

Timing and duration of spring staging of the Eurasian Greater White-fronted Goose (*Anser albifrons albifrons*) in relation to sex, age and progress of migration season

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Among Arctic-breeding waterfowl species, spring stopovers are critical to individuals as a means to accumulate fat and nutrient stores to invest in both migration and their breeding attempt in the tundra zone. We studied the influence of possible factors (age, sex, progress of migration season) on the stopover duration of one such species, the Eurasian Greater White-fronted Goose (*Anser albifrons albifrons*), by analysing records of 1,115 neck-banded birds spotted at their Biebrza Basin stopover site on spring migration in Poland. As expected, because most mature birds are paired, there were no differences between the sexes in stopover duration. Generally, adults stayed for shorter periods than immatures and stopover duration was shorter later in the season. Data from individuals of known age showed that the rate of decrease in stopover duration with season was faster among older than younger geese. Immature birds, still not ready to breed, do not face the pressure to attain breeding condition and therefore may stay longer in the stopover areas. We think these patterns may reflect the greater experience of older birds, as well as the stronger pressure on them to reach the breeding grounds as early as possible. As the breeding season approaches and foraging opportunities at migration sites further up the flyway become more accessible and of higher quality, geese stay for shorter periods later in the season.



1. Introduction

Bird migration consists of two main components: flight bouts and stopovers (Schaub *et al.* 2008). Birds use staging areas to rest and accumulate fat and nutrient supplies for investment in subsequent flight bouts. The time spent on stopovers depends on various factors, both intrinsic (e.g., current fat load, fuel deposition rate, endogenous time programme) and environmental (e.g., food resources, wind conditions, predators; Schaub *et al.* 2008). In reality, the time spent at stopovers constitutes the majority of the overall migration time (e.g., Berthold 1993, Schaub *et al.* 2001, Erni *et al.* 2002). Finding appropriate stopover sites, which allow for effective replenishment of fat and nutrient stores, is crucial for successful migration (Farmer & Parent 1997). This is particularly the case in migratory waterbirds, which depend greatly on scattered stopover sites (Verkuil *et al.* 2006).

Among migratory waterbirds, Arctic-nesting swans and geese depend more heavily on the stopover sites in spring than in autumn, as they need to gain fat in preparation for both migration and for investment in the short breeding period in the tundra zone (e.g., Kear 2005, Nolet 2006, Drent *et al.* 2007, Hübner *et al.* 2010). Thus, conditions at stopover sites are likely to be the key factors influencing their breeding success in the subsequent breeding period (Farmer & Parent 1997, Drent *et al.* 2007). However, the stopover ecology of these birds is still insufficiently understood and relatively few papers addressing this issue have been published (e.g., Arzel *et al.* 2006, Hübner *et al.* 2010, Kölzsch *et al.* 2016, Polakowski *et al.* 2018).

The Eurasian Greater White-fronted Goose (*Anser albifrons albifrons*) is a widespread species breeding in the tundra zone of northern Eurasia (Madsen *et al.* 1999; Banks 2011), which migrates on a broad front from wintering areas in the Netherlands and Germany eastwards to Lithuania and further on to Russia (Madsen *et al.* 1999, Kruckenberg *et al.* 2008). During spring migration, they concentrate in great numbers in the Biebrza Basin (north-eastern Poland; Polakowski *et al.* 2011), which is one of the most important staging sites for the species in Central Europe (Polakowski *et al.* 2011).

In this study, we examined the influence of several factors on the stopover duration of Eurasian Greater White-fronted Geese in the Biebrza Basin, using sequential records of neck-banded individuals collected in the field. We expected the age of the birds to be one of these factors. For adult birds spring migration is more time-limited, as they have to arrive at the breeding sites not only in the best condition, but also early enough to utilize best the short breeding period in the Arctic tundra zone and thus optimize their chance of reproductive success.

