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Fuelling rates by spring-staging Ruffs *Philomachus pugnax* in southern Belarus

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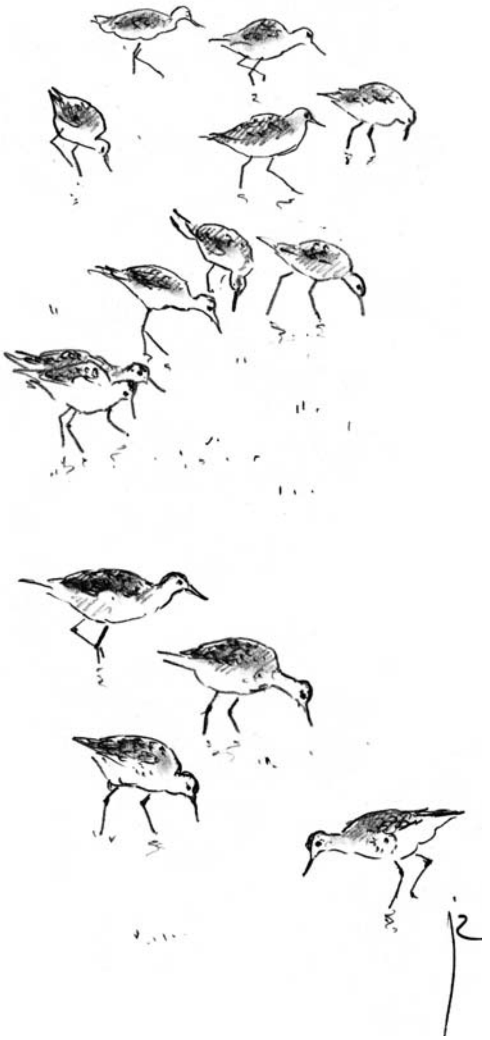

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On the floodplain meadows of the Pripyat River in southern Belarus, Ruffs *Philomachus pugnax* form concentrations of up to 30,000 individuals during spring migration. The Ruffs replenish their energy reserves before continuing their northwards migration. Over eight spring seasons, between late March and middle May 2001–2008, we measured the body mass increase in a sample of 2839 adult and 342 immature males, and 2058 adult and 136 immature females caught in the middle Pripyat near Turov. Body mass increased in two phases in the spring season, rising slowly in the first and faster in the second phase; the breakpoint date between the two phases differed between the sexes (24 April and 3 May, respectively) and showed less variation in females than in males. Adult males gained an average of 1.1 g/day in the first phase and later 2.4 g/day. Immature males gained 0.39 g/day in the earlier phase and 1.7 g/day later. Adult females gained on average 0.56 g/day in the early phase and 1.22 g/day later. In immature females the rate of body mass gain was not significant. The rate of body mass increase varied among years. The water level had a negative impact on the body mass increase in females, but not in males. Presumably, males are less affected by the water level as they have much longer legs and are able to forage in deeper water. According to the estimated flight ranges, both sexes were able to reach at least the breeding grounds in the western part of Siberia in one nonstop flight, except in years with higher water levels. The middle Pripyat is probably the last stopover site before their breeding grounds for at least a portion of these birds.

Key words: waders, *Philomachus pugnax*, spring migration, stopover, body mass, Belarus

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Fuelling at staging sites during migration is a crucial strategy enabling birds to complete their migration successfully (Baker *et al.* 2004, Morrison 2006, Morrison *et al.* 2007). The rate at which they replenish energy reserves depends on environmental variables and may also differ between sexes, age groups or migrants passing early and late in the season. These differences might explain variation in migration timing and migration strategy observed within a species (Goede *et al.* 1990, Farmer, & Wiens 1999, Swanson *et al.* 1999).

The Ruff *Philomachus pugnax* is a medium-sized wader that undertakes long seasonal migrations between its wintering grounds in Africa and Asia and breeding grounds throughout Eurasia (Cramp & Simmons 1983). During spring migration, tens of thousands of Ruffs are regularly observed at inland wetlands and grasslands in Europe (Baccetti *et al.* 1985, Chernichko *et al.* 1991, Wymenga 1999, Nowakowski & Górski 2002, Karlionova *et al.* 2008, Kohler & Rauer 2008). Similar large assemblages have also been reported from grain fields in northern Kazakhstan (Berezovikov 2007). In the past few decades, breeding populations of Ruffs have declined across temperate Eurasia. Most breeding Ruffs are now confined to habitats in the Arctic (Rakhimberdiev *et al.* 2011) and only 8,000–14,000 females still breed in the wet grassland habitats of Europe (Zöckler 2002). A substantial decline has also been recently reported in the number of Ruffs staging in agricultural grasslands of The Netherlands during spring migration (Verkuil 2010). It was suggested that the quality of the habitat at stopover sites has declined because of changes in agricultural practices (Schekkerman & Beintema 2007), which has caused Ruffs to move to alternative staging areas on the more eastern migration route (Rakhimberdiev *et al.* 2011). The middle Pripyat in Belarus is one of these sites: large spring concentrations of this species occur regularly (Karlionova *et al.* 2008) and the number of staging Ruffs has increased significantly between 2001 and 2008 (N. Karlionova, unpubl. data). These observations indicate that this area offers high-quality stopover sites for migrating Ruffs and that the birds are able to build up sufficient energy stores in time for a successful migration.

This paper aims to identify variation between years in the refuelling rates of Ruffs in relation to habitat availability (i.e. water level) and to test for sex and age differences in their refuelling rates at a spring stopover site in the Pripyat on their eastern flyway. Additionally, we estimate potential flight ranges of Ruffs after they leave the Pripyat.

