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Population trend and breeding productivity of some migrant passerines in Hungary

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Abstract This study aimed to monitor the demographic changes of some closely related species based on bird ringing data from the CES (Constant Effort Sites) program in Hungary between 2007 and 2018, and to explore the reasons for these demographic changes. The CES program tracks breeding bird populations with standard methods. The studied species breeding in Hungary were from genera *Sylvia*, *Curruca,* and *Phylloscopus*. Among these species, the trends of some forest birds, like Eurasian Blackcap *(Sylvia atricapilla)*, Lesser Whitethroat *(Curruca curruca)*, Common Chiffchaff *(Phylloscopus collybita)* and Willow Warbler (*Ph. trochilus)* showed no substantial changes, and one of the open-habitat species, the Barred Warbler *(Curruca nisoria)* – a long distant migrant – showed decreasing trends. The Garden Warbler *(Sylvia borin)* – a trans-Saharan migrant but forest dweller – also experienced population declines. Short-distance migrants maintained stable populations. Common Whitethroat productivity displayed an increasing trend to compensate for population decline. Upon examining the Eurasian Blackcap, this study detected a strong relationship between the number of adult birds, productivity, and the number of adults captured the following year.

Keywords: CES program, *Sylvia*, *Curruca*, *Phyllsocopus*, annual capture, demographic changes

Összefoglalás Kutatásunk célja, hogy kimutassuk néhány rokon faj demográfiai változását és ennek okait a CES programban 2007–2018 között gyűjtött gyűrűzési adatok alapján. A CES (Constant Effort Sites) program célja a hazai költőállományok hosszútávú monitorozása standard módszerek segítségével. A vizsgálatban résztvevő fajok a *Sylvia, Curruca* és *Phylloscopus* nemekbe tartozó Magyarországon költő fajok közül kerültek ki. Az ide tartozó erdei fajok – mint a barátposzáta *(Sylvia atricapilla)*, a kis poszáta *(Curruca curruca)*, a csilpcsalpfüzike *(Phylloscopus collybita)* és a fitiszfüzike *(Ph. trochilus)* – állományai nem változtak kifejezetten. Az elsősorban nyílt élőhelyekhez kötődő fajok közül a Szaharától délre telelő, hosszútávú vonuló karvalyposzáta *(Curruca nisoria)* és a szintén hosszútávú vonuló, de elsősorban erdei élőhelyeken fészkelő kerti poszáta *(Sylvia borin)* populációi csökkenő tendenciát mutatnak, ezzel szemben a rövid távú vonulók állományai stabilak vagy enyhén növekednek. A mezei poszáta produktivitása az évek során emelkedik, ezzel némileg ellensúlyozni tudja az egyedszámban bekövetkezett csökkenést. A barátposzáták esetében összefüggéseket találtunk az adult egyedek, a produktivitás és a következő évi adult egyedek száma között, ami sűrűségfüggő szabályozásra utal.

Kulcsszavak: CES program, *Sylvia*, *Curruca*, *Phyllsocopus*, éves fogás, demográfiai változások

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Introduction

Birds are the most abundant terrestrial vertebrates and the most studied group; the distributions, breeding ranges, habitat requirements, behaviours and migration routes of most species are well known (e.g. Cody 1985, Furness & Greenwood 1993, Csörgő *et al.* 2009, Haraszthy 2019, Keller *et al.* 2020, Szép *et al.* 2021). For this reason, their roles as indicator species in biodiversity monitoring are growing because their absence, presence, abundance or behaviour reflect environmental factors and changes (Báldi *et al.* 1999, Standovár 2000, Winkler 2000, Newton 2008).

Recently, more ornithological studies have focused on surveys covering the largest region possible to detect the local demographic changes and their causes and to gather data from the entire distribution-range level of a species (Gregory *et al.* 2008). Integrated international monitoring programs should collect such large data amounts from the whole distribution area of a species (Keller *et al.* 2020, Szép *et al.* 2021). Only a large amount of data can more precisely determine which parameters strongly influence population sizes in breeding grounds, wintering grounds and during migration (Goodenough *et al.* 2009).

