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Annual captures and low apparent survival rates in two tit species in western Hungary

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Abstract Adult and juvenile survival are important factors affecting the population dynamics of small passerines. Understanding variation in the population dynamics and survival rates is critical for ecological studies and nature conservation. The aim of this study was to investigate the annual capture-recapture, apparent survival and capture probabilities of the Blue Tit *Cyanistes caeruleus* and the Great Tit *Parus major* occurring in western Hungary. Data from 8,628 Blue Tits and 7,727 Great Tits came from a constant-effort ringing scheme, using three ringing periods, spanning 24 years (1998 to 2021). The annual captures did not show a significant linear trend from 1998 to 2021 in the study site for both tit species. The temporal variation of annual captures and the annual capture-recapture proportions of different ages and sexes of the tit species were similar. This indicated that the migration strategies of these two partial migrant species did not differ significantly. According to the best standard Cormack-Jolly-Seber model, apparent survival of first-year birds was lower than that for adults. The CJS model selection for the dataset indicated that the time and sex had no effect on apparent survival probabilities for both tit species. Capture probability in the juvenile groups was not significantly higher than that in the adult groups for both species.

Keywords: Cormack-Jolly-Seber model, apparent survival, capture-recapture, tits

Összefoglalás A különböző korú egyedek túlélése a madárpopulációk dinamikájának egyik legfontosabb meghatározó tényezője. A populációdinamika és a túlélési arányok változásainak megértése kiemelt jelentőségű az ökológiai vizsgálatokban és a gyakorlati természetvédelemben is. E tanulmány célja a kék cinege *(Cyanistes caeruleus)* és széncinege *(Parus major)* éves fogás-visszafogásainak, látszólagos túlélésének és fogási valószínűségének vizsgálata egy nyugat-magyarországi élőhelyen 1998 és 2021 között. A tanulmányban az Actio Hungarica és az Állandó Ráfordítású Gyűrűzés programokban 24 év alatt (1998–2021) gyűrűzött 8628 kék cinege és 7727 széncinege adatait használtuk fel. Az éves fogások egyik faj esetében sem mutattak lineáris trendszerű változást a vizsgált területen. A két cinege faj éves fogásainak időbeli változása, valamint a különböző korú és nemű egyedek éves fogás-visszafogási arányai hasonlóak voltak, ami arra utal, hogy e két részlegesen vonuló faj vonulási stratégiája nem különbözik jelentősen. A legjobb standard Cormack-Jolly-Seber-modell szerint az elsőéves madarak látszólagos túlélése alacsonyabb volt, mint a felnőtteké. Az adathalmazra vonatkozó CJS modellválasztás azt mutatta, hogy az időpont és az ivar nincs hatással a látszólagos túlélési valószínűségekre egyik cinegefajnál sem. A fiatal madarak fogási valószínűsége nem volt szignifikánsan magasabb, mint az felnőtt madaraké egyik cinegefajnál sem.

Kulcsszavak: Cormack-Jolly-Seber modell, látszólagos túlélés, fogás-visszafogás, cinegék

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Introduction

Annual counts of birds tell us how their numbers are changing, but the capture-recapture method is needed if we want to understand the mechanism of the changes observed. Various types of useful information can be recorded when birds are caught for ringing, including age and sex. If a bird is subsequently recaptured, repeated measurements can be used to study both apparent survival and capture probability (Silkey *et al.* 1999, Newton 2011). Capture-recapture is a powerful and efficient means of collecting critical data on demographic parameters such as survival (Nur *et al.* 2004).

