mass increased on average with about 50 g (in both sexes), suggesting a departure fuel load of 31–33% above lean body mass. In periods of high and stable mass increase, fuel was deposited at rates of about 0.8–1.3 g/d (or 0.5–0.8% of lean body mass/d). The heaviest males and females had a total body mass of 242 and 250 g, respectively. This kind of traditional natural history data forms an important complement to the new type of data emerging from modern tracking techniques.

Keywords

migration
fuel deposition
shorebirds
waders
hunting

INTRODUCTION

The Great Snipe *Gallinago media* breeds in northeast Europe and western Asia, and winters in sub-Saharan Africa (del Hoyo *et al.* 1996, Delany *et al.* 2009). It may be most famous for its spectacular lekking behaviour (Lindblad 1863, Glutz von Blotzheim *et al.* 1977, Cramp & Simmons 1983), but recent studies have revealed an equally spectacular migratory behaviour. A study based on geolocators of Swedish-breeding Great Snipes revealed that adult males (females were not studied) migrate 5,000–7,000 km non-stop in early autumn, at very high speed, from northern Europe to sub-Saharan Africa (Klaassen *et al.* 2011, Lindström *et al.* 2016). The snipes then make

a stopover of 2–4 weeks in the Sahel zone of West Africa, before continuing to the final winter grounds around the Equator in central Africa. After about seven months they make another long non-stop flight, this time northwards to eastern Europe, and from there they continue in smaller hops back to their Swedish breeding grounds (Klaassen *et al.* 2011, Lindström *et al.* 2016).

Whereas it was long known that Great Snipes winter in sub-Saharan Africa, there is clearly a shortage of data on their ecology from the eight months the snipes spend in Africa (Glutz von Blotzheim *et al.* 1977, Cramp & Simmons 1983, del Hoyo *et al.* 1996, Delany *et al.* 2009). Here we present data on the seasonal appearance, flight feather

Fig. 1. The four general sites in sub-Saharan Africa where Great Snipes were collected in 1990–2000: (1) Benin, (2) Gabon, (3) Cameroon, and (4) The Democratic Republic of Congo. The dark grey dots show where individual adult male Great Snipes from Scandinavia made a three-week-long stopover in late August–mid-October, according to data from geolocators (Lindström *et al.* 2016). The white dots show the general wintering grounds of the same birds.

moult, and body mass of Great Snipes in sub-Saharan West Africa, based on hunting bags of Great Snipes collected over 10 years.

The data presented originate from an unpublished doctoral thesis in veterinary science by EJMD at the Paul-Sabatier University in Toulouse, France, in 2003 (Debayle 2003). A small part of the data has been published previously by Devort & Paloc (1992).

METHODS

Study sites and collection

All the Great Snipe data in this study originate from hunters in Africa who voluntarily have sent in their information to MD, following a general call by MD through the International Club of Snipe Shooters. The main goal of this club is to protect snipe habitats and use the bagged birds for scientific purposes. Data on 3,247 Great Snipes were received from five localities in four countries in sub-Saharan Africa (Fig. 1). These birds would have been hunted anyway, but in this way there was a possibility to

gain knowledge that otherwise would have been extremely difficult to obtain. The timing and intensity of data collection could not be influenced by us, but at two sites the hunting started and ended with the general presence of snipes and, accordingly, was systematic enough to allow a description of seasonal patterns.

Benin – This site is close to the Benin coast, between Pahou and Ouidah, at about 6°23'N, 2°10'E (Devort & Paloc 1992). The site consists of 300 ha of damp meadows with varying water levels, some being cultivated during the dry season, and others grazed. In total 1,588 Great Snipes were reported by Mr. R. Paloc, with 50–449 birds per year in nine out of ten winter seasons from 1990/1991 to 1999/2000 (no data collected 1998/1999). Hunting was carried out about twice per week from the second half of August to January. The length of the hunting season was strictly governed by the presence of birds in the area (R. Paloc pers. comm.).

Gabon – In total 1,473 birds (7–337 per year) were collected by Mr. Babuin and Mr. M. Horent in the coastal marshes near Port-Gentil (0°41'S, 8°44'E), from early September to early May over eight seasons from 1992/1993

to 1999/2000. Also here the length of the hunting season was governed by the presence of birds in the area.