Immature individuals, being in their 2nd calendar year of life, are not yet ready to reproduce, are less time constrained and so may stay at the stopover site for longer periods. As the pressure on adults intensifies with the elapse of the migration period, we expected the stopover duration to decrease accordingly. Finally, as geese form lifelong pair bonds and pair members migrate together, we predicted no difference between the stopover durations of males and females.

2. Materials and methods

2.1. Study area

The study was conducted in the Biebrza Basin, north-eastern Poland (Fig. 1). This is one of the most important stopover sites for the Eurasian Greater White-fronted Geese in Central Europe, concentrating as much as up to 70% of the numbers migrating through Poland in spring and up to 10% of numbers wintering in Europe (Polakowski *et al.* 2011). Total numbers here can exceed 100,000 and individual flocks can hold up to 38,000 individuals (Polakowski *et al.* 2011). The Biebrza Basin is formed by the Biebrza valley and part of the Narew valley (Fig. 1).

The 260,000 ha study area, described in detail by Polakowski *et al.* (2011), Polakowski & Kasprzykowski (2016) and Polakowski *et al.* (2018), is one of the largest and best-preserved wetlands in the European lowlands (Grygoruk *et al.* 2013). Most of the Biebrza Basin is protected as a national park as well as two Natura 2000 SPA: “Ostoja Biebrzańska” (PLB200006) and “Bagno Wizna” (PLB200005). The Biebrza valley in the study area is 100 km long and up to 20 km wide, while

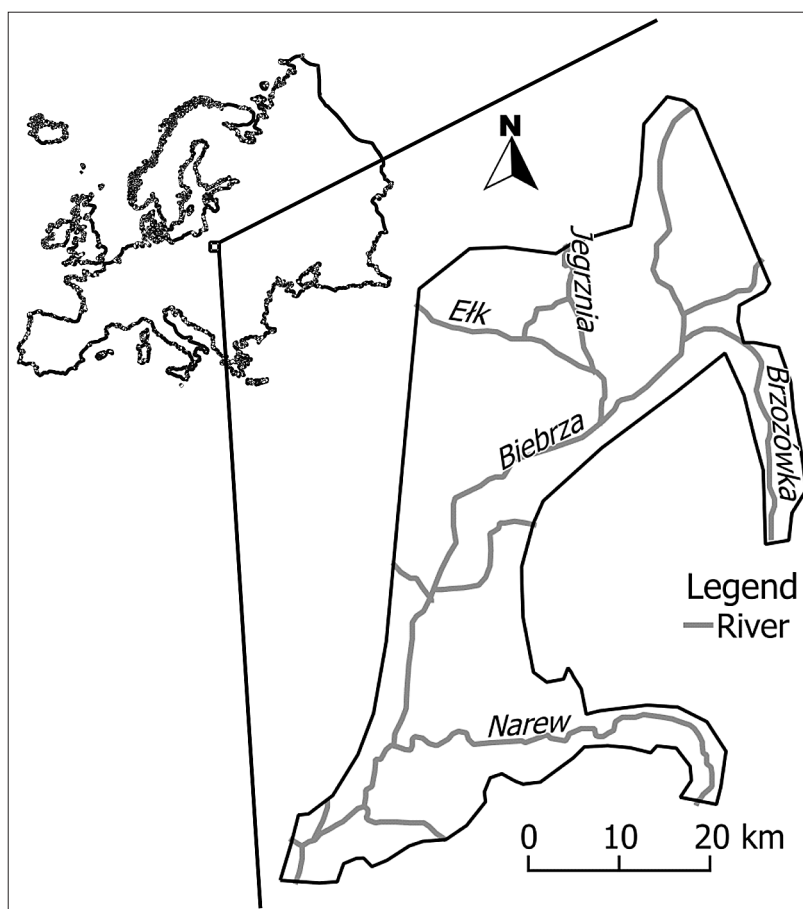


Fig. 1. Location of the study area in the Biebrza Basin, Poland.

the Narew valley is 65 km long and up to 15 km wide. Seasonally flooded green crops – mainly meadows and pastures – are the most important feeding and roosting sites for migrating geese in the basin (Polakowski *et al.* 2011, Polakowski & Kasprzykowski 2016).

