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Study of apparent survival and capture probabilities of some passerines in Hungary

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Abstract. Apparent survival rate is an important factor affecting the temporal changes of small passerine species. The aim of this study was to obtain information about the apparent survival and capture probabilities of some passerines breeding in Hungary. Data from 11,327 individuals come from a constant effort ringing scheme, using 12 ringing sites spread over Hungary, spanning 14 years (2004 to 2017). According to the best standard Cormack–Jolly–Seber model, apparent survival of first-year Eurasian Blackcap *Sylvia atricapilla* and Common Chiffchaff *Phylloscopus collybita* was found to be significantly lower than adult survival, but the apparent survival showed no difference between sexes. Male Eurasian Blackcap and Red-backed Shrike *Lanius collurio* had significantly higher capture probabilities than females in Hungary. The survival and capture probabilities of age and sex groups did not differ significantly for Barred Warbler *S. nisoria* and Lesser Whitethroat *S. curruca*. Time-dependent models were included in the analysis in all cases, but they always ranked lower than time-independent models. The capture rates of three species (Eurasian Blackcap, Barred Warbler, Common Chiffchaff) were male-biased in Hungary. Our study supports previous suggestions that female-biased mortality may be the most important explanation for male-biased adult sex ratios in birds.

Key words: Cormack–Jolly–Seber model, apparent survival, capture-recapture, passerines.

Introduction

Many European passerine populations are currently declining rapidly, although others are increasing and expanding (Sanderson et al. 2006, BirdLife 2017, Gyurácz et al. 2017). In order to understand the causes of population growth and decline, detailed demographic information must be collected. In bird populations, survival (Tinbergen & Boerlijst 1990, Adriaensen et al. 1998) and dispersal (Both et al. 2012, Mátrai et al. 2012) are often considered to be among the key population attributes underlying demographic mechanisms (Jankowiak et al. 2016).

Usually, studies dealing with both annual survival and capture probability in small passerines are based on identifying birds in the hand, through ringed individuals being captured and re-captured by mist-netting (Silkey et al. 1999). These methods appear to be a powerful and efficient means of collecting critical data on demographic parameters such as survival (Nur et al. 2004). In this study, we analysed capture-recapture data from Hungarian Constant Effort Sites (CES). The number of adults and juveniles captured in the CES program across many sites is a good indicator of the number of birds in the population (Feu & McMeeking 2004, Robinson et al. 2009). Many passerines show strong breeding-site fidelity in successive breeding periods. Consequently, standardized captures of ringed breeding birds can be an effective tool for estimating apparent survival rates of adults. Nevertheless, the accurate modelling of survival rate is burdened with uncertainty since capture probability can vary by individual characteristics, or according to the distance of territories from the CE sites (Robinson et al. 2009). We attempted to estimate the apparent survival and capture probability of birds ringed as juveniles or adults, considering that first-year birds have much lower recapture rates in subsequent years than adults on other CES projects (Peach & Bailie 2004).

The aim of the study was to obtain information about the apparent survival and capture probabilities of some passerines breeding in Hungary. We asked the following question: Do apparent survival and capture probability depend on the age and sex of the birds?

Material and Methods

Study area and data collection
Data are from a CES ringing scheme including passerine and near-passerine bird species, using 12 ringing sites spread over Hungary (Fig. 1), spanning 14 years (2004 to 2017). The Hungarian CES protocol is the same as that used by other CES schemes (Kestenholz 2007): birds were ringed during about 9 sessions, each separated by at least five days, covering the breeding period (mid-April to early July). Ringing sessions lasted from sunrise to noon; numbers, locations, types, and lengths of mist nets were held constant. Plumage features or brood patch and cloaca shape provide good criteria for determining age and sex in all species, allowing accurate distinction between adults and juveniles, males and females (Svensson 1992).

We used the data available for the Eurasian Blackcap *Sylvia atricapilla*, Garden Warbler *S. borin*, Barred Warbler *S. nisoria*, Lesser Whitethroat *S. curruca*, Common Whitethroat *S. communis*, Wood

Figure 1. Map showing the distribution of ringing sites involved in the study.

Warbler *Phylloscopus sibilatrix*, Common Chiffchaff *Ph. collybita*, Willow Warbler *Ph. trochilus* and Red-backed Shrike *Lanius collurio* since they are, with the exception of the Red-backed Shrike, related species, but their habitat preferences and migration strategies are different (Cramp 1998, Csörgő et al. 2009). A total of 11,327 individuals were ringed: Eurasian Blackcap 7,109; Garden Warbler 150; Barred Warbler 266; Lesser Whitethroat 492; Common Whitethroat 448; Wood Warbler 52; Common Chiffchaff 1,924; Willow Warbler 112; and Red-backed Shrike 774.