METHODS

We studied the refuelling rates of Ruff using the floodplain meadows of the Pripyat River in the vicinity of Turov, Belarus (Gomel Region, 52°04'N 27°44'E) (Fig. 1). At the height of spring migration, 10,000–30,000 staging Ruffs have been observed in this area (N. Karlionova, unpubl. data). One characteristic of the study area is the large fluctuation in water level on the flood plains of the Pripyat River over different years and seasons, which causes large variation between springs in the area of meadow available for waders (Pinchuk *et al.* 2005).

Field studies were conducted over eight spring seasons, from 2001–2008. We caught birds with walk-in traps (Meissner 1998) and occasionally with mist nets. Each individual was weighed to the nearest 1 g, and we took a standard set of measurements (for details see Karlionova *et al.* 2007), of which the total head length, tarsus length and wing length were used in this study. Two age classes were distinguished: adults, and immatures (second-year birds, hatched in the previous year), who were identified by the occurrence of juvenile inner median coverts (Prater *et al.* 1977) and other criteria, such as leg colour and the amount of wear of the primaries (Schmitt & Whitehouse 1976, Meissner & Scebba 2005). Birds with wings longer than 180 mm and with colourful tuft and ruff feathers we considered to be males and those with a wing length shorter than 170 mm we sexed as females (Karlionova *et al.* 2007). Intermediate birds were assigned to be faeders (female mimics, Jukema & Piersma 2006) but are not considered here.

Figure 1. Location of the study area in the Pripyat floodplain, Turov, southern Belarus (black dot).

We started catching waders at the end of March or the beginning of April and we finished at the end of May, which covered the total migration period of Ruffs through the study area (Mongin & Pinchuk 1999). Birds caught after 15 May were omitted from the analyses, because few Ruffs were caught in this period and their low body masses suggested they were local breeders. Indeed, at that time nests with eggs were found in the study area. Measurements of 2839 adult and 342 immature males and 2058 adult and 136 immature females were collected.

Body mass increase was analysed by regressing body mass against date, across the sample of caught birds, which represents the refuelling rate at the population level. When birds were caught twice or more we used data from the first capture only. This method is sensitive to the possible asynchronous arrival of individuals, which would lead to underestimates as new arrivals will have lower body masses (Gillings *et al.* 2009). To assess this possible underestimation, individual refuelling rates were estimated by changes in body mass of birds that were caught more than once in a season (retraps). Birds recaptured within one or two days of an earlier capture were excluded from this analysis, to avoid any underestimation of increases in body mass caused by the stress of being trapped. Data on 16 adult males and six adult females caught twice within a season remained for this analysis.

In adult males and adult females wing length decreased significantly during the spring season, by 0.72 mm and 1.62 mm, respectively, over the main migration period. Immature birds showed no such trend. Although we caught progressively smaller adult birds over the season, body mass was not adjusted for body size because we assume that this slight decrease in size had a negligible influence on the results showing a conspicuous increase in body mass over the staging period. Moreover, unadjusted body mass could be directly compared with data published from other parts of the flyway.

Body mass was not corrected for mass loss after capture since most birds were weighed within two hours of capture. However, when large catches were made with mist nets at night some birds were weighed up to four hours after capture and this might have led to a underestimation of body mass. Those large catches comprised about 300 males and 200 females, or about 10% of all the birds we analysed. Castro *et al.* (1991) showed that the loss of mass in waders kept for four hours after catching ranged between 3% and 9% and was much higher in temperatures above 30°C. Temperatures at nights, when we mist netted Ruffs, were below 15°C, so any bias would be small.

Preliminary analysis showed that body mass increase seemed to have two phases: a first slow phase and a second rapid phase. The significance of these two phases and the breakpoint date between phases was estimated using the standard procedure of stepwise linear regression in the nonlinear estimation module provided by STATISTICA 9.0 software (StatSoft 2009). Subsequently, body mass increase was estimated separately for males and females during the first and the second phase of fattening. To explore seasonal variation in migration the study period was divided into pentades (five-day periods), according to the standard pentade scheme (Berthold 1973).

We applied a Generalized Linear Model (GLZ) using Maximum Likelihood (ML) estimation with logarithmic link function provided by STATISTICA 9.0 (StatSoft 2009) to account simultaneously for the effects of the independent variables, water level per day and date (day number in the season), on body mass. The model included (i) the effect of water level on body mass increase, through the water level by date interaction, and (ii) the annual variation in body mass increase (year by date interaction). Immature birds were not taken into account because samples sizes were insufficient. The mean body mass in each year was calculated as the standard mean using the respective combinations of factor levels (weighed means). Because of large differences in body mass between the sexes, variation in body mass was modelled separately for adult males and adult females. Presence of heteroscedasticity in the models was tested following the procedure described by White (1980). Variance in body mass increased with date in adult females (White test, $\chi^2 = 111.35$, $P < 0.001$) and in males (White test, $\chi^2 = 219.87$, $P < 0.001$). To deal with the heterogeneity in variances we used the weighed least squares (WLS) method instead of ordinary least square (OLS) method (Carroll & Ruppert 1988, Wolberg 2006). The daily water level in the Pripyat was obtained from a gauge at Chernichi, 3 km downstream of the study area.