These habitats cover about 46.8% of the study area and are situated mostly in its central and southern parts. Arable fields lie mostly beyond the borders of the valley, covering 21.5% of the study area. Other habitats found in the study area play only a marginal role for geese (such as artificial surfaces and forests, in total about 31.7% of the area). Both rivers overflow their banks annually, flooding mainly meadows and pastures in the valleys. Spring floods in the Biebrza Basin last the longest in the middle and lower courses of the Biebrza and in the central part of the Narew valley within the study area.

2.2. Data collection

The neck-banded geese observed during the research and within the study area (with no leg-ringed individuals spotted) had been ringed mostly in the wintering areas in the Netherlands and Germany, while only fewer individuals in the breeding and moulting areas in Russia (Kolguyev Island and Pyasina Delta in Taimyr). Observations were conducted throughout the study area, mainly by Michał Polakowski and Monika Broniszewska, with the main focus on the sites where geese concentrated every year (Polakowski *et al.* 2011, Polakowski & Kasprzykowski 2016).

Most field surveys within the study area were carried out during 2–4 days (median 17.5 surveys per season) and the geese flocks, that were looked through, numbered from about 3,000 in the beginning and end of the season till approximately

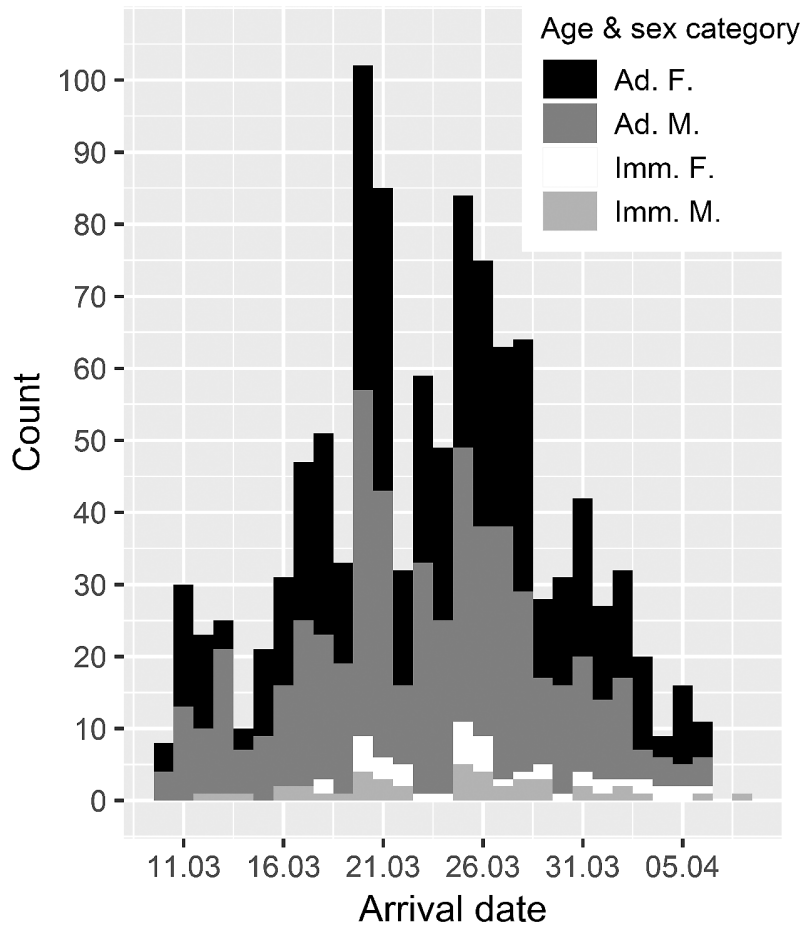


Fig. 2. Distribution of the numbers of observations of neck-banded individuals in the Biebrza Basin. Ad. F. – adult females, Ad. M. – adult males, Imm. F. – immature females, Imm. M. – immature males.