As part of a long-term monitoring study to understand passerines' population dynamics and migration (Gyurácz & Bánhidi 2008, Lukács *et al.* 2015, Gyurácz *et al.* 2021), here we report annual capture-recapture data, and estimate age- and sex-specific survival for one Palearctic and one European cavity-nesting and partial-migrant species of tits: Blue Tit *Cyanistes caeruleus* and Great Tit *Parus major* breed and migrate sympatrically in western Hungary (Gyurácz *et al.* 2017). The European breeding populations of Great Tit and Blue Tit appear to have increased moderately in recent decades (PECBMS 2021). In Hungary, the Great Tit overwintering population has increased, but changes in populations of overwintering Blue Tit were unclear between 1999 and 2018 (Gyurácz 2021, Szép *et al.* 2021). However, even within a country, population trends of tits can vary significantly across regions, as regional environmental factors affecting bird survival may also differ (Perdeck *et al.* 2000). In order to understand the causes of population dynamics, detailed demographic information is required. In bird populations, survival (Tinbergen & Boerlijst 1990, Adriaensen *et al.* 1998), dispersal and site fidelity (Both *et al.* 2012, Mátrai *et al.* 2012) are essential components for understanding the causes of population growth and decline (Jones *et al.* 2021). Survival, or fitness, may depend on the age, sex, behaviour, habitat and seasonal occurrence of the tits (Dhondt 1979, Horak & Lebreton 2008, Class *et al.* 2014).

Survival studies have usually been conducted during the breeding season (Orell & Ojanen 1979, Horak & Lebreton 2008, Bastianelli *et al.* 2021), though migration is the most risky season of the avian lifecycle (Newton 2007). Inclusion of birds captured in the pre- and post-breeding migration in the survival estimate is also needed to better understand the population limitations during the annual cycle (Salewski *et al.* 2013, Ward *et al.* 2018). In the present study, we investigated whether annual capture-recapture, apparent survival and capture probability differed between the two sympatric species, and whether juveniles and adults, and adult males and females have different apparent survival rates and capture probabilities that are linked to variations in behaviour or the role of the sex. First, we predicted that the two tit species have similar annual capture-recapture, apparent survival and capture probability due to their similar breeding, foraging and migratory strategies. Secondly, we predicted that juveniles would have lower apparent survival rates and capture probability than the adults, based on their lower dominance ranking status. Finally, based on different gender strategies in mating systems, parental care and migration, we predicted sex differences in apparent survival and capture probability in both tit species.

Material and Methods

Study area and data collection

The study was carried out at the Tömörd Bird Ringing Station in western Hungary (47°21'N 16°40'E). The study site has a typical continental climate with cold winters and warm summers. There are four natural habitat types around the station of Tömörd.

1. Scrubland: bushes and herbs make up compact, dense vegetation, which is dissected by small grass patches. Its characteristic plant is the blackthorn *(Prunus spinosa)*.
2. Forest edge: broadleaf trees and bushes form a compact, dense edge, forming an ecotone community with the Turkey oak *(Quercus cerris)* as the characteristic plant. These forests are characterized with regular felling and other forestry activities.
3. Grassland with shrubs: this habitat type represents a transition between the wet habitats of the swamp and the steppe communities that used to cover the agricultural land around the marsh. There are a few bushes in the grassland, with two small patches of the dwarf elder *(Sambucus ebulus)*. The grassland is not managed.
4. Marsh: a small (6 ha), permanent, and isolated wetland. The characteristic plant is the reedmace *(Typha latifolia)*.

Bird ringing for this study took place during the spring migration (an Actio Hungarica programme in March-April), the breeding (a Constant Effort Site programme from April to July) and post-fledging (also an Actio Hungarica programme from August to November) periods between 1998 and 2021. We used 23 (spring), 13 (breeding) and 28 (autumn), individually numbered Ecotone mist-nets (12 metres long and 2.5 metres high, with 5 shelves and a mesh size of 16 mm) for trapping. The nets were placed evenly in the four habitat types. Ringing sessions lasted from sunrise to noon (CES) or dusk, except on rainy and stormy days when the nets were closed; numbers, locations, types, and lengths of mist nets were held constant (Gyurácz *et al.* 2017). All birds were ringed, sexed and aged according to Svensson (1992). First-year birds that hatched in the year of ringing were defined as juveniles, while all older birds were defined as adults. Thus, in the case of juvenile birds, the sex of each individual could not be determined in the breeding season. We excluded all birds for which there was no sex or age data from the analysis.