Hungarian researchers use various methods for programs covering different periods and goals. The Common Bird Census (MMM) program employs observation-based methods (Szép & Nagy 2002, 2006, Szép *et al.* 2012) linked to the Pan European Common Bird Monitoring program (Gregory *et al.* 2003, 2005, PECBMS 2023). This method provides a large amount of data on species diversity, breeding population and abundance of a given area, even large areas, but is unsuitable for individual identification.

The AH (Actio Hungarica) and the CES (Constant Effort Sites) programs use standardised mark-recapture methods. The CES program focuses on the breeding season, and the AH focuses on the autumn and spring migration.

The CES program links directly to the program launched by the BTO (British Trust for Ornithology) and is now also active in many European countries and North America (MAPS) (Desante *et al.* 1995).

Each method can answer different questions and goals. Harmonising long-term systems and analysing them to detect population changes and understand their causes is indispensable.

The population trends of passerines show considerable variation between species (Sanderson *et al.* 2006, Szép *et al.* 2012, 2021, BirdLife International 2023) and geographical scales (Stanbury *et al.* 2017, Keller *et al.* 2020). According to the literature, the annual cycle, diet, habitat selection, migratory strategies, and environmental factors on the breeding or wintering grounds and along the whole migration route strongly influence songbird population dynamics (Wesołowski *et al.* 2006, Ockendon *et al.* 2014).

When considering changes in a songbird population, especially in migratory species, it is challenging to determine whether the most crucial effects occur at the breeding sites, wintering sites or migratory routes (Goodenough *et al.* 2009). Studies cannot focus on a single factor in the complex system that affects the population, because changes are driven by a combination of all factors, including abiotic, biotic, interspecific, and intraspecific effects. However, some may be more prominent during certain periods. For example, the presence or absence of food during the breeding period can strongly influence clutch size and breeding numbers, which affects productivity in a given year. Food availability depends on several factors: for insectivorous species during the breeding period, it primarily depends on weather conditions, especially spring temperatures and rainfall (Jones *et al.* 2003).

Examining population changes in a species requires a separate analysis of the effects at breeding sites, during migration routes and wintering grounds. Long-term changes are primarily determined by breeding success, which depends on habitat quality and the processes in the breeding area. Then, wintering grounds influence population size through survival rates (Ockendon *et al.* 2014), to which migration losses must be added. However, these losses can be compensated by higher productivity during the breeding season up to a specific limit. Weather conditions may also affect those trends locally (Gyurácz *et al.* 2016).

This study aimed to obtain information about the population dynamics of some passerines breeding in Hungary and to explore the reasons for those trends.

The closely related species have similar environmental requirements, but their habitat selection on breeding grounds and migration strategies vary, leading to differing changes to particular environmental factors (Cramp 1992, Csörgő *et al.* 2009, Haraszthy 2019); thus, we can use them as bioindicators (Winkler 2000).

The study included eight related passerine bird species, two of which – Eurasian Blackcap *(Sylvia atricapilla)* and Common Chiffchaff *(Phylloscopus collybita)* – are short-distance migrants. All other species winter south of the Sahara. Among these are forest bird species like Garden Warbler *(Sylvia borin)*, Lesser Whitethroat *(Curruca curruca),* Wood Warbler *(Phylloscopus sibilatrix)*, and Willow Warbler *(Ph. trochilus),* and species connected to open habitats like Barred Warbler *(Curruca nisoria)* and Common Whitethroat *(C. communis)*. Most of these species are abundant enough to indicate local and regional environmental changes.

Material and Methods

We analysed capture data from Hungarian Constant Effort Sites (CES) (Baillie 1990, Halmos & Karcza 2004), an international bird ringing program in the breeding season, through which it is possible to check local breeding population demographics (Baillie & Schaub 2009). The Hungarian CES Program began in 2004. The birds were captured with mist nets, a suitable method to estimate population size, relative abundance, species composition (Dunn & Ralph 2004, Halmos & Karcza 2004), and demographic parameters like productivity and apparent survival rates (Kiss *et al.* 2020, Gyurácz *et al.* 2022).

Only a few ringing sites participated in the CES program in its first three years, and the biometrics data were only identified from 2007 onwards. Therefore, this study uses data spanning 12 years (2007 to 2018). The CES program covers the breeding period from 15 April to 13 July. Nine visits occur during the season, with a minimum five-day gap between visits. The ringing starts at sunrise and ends at noon (Halmos & Karcza 2004).

