Annual captures, autumn migration phenology, and morphological traits of the Common Blackbird (*Turdus merula*) over 24 years

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Abstract. In this long-term study, the timing of autumn migration, stopover duration, wing and third primary length, body mass, fat load, and pectoral muscle of the Common Blackbird (*Turdus merula*) were studied between 1998 and 2022 in Tömörd, Hungary. We found a significant increase in Common Blackbirds passing through the study site. There was no substantial difference between the timings of autumn migration in the two sexes. Still, the adults started their migration slightly later than juveniles. This timing was unchanged between 1998 and 2022, indicating that juveniles and adults of both sexes use the same adaptation strategy to determine the departure time. We found that wing length slightly but significantly decreased in both age and sex groups, whereas there was an increase in the length of the third primary during the study period. In our view, these wing morphology changes cannot be explained by local adaptations but by a change in the population composition: most individuals captured are short-distance migrants. Our results indicated that body mass and condition of all groups increased from September to November within a year, which can be interpreted in two ways: on the one hand, it could be caused by an increase in the proportion of adults, and on the other hand, there could be an increase in the proportion of Common Blackbirds arriving from territories to the north of the Pannonian region as the autumn migration progresses. The similarity in changes in the phenology and morphological traits of the different age and sex groups during the study period emphasizes that environmental change caused no detectable intraspecific selection pressures.

Keywords: timing of migration, short-distance migrant, passerine biometrics, age, sex, West Hungary.

Introduction

Changes in morphological traits and other characteristics of bird populations, particularly a decline in body size, are expected to be one of many responses of birds to current global warming (Sheridan & Bickford 2011). Several studies show that major changes have occurred in many bird species' abundance, distribution, morphology, and phenology in the last few decades (Hüppop & Hüppop 2003, Visser & Both 2005). The extent of phenology changes can be influenced by many factors, including migration strategy, sex, age, etc. (Catry et al. 2006, 2007). Biometric features and the timing of migration may vary from one geographical area to another within the same species, as different subspecies or populations may change their migration patterns differently due to, for example, local or global weather changes and other ecological factors (Cotton 2003, Hubalek 2004, Rainio et al. 2006).

Based on our previous studies on changes in small passerine migration and body size (Gyurácz et al. 2016, 2021, 2022) and on the literature (Csörgő et al. 2017), we hypothesized that there had been some intraspecific age- or sex-dependent differences in phenology and/or biometrics during the last twenty-five years in a west Hungarian stopover site. We chose the typical partially migratory Common Blackbird (*Turdus merula*), whose migration strategies are relatively well-known (Main 2000, Csörgő & Gyurácz 2009). Analyses of the Hungarian population, however, have only been done on limited sample sizes (Csörgő & Kiss 1986, Ludvig et al. 1991, Móra et al. 1998, Csörgő et al. 2017, Orbán et al. 2019). Common Blackbirds are polytypic, with seven subspecies (Gill et al. 2020). The central European nominate subspecies has become progressively more sedentary (Berthold 1999, Main 2000). The Hungarian

Blackbirds have been recovered increasingly closer to their breeding grounds in the past decades, but their age and sex made no difference to the recovery distance (Németh 2017). Blackbirds usually have sex- and age-dependent migration strategies: males are less likely to migrate, and those that do migrate winter closer to the breeding sites than females (Bairlein et al. 2014), while the juveniles also tend to winter closer to the breeding areas than adults (Valkama et al. 2014). However, in the case of British Blackbirds, age groups showed no differential migratory behavior, and there was no difference in the tendency to migrate between male and female juveniles in Germany (Snow 1966, Schwabl 1983). There is a slight difference in migration dynamics of age groups in Swedish birds (Fransson & Hall-Karlsson 2008).

In Hungary, the Common Blackbird is a frequent passage migrant from late February to March in spring and from early September until mid-November in autumn, and some of them winter here (Gyurácz & Csörgő 2021). Most birds that breed in Hungary are residents, while the main wintering area for migrants covers the central Mediterranean Basin (Csörgő & Gyurácz 2009). The Common Blackbird is a very common passerine in the study area. The total annual captures (breeding and transient individuals) have significantly increased between 2001 and 2016. Migration starts in early September, followed by one long wave with a high peak from the 10th to the 20th of October. The median date of passage is 17th October, and migration finishes by mid-November (Gyurácz et al. 2017a). Despite intensive ringing activity, there have only been six recoveries in Hungary from north of the Carpathians, suggesting that northern Blackbirds avoid these high mountains (Csörgő & Gyurácz 2009). Only one individual (ringed in Poland) has been recaptured at Tömörd (BirdLife Hungary 2022).