To assess the theoretical flight range of adult males and adult females, the equation derived by Pennycuick (1975) was used. This formula does not take into account any improved body-drag coefficient (Pennycuick *et al.* 1996), so the results should be treated as the minimum distance the birds could fly in still air. Because the actual body mass of birds at departure remains unknown, the flight range was estimated (separately for males and females) using the mean body mass of the heaviest 25% of the birds caught between 10 May and 15 May. This selection takes into account that departure body mass varied among individuals, which has been found in other wader species (Jehl 1988, Battley & Piersma 2005). A similar approach was used in a previous study on Turnstone *Arenaria interpres* during autumn migration (Meissner & Kozirόg 2001). The final body mass (upon arrival at destination site) was calculated as the mean body mass of the lightest 10% of the birds in the whole sample. Additionally, the theoretical flight ranges were calculated for the heaviest individuals and for the birds that might have departed at the breakpoint date between slow and fast increase in body mass, using the mean body mass at the breakpoint for males and females separately. Ring recoveries were obtained from Belarusian Ringing Centre of Institute of Zoology National Academy of Sciences in Minsk.

RESULTS

Males arrived earlier than females, with the first arrivals usually being single birds observed in the first half of March. The earliest females arrived in the last days of March. A more intensive migration of males started in the second pentade of April (6–10 April) and of females two pentades later (16–20 April) (Fig. 2).

Stepwise linear regression distinguished two phases of increasing body mass in adults and in immature males. The first phase, ending on 24 April in adult males and on 3 May in adult females, was distinguished by a gentler slope of the regression line, which means that the rate of increase in body mass was slower than in the second phase (Fig. 3). In males the breakpoint was one week later for immatures than for adults (Fig. 3). Adult females reached the breakpoint 9 days later than adult males (Fig. 3). In immature females it was impossible to distinguish two phases of body mass increase (Fig. 3).

Before the breakpoint adult males gained on average 1.1 g/day, and afterwards 2.4 g/day. Immature males gained body mass at 0.39 g/day during the early phase, and after the breakpoint their body mass increased on average by 1.7 g/day. In the first period the rate of body mass increase did not differ significantly between adults and immatures (ANCOVA, $F_{1,2156}$= 1.10, P = 0.294), but in the second period it was higher in adults than in immature males (ANCOVA, $F_{1,1016}$ = 10.14, P = 0.001).

Adult females gained on average 0.56 g/day in the first phase of accumulating mass, and 1.22 g/day in the

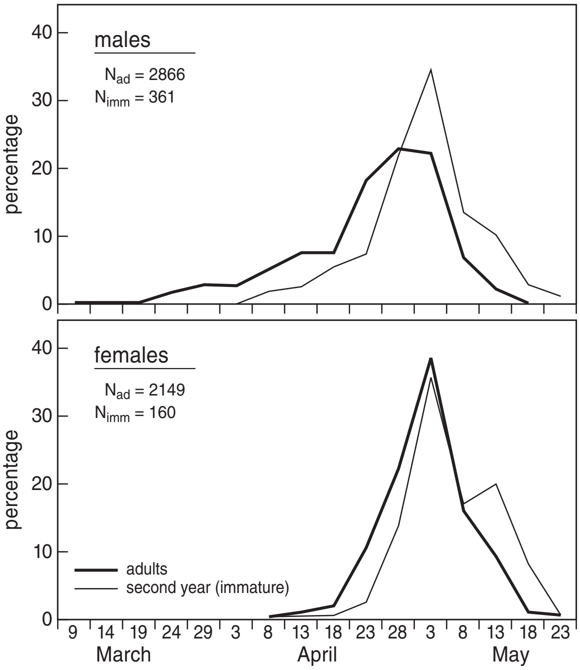

Figure 2. Phenology of spring migration of Ruffs in the Pripyat, Turov, southern Belarus, expressed as the percentage of migrant Ruffs caught at subsequent five-day periods (pentades) during spring 2001–08 (all years combined). The middle day of each pentade is indicated.