Ringing data were collected from 16 CES ringing sites spread over Hungary *(Figure 1)*. The sites included in this study were those that provided continuous data for at least 10 years during the study period (2007–2018). The numbers, locations, types, and lengths of

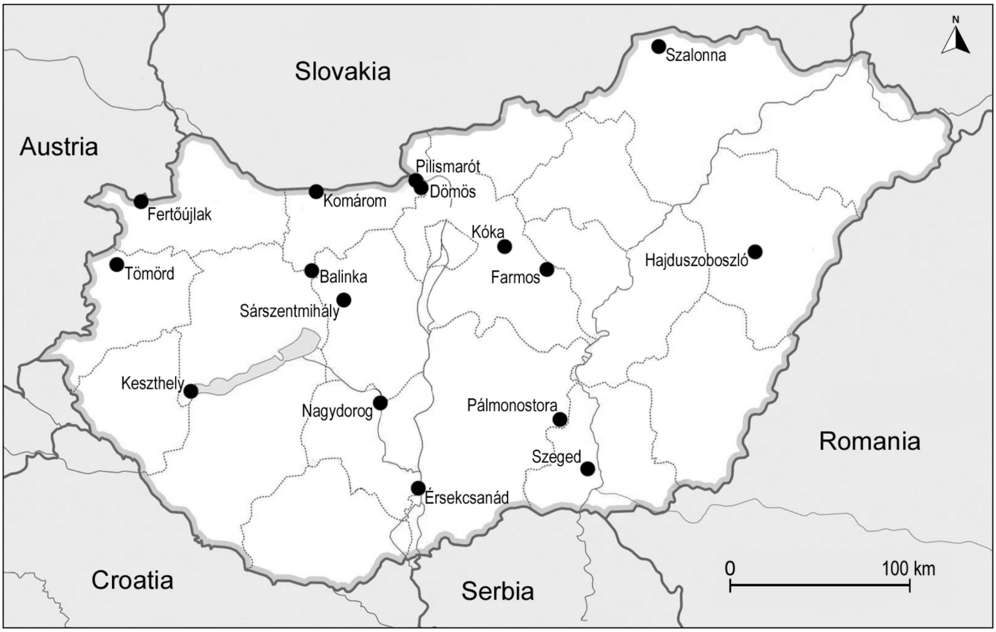

Figure 1. Study sites (bird ringing sites)
1. ábra Vizsgálati területek (gyűrűzőállomások)

mist nets at sites were constant between years, but each site used different amounts of mist nets. In order to ensure comparability the data was standardised per unified net surface and period. The captures were standardised to the number of birds caught by a net surface of 1,000 m^2 within 54 hours (six hours per day for nine days) on each site.

The CES protocol also includes the measurement of biometric data of the ringed individuals, according to Svensson (1992). However, in this study, we only used the age and sex data of birds. In the breeding season, we can determine age and sex in all studied species based on brood patch, cloaca shape or plumage features. We classified the first-year birds (hatched in the actual calendar year) as juveniles and signified them as “1y”. Birds hatched in earlier years were determined as adults and denoted as “1+”.

Based on the data obtained, we determined the population trends of birds ringed as juveniles or adults and their productivity, considering the proportion of the first-year birds to the total captures. Apparent survival rate was previously analysed in Kiss *et al.* (2020).

We tested whether the studied species showed similar trends and what behaviours influenced these trends. Furthermore, this study examined the relationships between productivity and the number of adults from the same year and the following years.

Generalized linear modelling (GLM) with identity link function was used to analyse the species trend slopes. Spearman’s correlation was used to quantify the relationship between productivity and the number of adults. The significance level was set at $P < 0.05$.

A hierarchical cluster analysis (with Euclidean distance) was used to detect similarities between the productivity of the studied species in consecutive years. All data analyses were conducted using the Past program version 4.03 (Hammer *et al.* 2001).