In the present study, we detected changes in the annual

captures of Common Blackbirds, the timing of autumn migration and stopover duration, and morphological variables at the Tömörd stopover site in western Hungary. We hypothesized that, probably as a consequence of climate change, the number of Common Blackbirds is increasing, and birds have shifted their migration to later in autumn. This could affect the migration timing of the males and females, juveniles and adults differently: the two sexes and ages may use different migration strategies. Furthermore, we hypothesized that the composition of migrants passing through the stopover site has also changed. We used wing length, third primary length, body mass, fat load, and pectoral muscles to examine how these variables have changed during the last 25 years: these biometric changes may represent changes in the composition of the migrants and possible shortening of the migration distance, thus indirectly showing effects of climate change.

Material and Methods

Study area
The study was carried out in western Hungary at the Tömörd Bird Ringing Station (47°21'N, 16°40'E), which is located 15 km from Szombathely. The study site has a typical continental climate with cold winters and hot summers. The study was performed in the four natural habitat types, which can be found around the station. The first habitat type is represented by scrublands, characterized by a compact and dense vegetation comprised of bushes and herbs crossed by small grass patches. The characteristic plant species in this habitat type is Blackthorn (*Prunus spinosa*). Forest edges represent the second habitat type; the broadleaf trees and bushes form a compact, dense edge, representing an ecotone area. The characteristic plant here is the Turkey Oak (*Quercus cerris*). Normal forest management and plenty of felling characterize the forest. The third habitat type, unmanaged grassland with shrubs, represents a transition between the wet habitats of the swamp and the steppe communities that previously covered the agricultural land surrounding the marsh. The vegetation in this grassland is characterized by a few bushes, with two small patches of Dwarf Elder (*Sambucus ebulus*). The marsh represents the last habitat type, an isolated and permanent wetland with a relatively small surface (6ha) and Broadleaf Cattail (*Typha latifolia*) as the characteristic plant species.

Data collection and analysis
The birds were captured and ringed, or recaptured, from 1998 to 2022 during the autumn migration between 1st September and the first weekend of November. The fieldwork time did not differ between the years, and this period covered 99% of the Common Blackbird migration period within the region, including the main migration waves (Gyurácz et al. 2017a).

For trapping, we used 28 numbered Ecotone mist nets, which were 12 m long and 2.5 m high, with five shelves and a mesh size of 16 mm. These were distributed evenly between the four habitat types. The number of nets and their location did not change throughout the study period. Birds were captured from dawn to dusk except for rainy and stormy days. All birds were ringed, sexed, and aged, according to Svensson (1992). First-year birds (1y) hatched in the year of ringing were defined as juveniles, while all older birds were defined as adults (1+). The flattened maximum wing length and length of the third primary (P3 length) were measured to the nearest millimeter using a graded wing ruler, and birds were weighed to the nearest 0.1 g (using a digital balance). The fat and pectoral muscle scores were estimated visually according to the SE European Bird Migration Network protocol (Busse & Meissner, 2015).

To determine whether biometric data follow a normal distribution, we created normal probability plots (where data are plotted against a normal distribution) and determined probability plot correlation coefficients (PPCC) as a measure of normality. All biometric data were roughly normally distributed (PPCC values for mass: 0.9942, wing length: 0.9962, third primary length: 0.9953, fat score: 0.9229, and muscle score: 0.8787); thus, we used parametric methods which are relatively insensitive to the normality conditions such as linear models and ANCOVA for comparisons. Data were characterized by mean, standard deviation, median, and percentiles. A simple linear regression on means was used to determine trends in the annual captures. Moreover, changes in the timing of migration intensity for a given proportion of the annual captures (10, 25, 50, 75, 90% - that means changes in the arrival of early birds vs. late birds) were determined by quantile regression (Cade & Noon, 2003). The minimum stopover duration was defined as the period from the first capture to the last recapture (Ellegren 1991). Annual changes in stopover duration and morphometric traits were also examined using simple linear regression.

