AUTUMN MIGRATION OF THE THRUSH NIGHTINGALE
(Luscinia luscinia) IN NORTHERN HUNGARY

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ABSTRACT


The autumn migration of the Thrush Nightingale was studied in Szalonna in northern Hungary in 1989-2010. Birds were mist-netted, ringed, aged, measured, weighed and fat scored. In total, 193 Thrush Nightingales were ringed during 22 years. Relations between arrival time and biometrical measurements were determined. Within the study period (6 August – 26 September) the migration curve was bimodal showing maximum on 22 August and 27 August. Immature birds arrived significantly earlier with lower body mass and shorter wing length and had more pointed wings in the first half of their passage. The distribution of fat score classes did not differ significantly between the early and late periods of the most intensive migration, although the mean of the deposited fat was the lowest during the peak of migration. Fat reserve distribution was bimodal in autumn suggesting that Thrush Nightingales probably start their journey from different breeding ranges (populations) or follow still undiscovered migration strategies of sex/age groups. The low proportion of recaptures proved that the area was not used as a stopover site or premigratory fattening area. Within 22 years of study, the median date of autumn migration of Thrush Nightingales shifted 7.9 days earlier, probably due to current climate change.

Key words: Luscinia luscinia, wing length, wing shape, body mass, fat reserves, age groups, timing of migration

INTRODUCTION

The climate change is one of the most important problems. In the last hundred years, the warming of the Earth increased by 0.5°C (IPCC 2001). Due to this fact, many avian taxa have shifted their timing of migration (Berthold 1990, Crick and Sparks 2006). Some species arrive earlier while others significantly later (Bradley et al. 1999, Zalakevicius and Zalakeviciute 2001). However, climate change affects
not only the timing of migration, but also morphological or physiological traits. In the last decades, breeding areas of many migratory species shifted towards the north and birds started their egg-laying period earlier (Thomas and Lennon 1999). Morphological characters (e.g. body size, wing shape, wing length) often correlate with migratory behaviour of birds. Populations of several species living in the north have relatively longer and more pointed wings than their southern counterparts, but these traits can also be influenced by the climate change (Leisler and Winkler 1985). Therefore, long-distance migratory bird species are basically suitable to describe the impacts of the global warming (Berthold 1990). Many avian taxa give a dynamic response to changing of external conditions (Baker 1978, Alerstam and Högstedt 1982, Alerstam 1990, Berthold 1996). Seasonal changes in survival and breeding are considered in migration systems (Moreau 1972, Alerstam and Högstedt 1982), which have been examined by research programs based on the analysis of the dynamics of migration and ringing recoveries (Gauthreaux 1996). Investigation of long-distance migrant species is very suitable to determine any changes in the timing and dynamics of migration, respectively (e.g. Sokolov et al. 1999, Tøttrup et al. 2006).

The Thrush Nightingale is a monotypic species, widespread in temperate Asia (mostly in Western Siberia) and north-eastern Europe, rarely nesting but regularly migrating in autumn in the Carpathian region (Cramp 1992). It is a medium-sized, ground-feeding, insectivorous, intercontinental migrant, which prefers gallery forests close to wider rivers. The wintering area lies from East Africa’s savannah via the Equator to latitude 28°S (Moreau 1972). Its western and central European populations migrate south east (Keith et al. 1992) to the southern areas of Africa (Hogg et al. 1984, Shirihai 1996). In Hungary, first migrants of transient birds arrive in the beginning of August, with a migration peak during the second half of August, and only a few individuals can be found after mid-September (Schmidt 1982). The European breeding populations migrate across the larger ecological barriers (e.g. Carpathians, Mediterranean Sea and Sahara).