Results

A total of 5,997 individuals of the studied species were ringed in the study period, including 4,400 Eurasian Blackcap, 67 Garden Warblers, 143 Barred Warblers, 296 Lesser Whitethroats, 193 Common Whitethroats, 22 Wood Warblers, 816 Common Chiffchaffs, and 60 Willow Warblers. This study excluded the Wood Warbler from further investigations due to the small amount of data collected on the species. For more detailed capture data by ringing station, see the Appendix.

The annual number of adult Garden Warblers ($r = –0.60$, $P < 0.05$) and Barred Warblers ($r = –0.74$, $P < 0.01$) decreased significantly. The remaining species showed no substantial changes. The annual number of juveniles of the studied species showed no clear trend over the study period *(Table 1, 2)*.

The productivity of Common Whitethroats showed a significantly increasing trend between 2007 and 2018, while the productivity of the other species did not change substantially and can be considered stable *(Table 3)*.

Two main groups are observable based on the cluster analysis using the yearly productivity data for each species *(Figure 2)*. The Common Chiffchaff and the Eurasian Blackcap are

Table 1. Standardised capture data of the adult birds (2007–2018) and generalized linear modelling (GLM) results. Species name abbreviations comprise the first three letters of the genus and the species name (HURING code)

1. táblázat Az adult madarak sztenderdizált éves fogási adatai (2007–2018) és az általánosított lineáris modell (GLM) eredményei. A fajnevek rövidítésénél a HURING kódokat alkalmaztuk

	PHYTRO	**PHYCOL**	**SYLATR**	**SYLBOR**	**CURCUR**	**CURNIS**	**CURCOM**
2007	13.40	96.62	901.86	26.67	70.19	53.34	69.33
2008	7.69	63.01	872.32	20.14	95.73	42.07	125.49
2009	4.17	83.57	791.72	16.67	36.82	84.89	37.10
2010	13.82	147.39	1018.12	31.03	72.83	64.16	42.86
2011	14.20	90.70	572.97	15.11	65.03	11.86	39.54
2012	18.96	73.79	1069.39	12.50	60.20	37.34	46.34
2013	11.79	87.56	830.37	37.50	72.30	25.31	45.11
2014	2.34	90.27	728.79	12.50	73.63	13.76	21.15
2015	5.34	114.92	923.47	18.58	71.69	26.92	68.89
2016	17.98	113.78	883.46	12.50	51.22	13.94	26.07
2017	16.11	89.09	734.61	2.78	96.96	4.17	49.99
2018	7.91	109.96	627.09	2.78	92.68	17.46	24.76
Slope	0.09	1.55	–13.51	–1.72	1.37	–4.98	–4.10
SE	0.48	1.88	12.21	0.73	1.50	1.44	2.12
Intercept	–178.22	–3021.00	28023.00	3488.6	–2683.00	10060.00	8305.40
SE	974.72	3792.00	24572.00	1471.5	3014.30	2904.00	4266.80
G	0.04	0.68	1.22	5.56	0.84	11.92	3.74
p(slope=0)	0.85	0.41	0.27	**0.02**	0.36	**0.01**	0.05

Table 2. Standardised annual capture of juveniles (2007–2018) and generalized linear modelling (GLM) results. Species name abbreviations comprise the first three letters of the genus and the species name (HURING code)

2. táblázat A fiatal madarak sztenderdizált éves fogási adatai (2007–2018) és az általánosított lineáris modell (GLM) eredményei. A fajnevek rövidítésénél a HURING kódokat alkalmaztuk

	PHYTRO	PHYCOL	SYLATR	SYLBOR	CURCUR	CURNIS	CURCOM
2007	2.78	68.62	747.53	0.00	15.06	25.32	0.00
2008	27.88	146.31	712.45	2.78	33.37	4.17	14.42
2009	0.00	84.26	759.07	4.86	8.33	4.65	0.00
2010	0.00	154.93	282.55	0.00	23.44	9.38	0.00
2011	0.00	195.50	755.11	0.00	23.40	5.13	5.13
2012	0.00	78.65	705.11	0.00	13.18	4.17	11.32
2013	13.68	146.32	438.23	0.00	12.33	4.17	5.13
2014	2.34	220.55	859.01	0.00	33.33	0.00	2.78
2015	4.69	96.55	499.26	0.00	6.73	8.33	10.90
2016	4.17	108.98	631.30	0.00	25.32	2.56	11.11
2017	0.00	68.34	617.07	0.00	23.40	6.73	12.82
2018	2.78	90.95	636.35	0.00	40.86	6.73	5.56
Slope	–0.62	–1.51	–6.46	–0.21	0.90	–0.76	0.58
SE	0.69	4.41	13.98	0.12	0.90	0.50	0.43
Intercept	1254.40	3162.50	13637.00	416.08	–1796.70	1531.80	–1160.00
SE	1394.10	8884.10	28124.00	240.31	1805.40	1012.90	864.01
G	0.80	0.12	0.21	2.99	1.01	2.27	1.82
p(slope=0)	0.37	0.73	0.65	0.08	0.31	0.13	0.18