30,000 individuals around the peak of migration (second half of March; Polakowski *et al.* 2011). Flocks were scanned with spotting scopes without causing disturbance and all neck-band numbers seen were recorded and reported to the central web database on colour-marked geese in Europe (www.geese.org).

The fieldwork in the Biebrza Basin was carried out during 10 spring seasons (March and April; records of neck-banded geese were scarce outside these two months) in 2007–2017 (excluding 2013, being characterized by an unusually long winter and extremely late spring, see Polakowski *et al.* 2018).

2.3. Data analysis

All records of marked birds were downloaded from the database www.geese.org. We analysed

the variation in stopover duration, which we defined as the number of days between the first and the last record of a marked bird within the season in the study area (minimum stopover duration). We described the migration period of geese as the time between the first and the last observations. We estimated the stopover duration of birds seen only once as one day. Although this approach likely underestimated the stopover duration (Chernetsov 2012), we considered it to be the most objective way to treat such records. The independent variables were 1) day of arrival (i.e., day of the first record of an individual, recorded as the day of the year), 2) age with two categories: adults (1,029 birds older than the 2nd calendar year of life) and immatures (86 birds in the 2nd calendar year of life, ringed in the wintering period preceding their spring migration), 3) sex (544 males, 571 females).

Table 1. Descriptive statistics of the day of arrival, day of departure and minimal stopover duration. All values are given in days. Q1 – lower quartile, Q3 – upper quartile, CI – 95% confidence interval.

| Adults, $n = 1029$ | Mean | Lower CI | Upper CI | Median | Q1 | Q3 | Min | Max |
|---------------------|------|-------------|-------------|--------|----|----|-----|-----|
| Arrival day | 82.1 | 81.7 | 82.4 | 82 | 78 | 86 | 59 | 96 |
| Departure day | 82.9 | 82.6 | 83.3 | 83 | 79 | 87 | 69 | 103 |
| Stopover length | 1.9 | 1.7 | 2.0 | 1 | 1 | 1 | 1 | 29 |
| Immatures, $n = 86$ | | | | | | | | |
| Arrival day | 84.5 | 83.2 | 85.8 | 84 | 80 | 88 | 71 | 98 |
| Departure day | 86.0 | 84.6 | 87.4 | 85 | 80 | 92 | 71 | 99 |
| Stopover length | 2.5 | 1.8 | 3.1 | 1 | 1 | 2 | 1 | 14 |
| Males, $n = 544$ | | | | | | | | |
| Arrival day | 81.8 | 81.3 | 82.4 | 82 | 78 | 86 | 59 | 98 |
| Departure day | 82.8 | 82.3 | 83.4 | 83 | 79 | 87 | 69 | 99 |
| Stopover length | 2.0 | 1.8 | 2.2 | 1 | 1 | 1 | 1 | 29 |
| Females, $n = 571$ | | | | | | | | |
| Arrival day | 82.6 | 82.1 | 83.1 | 83 | 79 | 87 | 61 | 96 |
| Departure day | 83.5 | 83.0 | 84.0 | 84 | 79 | 87 | 69 | 103 |
| Stopover length | 1.9 | 1.7 | 2.1 | 1 | 1 | 1 | 1 | 22 |
| All birds | | | | | | | | |
| Arrival day | 82.2 | 81.9 | 82.6 | 82 | 78 | 87 | 59 | 98 |
| Departure day | 83.2 | 82.8 | 83.6 | 83 | 79 | 87 | 69 | 103 |
| Stopover length | 1.9 | 1.8 | 2.1 | 1 | 1 | 1 | 1 | 29 |

We also modelled the interaction between the age category and day of arrival (to enable interpretation the variables were centred before the analyses; Schielzeth 2010), which would be excluded from the final model if they were statistically insignificant. We added year as a random effect (random intercept). We checked the full model with Poisson distribution for overdispersion: as it did not fit the data ($p < 0.05$), we used GLM (generalised linear mixed) models with negative binomial error distribution and log link function.