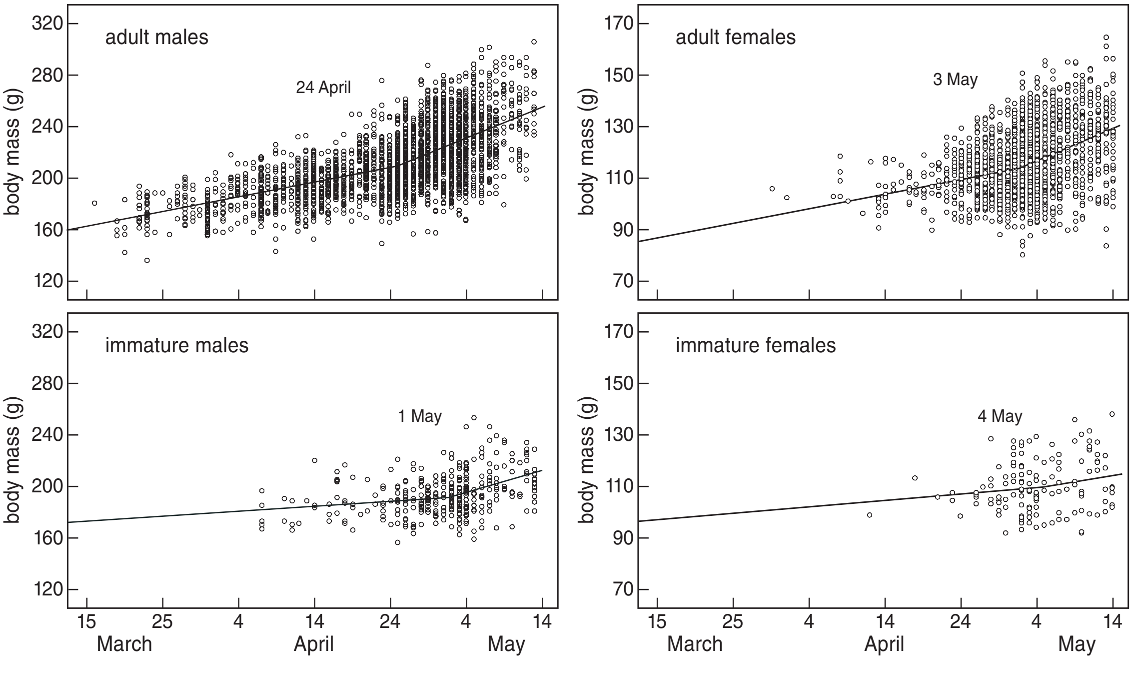

Figure 3. Body mass of adult and immature males and females caught during spring migration between March and May in 2001–08 in the Pripyat, Turov, southern Belarus. Lines show linear regression of body mass against date, before and after the breakpoint date (as estimated by stepwise linear regression).

second. Immature females showed no significant body mass increase in the whole period (the slope of the linear regression was not significantly different from zero; *t*-test, $t = 0.63$, $P = 0.53$).

The rate of body mass increase calculated from individual recaptured birds was 2.6 g/day (SD = 1.15, $n = 16$) in adult males, and 1.3 g/day (SD = 0.70, $n = 6$) in adult females. These rates were thus similar to the population mean rates of body mass increase in the second phase.

The rate of body mass increase of adult males and adult females differed significantly between years (Table 1), with a similar variation in body mass increase between subsequent years in males and females (Kendall tau –0.050, Z = 1.73, $P = 0.08$). In the first phase of fattening the highest rate of body mass increase occurred in 2001 in males (1.63 g/day) and in females (0.71 g/day), while it was the highest in the second phase in 2005 in males (5.18 g/day), and in 2007 in females (2.17 g/day). Over the years, the date of the breakpoint between the two phases differed by 12 days in males (extreme dates: 19 April in 2007 and 1 May in 2004) and four days in females (extreme dates: 1 May in 2004 and 2008, and 5 May in 2005).

Water level had a negative impact on the rate of body mass increase in females, but not in males (Table 1). The correlation between mean body mass increase and mean water level calculated for five-day periods is shown in Figure 4.

The mean departure body mass for adult males was 274.8 g and for adult females 141.1 g. The final (arrival) body mass was estimated at 176 g for adult males and 96 g for adult females. This value is close to the mean body mass of Ruffs wintering in Africa in December (Schmitt & Whitehouse 1976, Pearson 1981, OAG Münster 1998). Theoretical flight ranges of adult

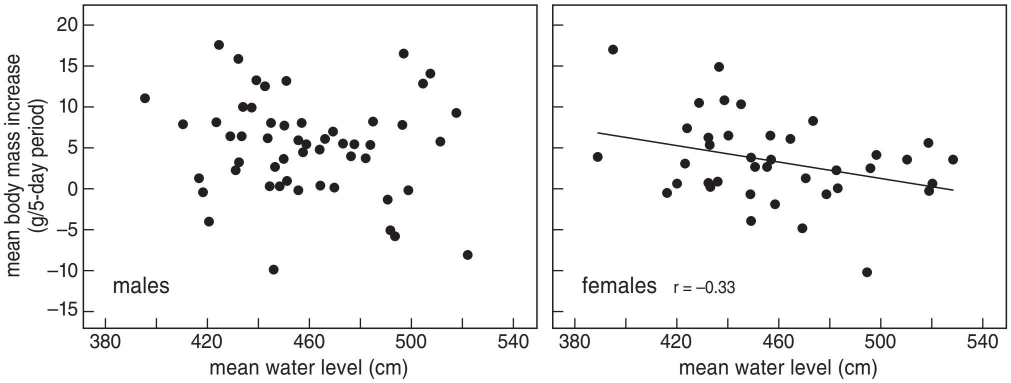

Figure 4. Relationship between mean water level and mean body mass increase of adult male and adult female Ruff in the Pripyat, Turov, southern Belarus. Each point represents the value for a five-day period (pentade).

Table 1. Results of generalized linear model showing the effect of water level, year and date (day number in the season) on the body mass of male and female Ruffs during spring passage at the middle Pripyat.

Sex	Parameter	Coefficient	SE	*df*	Wald's	*P*
Males	Constant	3.88	0.331	1	136.77	<0.0001
	Year			7	91.50	<0.0001
	Water level	0.0023	0.0007	1	11.86	0.0006
	Date	0.0015	0.0050	1	9.46	0.0021
	Water level × date	–0.00001	0.00001	1	1.37	0.2426
	Year × date			7	79.89	<0.0001
Females	Constant	2.96	0.562	1	27.79	<0.0001
	Year			7	53.68	<0.0001
	Water level	0.0032	0.0012	1	7.61	0.0058
	Date	0.0032	0.0075	1	19.92	<0.0001
	Water level × date	–0.0001	0.00001	1	14.61	0.0001
	Year × date			7	60.08	<0.0001