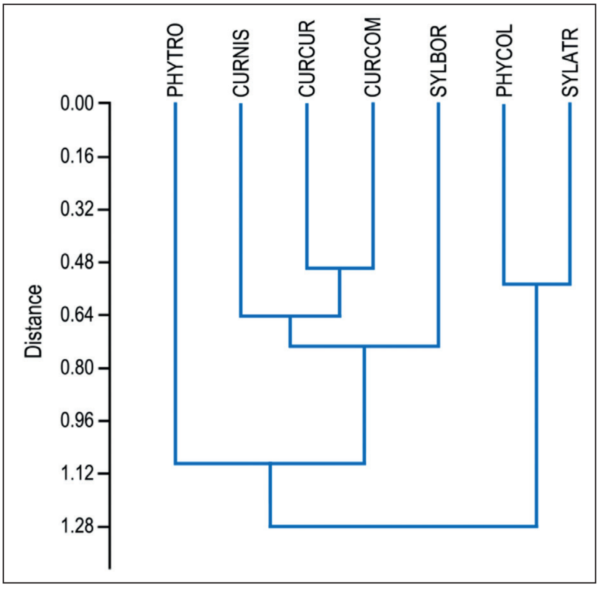

Figure 2. Dendrogram of the studied species' productivity (cluster analysis, Euclidean distance, P = 0.05). Species name abbreviations consist of the first three letters of the genus and the species name (HURING code)

2. ábra A vizsgált fajok produktivitásának hasonlósági vizsgálata klaszterezéssel (Euklideszi távolság, P = 0,05). A fajnevek rövidítésénél a HURING kódokat alkalmaztuk

Table 3. The productivity of the examined species in the study period (2007–2018) and generalized linear modelling (GLM) results. Species name abbreviations comprise the first three letters of the genus and the species name (HURING code)

3. táblázat A vizsgált fajok produktivitásának alakulása a vizsgált időszakban (2007–2018) és az általánosított lineáris modell (GLM) eredményei. A fajnevek rövidítésénél a HURING kódokat alkalmaztuk

	PHYTRO	PHYCOL	SYLATR	SYLBOR	CURCUR	CURNIS	CURCOM
2007	0.17	0.42	0.45	0.00	0.18	0.32	0.00
2008	0.78	0.70	0.45	0.12	0.26	0.09	0.10
2009	0.00	0.50	0.49	0.23	0.18	0.05	0.00
2010	0.00	0.51	0.22	0.00	0.24	0.13	0.00
2011	0.00	0.68	0.57	0.00	0.26	0.30	0.11
2012	0.00	0.52	0.40	0.00	0.18	0.10	0.20
2013	0.54	0.63	0.35	0.00	0.15	0.14	0.10
2014	0.50	0.71	0.54	0.00	0.31	0.00	0.12
2015	0.47	0.46	0.35	0.00	0.09	0.24	0.14
2016	0.19	0.49	0.42	0.00	0.33	0.16	0.30
2017	0.00	0.43	0.46	0.00	0.19	0.62	0.20
2018	0.26	0.45	0.50	0.00	0.31	0.28	0.12
Slope	0.00	–0.01	0.00	–0.01	0.00	0.02	0.02
SE	0.02	0.01	0.01	0.01	0.01	0.01	0.01
Intercept	2.42	16.16	–4.21	18.96	–8.36	–33.50	–34.72
SE	47.53	18.43	16.74	11.22	12.67	27.31	11.50
G	0.01	0.71	0.08	2.84	0.46	1.52	9.18
p(slope=0)	0.96	0.40	0.78	0.09	0.50	0.22	**0.01**