Apparent survival and capture analysis

Due to the lack of dispersion data, we could not distinguish between mortality and emigration. Consequently, we used the apparent survival, which underestimated the true survival (Schaub & Royle 2013). It was not possible to distinguish between local breeding birds and non-territory holders. Additionally, the number of "potential transients" (Ryu *et al.* 2016) was very low in the breeding and unknown in migration seasons: therefore, the data for all captured adults were pooled. The survival probabilities of passerines at a particular site are frequently analysed by using capture-recapture models: the Cormack-Jolly-Seber (CJS) formula is used most often (Lebreton *et al.* 1992, Naef-Daenzer *et al.* 2001, Williams *et al.* 2002, Greńo *et al.* 2008, Jones *et al.* 2021). In the CJS model, the probability of encounter (p) is explicitly modelled in order to correct possible biases in survival estimates (Jankowiak *et al.* 2016). In this study, analysis of bird survival and capture probabilities were based on capture-recapture, using the standard CJS model (Barker 1999). The analyses were performed using MARK software (White & Burnham 1999). We ran 22 models for both species to test for the effect of age, sex and time (year of capture) in survival estimates and capture probability for both species. The CJS model enables the calculation of apparent survival φ(i) (the probability that an individual survives from year i to year i + 1 and returns to the sampling area) and the probability of encounter p(i) (the probability that an animal in the sampling area at time i is encountered at time i). The most general model was selected based on the result of the goodness-of-fit (GOF) test performed in UCARE (Choquet *et al.* 2009). Passing all of the tests meant a solely time-dependent CJS model. Failure on test 3.SR (and passing the others) indicated an age-dependent model where survival and encounter probability after the first year (marked as a1 in the models) was different than in the consecutive years (a2). 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 in MARK). For the CJS model, model selection was performed using the information-theory approach. The Akaike Information Criterion, corrected for small sample size (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. If there were multiple most-probable models (QAICc values differed by less than 2 from the best-fit model), model parameters were calculated by model averaging (weighted average using QAICc weights) (White & Burnham 1999). Differences were considered significant if there were no overlaps between the 95% CI values of p and φ in each age and sex group. Variance due to model variation (MV) was calculated by the built-in routines of the MARK program when we performed parameter averaging. The multivariate linear model was used to determine trends in the annual capture-recapture rate, apparent survival, and capture probability of age and sex groups. The distribution of capture-recapture rates according to age and sex groups of the two species was compared with Fisher's exact test (χ^2). The correlation between annual captures of the two species was checked by Spearman rank correlation. The Past computer program was used for the statistical analysis (Hammer *et al.* 2001).

Results

Annual capture and recapture

A total of 16,355 individuals were ringed: 8,628 Blue Tits and 7,727 Great Tits. A total of 178 (2.06%) Blue Tits and 318 (4.11%) Great Tits were recaptured at the study sites *(Table 1)*. There was significant correlation between the annual captures of Blue Tit and Great Tit (r_s = 0.82, P = 0.001) *(Figure 1)*, whereas the distributions of annual capture (χ^2 = 3.15, P = 0.250) and annual recapture rates (χ^2 = 1.23, P = 0.611) of both age categories and sexes showed non-significant differences *(Table 1)*. With the exception of the annual recapture rates of juvenile Blue Tits and Great Tits, the annual capture rate, annual recapture rate, apparent survival and capture probability of both age categories and sexes did not show a significant linear trend from 1998 to 2021 for either species *(Tables 2, 3)*.

Effect of time, age and sex on apparent survival and capture probability

Apparent survival and capture probability were not time-dependent in any of the groups, they were constant during the study period for both species. Based on the result of the goodness-of-fit (GOF) test, for both species an age-dependent model was fitted to the

Table 1. Number of captures and recaptures of juvenile and adult birds at at Tömörd, western Hungary. R% = percentage of birds recaptured
1. táblázat A fiatal és felnőtt madarak fogásának és visszafogásának száma a nyugat-magyarországi Tömördön. R% = a visszafogott madarak százalékos aránya