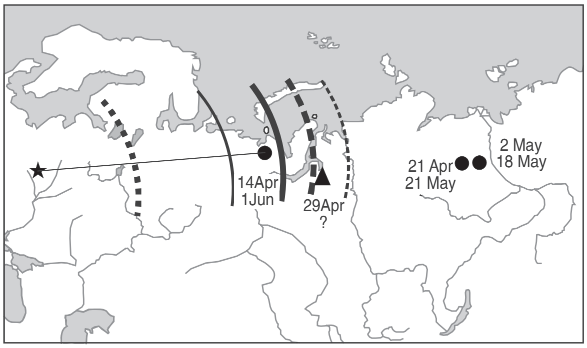

Figure 5. Theoretical flight ranges of adult male and adult female Ruff departing in spring from the Pripyat, Turov, southern Belarus (asterisk). Thick lines = males, thin lines = females. Dashed lines = the flight range of the heaviest individuals, solid lines = birds with the estimated mean body mass. Dotted line = estimated flight range calculated for mean body mass at the breakpoint (similar distances for males and females). Black symbols: location of ringing recoveries of one immature (triangle) and three adult (circles) males. The dates near the symbol show the date of ringing (top date) and date of recovery (bottom date; ? = exact date unknown). A straight line indicates a recovery obtained within the same spring season.

males and adult females after departure from the study area were 2700 km and 2000 km respectively (Fig. 5). The estimated flight range was 3000 km for the heaviest male (305 g) and 3300 km for the heaviest female (165 g) in the sample. In 2006 the water level was highest (mean 501.5 cm, SD = 26.2; for other seasons: mean = 447.0, SD = 24.4), and in this year the estimated flight range of females was as low as 2200 km and 1600 km for males. The theoretical flight range was about 1000 km for both males and females that would have left at the breakpoint date between the periods of slower and faster body mass increase (Fig. 5).

Four ringing recoveries east of the study area comprise one immature and three adult males, including one bird recovered after 48 days (direct recovery). The body mass of this bird at ringing was 189 g, and we do not know if this male put on weight in Turov or at the next stopover site. This male and another bird were recovered within the estimated flight range (2237 km and 3082 km from the ringing site), but two other males were shot about 5100 km from the ringing site (Fig. 5).

DISCUSSION

Differences in the timing of spring migration of male and female Ruffs have been reported in various studies. On the African wintering grounds adult females start their premigratory fuelling later than adult males, which suggests that they also depart later (Pearson 1981, OAG Münster 1998). Indeed in Italy, France, Germany and The Netherlands the proportion of females caught increased gradually between the end of March and the end of April (OAG Münster 1989, Verkuil & de Goeij 2003, Wymenga 1999). Census counts in the study area showed that the first males arrived 1 to 3 weeks earlier than females (N. Karlionova and P. Pinchuk, unpubl. data). However, it seems that closer to the breeding grounds, the difference in timing between males and females decreases, because in Turov the peak migration of both sexes occurred at about the same time (Fig. 2).

Individual body mass increase calculated for birds trapped twice during a season was similar to the body mass increase computed on population level in the second period. Thus, after the breakpoint, the possible underestimation of the body mass increase due to asynchronous arrival of individuals was likely to be small, and this also shows that correction for structural size was not necessary. However, the slower rates of body mass increase at the population level in the first phase, before the breakpoint, could be an underestimate resulting from a constant influx of new arrivals with lower body mass.

The mean body mass and the rate of body mass increase for Ruffs staging in the middle Pripyat were within the range reported for Ruffs that were fuelling before departure from their wintering grounds (e.g. Glutz von Blotzheim *et al.* 1975, Melter & Bergman 1996, OAG Münster 1998). In the middle Pripyat, adult Ruffs were able to accumulate energy reserves faster and had higher body masses than immatures, a phenomenon also found in other wader species preparing to migrate (e.g. Hockey *et al.* 1998, Wichmann *et al.* 2004). This might be a consequence of the lower foraging proficiency of young waders in comparison with adults, which results in delayed spring migration of immatures and later arrival on the breeding grounds (Hockey *et al.* 1998).

The water level had a negative impact on the body mass increase of females, but not of males, this difference may be due to the pronounced sexual dimorphism in Ruffs. Males are much larger, have longer wings, legs and bills than females (Karlionova *et al.* 2007). Differences in feeding techniques are common even in waders where sexual dimorphism is less pronounced (Puttick 1981, Summers *et al.* 1990, Durell *et al.* 1993, Both *et al.* 2003, Mathot & Elner 2004, Fernández & Lank 2008) and may lead to a sexual segregation of foraging niches (Lifjeld 1984, Davis & Smith 2001). Ruffs on the floodplains forage mostly in deep water using deep probing (Krupa *et al.* 2009). The size difference between the sexes might result in different diets or feeding techniques. Males are able to forage in deeper water than females and that is why their body mass increase did not show a negative relationship with water level, although males also had a shorter flight range in the year with the highest water level.

In the Pripyat the area of foraging habitat is determined by the scale of the flood after the spring thaw. When the water level in the river is exceptionally high, most riverside pastures and meadows are flooded and hence feeding areas are inaccessible to waders. However, in the studied section of the Pripyat river the relationship between water level and the quality of feeding areas seems to be quite complicated. Birds might move between different parts of the Pripyat searching for the best feeding conditions and gather in the evenings at night roosts, where they were mist netted. Also, the relationship between water level and the abundance of invertebrates in the study area remains unknown.