Table 4. Relationship between the annual capture of adults and annual productivity (Spearman correlation) Species name abbreviations comprise the first three letters of the genus and the species name (HURING code)

4. táblázat Az öregek éves fogása és az éves produktivitás közti kapcsolat. A fajnevek rövidítésénél a HURING kódokat alkalmaztuk

	number of adults /productivity in the same year		productivity in a year / number of adults in the following year	
	Spearman r	P-value	Spearman r	P-value
PHYTRO	-0.54	0.07	-0.56	0.07
PHYCOL	-0.43	0.17	-0.01	0.98
SYLATR	-0.86	**0.00**	0.72	**0.01**
SYLBOR	0.18	0.57	0.40	0.23
CURCUR	0.20	0.54	0.01	0.98
CURNIS	-0.41	0.18	-0.25	0.45
CURCOM	-0.16	0.62	-0.03	0.94

grouped together, separated from other species. The separation of the Willow Warbler in the second main group deserves mention.

The comparison of productivity and the number of adults in the following year resulted in a significant relationship in Eurasian Blackcaps: productivity decreases as the number of adults increases *(Table 4)*, suggesting density-dependent regulation. Higher productivity in a given year ensures more adults in the following year. Thus, more fledged birds return to breed. This study observed no significant relationship between productivity and adult catch number in the other species.

Discussion

Reproductive success and the survival rate during migration and overwintering largely determine the population size of a species, suggesting that the population size peaks after the breeding season and then declines steadily until the following season. However, environmental factors like habitat conditions over the lifecycle or local weather conditions can strongly influence this basic model (Newton 1998).

Songbird population changes show much variation within their distribution area, but main trends based on long-term studies can be determined (Reif 2013, Hanzelka *et al.* 2015, Buchanan *et al.* 2016, Brlík *et al.* 2021, Reif *et al.* 2022, Wesołowski *et al.* 2022, Virkkala *et al.* 2023). Based on our current results, the annual number of adult Garden Warblers and Barred Warblers showed a decreasing trend during the study period. The decline is significant in Garden Warblers, with 80% of the population having disappeared since the 2000s. This decline occurred throughout the country in all habitat types (Csörgő & Gyurácz 2021). With some minor exceptions, the breeding range of Garden Warblers has remained the same, but their populations show a slight decline everywhere in Europe (PECBMS 2023). According to Johnston *et al.* (2016), this decline is linked to the survival of adult birds.

Garden Warblers and Barred Warblers are long-distance migrants with wintering areas beyond the Sahara (Csörgő *et al.* 2009). Many detailed studies have pointed out the declines of Afro-Palearctic migrant birds, but the temporal pattern of these decreases was disproportionate (John 1992, Sanderson *et al.* 2006, Wesołowski *et al.* 2010). Migratory species, especially long-distance migratory birds, are at high risk because they must adapt to the changed environmental conditions at the breeding grounds, along the migratory route, in wintering areas, and stopover sites (Newton 2008). They are mostly obligatory migrants, meaning the routes and timing of the migration and the wintering grounds are genetically encoded (Morelli *et al.* 2022). Such species have less plastic behaviour and, with a few exceptions (e.g. Jonzén *et al.* 2006), cannot adapt quickly enough to the changed circumstances. They still winter in locations where they survived the last ice age (Berthold 2001). Long-distance migrant declines occur mainly along their migration routes or in wintering grounds. For the trans-Saharan migrants, the main threat may be the expanding Sahara Desert, which forces them to fly greater distances without food and water, and droughts in the Sahel (Hagemeijer & Blair 1997, Marchant *et al.* 1997).

Most long-distance migrants are insectivorous or mixed-feeders, and their food availability peak is influenced by local habitat and climatic conditions to which they cannot adapt as quickly as obligate migrants. Climate change shifts the peak availability of prey in wintering areas and stopover sites (Both *et al.* 2009). The number of migratory songbird species with strong links between population fluctuations and climatic conditions in the Sahel region of West Africa is remarkably high (Newton 2004a).