Two-way ANCOVA was used for the determination of the relationships between the dependent biometric variables (wing length, P3 length, body mass, fat, and pectoral muscle scores) and the independent factors (age, sex) and the covariate (year). We analyzed only the first capture data of each individual in a given year: as arriving migrants are predominantly captured shortly after arrival (Kovács et al. 2012), our biometrics represent the condition of newly arrived birds. True stopover time (time spent by recaptured birds at the study area) was estimated based on the daily capture history of each year. Pooling the data was not rational because most birds stayed only 1-2 days in the study area. Standard Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992) were used for the estimation of apparent survival (Φ) and seniority (γ; based on the reversed capture history) parameters (Schaub et al. 2001). Goodness-of-fit tests, implemented in the MARK program, were used to validate the CJS model. Stopover duration was calculated as $-\ln(1/\Phi) - \ln(1/\gamma)$. Model adjustments for less-than-optimal fit were performed by changing the ĉ value (ĉ was calculated based on the result of the GOF bootstrapping test). The Quasi-Akaike Information Criterion corrected for small sample sizes (QAICc) was used to rank the fit of models to the data. The model with the lowest QAICc was considered to be the best fit. These analyses were performed using MARK and RMARK software (White & Burnham 1999). We used the records of 4,638 males, 3,988 females, 6,779 juveniles, and 1,935 adults trapped and ringed between September and early November within the study period (1998–2022). All statistical analyses were performed using R 3.6.0. (R Core Team, 2015).

Results

Changes in annual captures and timing of migration
There was a strong increasing trend in the annual captures of Common Blackbirds in the autumn migration seasons between 1998 and 2022, also for all age and sex classes (Table 1). The ratio of females to males was 1:1.16, and the ratio of adults to juveniles was 1:3.50.

The mean first capture day and minimum stopover duration are shown in Table 2. ANCOVA showed a significant age effect on both factors (Table 3). The stopover duration estimated using the CJS model (e.g., juvenile 38.68 ± 4.46 days, mean ± SE) was higher than the measured minimum stopover duration. The goodness-of-fit (GOF) test suggested that the standard CJS model fitted well to the capture-recapture data (p > 0.05). Based on the result of the CJS model, the apparent survival, thus stopover duration, was also dependent on age, not sex (Table 4).

Figure 1 shows the relative frequency of daily captures in

age and sex groups during the study period. Between 1998 and 2022, the quantile regression for all birds, males, females, juveniles, and adults showed no significant shifts (p > 0.05) in the timing of first captures (Table 5, Figure 2). The minimum stopover durations of females (r = −0.17, SE = 0.08, t = −2.21, p = 0.028) and adults (r = −0.31, SE = 0.12, t = −2.57, p = 0.011) showed significant decreasing trends. All birds, males and juveniles, showed no significant trend between 1998 and 2022. Based on the result of the CJS model, the apparent survival, thus stopover duration, depended on the year, but not necessarily linearly (Table 4).

Changes in morphological traits

The morphological traits varied between ages and sexes, with significant interaction between both factors (Table 3). The males and adults passing through at Tömörd had significantly longer wing and third primary and higher body mass, fat, and pectoral muscle scores than females and juveniles (Table 2). The wing lengths of all birds, sexes, and juveniles decreased significantly between 1998 and 2022 (Table 6). The third primary of all birds, age groups, and males increased significantly between 1998 and 2022. The body masses of all birds, males and juveniles, increased significantly. The fat scores of all birds, age, and sex groups increased significantly. The pectoral muscle scores of all birds, age, and sex groups also increased significantly. The wing lengths of adults, the third primary lengths, and body masses of females and adults did not change significantly during the study period (Table 6). The morphological traits of all groups increased significantly from the beginning to the end of the autumn migration season (Table 7).

Table 1. Changes in annual captures of Common Blackbirds (A) and results of linear regression for all birds, also for the age and sex classes (B)

A				
Birds	Coefficient	SE	t value	p-value
All	17.41	4.23	4.11	**0.0004**
Male	9.58	2.35	4.07	**0.0005**
Female	7.84	1.99	3.95	**0.0006**
Juvenile	13.86	3.56	3.89	**0.0007**
Adult	3.64	1.01	3.61	**0.001**
B				
Year	Male	Female	Juvenile	Adult
1998	97	52	126	23
1999	104	87	150	46
2000	72	66	101	44
2001	93	62	120	38
2002	66	53	79	40
2003	73	51	107	21
2004	77	79	107	53
2005	88	80	133	35
2006	99	93	152	42
2007	288	259	456	94
2008	132	116	186	64
2009	217	225	320	125
2010	193	177	282	89
2011	191	230	359	64
2012	260	281	377	164
2013	104	90	167	47
2014	236	179	317	102
2015	326	263	488	102
2016	377	313	553	139
2017	443	310	663	98
2018	174	171	269	77
2019	353	302	462	194
2020	139	118	220	39
2021	152	136	190	101
2022	284	195	395	94
All	4,638	3,988	6,779	1,935