Cameroon – Birds were collected by Mr. Gamel, Mr. Pichavant and Mr. Blay in a non-systematic way, from the end of September to early November at two ‘wet’ sites with grazed grassland: Garoua (9°19'N, 13°26'E) and Ngaoundere (7°21'N, 13°37'E). The sites are situated around 1,200 m above sea level (a.s.l.) and about 250 km apart. Birds were collected in Garoua ($n = 99$) in 1994 and 1998, and in Ngaoundere ($n = 65$) in 1992, 1994 and 1995. Data from the two Cameroonian sites are lumped in the analyses ($n = 164$).

The Democratic Republic of Congo (DR Congo) – In total 22 Great Snipes were collected by Mr. Fagel near Bianco on the Manika plateau (10°13'S, 26°05'E, 1,800 m a.s.l.) on 9–12 December 1990 ($n = 3$) and 23–24 February 1991 ($n = 19$).

Measurements, ageing, sexing and moult scoring

Upon collection, the birds were weighed to the nearest 1 g, or sometimes 10 g. Birds collected in Cameroon were not weighed. Bill + head length (*BillHead*) was measured to the nearest half or full mm, from the back of the skull to the tip of the bill (Green 1980). This was done by the hunter directly after the hunt (i.e. on freshly dead birds). One wing and the tail were taken from each bird, stored in an envelope and sent to MD.

In total 1,481 of the Benin birds were determined to sex and age through autopsy (all done by R. Paloc, directly upon collection). Sexing was based on the presence of either testes or ovaries and oviducts. Ageing was based on the presence of Fabricius bursae in juvenile birds, which adults do not have. In females, additional indications of age can be found in the sexual organs. In adults the oviduct is wide and sinuous since eggs have gone through, whereas in juveniles it is straight and thin. All birds were later aged also by MD, based on the presence of juvenile wing coverts, tertials and tail feathers, where juveniles have barred outer tail feathers, and narrow and duller white edges to wing coverts. Birds that were not autopsied were sexed on the basis of *BillHead* length, as gauged on the basis of the Benin sample (see *Results*).

The moult of the 10 primaries and 11 secondaries was scored by MD on the collected wings, according to Ginn & Melville (1983). An old feather scores 0. A missing (shed) feather, or a growing feather still in pin, scores 1. Growing feathers no longer in pin score 2–4 depending on their length in relation to the full-grown feather, and a fully-grown feather scores 5. Accordingly, the total moult score (MS) for one wing may vary between 0 (all flight feathers unmoulted) and 105 (all flight feathers replaced).

Two birds with the same MS can be in quite different stages of moult. For example, a MS of 20 can be achieved by moulting at high intensity, having two fully grown feathers, one feather in moult stage 1, three in moult stage 2 and one in stage 3, but also by not moulting actively, having four new fully-grown primaries but no

actively growing feathers. The birds in these two examples are in different ecological phases (actively moulting versus not moulting, respectively). To account for these ecological differences, all adults were grouped according the following criteria: *Not started* (MS = 0), *Active moult* (one or more growing with at least one of them in score 2 or 3), *Stopping* (several new fully grown feathers, 1–3 in score 4 and at least one feather score 0, suggesting the bird is about to suspend moult), *Suspended* (solely fully grown feathers, where both score 0 and 5 occur), *Resuming* (similar to *Suspended*, but with 1–3 feathers with score 1), and *Completed* (all primaries and secondaries new and fully grown; MS = 105).

We have analysed the data per site, given that different breeding populations may be involved and that there are most likely movements within sub-Saharan Africa in the non-breeding season (Lindström *et al.* 2016). However, we lumped data from all years per site, since we first of all want to describe the general pattern of Great Snipe occurrence in sub-Saharan Africa. In addition, with data from up to nine seasons per site, between-year variation should largely even out. On a few occasions we still refer

Table 1. The distribution of males and females Great Snipes in relation to head + bill size. All birds were collected in Benin and sexed by autopsy (see *Methods*).

Head+Bill (mm)	Males <i>n</i>	Females <i>n</i>	Total <i>n</i>
87	2		2
88	2		2
89	14		14
90	46		46
91	87	1	88
92	168		168
93	204	1	205
94	157	1	158
95	86	3	89
96	27	26	53
97	8	64	72
98	3	108	111
99	5	117	122
100		158	158
101		99	99
102		60	60
103		25	25
104		7	7
105		1	1
106			
107		1	1
Total	809	672	1,481

Fig. 2. The number of Great Snipes of different sex and age classes collected per half month (Aug I, Aug II, etc.) in Benin, Gabon and Cameroon in 1990–2000 (cf. Fig. 1). Ad = adult, Juv = juvenile, M = male, and F = female.

to individual years, mainly to make clear that the overall pattern was not dependent on data from single years. Statistical analyses were carried out using R 3.2.0 (R Core Team 2015).