The Carpathian Basin plays a special role in the migration of European passerines. Depending on location of the breeding areas and migration strategies, most Palaearctic migrants simply avoid, while others fly across this region (Csörgő and Lövei 1990). To understand the migration strategies, the relations among morphology, body mass condition, fat reserves and timing are necessary to determine. Descriptions of migration dynamics at a stopover site where the species occurs during their autumn migration only, are essential to understand their behaviour. Presently, the migration phenology (e.g. the timing of migration) and stopover ecology are still poorly known for the Thrush Nightingale in the Carpathian Basin. Although its stopover phenology and recurrence behaviour have been relatively well studied in central Hungary (Schmidt 1986, Csörgő and Lövei 1995), the dynamics of autumn migration is virtually unknown in the northern part of the country.

The aim of this study was to describe the dynamics of autumn migration and the changes of wing lengths, wing shapes, body mass and fat reserves of Thrush Nightingales in northern Hungary (Szalonna) using the data of 22 years. Further aim was to examine the migration phenology and possible impacts of the climate change using standard, long-term mist-netting and ringing data.
STUDY AREA

The research was carried out at the Bódva Valley Bird Ringing Station in the Aggtelek National Park at Szalonna (48°27'N, 20°42'E) (Fig. 1). The study area was situated between two medium-altitude hills covered by deciduous forest vegetation (see the darker area on Fig. 1). The vegetation is primarily dominated by soft-wood riparian forests (Salicetum albae-fragilis) consisting of the White Willow (Salix alba), Crack Willow (S. fragilis), White Poplar (Populus alba) and Black Poplar (P. nigra), which play an important role in the general ecological functioning of those wetlands. The habitat structure of the sampling locations consists of mixed old hard-wood riparian (gallery) forests dominated by the Common Oak (Quercus robur), European White Elm (Ulmus laevis), Field Elm (U. minor), European Ash (Fraxinus excelsior) or Narrow-leafed Ash (F. angustifolia), White and Black Poplars and different sections of associated small oxbow lakes and backwaters with the Common Alder (Alnus glutinosa), White Willow, White Poplar and low amount of the European Elder (Sambucus nigra). The climate is dominantly continental with a mean annual temperature of 9.5-10°C (±0.5), and with a mean annual precipitation of 550-700 mm.

MATERIAL AND METHODS

Ringing data were collected during post-breeding and autumn migration between 1989-2010. The birds were caught in bushy vegetations and sub-mountain forest associations using 12 m long and 2.5 m high Ecotone® mist-nets. Altogether 40 mist-nets (1200 m2) were set up at standard locations in every year. Mist-netting was permanent between mid-August and mid-October, started daily at 5.00 and lasted to 20.00. Nets were controlled every hour. All birds were ringed and aged as follows: immature (Imm.) – hatched in the year when they moulted partially and retained juvenile pri-
maries; adult (Ad.) – more than one-year old birds, individuals with the same generation of all feathers after post-nuptial moult. The Thrush Nightingale is a sexually monomorphic species (Svensson 1992) and thus, sexing adults was impossible in autumn. Ageing was based on criteria given by Busse (1990) and Svensson (1992). After ringing and measurements all birds were released.

To analyse the phenological changes in arrival time of migrating populations, standardized data are essential. Hence, mist-netting and ringing were standardized per unified period and net surface. The captures were standardized to the average number of birds caught by a net surface of 1200 m² within 100 h.

The averaged number of individuals was used when calculating the population indices. According to Greenwood et al. (1993), the „chain” index can be calculated as follows:

\[ I_s = \frac{N_s}{N_{s-1}} \times I_{s-1} \]

where:
- \( I_s \) – the chain index of the specific year,
- \( I_{s-1} \) – the chain index of the previous year,
- \( N_s \) – the number of birds captured on 1200 m² net surface in 100 h in the specific year,
- \( N_{s-1} \) – the number of birds captured on 1200 m² net surface in 100 h in the previous year.

The passage time trend and long term population dynamics were checked by linear regression and described as regression equation, Pearson’s \( r \) and statistical significance \( p \).

Individuals of the migrating population were characterized by the time of arrival, wing length, wing shape, body mass and fat score classes. Both age groups were compared considering the morphometrical measurements during the migration period, to find any differences.