Table 2. Descriptive statistics of first capture day, minimum stopover duration, and morphometric traits of captured Common Blackbirds at Tömörd

	Age	Sex	Mean	SE	Conf.low	Conf.high
First capture day	Adult	Male	288.81	0.48	287.87	289.76
		Female	288.33	0.50	287.35	289.31
	Juvenile	Male	282.52	0.25	282.03	283.01
		Female	282.42	0.27	281.88	282.96
Minimum stopover duration (day)	Adult	Male	7.82	1.34	5.38	10.26
		Female	8.67	1.18	6.36	10.98
	Juvenile	Male	14.23	0.44	13.36	15.09
		Female	13.57	0.48	12.63	14.52
Wing length (mm)	Adult	Male	129.93	0.10	129.73	130.13
		Female	124.75	0.10	124.54	124.95
	Juvenile	Male	126.92	0.05	126.82	127.02
		Female	123.26	0.06	123.15	123.36
3rd primary length (mm)	Adult	Male	98.88	0.09	98.69	99.06
		Female	94.62	0.10	94.43	94.81
	Juvenile	Male	96.15	0.05	96.06	96.24
		Female	93.17	0.05	93.07	93.27
Body mass (g)	Adult	Male	92.08	0.20	91.69	92.46
		Female	89.27	0.20	88.87	89.67
	Juvenile	Male	90.11	0.10	89.91	90.31
		Female	87.85	0.11	87.63	88.07
Fat score	Adult	Male	1.33	0.04	1.26	1.41
		Female	1.38	0.04	1.30	1.45
	Juvenile	Male	1.09	0.02	1.05	1.13
		Female	1.12	0.02	1.08	1.16
Pectoral muscle score	Adult	Male	1.94	0.02	1.90	1.98
		Female	1.86	0.02	1.82	1.90
	Juvenile	Male	1.84	0.01	1.82	1.86
		Female	1.87	0.01	1.84	1.89

Table 3. Results of ANCOVA of Blackbird capture phenology and morphometrics in relation to sex and age (capture year is a covariate)

	df	Sex		Age	
		F	p	F	p
Capture day	1;8624	0.32	0.57	241.20	0.001
Stopover duration	1;1697	0.57	0.45	37.67	0.001
Wing length	1;7894	3566.93	0.001	784.97	0.001
Body mass	1;8450	312.48	0.001	111.99	0.001
3rd primary length	1;7112	2767.12	0.001	777.23	0.001
Fat score	1;8465	2.04	0.15	68.57	0.001
Pectoral muscle score	1;7938	0.01	0.98	9.44	0.002

Table 4. Cormack-Jolly-Seber model selection results examining apparent survival and capture probability of Common Blackbird, western Hungary 1998-2022, as a function of sex, age, and year. QAICc = Quasi-Akaike Information Criterion values corrected for small sample sizes; ΔQAICc = difference of models' QAICc values in relation to the best-fitting model; QAICc values were calculated using a ĉ (variance inflation factor) of 1.24.

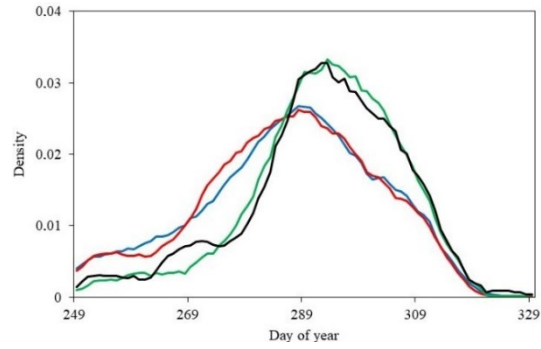| Model	QAICc	ΔQAICc	QDeviance	No. Par
φ(~Year+Age)p(~Year+Age)	19410.57	0.00	14522.32	52
φ(~Year+Age)p(~Year+Age+Sex)	19412.13	1.55	14521.86	53
φ(~Year+Age+Sex)p(~Year+Age)	19412.59	2.01	14522.32	53
φ(~Year+Age+Sex)p(~Year+Age+Sex)	19413.87	3.30	14521.58	54
φ(~Year+Age)p(~Year)	19421.63	11.06	14535.40	51
φ(~Year+Age+Sex)p(~Year)	19423.65	13.07	14535.40	52
φ(~Year)p(~Year+Age)	19424.84	14.28	14538.61	51
φ(~Year)p(~Year+Age+Sex)	19426.42	15.85	14538.17	52
φ (~Year)p(~Year)	19530.87	120.03	14646.66	50