We can quantify migration and overwintering loss by apparent survival rate. The returning rate of the first-year bird is low, i.e., most young birds hatched in a given year will not return from the wintering area. This survival may be much higher for second and third-year birds (Kiss *et al.* 2020). Migration losses cannot be recovered after the return to breeding areas because the return time often does not coincide with the peak in food availability, which affects breeding success and clutch size (Both *et al.* 2006).

Common Whitethroat productivity showed a rising trend during the study period, suggesting that the carrying capacity of the habitat in the breeding area and subsequent higher productivity are high enough to compensate for wintering loss, resulting in a moderately growing European population (PECBMS 2023). Common populations decreased considerably across Europe by the 1960s, possibly due to African drought (Zwarts *et al.* 2015). Populations have since recovered in several areas (Birdlife International 2023) thanks to favourable climatic conditions, especially in northern and western European countries (Balmer *et al.* 2013, Sovon Vogelonderzoek Nederland 2018, Kalyakin & Voltzit 2020).

The migration route, its length, and the habitat in the breeding areas greatly determine population sizes. The more diverse and heterogeneous a habitat, the more species and individuals it supports and the more resilient the community. Thus, forests – which are in a more natural state – are less disturbed habitats in which the birds can better adapt to habitat and structural changes like forest fragmentation and forest management (Angelstam *et al.* 2004, Wesołowski *et al.* 2010, Bakermans *et al.* 2012, Czeszczewik *et al.* 2015). Forest management considerably influences changes in forest species populations. The increasing proportion of forests is one of the reasons why the nesting population of the Eurasian Blackcap is stable or moderately rising in Hungary (Csörgő & Gyurácz 2021) and increasing across Europe (BirdLife International 2023).

The Barred Warbler and especially the Common Whitethroat are connected to open habitats (including farmlands and shrublands); they forage on fields and nest in shrubs along the edges. Numerous detailed studies in recent decades have reported on declining farmland songbird populations, including Tucker and Heath (1994), Siriwardena *et al.* (1998), Pitkänen & Tiainen (2001), Gregory *et al.* (2004), Newton (2004b), Wretenberg *et al.* (2006), Reif *et al.* (2008) and Báldi and Batáry (2011). Agricultural intensification is the main reason behind the large-scale decrease (Verhulst *et al.* 2004, Németh 2017). Such intensification comprises large homogeneous fields, increased isolation of habitat patches due to the conversion of previously unused land to production, lack of bushes on field edges, the application of a large number of pesticides, chemicals and fertilisers, heavy mechanisation or overgrazing (Hallmann *et al.* 2014, Traba & Morales 2019, Valavanidis 2021). Population changes of the Barred Warbler can vary immensely from area to area. This study observed a slight decrease in the breeding population; however, based on the

Hungarian Monitoring of Common Birds programme, the population east of the Tisza River shows an increasing trend (Csörgő & Gyurácz 2021). European research also indicates a stable population (PECBMS 2023).

Our results show no significant trend in the remaining species, either in the numbers of adults or juveniles.

The comparison of productivity based on the cluster analysis shows a clear distinction between certain species groups. The Common Chiffchaff and Eurasian Blackcap, predominantly overwintering in the Mediterranean, are separated from all other species, which overwinter mainly or exclusively south of the Sahara. According to Gregory *et al.* (2007), the populations of short-distance or partial migrants like the two species mentioned above are stable, because they are exposed to fewer risks and have more plastic behaviour. Short-distance or partial migrants are mostly facultative migrants whose migration strategies are affected by weather events. Thus, they respond quicker to changes to the environment or local food resources (Berthold 2001). Weather parameters also influence peak food availability. Facultative migrants adapt to such changes by arriving earlier and laying eggs sooner, providing them with a remarkable advantage compared to long-distance migrants (Mitrus 2003, Czeszczewik 2004, Wesołowski & Maziarz 2009). Consequently, their populations are more stable or can increase. However, early returns or remaining in place also exposes them to dangers like sudden temperature drops and snowy winters (Gregory *et al.* 2007).