Species		juvenile	adult male	adult female
Blue Tit *(Cyanistes caeruleus)*	Capture	7455 (86%)	451 (5%)	722 (9%)
	Recapture	151 (85%)	18 (10%)	9 (5%)
	R%	2.03	4.91	1.25
Great Tit *(Parus major)*	Capture	6248 (80%)	899 (12%)	580 (8%)
	Recapture	252 (79%)	39 (12%)	27 (9%)
	R%	4.03	4.34	4.65

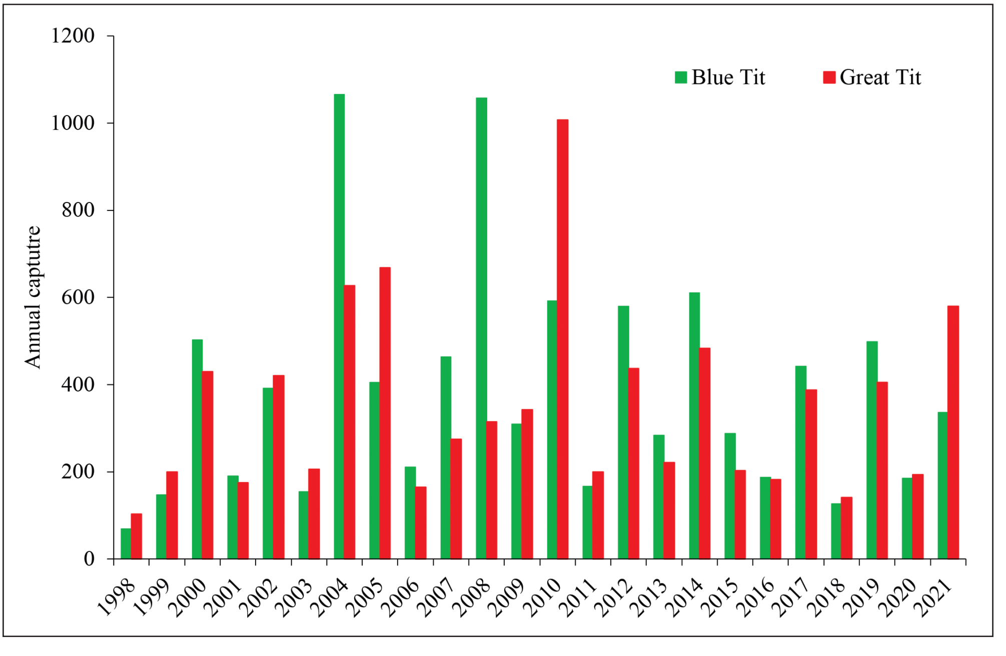

Figure 1. Annual captures of Blue Tit and Great Tit between 1998 and 2021 in Tömörd
1. ábra A kék cinege és a széncinege éves fogásai Tömördön 1998–2021 között

Table 2. Results of the multivariate linear model test of recaptured Blue Tits at Tömörd, western Hungary. Dependent variables: annual capture (C), annual recapture rate (aR%), apparent survival (φ) and capture probability (p). Independent variable: year

2. táblázat A többváltozós lineáris modell vizsgálatának eredményei a nyugat-magyarországi Tömördön visszafogott kék cinegékre vonatkozóan. Függő változók: éves fogási arány (C), éves visszafogási arány (aR%), látszólagos túlélés (φ) és fogási valószínűség (p). Független változó: év

Group	Variable	Slope	Error	Intercept	Error	r	p
Juvenile	C	0.481	7.444	–643.130	14963.000	0.014	0.949
	aR%	0.003	0.001	–5.094	1.609	0.571	**0.004**
	φ	–0.001	0.010	2.148	19.400	–0.022	0.922
	p	0.007	0.013	–14.488	25.237	0.128	0.562
Adult male	C	–0.165	0.478	351.300	960.410	–0.075	0.733
	aR%	0.002	0.002	–3.880	3.944	0.213	0.330
	φ	–0.008	0.009	17.188	17.658	–0.206	0.347
	p	0.008	0.013	–15.023	26.351	0.128	0.561
Adult female	C	0.953	0.715	–1883.300	1437.200	0.279	0.197
	aR%	0.001	0.001	–1.595	1.649	0.208	0.340
	φ	–0.012	0.014	24.611	27.203	–0.191	0.382
	p	0.014	0.011	–28.486	21.797	0.277	0.201