RESULTS

Sex and age determination

In the Benin birds, *BillHead* differed significantly between sex and age groups (two-way ANOVA, effect of sex: $t = 70.5$, $P < 0.001$, effect of age: $t = 2.66$, $P = 0.008$, after removing a non-significant interaction term). The average *BillHead* for the different groups were: adult males 92.7 ± 1.7 (SD) mm ($n = 284$), adult females 99.4 ± 1.9 mm ($n = 238$), juvenile males 93.0 ± 1.8 mm ($n = 525$), and juvenile females 99.6 ± 1.7 mm ($n = 434$).

Although the difference due to age is statistically significant, it is minute in biological terms (0.2–0.3 mm), especially compared to the difference between the sexes (6.6–6.7 mm). We therefore lumped the age groups when using *BillHead* for sex determination in birds not autopsied. Birds <96 mm were considered males and birds >96 mm

Fig. 3. The proportion of males among adult and juvenile Great Snipes per half month in Benin and Gabon in 1990–2000. Only half-month periods with more than 10 birds are included. For sample sizes, see Fig. 2.

as females. Using this criterion for sexing the autopsied birds, 98% of the males and 99% of the females would have been sexed correctly (Table 1). In the analyses including sex differences, the 130 birds with a *BillHead* of 96 mm were left out.

Seasonal occurrence

At two of the sites, birds were sampled over sufficiently long periods per season to allow an analysis of the seasonal occurrence (Fig. 2). In Benin, sampling started as soon as the first birds arrived (Mr. Paloc was waiting for them). There was a dominance of adult birds from the beginning. Their numbers peaked from late September to early November and then dropped drastically in the second part of November (Fig. 2). The adult Great Snipes were generally gone by mid-January. Except for a particularly high proportion of males in the second half of August, the proportion of males among adults increased slowly over the season (Fig. 3). It should be noted that the data from the second half of December and onwards come from three seasons only (1993/1994, 1996/1997 and 1997/1998) when good conditions for the snipes lasted longer into the winter. The juveniles arrived in Benin on average later than adults and numbers built up gradually until late October. The proportion of juveniles in the population increased steadily from around 10% in late August, to 50% in early December, and 100% in late February. In the second half of February the number of birds had decreased to such extent that hunting ceased. Juvenile males peaked in numbers later than juvenile females. The proportion of males among the juveniles increased steadily from 27% in early September to 60–80% in early December and onwards (Fig. 3).

In Gabon, 1,100 km southeast of Benin, Great Snipes arrived later, with only few birds collected in September. Numbers increased dramatically in early October, when mainly adults entered the area. Their numbers peaked in late October and early November. From then on, the number of adults was low but fairly steady until April. The first juveniles arrived in late October, on average a month later than the first adults. The number of juveniles increased into December and then stayed fairly constant until early April. The proportion of males among the Gabon birds increased slowly from 50–60% in September–October to 80–90% in the second half of March (a similar pattern in both age groups; Fig. 3). In adults the proportion of males subsequently dropped dramatically down to 38% in early April and 4% in late April. The corresponding values among juveniles were 55% and 31%.

In Cameroon, the sampling period in autumn was quite short. The numbers of snipes were highest in the two first sampling periods (late September–early October), but much lower already by the end of October (Fig. 2). This suggests that there was a ‘wave’ of birds coming through in early autumn. There was no obvious pattern according to age, but possibly females (of both ages) dominated in early October.

The three birds in December in DR Congo were two juveniles and one adult (not sexed). In late February, 19 birds consisted of one juvenile male, one unsexed adult, one adult male and 16 adult females.

Moult

We do not describe the details of the flight feather moult of Great Snipes, but the general pattern is the following. Primary moult progresses in one sequence from P1 (the innermost primary) toward P10 (the outermost primary). Normally two to three primaries grow simultaneously, but on a few occasions four or even five. The secondary moult starts simultaneously with S1 (the outermost) and S11 (the innermost) and is conducted in a centripetal way. The secondary moult begins when about six primaries are fully grown, and once started it is very fast, to the point that it is normally completed before P10 is fully grown.