Rates of body mass increase were highly variable between years, and differed largely between the two phases. Part of the annual variation was explained by water level, but body mass increase might also depend on other environmental conditions, especially food abundance (Maron & Myers 1985). The two phases in body mass increase might reflect an improvement in feeding conditions as spring progresses, because more invertebrates become available for waders in May when temperatures rise. The later and more stable date of the breakpoint in the body mass increase of females might be the result of endogenous control, whereas in males, who arrive earlier, the timing of the beginning of rapid fattening is more flexible and depends on when food availability starts to improve. When food became more abundant, both sexes gained energy reserves fast and left the study area at about the same time. On the other hand, it is also possible that different groups of migrants occur in Turov. Early migrants could leave the study area before the last decade of May, heading to the next stopover site or flying directly to breeding grounds situated closer than those of the later migrants. Similar situations were described for Dunlins *Calidris alpina* staging in spring at the Dutch Waddenzee, where two groups of migrants differed in migration timing, rates of body mass increase and probably also in destination (Goede *et al.* 1990). However, the hypothesis that the observed phases are due to early and late migrants was not fully supported by our data, because out of the 22 retraps 45% (10 individuals) were caught before and after the date of the breakpoint in the body mass increase rate. The other 12 birds were trapped both times during the second phase of the body mass increase.

According to the flight ranges we estimated, both sexes are able to reach at least the western part of Siberia in one nonstop flight. Thus the middle Pripyat is probably the last stopover site for these birds heading to their breeding grounds. However, in years with high water levels both males and females accumulate fewer reserves than in other seasons, which affected their theoretical flight range. However, the use of different assumptions and models for flight cost strongly affects the estimates of flight range (Davidson 1984, McWilliams *et al.* 2004). For example, according to Davidson's (1984) formula the flight range of Ruffs departing from Turov would be about 6000 km. But aerodynamic models based on Pennycuick's equation (1975) are often preferred because they can account for body mass, morphometry, air density and other factors that affect the costs of flight (McWilliams *et al.* 2004). Adult males are assumed to have a larger flight range than adult females, due to their higher energy reserves. However, in males energy reserves might be used not only for migration, but also for displaying activities on the leks. Females might use their reserves as a buffer during incubation or to enhance their production of fledglings (Farmer & Wiens 1999). Although waders nesting in the Arctic are not capital breeders (Klaassen *et al.* 2001), there are no such data for Ruffs, which breed at relatively low latitudes.

Our study conducted in spring in the middle Pripyat showed that the rate of body mass increase of Ruffs is variable between years and within season. The two phases of body mass gain probably reflect improvement in feeding conditions in the second part of the spring season. Rapid fattening during the second phase allowed Ruffs to accumulate stores sufficient for the next and probably last stage of migration toward the breeding grounds. Departure body mass depends on feeding conditions at the staging site and has a crucial influence on survival of migrants preparing for long-distance flights (Baker *et al.* 2004). Thus, adequate protection of the floodplain meadows in the Pripyat is essential for the conservation of Ruffs, especially because there is growing evidence that the importance of the area for Ruffs is increasing due to a shift from West European spring staging sites towards Eastern Europe (Rakhimberdiev *et al.* 2011).

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REFERENCES

Baccetti N., Farronato J., Forcellini C., Lacatelli A., Piacentini D., Scappi A., Spina F. & Tinarelli R. 1985. Progetto Combattente: primi dati da alcune zone umide dell'Emilia Romagna. In: Fasola M. (ed.) Atti III Conv. It. Orn.: 88–91.

Baker A.J., Gonzalez P.M., Piersma T., Niles L.J., Atkinson P.W., Clark N.A., Minton C.D.T., Peck M. & Aarts G. 2004. Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. Proc. R. Soc. Lond. B 271: 875–882.

Battley P.F. & Piersma T. 2005. Body composition and flight ranges of Bar-tailed Godwits (*Limosa lapponica baueri*) from New Zealand. Auk 122: 922–937.

Berezovikov N.N. 2007. Trophic relations of ruffs *Philomachus pugnax* with grain fields during spring migration in Northern Kazakhstan. Russian J. Ornithol. 350: 394–397. (in Russian)

Berthold P. 1973. Proposals for the standardization of the presentation of data of animal events, especially migratory data. Auspicium 5: 49–57.

Both C., Edelaar P. & Renema W. 2003. Interference between the sexes in foraging Bar-tailed Godwits *Limosa lapponica*. Ardea 91: 268–272.

Carroll, R.J. & Ruppert D. 1988. Transformation and weighting in regression. Chapman & Hall.

Castro G., Wunder B.A. & Knopf F.L. 1991. Temperature-dependent loss of mass by shorebirds following capture. J. Field Ornithol. 62: 314–318.

Chernichko I.I., Grinchenko A.B. & Siokin V.D. 1991. Waders of the Sivash Gulf, Azov-Black Sea, USSR. Wader Study Group Bull. 63: 37–38.

Cramp S. & Simmons K.E.L. (eds) 1983. The Birds of the Western Palearctic, Vol. III. Oxford University Press, Oxford.

Davidson N.C. 1984. How valid are flight range estimates for waders? Ring. Migrat. 5: 49–64.

Davis C.A. & Smith L.M. 2001. Foraging strategies and niche dynamics of coexisting shorebirds at stopover sites in the southern Great Plains. Auk 118: 484–495.

Durell S.E.A. Le V. Dit, Goss-Custard J.D. & Caldow R.W.G.1993. Sex-related differences in diet and feeding method in the Oystercatcher *Haematopus ostralegus*. J. Anim. Ecol. 62: 205–215.

Farmer A.H. & Wiens J.A. 1999. Models and reality: time-energy trade-offs in Pectoral Sandpiper (*Calidris melanotos*) migration. Ecology 80: 2566–2580.

Fernández G. & Lank D.B. 2008. Foraging behaviour of non-breeding Western Sandpipers *Calidris mauri* as a function of sex, habitat and flocking. Ibis 150: 518–526.