Table 3. Results of the multivariate linear model test of recaptured Great Tits at Tömörd, western Hungary. Dependent variables: annual capture (C), annual recapture rate (aR%), apparent survival (φ) and capture probability (p). Independent variable: year

3. táblázat A többváltozós lineáris modell vizsgálatának eredményei a nyugat-magyarországi Tömördön visszafogott széncinegékre vonatkozóan. Függő változók: éves fogási arány (C), éves visszafogási arány (aR%), látszólagos túlélés (φ) és fogási valószínűség (p). Független változó: év

Group	Variable	Slope	Error	Intercept	Error	r	p
Juvenile	C	1.552	5.557	–2847.100	11165.000	0.061	0.783
	aR%	0.004	0.001	–7.094	2.766	0.491	**0.017**
	φ	–0.011	0.010	23.189	20.025	–0.242	0.266
	p	0.013	0.012	–25.436	23.487	0.233	0.284
Adult male	C	–1.683	0.972	3419.800	1952.500	–0.353	0.098
	aR%	0.004	0.002	–8.712	4.684	0.378	0.075
	φ	–0.002	0.011	3.553	22.271	–0.032	0.883
	p	0.014	0.014	–27.222	27.656	0.214	0.326
Adult female	C	–0.263	0.666	553.270	1338.700	–0.086	0.697
	aR%	0.002	0.002	–3.339	3.321	0.218	0.318
	φ	–0.013	0.009	26.912	17.252	–0.321	0.136
	p	0.024	0.012	–47.968	24.684	0.394	0.062

Table 4. Cormack-Jolly-Seber model selection results examining apparent survival and capture probability of (a) Great Tit and (b) Blue Tit, western Hungary 1998-2021, as a function of age and sex. QAICc = small sample sizes corrected Akaike values; ΔQAICc = difference of models' QAICc values in relation to the best-fit model; QAICc values were calculated using a ĉ (variance inflation factor) of 2.14 for Blue Tit, 2.40 for Great Tit; No. Par. = number of parameters. Only the top models (ΔQAICc<5) are shown

4. táblázat A Cormack-Jolly-Seber-modell szelekciós eredményei, amelyek a) a széncinege és b) a kék cinege látszólagos túlélését és fogási valószínűségét elemezték az életkor és a nem függvényében Nyugat-Magyarországon 1998 és 2021 között. QAICc = kis mintanagysággal korrigált Akaike-értékek; ΔQAICc = a modellek QAICc-értékeinek különbsége a legjobban illeszkedő modellhez képest; a QAICc-értékeket a ĉ (varianciainflációs faktor) 2,14-es értékével számoltuk a kék cinegék esetében, 2,40-es értékével a széncinegék esetében; No. Par. = paraméterek száma. Csak a legjobb modellek (ΔQAICc<5) vannak feltüntetve