Moult scores – Only adult birds were found to moult flight feathers. We here present data on primary and secondary moult combined, from now on referred to as ‘moult’. Most moult data come from Benin and Gabon (Fig. 1). The general change in moult score over time was upon visual inspection similar between years at both sites (nine and eight seasons, respectively), and we therefore, for each site, combined the data from all years in our analyses (Fig. 4).

At both sites, males were ahead of females in moult, and in the MS range of 30–95 (the central part of moult), for a given half-month period, the MS of males were consistently 22–38 points higher than in females. This difference between the sexes can also be described as, for a given moult score, males being about 1–1.5 months ahead of the females. In Benin, in total 15 birds had not yet commenced moult (MS = 0), of which the last bird was

Fig. 4. The average ($\pm$ SD) moult score (primaries and secondaries combined) of adult male and female Great Snipes per half month in Benin, Gabon and Cameroon in 1990–2000. The maximum possible moult score is 105. To improve readability, only one of the error bars per sample is shown. Sample sizes are given above each graph, with male values on top.

recorded in the first half of November. All were females. Only one bird in Gabon had not commenced moult, a male shot in the first half of October. This stands out as the only adult male in our sample that was trapped in MS 0. However, since it had a *BillHead* of 95 mm, it cannot be ruled out that this could have been an unusually small female.

The earliest birds with a completed moult (MS = 105) were recorded in the first half of October, both in Benin (three birds in three different years) and Gabon (five birds in three different years). All were males, apart from one of the Gabon birds. The earliest period in the total

Fig. 5. The proportion of male and female adult great snipes in different moult stages (see *Methods*) per half month in Benin and Gabon in 1990–2000. Sample sizes are given above each graph.

data set in which all males were fully moulted was the second half of December, both in Benin and Gabon (four and 18 birds, in two and six years, respectively). From then on, all males were fully moulted at both sites, apart from a male with MS 83 in early January and one with MS 80 in the second half of April.

In females, the picture was quite different between sites. In Benin, the first period when all females were fully moulted was already by the second half of December (three birds in one year), just as in males. In Gabon, a completed moult in all females was not reached until early March (three birds in three years). Per half month, a majority of the females had completed moult from the first half on January onwards, but birds with growing feathers were recorded up to the second half of February. All birds recorded after that with a MS lower than 105 had suspended their moult; i.e. no feathers were growing, but they still had old feathers. Among them, five birds in two years had 3, 3, 4, 5 and 8 old retained wing feathers each (all birds recorded in April). In general, in the most intense period of moult (August–October), the Benin

birds (both sexes) had a MS of about 10–20 points higher than the Gabon birds, and were about half a month ahead for a given MS.

The moult of the birds in Cameroon was somewhat in between that recorded in Benin and Gabon (Fig. 4). The 16 adult females from late February in DR Congo had an average moult score of 66, which is much lower than the average of 98 (almost finished moult) found among adult females in Gabon in the same period. However, the birds from DR Congo belonged to two clear groups, where twelve were in active mid-moult (MS 44–78) and three had completed moult (MS = 105). One bird had suspended moult at MS 45.

Moult stages – Moult score gives a measure of how moult has progressed overall. However, birds with a given moult score can be in different moult stages (e.g. active, suspended, just resumed). These moult stages give additional information on moult progress and how it may relate to season and geographic location (Fig. 5).

In Benin and Gabon, almost all birds up to the end of October were either just resuming moult or were in active moult. Some additional birds, particularly males in August and early September, were in suspended moult. Some females had not yet started moult at all. This strongly suggests that flight feather moult in both sexes is activated directly upon, or soon after, arrival to sub-Saharan Africa. Most males resume the primary moult they initiated (and suspended) on the breeding grounds, whereas most females initiate primary moult. From November (males) and December (females) a majority of birds have finished moult. It should be noted, though, that there are birds in suspended moult or in various active stages far into the winter, not least in Gabon females, showing the large variation that exists in moult stage among Great Snipes in sub-Saharan Africa.

In Cameroon, the situation was similar to that in Benin, with most birds resuming or in active moult in September–October. Interestingly, in early November, five out of seven birds were either stopping or had suspended moult. In DR Congo in February, the moult stages were resuming (1), active (11), suspended (1), and completed (3).