In our second approach, we were able to compute the exact age of birds ringed as immatures ($n = 380$) and later recorded in the Biebrza Basin. Here we examined age as a continuous variable in relation to the variability of the stopover duration. The other independent variables were sex (183 females, 197 males) and day of arrival, incorporating the interaction between the exact age and day

of arrival (to enable interpretation the variables were centred before the analyses; Schielzeth 2010), which would be excluded from the final model if they were statistically insignificant. We checked the full model with Poisson distribution for overdispersion and found that it did not fit the data ($p < 0.05$). Thus, we used GLM models with negative binomial error distribution and log link function. We used the “MASS” package (Venables & Ripley 2002) in R software (R Core Team 2018) for the analyses.

3. Results

We recorded 1,029 adults and 86 immatures, 544 males and 571 females – altogether 1,115 neck-banded Eurasian Greater White-fronted Geese, 228 of which were seen more than once within a

Table 2. Models describing variation in stopover duration of Greater White-fronted Geese. Two models are presented: first, where all the data were used, and second, where only the individuals of exact known age were included. The independent variables in the first model include age category (Age_cat), arrival date and sex. The continuous variables in the second model were age and arrival date. Year was a random effect – r(year) – in both models.

| | Estimate | Std. Error | z value | P |
|---|----------|------------|---------|------------------|
| Whole data set, $n = 1,115$ | | | | |
| (Intercept) | 5.424 | 0.421 | | |
| Age_cat[immatures] | 0.498 | 0.102 | 4.907 | <0.001 |
| Arrival date | -0.060 | 0.005 | -12.091 | <0.001 |
| Sex[M] | 0.026 | 0.056 | 0.458 | 0.647 |
| r(year) | 0.141 | 0.375 | | |
| Data with exact age of birds, $n = 380$ | | | | |
| (Intercept) | 0.575 | 0.137 | | |
| Age | -0.067 | 0.017 | -4.073 | <0.001 |
| Arrival date | -0.062 | 0.008 | -7.926 | <0.001 |
| Sex[M] | -0.058 | 0.100 | -0.579 | 0.563 |
| Age × arrival date | -0.006 | 0.002 | -2.644 | 0.008 |
| r(year) | 0.131 | 0.362 | | |

season (for those individuals the minimal stopover duration was longer than 1 day). The distribution of observations of neck-banded geese is shown on Fig 2. The migration period lasted from 11 March to 10 April, peaking between 18 March and 30 March. The median arrival day for all the birds was 23 March and the mean stopover duration was 1.9 days (Table 2). Adults arrived in the Biebrza Basin on average 2 days earlier than immatures, and females arrived on average one day later than males (Table 1).

In the first analysis, which included all the individuals ($n = 1,115$), we found no interactive effect of age category and arrival date ($p > 0.05$), so it was excluded from the final model (which is shown in Table 2). Sex did not affect the stopover duration (Table 2; predicted means [days] \pm SE: males = 2.1 ± 0.3 ; females = 2.1 ± 0.3). Meanwhile, there were differences between age groups: immatures stayed significantly longer than adults (Table 2, Fig. 3; predicted means [days] \pm SE: immatures = 2.7 ± 0.4 ; adults = 1.6 ± 0.2). Stopover duration decreased with arrival date (Fig. 3). The stopover duration at the beginning of the season was longer (e.g., on the 11 March for adults 3.4 days, for immatures 5.6 days) in comparison with the end of the season (e.g., on the 26 March for

adults 1.4 days and for immatures 2.3 days; Table 2, Fig. 3). When using the data with known age ($n = 380$), there was an interaction between age (as a continuous variable) and arrival date (Table 2, Fig.4). With the advancement of the migration season, the stopover periods of older birds shortened at a faster rate than those of younger birds. Sex was not associated with stopover duration.