Model	QAICc	ΔQAICc	QDeviance	No. Par
Blue Tit *Cyanistes caeruleus*				
φJ(a1)J(a2)AM(.)AF(.) pJ(a1)J(a2)AM(.)AF(.)	847.9	0.00	153.0	8
φJ(a1)J(a2)AMAF(.) pJ(a1)J(a2)AM(.)AF(.)	848.0	0.14	155.2	7
φJ(a1)J(a2)AMAF(.) pJ(a1)JAM(a2)AF(.)	848.0	0.15	157.2	6
φJ(a1)J(a2)AMAF(.) pJ(.)AMAF(.)	849.0	1.14	160.2	5
φJ(a1)JAM(a2)AF(.) pJ(a1)J(a2)AM(.)AF(.)	849.0	1.14	158.2	6
φJ(a1)JAMAF(a2) pJ(a1)J(a2)AMAF(.)	849.2	1.27	160.3	5
φJ(a1)J(a2)AMAF(.) pJ(t)AMAF(.)	850.3	2.37	117.2	27
φJ(a1)J(a2)AM(.)AF(a2) pJ(a1)J(a2)AMAF(.)	850.5	2.58	159.6	6
φJ(a1)J(a2)AMAF(.) pJ(a1)J(a2)AMAF(.)	850.5	2.66	159.7	6
φJ(a1)J(a2)AM(.)AF(.) pJ(a1)J(a2)AMAF(.)	850.9	3.00	158.0	7
Great Tit *Parus major*				
φJ(a1)J(a2)AMAF(.) pJ(.)AMAF(.)	1181.22	0.00	240.8	5
φJ(a1)J(a2)AMAF(.) pJ(a1)J(a2)AMAF(.)	1182.39	1.17	240.0	6
φJ(a1)J(a2)AMAF(.) pJ(a1)JAMAF(a2)	1183.31	2.09	242.9	5
φJ(a1)JAMAF(a2) pJ(a1)J(a2)AMAF(.)	1183.81	2.59	243.4	5
φJ(a1)J(a2)AMAF(.) pJ(a1)J(a2)AM(.)AF(a2)	1184.25	3.03	241.8	6
φJ(a1)J(a2)AMAF(.) pJ(a1)J(a2)AM(.)AF(.)	1184.28	3.06	239.8	7
φJ(a1)J(a2)AM(.)AF(.) pJ(a1)J(a2)AMAF(.)	1184.38	3.16	239.9	7
φJ(a1)J(a2)AMAF(.) pJAMAF(.)	1184.51	3.29	246.1	4
φJ(a1)J(a2)AM(.)AF(a2) pJ(a1)J(a2)AM(.)AF(.)	1185.06	3.84	242.6	6
φJ(a1)J(a2)AMAF(.) pJ(a1)JAM(a2)AF(.)	1185.30	4.08	242.9	6
φJ(a1)JAM(a2)AF(.) pJ(a1)J(a2)AM(.)AF(.)	1185.62	4.40	243.2	6
φJ(a1)J(a2)AM(.)AF(.) pJ(a1)J(a2)AM(.)AF(.)	1186.10	4.88	239.7	8

Table 5. Summary of average values for the different parameters (φ = apparent survival rate, p = capture probability, J = constant parameter for juveniles across study years, AM = constant parameter for adult males across study years, AF = constant parameter for adult females across study years, J(a)1 = juveniles in their first year, J(a)2 = juveniles in their second and following years) for two tit species, according to the best models from the CJS analysis. SE = unconditional standard error, CI = confidence interval, MV = percent of variation attributable to model variation. Significant differences in bold

5. táblázat A különböző paraméterek (φ = látszólagos túlélési ráta, p = fogási valószínűség, J = a fiatal egyedekre vonatkozó konstans paraméter a vizsgálati években, AM = a felnőtt hímekre vonatkozó konstans paraméter a vizsgálati években, AF = a felnőtt tojókra vonatkozó konstans paraméter a vizsgálati években, J(a)1 = a fiatal egyedek az első évben, J(a)2 = a fiatal egyedek a második és az azt követő években) átlagos értékeinek összefoglalása a két cinegefaj esetében, a CJS elemzés legjobb modelljei szerint. SE = feltétel nélküli standard hiba, CI = konfidenciaintervallum, MV = a modellváltozatoknak tulajdonítható eltérés százalékos aránya. A szignifikáns különbségek félkövér betűvel szedve

Parameters	Weighted averages	SE	95% CI		MV%
Blue Tit *Cyanistes caeruleus*					
φJa1	0.025	0.007	**0.014**	**0.044**	0.025
φJa2	0.302	0.080	**0.171**	**0.477**	0.302
φAM	0.191	0.115	0.052	0.504	0.191
φAF	0.221	0.142	0.053	0.588	0.221
pJa1	0.612	0.189	0.249	0.882	0.612
pJa2	0.492	0.205	0.162	0.829	0.492
pAM	0.216	0.237	0.017	0.811	0.216
pAF	0.074	0.070	0.011	0.373	0.074
Great Tit *Parus major*					
φJa1	0.051	0.008	**0.036**	**0.070**	5.78
φJa2	0.338	0.065	**0.224**	**0.476**	26.62
φAM	0.176	0.077	0.071	0.376	51.92
φAF	0.177	0.079	0.069	0.383	53.70
pJa1	0.587	0.095	0.398	0.754	9.13
pJa2	0.500	0.124	0.275	0.725	31.58
pAM	0.232	0.129	0.068	0.555	58.83
pAF	0.243	0.139	0.068	0.584	59.68