Figure 1. Mean daily captures of Common Blackbirds during the study period, blue: juvenile male, red: juvenile female, green: adult male, black: adult female
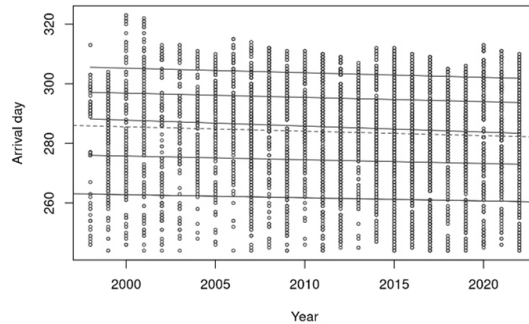

Figure 2. Scatter plot of first capture day of each bird in each year. Lines were fitted by quantile regression (10, 25, 50, 75, 90% solid line, linear regression broken line) to the arrival times of autumn migration of all Common Blackbirds.

Table 5. Changes in the timing of autumn migration of Common Blackbirds: results of linear regression for the mean, 10%, 25%, 50%, 90% quantile regression

Birds	Quantiles	1998	2022	Coefficient	SE	t value	p-value
All birds	Mean	12 Oct	10 Oct	−0.08	0.08	−1.11	0.276
	10%	19 Sep	20 Sep	0.05	0.16	0.31	0.757
	25%	1 Oct	2 Oct	0.03	0.12	0.25	0.806
	50%	15 Oct	12 Oct	−0.12	0.08	−1.39	0.176
	75%	23 Oct	22 Oct	−0.09	0.11	−0.78	0.441
	90%	2 Nov	29 Oct	−0.19	0.11	−1.67	0.109
Male 1y, 1+	Mean	13 Oct	10 Oct	−0.09	0.08	−1.17	0.254
	10%	19 Sep	19 Sep	0.02	0.15	0.14	0.890
	25%	3 Oct	1 Oct	−0.06	0.05	−0.41	0.686
	50%	14 Oct	12 Oct	−0.09	0.11	−0.81	0.425
	75%	25 Oct	21 Oct	−0.16	0.11	−1.40	0.174
	90%	2 Nov	29 Oct	−0.18	0.11	−1.67	0.108
Female 1y, 1+	Mean	13 Oct	10 Oct	−0.11	0.07	−1.47	0.156
	10%	24 Sep	20 Sep	−0.15	0.17	−0.93	0.359
	25%	2 Oct	2 Oct	−0.00	0.12	−0.02	0.981
	50%	14 Oct	11 Oct	−0.11	0.08	−1.34	0.194
	75%	23 Oct	21 Oct	−0.11	0.11	−1.05	0.303
	90%	2 Nov	29 Oct	−0.18	0.13	−1.37	0.183
Juvenile M, F	Mean	11 Oct	9 Oct	−0.09	0.09	−1.14	0.267
	10%	18 Sep	18 Sep	−0.00	0.16	−0.03	0.978
	25%	30 Sep	29 Sep	−0.03	0.14	−0.19	0.848
	50%	12 Oct	10 Oct	−0.09	0.11	−0.89	0.384
	75%	23 Oct	19 Oct	−0.16	0.12	−1.35	0.190
	90%	31 Oct	29 Oct	−0.15	0.12	−1.32	0.199
Adult M, F	Mean	15 Oct	15 Oct	0.01	0.10	0.11	0.910
	10%	26 Sep	30 Sep	0.18	0.21	0.86	0.396
	25%	5 Oct	11 Oct	0.19	0.14	1.39	0.178
	50%	18 Oct	19 Oct	0.03	0.14	0.23	0.818
	75%	28 Oct	23 Oct	−0.15	0.12	−1.25	0.225
	90%	3 Nov	29 Oct	−0.18	0.14	−1.32	0.199

Table 6. Results of the linear model with morphological traits of captured Common Blackbirds at Tömörd, western Hungary, as the dependent variables, and year as the independent variable