**Biometric measurements**

When analysing the dynamics of migration for a population it is important to control the possible differentiations in wing lengths, wing shapes, body mass and fat reserves as well. For this purpose, each captured bird was measured following the recommendations of the Hungarian Bird Ringing Protocol (Szentendrey et al. 1979). Specifically, the variables of maximum chord wing length (\( WL \) – in millimetres) and body mass (\( BM \) – in grams) were recorded for each individual. Wing characteristics were measured with a plastic ruler to the nearest millimetre according to maximum chord method by Svensson (1992), where the wing is flattened and straightened sideways.

Wing formula was recorded in all cases of not active moult observed. Distances were measured from the tip of wing to the tip of each primary on the closed wing in millimetres and numbered in an ascending order. The wing formula measurements were used to calculate two indices, using the Holynsky (1965) equations:

\[ W_s = \frac{100 \times (dPF - dDF)}{WL} \]
\[ W_{sym} = \frac{dPF}{dDF} \]

where:
- \( W_s \) – the index of wing pointedness,
- \( W_{sym} \) – the index of wing symmetry,
**Results**

In total, 193 Thrush Nightingales were captured, ringed and measured during the period of 22 years. Of these, 46 were identified as adults and 147 as immatures. The earliest record was on 6 August and the latest on 26 September; the maximum of migration was observed on 22 August and 27 August (Fig. 2). Only 10 individuals were recaptured on 19 occasions during 1989-2010 (excluding cases of ringing and recapture on the same day). Taking into account all the birds ringed at Szalonna, 1.03% was recaptured in later years. The low proportion of recaptures proved that the area was not used as a stopover site or premigratory fattening area.

The population indices \( I_t \) of migrating Thrush Nightingales increased \( (r = 0.205) \), but it is worth to point out that after excluding the very abnormal value in 1992, \( r \) value was much higher and statistically significant (Fig. 3). The mean value of the autumn migration of the species (Fig. 4) shifted significantly \( (r = -0.17, p < 0.05) \) 7.9 days earlier (mean day = 23/24 Aug. or 235.5 day of the year, \( SD = 7.91 \)).
For an analysis the migration period was divided into two sub-periods (Table 1). The relation of immature birds to adults was 3.75 in the first half of the migration while 2.23 in the second one, which means that adults arrive later in the Bódva Valley. In the first wave of migration, the immature birds had significantly lower body mass, while adult birds did not show statistical differences between the two periods of migration (Table 1). Within the first wave of migration, the immature birds differed from the adults significantly in relation to the body mass ($t$-test, $t = 3.157$, $p < 0.005$), while in the second period no significant difference was found between the two age groups ($t$-test, $t = 1.082$, $p > 0.30$). Wing lengths tended to be spread out and were not concentrated near the mean. The minimum and maximum wing lengths were 82 and 96 mm respectively, with a mean of 87.58 mm ($SD = 3.84$, $n = 120$). In the wing length distribution both age groups differed significantly between the periods of autumn migration. Immatures had shorter wing length in the first half of the migration than in the second one. In the case of adults, no significant difference was found.
As in the case of body mass, similar pattern was observed in the wing length between the two age groups. Moreover, highly significant difference was noted in the first half of the migration between adult and immature birds ($t = 2.743, p = 0.008$). In the second wave, no difference was found in this respect ($t = 1.163, p > 0.26$). Immature birds with significantly more pointed wings arrived earlier. In the second half of migration, adult individuals showed more pointed wings, but there was no significant difference between the early and later stages of their migration. Further, no significant difference was found in the wing symmetry index in both age groups between the first and second half of migration. In the first phase of migration immature migrants had more symmetric wings than in the second half, although the difference was insignificant. In relation to the wing pointedness and wing symmetry indices, age groups did not differ significantly within each period of their migration ($W/B_70$ and wave 1: $t = 1.002, p > 0.30$; wave 2: $t = 1.278, p > 0.20$; $W_{Im}$ and wave 1: $t = 1.723, p > 0.05$; wave 2: $t = 0.556, p > 0.50$).