4. Discussion

We found that young Greater White-fronted Geese (immatures in their 2nd calendar year of life) arrived later and stayed longer than adults at the stopover sites. More detailed analyses, in which the birds' exact age was known, confirmed that age was a crucial factor explaining the stopover duration. The adult birds of many different species fly rapidly to their breeding grounds in spring to occupy the best territories and start breeding as early as possible in the best possible conditions (e.g., Berthold 1993, Prop *et al.* 2003, Arzel *et al.* 2006, Drent *et al.* 2006, Newton 2008). This may also explain the shorter stopover duration in more advanced part of the spring migration period in comparison with the earlier part of the season.

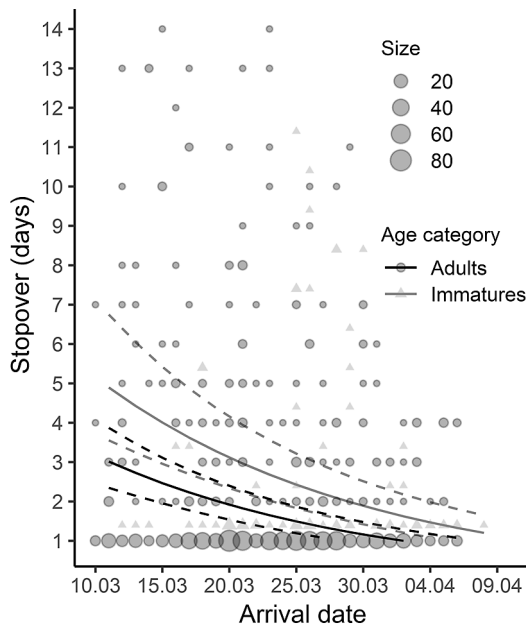


Fig. 3. Prediction of stopover duration for Greater White-fronted Geese. Lines represent the prediction from the negative binomial model with 95% confidence intervals (dashed lines) and they show the additive effects of age category (Adults: older than the 2nd calendar year of life; Immatures: in the 2nd calendar year of life) and date of arrival. The raw data are shown as a bubble plot and the sizes of the triangles and circles represent the sizes of the groups. The triangles have been shifted by a value of 0.4 above the integer stopover values so as to avoid overlap with the circles.

Geese appear to time their reproduction to synchronise the raising of their offspring with the period of nutrient-rich herbaceous plants growth in the breeding areas. In order to do this, they initiate egg-laying as early as possible, when only a few places are free of snow and competition for good nesting sites is strong (van Wijk *et al.* 2012). This competition probably compels dominant adults to leave the stopover sites as soon as they can, once they have accumulated sufficient nutrient and energy stores through foraging.

We found that mature geese arrived earlier in the Biebrza Basin. This could also be linked to the pressure of the oncoming breeding season: early arriving adults would be ready to continue their migration earlier. On the other hand, geese are “capital” rather than “income” breeders, so they have to acquire energy and store the nutrients re-

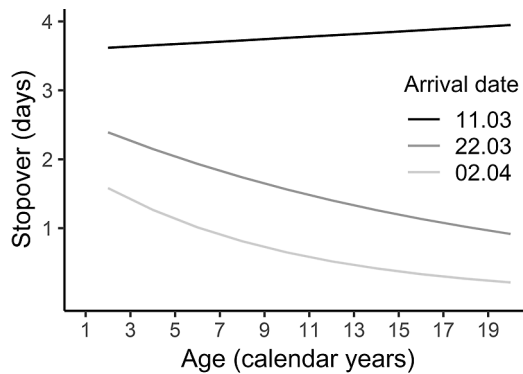


Fig. 4. Prediction of stopover duration of Greater White-fronted Geese when the exact age of the birds was known. The figure shows the interactive effect of age and date of arrival (continuous variable, represented on the panel by days of arrival) and also that the older the birds, the sharper the decrease of the stopover duration during the migration period.