	Birds	Coefficient	SE	t value	p-value
Wing length	All birds	−0.03	0.01	−4.99	**0.001**
	Male J + A	−0.03	0.01	−4.03	**0.001**
	Female J + A	−0.04	0.01	−5.09	**0.001**
	Juvenile M + F	−0.06	0.01	−6.91	**0.001**
	Adult M + F	0.03	0.02	1.74	0.081
3rd primary length	All birds	0.03	0.01	4.26	**0.001**
	Male J + A	0.03	0.01	3.10	**0.002**
	Female J + A	0.02	0.01	1.62	0.105
	Juvenile M + F	0.03	0.01	3.10	**0.002**
	Adult M + F	0.06	0.02	3.37	**0.001**
Body mass	All birds	0.02	0.01	2.22	**0.027**
	Male J + A	0.03	0.01	2.20	**0.028**
	Female J + A	0.01	0.02	0.77	0.439
	Juvenile M + F	0.03	0.01	2.25	**0.025**
	Adult M + F	0.02	0.02	0.90	0.367
Fat score	All birds	0.02	0.00	10.43	**0.001**
	Male J + A	0.02	0.00	7.53	**0.001**
	Female J + A	0.02	0.00	7.32	**0.001**
	Juvenile M + F	0.02	0.00	8.29	**0.001**
	Adult M + F	0.03	0.00	6.70	**0.001**
Pectoral muscle score	All birds	0.01	0.00	10.34	**0.001**
	Male J + A	0.01	0.00	7.96	**0.001**
	Female J + A	0.01	0.00	6.50	**0.001**
	Juvenile M + F	0.02	0.00	7.00	**0.001**
	Adult M + F	0.02	0.00	8.99	**0.001**

Table 7. Results of the linear model with morphological traits of captured Common Blackbirds at Tömörd, western Hungary, as the dependent variables, and first capture day of the year as independent variable

	Birds	Coefficient	SE	t value	p-value
Wing length	All birds	0.02	0.00	8.09	**0.001**
	Male J + A	0.03	0.00	8.38	**0.001**
	Female J + A	0.01	0.00	4.30	**0.001**
	Juvenile M + F	0.01	0.00	3.71	**0.001**
	Adult M + F	0.02	0.01	2.22	**0.027**
3rd primary length	All birds	0.04	0.00	15.49	**0.001**
	Male J + A	0.04	0.00	13.59	**0.001**
	Female J + A	0.04	0.00	11.03	**0.001**
	Juvenile M + F	0.03	0.00	11.38	**0.001**
	Adult M + F	0.03	0.01	3.58	**0.001**
Body mass	All birds	0.06	0.00	12.92	**0.001**
	Male J + A	0.05	0.01	8.87	**0.001**
	Female J + A	0.06	0.01	9.49	**0.001**
	Juvenile M + F	0.05	0.00	10.07	**0.001**
	Adult M + F	0.06	0.01	5.52	**0.001**
Fat score	All birds	0.03	0.00	35.40	**0.001**
	Male J + A	0.02	0.00	25.44	**0.001**
	Female J + A	0.03	0.00	24.36	**0.001**
	Juvenile M + F	0.03	0.00	32.58	**0.001**
	Adult M + F	0.03	0.00	12.58	**0.001**
Pectoral muscle score	All birds	0.01	0.00	21.90	**0.001**
	Male J + A	0.01	0.00	15.31	**0.001**
	Female J + A	0.01	0.00	15.95	**0.001**
	Juvenile M + F	0.01	0.00	19.98	**0.001**
	Adult M + F	0.01	0.00	8.36	**0.001**

Discussion

Timing of migration

Many European passerine species' populations are declining rapidly, but there are also examples of increasing and expanding populations (BirdLife International 2022). According to the Hungarian common bird monitoring scheme, significantly increasing populations are more common among species that predominantly breed in Hungarian forests or other wooded and bushy habitats (Szép et al. 2012, Gyurácz & Csörgő 2021); this is seen all over Europe (BirdLife International 2022). Although there was considerable variation in inter-annual capture frequencies during autumn, we found a significant increase in the number of Common Blackbirds of all age and sex groups passing through the west Hungarian stopover site in this study. Recently, the Hungarian Blackbird population has increased both in the breeding period: $3.4 \pm 0.5\%$, $p < 0.01$, and wintering period: $2.5 \pm 1.3\%$, $p < 0.05$ (Gyurácz & Csörgő 2021). Because only small numbers of Common Blackbirds from areas to the north of the Carpathian Basin pass through Hungary (Csörgő & Gyurácz 2009), the increasing number of migrating individuals might be related to the extension of the forests of Hungary and its northern neighboring countries. The forested area of Hungary has increased by 7.1% in recent decades (Hungarian Central Statistical Office 2019), mainly due to acacia and poplar afforestation in areas previously used for farming. The proportion of forests has also increased in Slovakia and Ukraine (Forest Europe 2020). In addition, the increase in the number of birds passing through could be affected by climate change (Morrison et al. 2013): temperature and rainfall may affect the birds' survival and reproduction, as well as other demographic trends (Rodriguez & Bustamante 2003); and climate change is a particularly important driver of bird population trends (Reif 2013). The results of our earlier studies have shown that the high April and May temperatures have been favorable for the breeding productivity of the partial and two short-distance migrants, the Common Chiffchaff (*Phylloscopus collybita*) and the Eurasian Blackcap (*Sylvia atricapilla*) (Gyurácz et al. 2016, 2022). The abundance of Common Blackbirds during migration can also be influenced by changes in breeding areas, migration routes, and destinations. A good example of this is the case of migrating tits in Europe (del Hoyo et al. 2020).