Body mass development

For Benin and Gabon we present average body masses per half-month period for males and females separately, since females are clearly larger than males (Fig. 6). In Benin, within each sex, body mass was significantly affected by half-month period, but not by age (ANCOVA; males ($n = 532$), effect of period: $t = 2.36$, $P = 0.019$, effect of age: $t = 1.67$, $P = 0.09$; females ($n = 678$), effect of period: $t = 4.20$, $P < 0.001$, effect of age: $t = 0.76$, $P = 0.45$; non-significant interaction terms were removed in both cases). In Gabon, body mass was significantly affected by half-month period, but also by age (ANCOVA; males ($n = 847$), effect of period: $t = 17.9$, $P < 0.001$, effect of age: $t = 6.28$, $P < 0.001$; females ($n = 488$), effect of period: $t = 12.81$, $P < 0.001$, effect of age: $t = 5.24$, $P < 0.001$; non-significant interaction terms were removed in both cases).

Fig. 6. The average ($\pm$ SD) body mass of male and female Great Snipes per half month in Benin and Gabon in 1990–2000. To improve readability, only one of the error bars per sample is shown. Sample sizes are above each graph, with female values on top.

However, in Gabon, adults and juveniles within each sex had very similar overall seasonal pattern of body mass; i.e. juveniles also put on substantial amounts of fuel in spring. Further, the effect of age was relatively small (7.9 g for males, 8.9 g for females, according to model estimates) compared to the overall seasonal variation in body mass (Fig. 6). Because of the lack of a significant age effect in Benin, and the small absolute differences between age groups, we lumped adults and juveniles within each sex when presenting the body mass development over winter in Benin and Gabon (Fig. 6).

Both at Benin and Gabon, and in both sexes, there was a small average body mass increase of about 10 g from late September to early November, followed by a similar-sized drop in body mass until late January. In the first half of February body mass started to increase again, especially in males.

In Benin, where birds were only sampled up to the second half of February (although the data from second half of December onwards only come from three years), several heavy males were trapped in this last period (all in 1996/1997). The average of 194 g in late February is based on eight birds, of which four weighed more than 200 g and the heaviest 230 g. None of the six females sampled the same period weighed more than 200 g (despite the fact that females are generally larger than males).

In Gabon, where birds were sampled until early May, average body mass in males increased from a winter low

in late January of 154.9 ± 8.6 (SD) g to 205.8 ± 17.6 g in late April, an increase of about 50 g. Also in females the total mass increase in spring was about 50 g, from 166.8 ± 9.5 in early February to 218.3 ± 17.4 g in early May. Assuming lean body masses (the lowest half-month average recorded in late winter in each sex) of 155 g in males and 167 g in females, the fuel loads at the end of spring correspond to about 33% and 31% of lean body mass, respectively. To compare Great Snipe fuel deposition rates with published data on maximum rates in other migrant birds (Lindström 2003), we need to look at a period of high and rather stable mass increase. For males we used the period from late February to late March, when the fuel deposition rate of males was 1.27 g/d (around 38 g in 30 days). This is equivalent to a fuel deposition rate of 0.8% of lean body mass/d. Females had a longer fuelling period with high and stable rates, from late February to late April, when mass increased with 0.83 g/d (50 g in 60 days), or around 0.5% of lean body mass/d. The four heaviest males, presumably trapped just prior to departure, weighed 225, 230, 240 and 242 g (from two different years). Among females, there were two birds recorded at 245 g and four birds at 250 g (from three different years).

No birds were weighed in Cameroon. In DR Congo, 18 birds in late February weighed 153–181 g. The average mass of adult females was 164.6 g (155–181 g, $n = 16$). This is similar to the average for females in February in Gabon and Benin (Fig. 6).

DISCUSSION

Large, long-term datasets on seasonal occurrence, moult and body mass from tropical winter grounds of long-distance migrants are relatively uncommon. For Palaearctic-breeding waders spending their non-breeding season in Africa there are some notable exceptions, from both coastal (e.g. Summers & Waltner 1979, Zwarts *et al.* 1990) and inland sites (e.g. Pearson *et al.* 1970, Pearson 1987). The current study adds a significant amount of data from the African wintering grounds of a generally poorly studied inland wader species (Glutz von Blotzheim *et al.* 1977, Cramp & Simmons 1983, del Hoyo *et al.* 1996, Delany *et al.* 2009). Although our data come from a few locations only, they provide a basis for a first more systematic and detailed description of the seasonal pattern of occurrence, moult and body mass of Great Snipes in Africa. This kind of traditional natural history data forms an important complement to the new type of data emerging from modern tracking techniques (in the case of Great Snipes, see Klaassen *et al.* 2011, Lindström *et al.* 2016).