Gillings S., Atkinson P.W., Baker A.J., Bennett K.A., Clark N.A., Cole K.B., González P.M., Kalasz K.S., Minton C.D.T., Niles L.J., Porter R.C., Serrano I.D.L., Sitters H.P. & Woods J.L. 2009. Staging behaviour in Red Knot (*Calidris canutus*) in Delaware Bay: implications for monitoring mass and population size. Auk 126: 54–63.

Glutz von Blotzheim U.N., Bauer K.M. & Bezzel E. 1975. Handbuch der Vögel Mitteleuropas. Vol. 6. Akademische Verlagsgesellschaft, Wiesbaden.

Goede A.A., Nieboer E. & Zegers P.M. 1990. Body mass increase, migration pattern and breeding grounds of Dunlins, *Calidris a. alpina*, staging in the Dutch Wadden Sea in spring. Ardea 78: 135–144.

Hockey P.A.R., Turpie J.K. & Velasquez C.R. 1998. What selective pressures have driven the evolution of deferred northward migration by juvenile waders? J. Avian Biol. 29: 325–330.

Jehl J.R. Jr. 1988. Biology of the Eared Grebe and Wilson's Phalarope in the nonbreeding season: a study of adaptations to saline lakes. Stud. Avian Biol. 12: 1–74.

Jukema J. & Piersma T. 2006. Permanent female mimics in a lekking shorebird. Biol. Lett. 2: 161–164.

Karlionova N., Pinchuk P., Meissner W. & Verkuil Y. 2007. Biometrics of Ruffs *Philomachus pugnax* migrating in spring through southern Belarus with special emphasis on the occurrence of 'faeders'. Ring. Migrat. 23: 134–140.

Karlionova N., Meissner W. & Pinchuk P. 2008. Differential development of breeding plumage in adult and second-year male Ruffs *Philomachus pugnax*. Ardea 96: 39–45.

Klaassen M., Lindström Å., Meltofte H. & Piersma T. 2001. Arctic waders are not capital breeders. Nature 413: 794.

Kohler B. & Rauer G. 2008. Bestandsgrößen und räumliche Verteilung durchziehender Limikolen im Nationalpark Neusiedler See-Seewinkel in den Jahren 1995–2001. Egretta 50: 14–50.

Krupa M., Ściborski M., Krupa R., Popis R. & Wołoszyn J. 2009. Differences in foraging ecology of Wood Sandpiper *Tringa glareola* and Ruff *Philomachus pugnax* during spring migration in Sajna River valley (northern Poland). Ornis Svecica 19: 90–96.

Lifjeld J.T. 1984. Prey selection in relation to body size and bill length of five species of waders feeding in the same habitat. Ornis Scand. 15: 217–236.

Maron J.L. & Myers J.P.1985. Seasonal changes in feeding success, activity patterns, and weights of nonbreeding Sanderlings (*Calidris alba*). Auk 102: 580–586.

Mathot K.J. & Elner R.W. 2004. Evidence for sexual partitioning of foraging mode in Western Sandpipers (*Calidris mauri*) during migration. Can. J. Zool. 82: 1035–1042.

McWilliams S.R., Guglielmo C., Pierce B. & Klaassen M. 2004. Flying, fasting and feeding in birds during migration: a nutritional and physiological ecology perspective. J. Avian Biol. 35: 377–393.

Meissner W. 1998. Some notes on using walk-in traps. Wader Study Group Bull. 86: 33–35.

Meissner W. & Kozirόg L. 2001. Biometrics of Turnstone *Arenaria interpres* migrating in autumn through Gulf of Gdańsk region. Ornis Svecica 11: 181–188.

Meissner W. & Scebba S. 2005. Intermediate stages of age characters create dilemmas in ageing female Ruffs *Philomachus pugnax* in spring. Wader Study Group Bull. 106: 30–33.

Melter J. & Bergmann H.-H. 1996. Jahreszeitliches Aktivitätsmuster, Mauserzyklus und Körpermassenänderung bei Kampfläufern (*Philomachus pugnax*) unter Gehegebedingungen. Vogelwarte 38: 169–179.

Mongin E. & Pinchuk P. 1999. A survey of spring wader migration on the floodplain meadows of the Pripyat River in South part of Belarus during 1994–1998. Ring 21: 149.

Morrison R.I.G. 2006. Body transformations, condition, and survival in Red Knots *Calidris canutus* travelling to breed at Alert, Ellesmere Island, Canada. Ardea 94: 607–618.

Morrison R.I.G., Davidson N.C. & Wilson J.R. 2007. Survival of the fattest: body stores on migration and survival in red knots *Calidris canutus islandica*. J. Avian Biol. 38: 479–487.

Nowakowski J.J. & Górski A. 2002. Status of breeding population and sites of migratory concentrations of the Ruff (*Philomachus pugnax*) in the Narew river-basin and the lower Bug valley. Ring 24: 81–88.

OAG Münster 1989. Zugphänologie und Rastbestandsentwicklung des Kampfläufers (*Philomachus pugnax*) in den Rieselfelderm Münster anhand von Fangergebnissen and Sichtbeobachtungen. Vogelwarte 35: 132–135.

OAG Münster 1998. Mass of Ruffs *Philomachus pugnax* wintering in West Africa. International Wader Studies 10: 435–440.

Pearson D.J. 1981. The wintering and moult of Ruffs *Philomachus pugnax* in the Kenyan Rift Valley. Ibis 123: 158–182.