In contrast to the results of research in central Hungary, which found that the autumn timings of both adult and juvenile Common Blackbirds became slightly later between 1984 and 2016 (Csörgő et al. 2017), the first capture days and stopover durations of sexes and ages are unchanged between 1998 and 2022 at Tömörd. In Europe, North America, and the East Asian–Australasian flyway, there has been much variation in phenological change among species, especially in the autumn over the past decades. Usually, the autumn migration has become earlier for long-distance migrant passerines and later for short-distance migrants, but many species have exhibited no long-term change in migration phenology (Jenni & Kéry 2003, Buskirk et al. 2009, Ozarowska & Zaniewicz 2015, Allcock et al. 2022).

In our study site, the ratio of migrant females (46%) and males (54%) was very similar to that at the central Hungarian stopover site, Ócsa, 49% and 51%, respectively (Csörgő et al. 2017). During the breeding season, the capture rates of three species (Eurasian Blackcap, Barred Warbler *Curruca nisoria*, and Common Chiffchaff) were also male-biased in Hungary (Kiss et al. 2020). Female-biased mortality may be the most important explanation for a male-biased adult sex ratio in birds (Liker & Székely 2005, Székely et al. 2014, Lovász et al. 2018), but other factors such as home range, territorial behavior, capture probability, and stopover strategy might also play important roles (Amrhein et al. 2012).

As in central Hungary, there was no substantial difference between the autumn migration timings of the Blackbird sexes (Csörgő et al. 2017), unlike in other passerines, where females migrated slightly earlier than males (Gyurácz et al. 2003, 2022, Jakubas & Wojczulanis-Jakubas 2010, Csörgő & Harnos 2011, Bozó & Heim 2016). Our results and changes in migration distance in both sex groups in recent decades (Németh 2017) indicate that male and female Blackbirds do not use different adaptation strategies to determine the time of departure (Schwabl 1983). We also found no significant difference in stopover duration between the sexes. Some previous studies suggested that females would stay longer to avoid intraspecific competition, while males might be more dominant, allowing them to refuel faster (Newton 2010). As there were no significant differences, intersexual competition might be low, and both sexes might be able to follow a time-minimizing strategy. This result is consistent with other studies on passerines (Polak & Szewczyk 2007, Gyurácz et al. 2017b, Collet & Heim 2022).

Adult Blackbirds, in contrast to the Swedish experience that adults migrate a little earlier and faster (Fransson & Hall-Karlsson 2008), start their migration slightly later than juveniles at Tömörd. Because adult Blackbirds undertake a complete moult after breeding, their flying ability is reduced, and they can only leave after moulting is completed (Svensson 1992). Juveniles, however, retain their first flight feathers, and their flying ability is unaffected by moult. The Common Blackbird usually breeds twice a year in April – May and June – July (Haraszthy 2019). The second clutch might also cause the late migration of adults: juveniles that migrate early are probably from the first brood. Juvenile Blackbirds stayed at Tömörd significantly longer than adults, consistent with other songbird studies (Rguibi-Idrissi et al. 2003, Newton 2010, Collet & Heim 2022). Age-dependent improvements in foraging efficiency have been clearly shown in Blackbirds (Desrochers 1992): adults are more experienced and, therefore, can search the most profitable parts of the stopovers and accumulate fat faster than juveniles (Polak & Szewczyk 2007).

Morphological traits and migration

Correlations have been observed between migration distance, wing length, and wing pointedness (measured by P3 length; Lockwood et al. 1998, Vágási et al. 2016). Northern populations, with a longer migration route to the wintering area, have longer wings than southern populations of conspecifics (Milá et al. 2008, Nowakowski et al. 2014). According to studies on Blackcaps, in which different populations present a wide variety of migration behaviors, the increase in wing length is about 1 mm for each 1,000 km of migration distance, and wing pointedness significantly