Our data were collected through hunting only. Although the actual method of sampling (whether the bird was killed by a bullet or captured in a mist-net or other trap) should not influence the data collected on a given individual, the sampling method has potential consequences for the interpretation of the data. In birds that are trapped and released, all birds that intended to stay in an area can do so, and they can get recorded again. A bird shot cannot be

sampled more than once. Clearly, as shown in our study, at some spots from many tens up to several hundred Great Snipes could be shot throughout the season, which implies that there was a constant movement of birds around these sites. Barth (1881) reported from lowland sites in southern Norway, during early autumn migration (August–September), that there was a continuous movement of Great Snipes, since “even when you shot all birds at a given site in one day, there could be just as many of them the next day” [our translation].

We do not know to what extent the new birds have arrived from near or afar. Although this holds also for ordinary trapping and ringing, in a study based on hunting we cannot know whether these ‘newcomers’ would have come into the area if the shot birds had not been removed. Conversely, if birds in some parts of the year are more sedentary, the seasonal decline in numbers at some sites, for example the sharp decline in adult numbers in Benin in November, could in principle be an effect of shooting out the birds settling in the area, birds that otherwise would have stayed much longer. These caveats must be borne in mind when interpreting the data, not least since, to our knowledge, there are no ringing-recapture studies of Great Snipes to compare with.

Seasonal patterns of occurrence

Arrival and within-Africa migrations – Of the two study sites with good coverage (Benin and Gabon), Benin was the first to record large numbers of Great Snipes in autumn, with significant numbers, mainly males, showing up in the second half of August. That Great Snipes start arriving in West Africa in late August is long known (e.g. Elgood 1994, Delany *et al.* 2009). Indeed, tracks of Swedish-breeding males showed that they on average arrived in sub-Saharan West Africa on 29 August (20 August–20 September, $n = 18$). Although most of the latter birds seemed to have stopped just south of the Sahara, some of them may have stopped close to the coast, i.e. at sites close to or similar to the Benin site (Lindström *et al.* 2016). Adult females seemed to arrive somewhat later than males on average. The main bulk of juveniles seemingly arrived 1–2 months later still than the adults. In November, the number of Great Snipes declined dramatically, suggesting that the Benin site is mainly a transit site and not a wintering site for Great Snipes. Only in a few years, when suitable (damp) habitat was preserved during an unusually long period, did some Great Snipes stay into January and February (R. Paloc pers. comm.).

Swedish-breeding males left sub-Saharan West Africa for their final wintering sites near the Equator on average 22 September (4 September–22 October, $n = 19$; Lindström *et al.* 2016). Possibly a proportion of the snipes sampled in August–September originates from Sweden, whereas some of the birds sampled later in the autumn may have had different breeding origin. The short sampling period in Cameroon precludes stronger conclusions, but this northern site is most likely also a transit site. This type of within-Africa migration, from sub-Saharan savannah

Fig. 7. Flooded grazed meadows on the Jos Plateau, central Nigeria, in late September 2015. This time of the year, Great Snipes are commonly found here. A few weeks later, these meadows have dried out. Photo and information: Ulf Ottosson.

towards the Equator and beyond, most likely a response to seasonal moving rain fronts and hence habitat suitability, has since the pioneering studies of passerine migration in East Africa (Pearson & Backhurst 1976) been described for many Palaearctic migrants in Africa (Alerstam 1990, Newton 2008, Thorup *et al.* 2017). Adult Great Snipes clearly make use of the benign conditions just south of the Sahara in August–September (Fig. 7) to moult flight feathers to a varying degree (more below).

Also Gabon seems to be primarily a staging site for adult birds, with large numbers in September–October, but a rapid decline in November (much in parallel to the pattern in Benin). However, some adult birds seem to remain throughout the rest of the winter, suggesting that this site also is a wintering site for some adults. Indeed, all Swedish-breeding males tracked wintered near the Equator, and one bird was estimated to have wintered very close to the Gabon site (Lindström *et al.* 2016). Conversely, the Gabon site held a large number of juveniles throughout the winter, suggesting this is an important wintering site for juveniles, and that juveniles and adults may choose different sites for their final wintering grounds.