data the best, which discriminated between first year – J(a1), and consecutive year – J(a2) captures in the case of those birds which were first captured as juveniles *(Table 4)*. In juveniles, apparent survival was significantly lower in the first year than in the second (2-age-group model). The apparent survival rate of first-year birds was very low: only 2.5% of Blue Tits and 5.1% of Great Tits survived and were recaptured in their second year. This means that an unknown proportion of the remaining 94.9–97.5% of birds died and an unknown proportion did not return to the ringing site. The apparent survival probability of second-year birds was significantly higher: 30.2% of Blue Tits and 33.8%

of Great Tits survived the following year. Apparent survivals of males (19.5% of Blue Tits, 17.6% of Great Tits) and females (22.5% of Blue Tits, 17.7% of Great Tits) were similar. Apparent survival in the second year in the juvenile group was not significantly different from apparent survival in the adult male or female groups for both species. Capture probabilities of sexes were similar for both species. Capture probability in the first and second year in the juvenile groups was not significantly higher than capture probability in the adult groups for both species *(Table 5)*.

Discussion

Population dynamics: annual capture-recapture

In Europe, the Blue Tit and Great Tit populations have increased moderately during the recent decades, although there have been regional differences in the changes in both the breeding and overwintering populations, even within Hungary (Gyurácz 2021, Szép *et al.* 2021). Our annual captures also suggest stabile populations in this western Hungarian study site (Tömörd) for both tit species. The results of an earlier study showed that high temperatures in the breeding season was the key determinant of increased annual captures of first-year birds of some short-distance migrants (Gyurácz *et al.* 2016). The increasing and stable populations of forest tit species is most likely due to the expanding forested area of Hungary. In Hungary, the average annual temperature rose by 1.7 °C between 1981 and 2020. The forested area increased by 7.6% in Hungary between 2000 and 2015 (www.ksh.hu), mainly due to acacia and poplar afforestation in areas previously used for farming. Both environmental changes are favourable for tit species. This is also indicated by the significant increasing linear temporal trend in the recapture rates of juvenile Blue Tit and Great Tit between 1998 and 2021 at the study site. However, the annual captures did not show a linear trend between 1998 and 2021, but fluctuated, being very high in a few years (2004 and 2008 for Blue Tit, 2010 for Great Tit). In these invasion years, the most birds were captured primarily in the second half of the autumn migration (Gyurácz *et al.* 2017). The temporal variation of annual captures and the annual capture-recapture proportions of ages and sexes of the closely-related tit species were similar. This indicated that the migration strategies of these two partial migrants did not differ significantly. The partial migration for widely-distributed species like the Blue Tit and Great Tit, involving a mixture of resident and migratory birds in most populations, is associated with general selection for a short migration distance (Nilsson *et al.* 2008). The slightly higher proportions of first-year and adult female Blue Tits indicated that irruptive migration is a little more typical in this species than in the Great Tit. The body-size and the dominance hypothesis can explain the difference in migratory behaviour between species, ages and sexes (Smith & Nilsson 1987, Nyquist 2007). The intensive Blue Tit (2004, 2008) and Great Tit (2010) migration in the study site could be connected with the reduced beech *(Fagus sylvatica)* crop and the large tit populations breeding in the Alps and in the Carpathians as well as further north, e.g. northwest Russia, Poland

and the Baltic region (Heldbjerg & Karlsson 1997). According to our results and the winter-food limitation hypothesis (Perdeck *et al.* 2000), contrary to the conclusion of Nowakowski and Vähätalo (2003), the Great Tits, similarly to the Blue Tits, behave like irruptive partial migrants, with the migration in central Europe also being affected by the population density and beech crop fluctuations.