increases with an increasing wing length of migrating birds (Fiedler 2005, Ozarowska et al. 2021). We found in this study that the wing length showed a small but significant decrease in both age and sex groups of Common Blackbirds, while P3 length increased during the study period. If wing length decreases and P3 length increases, the wing becomes rounder, i.e., the wing pointedness of birds migrating through at Tömörd has decreased over the study period. In our view, these changes in wing morphology cannot be explained by local adaptations but by the change in the population composition: most of the captured individuals are short-distance migrants. According to many studies, morphological changes in birds could be related to climatic factors (Kaňuščák et al. 2004, Tryjanowski et al. 2004). Temperatures in Europe, both annual and seasonal averages, have increased over the last four decades (Guiot et al. 2010); therefore, Hungarian Blackbirds are recovering increasingly closer (−5.9 km/year) to their breeding grounds. Hungarian Blackbirds can be both migratory and resident. If wing length continues to decrease and P3 length continues to increase, the adaptive benefits of migratory behavior could be reduced so that selection will not maintain it in the population, and the Hungarian population will become entirely sedentary (Németh 2017). Ozarowska et al. (2016) also noted a remarkable decrease in the wing length of juvenile Blackcaps migrating in autumn through the south Baltic region, which may indicate a pronounced increase in the number of short-distance compared to long-distance migrants. The mean migration distance of many other species and the proportion of migratory individuals within populations have decreased in recent decades, presumably due to climate and habitat changes (Visser et al. 2009). However, it should be noted that wing length, wing pointedness, and their changes are not only affected by migration constraints but also by other environmental factors (e.g., breeding site vegetation, feeding conditions, parasites, predation risk, changes in climate and weather, etc.) (Ciach 2009, Sheard et al. 2020).

Our results indicated that the body mass and condition of Blackbirds in this study increased over the study period, but even the highest body mass averages of sex and age groups (e.g., adult male 94.40 ± 7.05 g) were lower than averages measured in England between September and March (e.g., adult male 102.8 ± 10.4 g, Macleod et al. 2005). This difference is due to the weight increasing towards a maximum in mid-winter (Lehikoinen 1987). Two factors that could be responsible for the Blackbird body mass increase over many years are changing food availability caused by climate and habitat changes (Bednekoff & Krebs 1995). The alternative hypothesis that a bird's condition is limited by food availability is not supported: this would lead to peak body mass and fat reserves when berry crops were in greatest mass during the autumn migration. Therefore, body mass, fat load, and pectoral muscle seem to be under behavioral control, with the bird responding strategically to environmental factors to minimize the risk of starvation and predation (Witter & Cuthill 1993, Creswell 1998). Increased body mass can improve survival and reproductive success in birds by using stored energy reserves as insurance against unpredictable environmental factors (Thomas 2000). Consequently, increasing body mass and fitness may also have contributed to the increasing annual captures during the study period.

The increasing values for all the morphological traits of all sex and age groups from September to November can be interpreted in two ways: on the one hand, it could be caused by an increase in the proportion of adults; on the other hand, it could be the result of an increase in the proportion of Common Blackbirds arriving from territories to the north of the Pannonian region as the autumn migration progresses (BirdLife Hungary 2022). The body mass, fat score, and pectoral muscle score covary for both pre- and sub-Saharan migrants (Salewski et al. 2009, Lupi et al. 2016), and change in fat score proved to be a good predictor of the change in migratory restlessness, while individuals accumulating a lot of fat showed a strong increase in restlessness (Eikenaar et al. 2021). Therefore, the increasing trend in body mass, fat reserve, and pectoral muscle of sex and age groups from September to November also indicates that sex and age classes of Hungarian Blackbirds could use similar refueling and time-minimizing stopover strategies during autumn migration (Alerstam & Lindström 1990). During this period, passerines adopt a diurnal mass gain method that reduces predation risk when starvation risk is low (Houston et al. 1993). Such a strategy is common in passerines migrating in the spring but could also benefit autumn migrants (Arizaga et al. 2008, Yosef & Wineman 2010, Bozó et al. 2020).

Conclusions

Based on the increasing number of birds captured annually, we suggest that the Common Blackbird, as a response to environmental conditions, may adapt morphologically to selection pressures created by their behavior. We have clearly shown that juveniles migrate earlier than adults in autumn. However, the autumn migration timings of sex and age groups appear to be unchanged between 1998 and 2022, indicating that juveniles and adults of both sexes could use the same adaptation strategy to determine the departure time. Of the morphological variables, wing length and wing pointedness are the best indicators of the annual change in the proportion of birds with different migration strategies. We suggest that Blackbirds use a time-minimization model for the autumn migration and that the birds are still adapting to this strategy. In the future, we plan to make further studies involving other species, including more variables and factors, to understand better the effects of climate warming and land cover change on bird migration strategy.

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