The ratio of adults and productivity shows an interesting pattern in the Eurasian Blackcap. This study found that productivity decreased with more adults returning. Higher productivity can compensate for the loss of migration and wintering when fewer adults return, suggesting density-dependent population regulation. Following a period of high productivity over several years, fewer adult birds returning in the spring are often observed, indicating density-independent regulation during migration and wintering (Newton 1998). Temperature is the most crucial factor determining Eurasian Blackcap density (Knaus 2020). In addition to abundance, the success of juveniles also contributes to species productivity. Our previous studies at the Tömörd Bird Ringing Station showed that temperatures at the beginning of the breeding season influenced Eurasian Blackcap fledgling success. Milder spring weather resulted in increased fledging success, while cooler spring weather increased the mortality of first-year birds (Kiss *et al.* 2016). The proportion of overwintering Eurasian Blackcaps has increased in northern and central Europe over the last decade, especially in urban and peri-urban areas. Earlier spring arrivals have been observed in northern and western Europe (Lundberg & Edholm 1982, Fransson 1995, Hüppop & Hüppop 2011). In addition, the migratory routes of migrants are shorter, which has also resulted in earlier breeding (Aymí *et al.* 2020).

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Appendix

Standardised annual capture (mean ± SD) of the studied species in the ringing stations during the CES sessions (2007–2018)
A vizsgált madárfajok sztenderdizált fogásszámának éves átlaga és szórása az egyes gyűrűzőállomásokon a CES időszakban (2007–2018)

	PHYTRO	PHYCOL	SYLATR	SYLBOR	CURCUR	CURNIS	CURCOM
Dömös	0	15.3 ± 12.4	185.7 ± 52.1	0.3 ± 1.2	0.7 ± 1.6	0.3 ± 1.2	0.7 ± 1.6
Balinka	0.6 ± 1.9	6.8 ± 9.4	149.5 ± 47.6	0	0	0	0.6 ± 1.9
Érsekcsanád	1.1 ± 3.8	16.3 ± 10.9	201.9 ± 44.5	1.5 ± 2.9	4.1 ± 4.4	0.4 ± 1.3	11.1 ± 10.8
Farmos	0	0	0.8 ± 1.2	0.2 ± 0.7	0.4 ± 0.9	0	0.8 ± 1.6
Fertőújlak	1.7 ± 3.0	1.1 ± 2.6	10.1 ± 8.7	0.6 ± 1.9	0	0	1.7 ± 4.1
Hajdúszoboszló	0	6.3 ± 4.9	56.5 ± 34.9	1.6 ± 1.9	6.2 ± 7.4	0	0,5 ± 1.7
Keszthely	2.3 ± 2.6	12.0 ± 6.0	29.9 ± 13.8	1.8 ± 3.8	1.6 ± 2.2	0	2.1 ± 2.4
Kóka	0.4 ± 1.4	28.0 ± 13.6	185.9 ± 53.0	0.3 ± 1.2	0.4 ± 1.4	1.1 ± 2.9	4.9 ± 10.5
Komárom	0	0	68.5 ± 47.9	0	0	0	0
Nagydorog	1.3 ± 2.2	27.2 ± 13.8	94.4 ± 23.0	1.4 ± 2.1	1.9 ± 2.1	5.5 ± 4.5	3.9 ± 3.3
Pálmonostora	0	0.3 ± 1.2	0.7 ± 1.6	0	0.3 ± 1.2	0	1.7 ± 2.1
Pilismarót	0.3 ± 1.2	2.3 ± 3.2	176.3 ± 42.9	0.3 ± 1.2	4.0 ± 4.2	2.3 ± 3.6	0.7 ± 1.6
Sárszentmihály	0	2.9 ± 4.6	14.9 ± 28.6	0	0	0	5.0 ± 6.1
Szalonna	2.8 ± 2.7	32.6 ± 16.4	172.3 ± 36.4	2.8 ± 2.7	57.6 ± 20.6	21.4 ± 19.5	4.9 ± 6.1
Szeged	0.2 ± 0.6	0	0.3 ± 0.8	0.2 ± 0.6	0.2 ± 0.5	0	0.5 ± 1.2
Tömörd	5.2 ± 6.3	67.0 ± 36.4	118.8 ± 34.5	8.0 ± 3.7	15.8 ± 6.4	8.7 ± 6.4	17.5 ± 12.1