In both Benin and Gabon the proportion of males increased over winter. This suggests that the sexes differ in their migration patterns, but exactly how they differ is unclear. So far only male Great Snipes have been tracked by geolocators (Lindström *et al.* 2016), since they are more likely to be re-trapped between seasons, a prerequisite for the geolocator method. A possibility would be that females on average move further south in Africa during winter, leading to increasing proportions of males at northern sites, such as Gabon. Great Snipes are regularly found much further south in Africa (Delany *et al.* 2009), but it is not known whether they are a subset of the breeding populations we have studied or have a completely different breeding origin. Overall, the seasonal appearance at Benin and Gabon strongly suggests that the spatio-temporal

distribution of Great Snipes in winter varies in relation to both sex and age.

Departure from Africa – As indicated by the dramatic drop in the proportion of males among adults (Fig. 3), male Great Snipes clearly started to depart from Gabon in late March and early April, concomitant with the highest body masses recorded in our study. This timing fits nicely with the departure dates recorded for 13 Scandinavian adult males, which left their wintering grounds around the Equator (Fig. 1) on average on 18 April (range 3–28 April; Lindström *et al.* 2016). Given the close proximity of the Gabon site to the wintering areas of Scandinavian males (Fig. 1), it is reasonable to assume that the birds in Gabon at least partly belong to the Scandinavian population, and, conversely, the disappearance of the males reflects their spring migratory departure from Africa. The females seem to depart about 2–4 weeks later than the males.

Flight feather moult

Many adult males, and some adult females, arrived at sub-Saharan stopover sites with a number of inner primaries already moulted. This moult took place on the breeding ground and was apparently suspended prior to the southward departure, most likely to avoid the extra cost associated with flying with growing flight feathers (Hedenström & Sunada 1999). Males on average had moulted more primaries than females, which most likely reflects the differences in parental duties. Males have plenty of time to start moult already in the breeding area after the lekking period is over in July, in contrast to females that incubate and care for the young for yet a few weeks.

It seems as if a majority of the adult Great Snipes resume or initiate primary moult almost immediately upon arrival in sub-Saharan Africa. From then on, flight feather moult may continue almost uninterrupted until it is completed from early October to early December (Fig. 8). However, in the period up to early December, it seems as if most individuals make an intra-Africa migration (del Hoyo *et al.* 1996, Lindström *et al.* 2016, this study). From our data it is not possible to figure out how many birds finish moult before the intra-African migration. The Swedish-breeding males stayed on average three weeks before moving on (Lindström *et al.* 2016), a time span that seems too short for most of them to finish moult. Our data, not least from Gabon, clearly suggest that others suspend moult (again?) in order to finish moult at the final wintering site. It is of course also possible that some birds make the relatively 'short' intra-African migration with growing primaries. Given the potentially high energy cost of moult (Lindström *et al.* 1993), and that the birds migrate between sites in a way that coincides with peaks in habitat quality, it makes sense that they moult both during sub-Saharan stopover and upon arrival to the final wintering sites. A moult strategy where primary moult is initiated and suspended at the breeding site, and completed at a stopover or a wintering site, has been reported in several other species of migrating waders

Fig. 8. The wing of an adult male (minimum 6 years old) Great Snipe in late May, in Jämtland, Sweden. The primaries are quite fresh despite the fact that they were grown in September–October in sub-Saharan Africa. Photo: Åke Lindström.

wintering in sub-Saharan Africa, such as Black-tailed Godwit *Limosa limosa*, Marsh Sandpiper *Tringa stagnatilis*, and Spotted Redshank *Tringa erythropus* (Newton 2008).

The females are clearly behind the males in the progress of flight feather moult, a difference that originates from the males' early start at the breeding grounds. At the population level, it seems as if the females moult at a similar speed, or possibly, as suggested by the Gabon dataset, somewhat slower. As discussed above, based on the seasonal change in sex ratio, females may move further south in Africa following the stop in sub-Saharan West Africa. How such a difference in migration may interact with the flight feather moult needs more investigation, but both the Benin and Gabon data suggest that suspended flight feather moult in October and November is much more common in females than in males.