### Table 1

Biometrical parameters differentiation between two periods of migration (see text). $N$ given in brackets.

<table>
<thead>
<tr>
<th>Age group</th>
<th>Migration period</th>
<th>Imm.</th>
<th>1.</th>
<th>2.</th>
<th>Ad.</th>
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</thead>
<tbody>
<tr>
<td>Body mass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>[g]</td>
<td>$t$-test</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>25.52 ± 4.92</td>
<td>$t = 1.992; p &lt; 0.05$</td>
<td>27.30 ± 5.43</td>
<td>($89$)</td>
<td>($56$)</td>
<td>29.57 ± 6.20</td>
</tr>
<tr>
<td>Wing length [mm]</td>
<td>$t$-test</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>86.62 ± 4.08</td>
<td>$t = 2.943; p &lt; 0.005$</td>
<td>88.13 ± 2.22</td>
<td>($109$)</td>
<td>($38$)</td>
<td>88.90 ± 3.95</td>
</tr>
<tr>
<td>Wing pointedness index</td>
<td>$t$-test</td>
<td></td>
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<tr>
<td>67.52 ± 8.15</td>
<td>$t = 3.171; p &lt; 0.005$</td>
<td>63.86 ± 5.24</td>
<td>($109$)</td>
<td>($38$)</td>
<td>65.83 ± 8.05</td>
</tr>
<tr>
<td>Wing symmetry index</td>
<td>$t$-test</td>
<td></td>
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<td></td>
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<tr>
<td>48.00 ± 4.65</td>
<td>$t = 1.966; p &lt; 0.05$</td>
<td>50.18 ± 6.26</td>
<td>($109$)</td>
<td>($38$)</td>
<td>50.70 ± 8.09</td>
</tr>
</tbody>
</table>

The fat score classes showed a bimodal distribution during autumn migration. The median fat score was 2 for specimens captured in the first half of migration and 3 in the second period. The distribution of fat scores in the early and late peak periods of the migration did not differ from each other significantly (wave 1: mean = 2.32, $SD = 1.72, n = 118$; wave 2: mean = 2.63, $SD = 1.82, n = 59$; $t = 1.311, p > 0.10$). Therefore, the studied individuals migrate with homogenous fat reserves in Szalonna. The median of the fat score frequency was 2.00 (mean = 2.45, $SD = 1.76, n = 177$). The frequency of fat score classes of 2 and 3 was 23.7 and 18.6%, respectively. The lowest proportion of birds with fat scores of 0 and 1 was 16.1 and 15.3%. Changes in fat scores and body mass are given in Figure 5. The curve of fat scores was relatively parallel with that of body mass, although the fat line is somewhat stretched.
DISCUSSION

In autumn, birds usually optimize their migration for survival. Within this period, the Thrush Nightingale mainly feeds on elderberries (Csörgő and Lövei 1995). Based on this experience, one reason for the early arrival may be that the birds must coordinate the timing of their migration to ripening berries. Due to climate change, breeding populations have to start their journey earlier in order to find ripe elderberries. Presumably, individuals with minimal fat reserves came from a relatively short distance from the study area, or came from more distant northern breeding grounds and their fat reserves were depleted. Avian wing size, wing shape and body mass may be affected by many factors, such as climate, migratory strategies and behaviour or developmental conditions (Tellería et al. 2001).