quired for breeding en route. Therefore, they need enough time to acquire an appropriate level of fat reserves, which is an important factor influencing stopover duration (Spaans *et al.* 2007, Inger *et al.* 2008, van Wijk *et al.* 2012, Kölzsch *et al.* 2016). Energy loads accumulated by birds on stopover influence the overall time of migration, the energy costs of transport as well as the total energy cost of migration (Hedenström & Ålerstam 1997). Accumulation of appropriate energy resources during the spring passage may be crucial to subsequent breeding success. It may be the reason why, according to some studies (e.g., Kölzsch *et al.* 2016), spring migration in geese can be much longer than the autumn one.

On the other hand, longer stopover duration could reflect more limited experience and poorer foraging techniques, a phenomenon well-known among young birds of many different species (e.g., Berthold 1993, Wichmann *et al.* 2004, Polakowski & Jankowiak 2012). In other words, older and more experienced geese are more capable of “managing” their refuelling, which could result in the sharper decline of stopover duration as the migration period advanced. Inexperienced birds may require more time for feeding in order to maintain high food intake rates. This refers mostly to the second calendar year birds, which are not mature yet and belong to the non-breeding part of the population (Kear 2005). Therefore, as they are not

under pressure of the approaching breeding season, they can afford to arrive later and stay longer at the stopover sites, thereby compensating for less efficient fat deposition.

We found no differences between the stopover durations of males and females. Initial pair formation in adult birds occurs in winter or spring, mainly in their second or third year of life, and the birds maintain pair bonds throughout their lives and raise their offspring together (Fox & Stroud 1988, Warren *et al.* 1992, Kear 2005). Both pair members migrate together and arrive at the breeding grounds at the same time. Because of the pair bonds, it is likely that males are slowed down by their females, which have to carry an extra fat load for breeding (van Wijk *et al.* 2012).

In conclusion, both age and timing within the migration season seem to play a key role in influencing the stopover duration of the geese. Adults of both sexes migrate together and do so more rapidly in comparison to non-mature immature birds. This is related to their need to attain the best condition and arrive at the nesting areas as early as possible, which shortens the duration of their stopover, especially in the later stages of the spring migration season. On the other hand, immature birds are not ready to breed yet and therefore do not face such time pressure. Consequently, they can afford staying longer in the stopover areas.

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Tundrahanhen kevätmuuton levähdysten ajoitus ja kesto: sukupuolen, iän ja muuton ajankohdan vaikutus

Pohjoisella pallonpuoliskolla pesiville vesilinnuille kevätmuuton pysähdykset ovat tärkeitä rasva- ja energiavarastojen tankkauspisteitä. Tutkimme iän, sukupuolen ja muuton etenemisen vaikutusta levähdyskäyntien kestoon tundrahanhilla. Aineistona käytimme Puolan (Biebrza Basin) levähdyspaikalla havaittuja, 1 115 kaularengastettua hanhea. Sukupuolten välillä ei havaittu eroja levähdyskäynnin pituudessa, johtuen todennäköisesti siitä että aikuiset hanhet ovat jo pariutuneet. Aikuiset hanhet jäivät levähdyspaikoille lyhyemmäksi aikaa kuin nuoret hanhet. Levähdykset olivat lyhempiä myöhemmin keväällä. Erityisesti iäkkäämmillä hanhilla levähdysten pituus lyheni jyrkemmin kauden edetessä.

Todennäköisesti nämä tulokset selittyvät vanhempien lintujen kokemuksella, sekä sillä että niillä on enemmän kiire lisääntymisalueille kuin nuorilla, ei-lisääntymiskykyisillä yksilöillä. Lisäksi kauden loppupuolella pohjoisemmatkin levähdysalueet sulavat ja tarjoavat hyvälaatuista ravintoa, mikä voisi selittää lyhyempää levähdysaikaa myöhemmin keväällä.

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