Apparent survival, capture probabilities across ages and sexes

Apparent survival is one of the most important factors affecting the annual variations in the populations of small passerine species (Peach & Baillie 2004). The average apparent survival probabilities of Blue Tit (ranging 0.025 to 0.302) and Great Tit (ranging 0.051 to 0.338) age and sex groups in western Hungary was lower than in most other European studies, which range from 0.26 to 0.56 (Orell & Ojanen 1979, Horak & Lebreton 2008). Our lower survival probabilities may have been due to the high proportion of "potential transients" during migration seasons. The CJS model selection for the dataset indicated that the time and sex had no effect, but age had an important effect on apparent survival probabilities for both tit species. The first-year birds had a lower apparent survival than individuals in their second year and older male and female adult tits. These age-related differences in survival are found in most bird species, because first-year birds have less experience or hold poorer-quality territories (Martin 1995, Siriwardena *et al.* 1998, Kiss *et al.* 2020). Some studies have given general support to the early-breeding hypothesis for the survival of first-year individuals (Ringsby *et al.* 1998, Yackel *et al.* 2006). However, adult males (AM) and females (AF) also had a lower apparent survival than first-year breeders in their second year J(a2), but J(a2) and AM, AF confidence intervals largely overlapped. In other studies, survival probabilities have also been shown to rapidly decrease with age after two years in the Blue Tit and Great Tit (Bastianelli *et al.* 2021, Bouwhuis *et al.* 2012). Population density had a significant negative impact on adult survival in the less productive habitats, suggesting higher breeding competition (Tremblay *et al.* 2005, Bastianelli *et al.* 2021). Maness and Anderson (2013) reviewed the literature on the predictors of juvenile survival in birds. Factors other than body weight, size and sex can influence juvenile survival, including hatching date, hatching order, brood size and nestling growth rate. Body size and weight predict juvenile survival in many bird species, so sex-biased survival might be expected in species with sexual size dimorphism. However, according to our results, there were no significant differences in survival probability between sexes in both species, although the capture rate of the Blue Tit was female-biased, and the Great Tit was male-biased at the study site. According to our earlier study, the apparent survival is also not sex-related in other passerines in Hungary (Kiss *et al.* 2020). Higher survival of males than females has been reported in most of the earlier studies of Great Tits (Orell & Ojanen 1979), as well as in many other bird species (Breitwisch 1989, Payevsky 1993). However, Clobert *et al.* (1988) found no clear differences between survival of adult male and female Great Tits in Wytham, Oxford. Dhondt *et al.* (1990) found no sex differences in survival in the Blue Tit in Belgium. Female Blue Tits survived slightly better in Corsica, while males survived better in Provence (Blondel *et al.* 1992). Females survived better than males, and the survival probabilities varied over time in Estonia (Horak & Lebreton 2008). These contradictory results suggest that regional environmental conditions (e.g. weather conditions, food supply) could drive survival fluctuations across populations.

Unlike other results (Burton & DeSante 2004, Nur *et al.* 2004), the CJS models in the present study did not reveal an important effect of age and sex on capture probabilities for either tit species. In Hungary, male Eurasian Blackcap *(Sylvia atricapilla)* and Red-backed Shrike *(Lanius collurio)* had significantly higher capture probabilities than females during the breeding season, perhaps due to the sex differences in territorial behaviour and breeding strategy (Amrhein *et al.* 2012, Kiss *et al.* 2020). Similar capture probabilities for ages and sexes of the two tit species in western Hungary may be explained because most of the birds were captured during the autumn migration, when there is less territorial behaviour than in the breeding season, but this needs to be examined directly.

Conclusion

We produce the first robust annual capture-recapture study and estimates of apparent survival and capture probability for Blue Tit and Great Tit in Hungary. We demonstrate annual captures with high year-to-year fluctuation, and low apparent survival probabilities in both tit species. Our results demonstrate that apparent survivals of juveniles and adults are unlikely to drive population trends in these species. Future work should focus on other lifestyle characteristics, such as overwintering survival, stopover strategies and habitat selection, as well as parallel studies of the apparent survival of this species at other sites in Hungary; investigating the annual capture-recapture and apparent survival in other closely-related tit species would also be important for understanding the causes of population dynamics of tits.

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