The Intergovernmental Panel on Climate Change (IPCC) expects the average global surface temperature to rise by 0.6 to 2.5°C in the next fifty years, and 1.4 to 5.8°C in the next century, with significant regional variations. Climate change may affect large-scale spatial distribution, phenology of migration and breeding, pattern of moulting as well as biometrical parameters (e.g. wing characters) of birds. Recently, research on many indicator species has become increasingly important. Within the last decades, many migrant passerines have changed in their migration phenology (Cotton 2003, Leikoinen et al. 2004, Crick and Sparks 2006, Zalakevicius et al. 2006), moulting (Hedenström et al. 2007), the timing of breeding (Crick et al. 1997, Forchhammer et al. 2002, Both et al. 2004), distribution factors (Berthold 1993, Crick 2004, Seather et al. 2004) and biometrics (Yom-Tov et al. 2006), presumably due to climatic factors (Williamson 1975, Lundberg and Edholm 1982, Berthold 1990). Short- and medium-distance migrants adapt more quickly to changed conditions than long-distance migrant species subjected to stronger genetic controls (Berthold 1996, Pulido et al. 2001, Butler 2003). The timing of migration of many bird species has changed recently, probably due to climatic factors. Migration is a dynamic re-

Fig. 5. Changes of fat score (T – right y-axis) and body mass (left y-axis)
sponse of birds to changing environmental conditions through which many populations and species track seasonal productive outputs across climatic gradients (Baker 1978, Berthold 1996). However, it is still not clear whether the evolutionary change or simply the flexibility of the phenotypes is in the background (Coppack and Both 2002, Gienapp 2007).

In spring, the Thrush Nightingale does not migrate through the Bódva Valley (Farkas pers. comm.), and thus, this species is probably a loop migrant. Based on the number of mist-netted birds during autumn season, immature Thrush Nightingales start their autumn migration earlier, while adults arrive later in the Bódva Valley. For the immatures the mean wing length and body mass were significantly larger in the second half of the migration than in the first one. The timing of migration may depend on the developmental and physiological condition of birds and geographical location of the population as well (Csörgő and Lövei 1995). Therefore, more developed Thrush Nightingales with longer wings and larger body mass might start their journey later, while weaker ones have to depart earlier. Significant differences in the wing shape indices were found only in relation to the wing pointedness – the immature migrants had more pointed wings. The first possible explanation is that immature birds having more pointed wings are more advantageous compared to adults. On the other hand, immature and adult Thrush Nightingales may come from various breeding areas or populations, and thus, could show differences in biometrics. In general, wing length and wing shape show clinal variation with latitude: northern breeders have relatively more pointed and longer wings than birds breeding in southern areas (Klein et al. 1982). This trend has already been known for some other transcontinental migrants, e.g. Phylloscopus species (Gaston 1974, Lövei 1983, Csörgő and Lövei 1990, Berthold 1993).

Stopovers are crucially important for most small passerines since it is not possible to complete their intercontinental migration period without refuelling (Berthold 1975, Blem 1980). Thus, the typical migratory journey is made up of several flight periods, where fat load is used as fuel, and stopover periods (Alerstam and Hedenström 1998). The process of fattening prior to departure and utilizing fat reserves during active passage can be very dynamic. For example, long-distance migrants can lose 30% of their body mass at start. However, the mean fat score during the migratory period is thought to be more or less stabilized (Ścisłowska and Busse 2005). Larger areas covered by elderberries, which are one of the most important food source for insectivorous passerines in autumn, cannot be found in the Bódva Valley. Thus, the structure of vegetation could play a different role (than only food source) during migration. For instance, another study area (Ócsa Landscape Reserve) is used for stopover and premigratory fattening in Central Hungary (Csörgő and Lövei 1995), because the site is similar to the Thrush Nightingale’s preferred habitat during breeding (Sorjonen 1980). Only 1.03% of birds were recaptured in Szalonna. These individuals with mean fat score equal to 2, ranged 0-1 in August, were in a relatively poor condition. The low recapture rate and the mean fat score of captured birds suggest that Thrush Nightingales did not increase their fat reserves but only rest at the study site. It is possible that birds continue their journey to the south to find areas where they can refuel their fat reserves effectively (especially in the Upper-Tisza valley or more
southern regions). The lowest body mass and fat deposits detected towards the end of August (Fig. 5) proved that birds migrating at that time did not accumulate enough substantial fat reserves before starting, or they came from so far that by the time they reached the Bódva Valley they had run out of fuel. The latecomers (probably originating from northern areas) with greater body mass and higher fat scores were in better condition. Populations with unique migratory strategies have different routes, fat refuelling and timing parameters. Specimens with lower fat reserves can migrate in shorter stages only, while birds with larger fat reserves (and body mass) prefer a non-refuelling strategy over longer distances (Dowsett-Lemaire and Dowsett 1987, Thorup and Rabøl 2001). For the reasons mentioned above both of them did not stopover in the Bódva Valley for a long time.