Body mass development

Upon arrival to sub-Saharan Africa, the body mass of Great Snipes is similar to the lowest general levels reported in the literature (Cramp & Simmons 1983), suggesting that, to no surprise, they arrive with no or very small fuel loads. It is not obvious what the subsequent 10-g general increase in body mass up to November signifies. First, the birds may increase somewhat in mass to restore muscle and gut tissue that may have been burned to sub-optimal levels before and during the long flight (*cf.* Piersma & Gill 1998, Battley *et al.* 2000). What speaks against this explanation is that they apparently return to the same low body masses in January, for no obvious reason. Second, it is common that birds increase in mass during flight feather moult, which is caused by a higher body water content (Dolnik & Gavrillov 1979, Lindström *et al.* 1993). However, when the peak in mass occurs in November, the proportion of birds moulting flight feathers has decreased considerably compared to the previous months, not least in males. Third, at temperate wintering

grounds, many waders have a mid-winter peak in mass, due to fuel loads put on as insurance to cold and unpredictable feeding conditions (e.g. Johnson 1985). That a similar explanation can be applied on wintering Great Snipes seems unlikely in Africa. Fourth, the November mass peak represents the fuelling for intra-African migration. However, also here the peak seems to come too late. Most of the Swedish-breeding males tracked by geolocators carried out their intra-African migration already in late September and had all reached their final wintering grounds by the end of October (Lindström *et al.* 2016). Still, fuelling for migration may be the most likely explanation for the general increase in body mass from September to November.

Following a general dip in body mass in January, the most prominent change in body mass among Great Snipes in sub-Saharan Africa takes place from February to April. If we assume that individuals continue to increase in mass right up until spring departure, the levelling out of the mass increase in Gabon from March onwards suggests that the first males depart in late March and the first females in late April.

Based on the information from Gabon, both males and females increase by about 50 g (obtaining a fuel load of 31–33% above lean body mass) before departing Africa for their northern breeding grounds. The peak individual body masses were about 240 and 250 g in males and females, respectively. There are very few data from the spring departure from Africa to compare with. Five birds in May in Tanzania weighed 191–255 g (Urban *et al.* 1986). From autumn there are more data on body mass close to migratory departure, and several studies report body masses well above 200 g, but almost never more than 250 g (Lindblad 1863, Barth 1881, Cramp & Simmons 1983). The heaviest individual reported in the literature weighed 265 g and was shot in Norway in autumn (Barth 1881).

Fuel loads of just above 30% of lean body mass in late spring in Africa, and possibly rarely above 50% in some individuals, are surprisingly low for birds supposedly bound for non-stop flights of 4,300–5,900 km (*cf.* Swedish-breeding male Great Snipes; Lindström *et al.* 2016). For comparison, populations of the 134-g Red Knot *Calidris canutus* and 105-g Ruddy Turnstone *Arenaria interpres* regularly put on fuel loads of 40–56% and 50–73% above lean body mass, respectively, before their non-spring migration flights of ‘only’ 1,850–4,700 km (review by Gudmundsson *et al.* 1991). As discussed by Lindström *et al.* (2016), one possibility for the apparently low fuel loads of Great Snipes is that the very fattest snipes have not yet been recorded. There are indeed comparatively few data on migration-related body mass in this species (Glutz von Blotzheim *et al.* 1977, Cramp & Simmons 1983, Urban *et al.* 1986). Alternatively, the flight conditions for the different wader species, or their flight capacity, differs dramatically between species. There is clearly a strong need for more Great Snipe body mass data from the period just before departure (Lindström *et al.* 2016).

The fuel deposition rate in spring, again based on data from Gabon, of 0.5–0.8% of lean body mass/d, is comparatively low. The highest recorded population-average fuel deposition rates in 17 wader species varied between 1.2 and 8.5% of lean body mass/d (Lindström 2003). Since maximum fuel deposition rates decrease with increasing body mass, one should ideally compare with similar-sized birds. Three wader species of 150–200 g fuelled at a rate of 1.2–1.9% of lean body mass/d (Lindström 2003). How representative the values of 0.5–0.8% of lean body mass/d are for individual Great Snipes we do not know. We also do not know whether the fuelling rates are low because the birds are constrained in their feeding rates due to low food abundance or poor food quality, or simply do not need to fuel (feed) at a higher rate, with the potential costs that high feeding rates may incur (e.g. Metcalfe & Furness 1984). Given that Great Snipes probably spend around seven months in the same general wintering area before spring departure (Lindström *et al.* 2016), there should at least be no general time stress. But of course, changes in habitat quality may well set limits to when, and at what speed, fuel can be deposited. For example, Whimbrels *Numenius phaeopus* in Mauritania could not start fuelling in spring until their main prey changed behaviour so that they were available to Whimbrels for longer periods of the day (Zwarts 1990). Detailed studies of Great Snipe feeding ecology in equatorial Africa are needed to answer these questions.

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