Pennycuick C.J. 1975. Mechanics of flight. In: Farner D.S. & King J.R. (eds) Avian Biology vol 5: 1–75. Academic Press, London.

Pennycuick C.J., Klaassen M., Kvist A. & Lindström Å. 1996. Wingbeat frequency and the body drag anomaly: windtunnel observations on a Thrush Nightingale (*Luscinia luscinia*) and a Teal (*Anas crecca*). J. Exp. Biol. 199: 2757–2765.

Pinchuk P., Karlionova N. & Zhurauliou D. 2005. Wader ringing at the Turov ornithological station, Pripyat Valley (S Belarus) in 1996–2003. Ring 27: 101–105.

Prater A.J., Marchant J.H. & Vuorinen J. 1977. Guide to the identification and ageing of Holarctic waders. BTO, Tring.

Puttick G.M. 1981. Sex-related differences in foraging behaviour of Curlew Sandpipers. Ornis Scand. 12: 13–17.

Rakhimberdiev E.N., Verkuil Y.I., Saveliev A.A., Väisänen R.A., Karagicheva J.V., Soloviev M.Y., Tomkovich P.S. & Piersma T. 2011. A global population redistribution in a migrant shorebird detected with continent-wide qualitative breeding survey data. Divers. Distrib. 17: 144–151.

Schekkerman H. & Beintema A.J. 2007. Abundance of invertebrates and foraging success of Black-tailed Godwit *Limosa limosa* chicks in relation to agricultural grassland management. Ardea 95: 39–54.

Schmitt M.B & Whitehouse P.J. 1976. Moult and mensural data of Ruff on the Witwatersrand. Ostrich 47: 179–190.

StatSoft Inc. 2009. STATISTICA (data analysis software system), version 9.0. www.statsoft.com.

Summers R.W., Smith S., Nicoll, M. & Atkinson N.K. 1990. Tidal and sexual differences in the diet of Purple Sandpipers *Calidris maritima* in Scotland. Bird Study 37: 187–194.

Swanson D.L., Liknes E.T. & Dean K.L. 1999. Differences in migratory timing and energetic condition among sex/age classes in migrant ruby-crowned kinglets. Wilson Bull. 111: 61–69.

Verkuil Y.I. 2010. The ephemeral shorebird: population history of ruffs. PhD thesis, University of Groningen. http://dissertations.ub.rug.nl/faculties/science/2010/y.i.verkuil.

Verkuil Y.I. & de Goeij P. 2003. Do Reeves make different choices? Meadow selection by spring staging ruffs *Philomachus pugnax* in Southwest Friesland. Limosa 76: 157–168. (In Dutch)

White H. 1980. A heteroscedasticity-consistent covariance matrix extimator and a direct test for heteroscedasticity. Econometrica 48: 817–838.

Wichmann G., Baker J., Zuna-Kratky T., Donnerbaum K. & Rössler M. 2004. Age-related stopover strategies in the Wood Sandpiper *Tringa glareola*. Ornis Fenn. 81: 169–179.

Wolberg J. 2006. Data analysis using the method of least squares. Springer, Berlin.

Wymenga E. 1999. Migrating Ruffs *Philomachus pugnax* through Europe in spring. Wader Study Group Bull. 88: 43–48.

Zöckler C. 2002. Declining Ruff *Philomachus pugnax* populations: a response to global warming? Wader Study Group Bull. 97: 19–29.

SAMENVATTING

In de vloedvlaktes van de Pripyatrivier in het zuiden van Belarus (Wit-Rusland) worden in het voorjaar concentraties van wel 30.000 Kemphanen *Philomachus pugnax* gevonden. De Kemphanen bouwen hier lichaamsreserves op voordat ze hun trek naar het noorden voortzetten. Gedurende acht jaar (2001–2008) bepaalden de auteurs tussen eind maart en half mei het lichaamsgewicht van in totaal 5.375 Kemphanen gevangen nabij Turov, gelegen in de het centrale stroomgebied van de Pripyat. Elk jaar namen de gewichten tijdens de verblijfsperiode gestaag toe. Deze toename was echter niet constant. De auteurs vonden een vrij abrupte versnelling van de gewichtstoename in het laatste deel van het seizoen. De datum van dit omslagpunt in de snelheid van opvetten was gemiddeld 24 april voor de mannetjes, maar varieerde sterk tussen jaren. Voor de vrouwtjes viel dit omslagpunt later rond 3 mei. De gewichtstoename van volwassen mannetjes was in de eerste fase gemiddeld 1,1 gram per dag, later 2,4 gram per dag. Volwassen vrouwtjes namen in de eerste fase gemiddeld 0,6 gram per dag toe, daarna 1,2 gram per dag. De snelheid van opvetten varieerde tussen jaren. Naarmate het waterniveau in het voorjaar hoger was, lag de snelheid van opvetten bij vrouwtjes lager. Bij mannetjes werd dit verband niet gevonden. De auteurs denken dat mannetjes minder afhankelijk zijn van het waterniveau dan vrouwtjes, doordat ze, dankzij hun langere poten, in dieper water kunnen foerageren. Schattingen van de afstanden die kunnen worden afgelegd met de opgeslagen reserves, suggereren dat volwassen mannetjes en vrouwtjes op zijn minst de broedgebieden in westelijk Siberië in een non-stop vlucht kunnen bereiken, behalve in de jaren met hogere waterniveaus. De auteurs concluderen dat de midden-Pripyat waarschijnlijk de laatste pleisterplaats is voor de meeste Kemphanen die dit gebied aandoen op weg naar de broedgebieden. (YIV)

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