The timing of migration may depend on sex, but this has not been documented for the Thrush Nightingale (Zink 1975, Cramp 1992, Svensson 1992). However, the timing of the autumn migration may also be determined by population groups, age classes and the physiological condition of the birds. Climate change can strongly influence the previous migration system of the species. Thus, long-winged birds have to start sooner because their breeding area is gradually shifting northwards probably due to climate change (e.g. Thomas and Lennon 1999). If short-winged birds breed closer to the studied area, they should not arrive earlier than long-winged ones. The timing of autumn migration of other trans-Saharan migrants has already changed, probably due to climatic factors. The arrival of juvenile Garden Warblers (Sylvia borin) shifted 13 days later over a study period of 24 years (Miholcsa and Csörgő 2007, Miholcsa et al. 2008, Csörgő et al. 2009).

Environmental changes have had a major impact on birds, affecting their distribution and ecological behaviour (Thomas and Lennon 1999, Crick and Sparks 2006). Long-distance migratory species such as the Reed Warbler (Acrocephalus scirpaceus), Marsh Warbler (A. palustris), Wood Warbler (Phylloscopus sibilatrix) or Garden Warbler are expected to respond to global warming by increasing the time spent in their breeding areas or expanding their ranges (Burfield and Van Bommel 2004, Miholcsa and Csörgő 2007, Miholcsa et al. 2008). In order to better understand the whole migration pattern of the species, the phenology of spring arrival in the breeding areas should also be examined. The changing weather conditions in Africa (e.g. the absence of rainfall) suggest that food might be limited and therefore spring migration may be slowed down (Gordo et al. 2005). Thus, in spring, these birds usually arrive at their breeding grounds later and so their survival chance might decrease (Both and Visser 2001). However, warmer spring temperatures and earlier breeding initiation in the northern Europe potentially enable migrants to complete the reproductive cycle earlier (Thorup et al. 2006) and therefore, their timing of departure can be shifted earlier. Similarly to the Thrush Nightingale, the autumn migration of the Garden Warbler has also shifted to earlier dates in Denmark (Christiansø) and England (Oxfordshire) (Cotton 2003, Thorup et al. 2006), although age groups were not treated separately in these analyses.

In conclusion, this study provides some insight to migration strategy of the Thrush Nightingale in the northern Hungary. The observed shift in autumn migration dates of the studied species (7.9 days earlier in Szalonna), suggest that environmental con-
ditions (e.g. weather, climate) probably changed in the last two decades. The surviv-
ability may also depend on the weather conditions and available food resources at the
wintering sites in Africa and along the Nile (Csörgő pers. comm.). However, the sur-
vival rate of the Thrush Nightingale and its migration strategy in Africa, is still poorly
known. In general, the long-distance migrant passerines have to accumulate suffi-
cient fat reserves to make their journey (Blem 1980). Based on some calculations,
Thrush Nightingales with maximal fat reserves can reach their wintering ranges
without stopping or refuelling (Csörgő and Lövei 1986). After leaving Europe, the
first available refuelling sites are in the northern part of Africa, before they fly across
the Sahara. Because the birds follow the winter rainfalls along the Nile to southern
wintering sites (Lack 1983), the timing of migration has to be adjusted to this. With
the expansion of global warming, drier periods often come sooner, and it is possible
that autumn migration of some long-distance migrant passerines have shifted their
migration earlier.

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