Apparent survival and capture analysis

Dispersion means that the bird was ringed as a juvenile or as an adult and recaptured elsewhere (distance ≥ 1 kilometer) one or more years later (Mátrai et al. 2012). Unfortunately, the data set of Hungarian CES did not provide possibilities to assess the short distance dispersal. That would need a dense network of catching sites that was not the case here. Among all of the recaptures, only one young male Eurasian Blackcap was recaptured at a different site from the original capture: it was recaptured 101 kilometers away from its original ringing site, two years after the first capture. 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, as well as the rate of the "potential transients" (Ryu et al. 2016) was very low in the CES program: 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) formulation is the one used most often (Lebreton et al. 1992, Naef-Daenzer et al. 2001, Williams et al. 2002, Greńo et al. 2008). 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 Cormack–Jolly–Seber (CJS) model (Barker 1999). The analyses were performed using MARK software (White & Burnham 1999). The CJS model enables the calculation of apparent survival Phi(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 probability of encounter was, in fact, the probability that birds occurring at the ringing sites were captured during study periods. The selection of the most general model was based on the abundance of the available data (if there was no recapture of juvenile birds, we could not incorporate age-factor in the models, we could test only the effect of sexes) and on the result of the Goodness of Fit test performed in U-CARE program (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 (AICc), was used to rank the fit of models to the data. The model with the lowest AICc was considered to be the best fit. If there were multiple most-probable models (AICc values differed by less than 2 from the best fit model) model parameters were calculated by model averaging (weighted average using AICc weights) (White & Burnham 1999). Differences were considered significant if there were no overlaps between the 95% CI values of p and Phi 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.

Results

From the nine target species (Table 1), the most captured species was the Eurasian Blackcap with 7,509 individuals, followed by the Common Chiffchaff (1,675 ind.) and the Red-backed Shrikes (760 ind.). The Barred Warbler, the Lesser Whitethroat, and the Common Whitethroat were caught in similar numbers (215 to 248 ind.), while the Willow Warbler, the Garden Warbler, and the Wood Warbler were represented by fewer than 100 individuals. Since there were no or very low number of local recaptures of Garden Warblers, Wood Warblers, Common Whitethroats, and Willow Warblers, we were therefore unable to perform any model analyses on the age- and sex-dependence of survival or capture probabilities due to the lack of data.

Time (year of capture)-dependent models were included in the analysis in all cases, but they always ranked lower than time-independent models.

Table 1. Number of captures and recaptures of juvenile; male and female (age groups pooled) birds in CES, Hungary. R% = percentage of birds recaptured.

Species		juvenile	male	female
Eurasian Blackcap	Capture	3281	2320	1908
(Sylvia atricapilla)	Recapture	185	280	115
	R%	5.64	12.07	6.03
Garden Warbler	Capture	14	14	12
(Sylvia borin)	Recapture	0	0	0
	R%	0	0	0
Barred Warbler	Capture	38	103	107
(Sylvia nisoria)	Recapture	0	9	5
	R%	0	8.74	4.67
Lesser Whitethroat	Capture	113	38	64
(Sylvia curruca)	Recapture	4	4	9
	R%	3.53	10.53	14.06
Common Whitethroat	Capture	41	99	77
(Sylvia communis)	Recapture	0	0	1
	R%	0	0	1.30
Wood Warbler	Capture	12	4	2
(Phylloscopus sibilatrix)	Recapture	0	0	0
	R%	0	0	0
Common Chiffchaff	Capture	1212	272	191
(Phylloscopus collybita)	Recapture	78	49	23
	R%	6.44	18.01	12.04
Willow Warbler	Capture	44	4	7
(Phylloscopus trochilus)	Recapture	1	0	1
	R%	2.27	0	14.28
Red-backed Shrike	Capture	98	407	255
(Lanius collurio)	Recapture	3	28	2
	R%	3.06	6.88	0.78

A total of 450 (6.33%) Eurasian Blackcaps were recaptured at the ringing sites. Based on the result of the Goodness of Fit (GOF) test, an age-dependent model was fitted to the data which discriminated between first year (Age group 1 / A1) and consecutive year (Age group 2 / A2) captures in the case of those birds which were first captured as juveniles (1yA1 and 1yA2 groups). For adult male (group M) and female (group F) birds the standard CJS model was used.

Table 2. Cormack–Jolly–Seber models used to estimate apparent survival rate (Phi) and capture probability (p) parameters of bird species. We tested hypotheses with two age and two sex categories, with constant parameters and age dependence of juveniles. 1y = constant parameter for juveniles across study years; M = constant parameter for adult males across study years; F = constant parameter for adult females across study years. Juveniles were also parametrized as age-dependent with two categories: 1yA1 = juveniles in their first year; 1yA2 = juveniles in their second and following years. AICc = small sample sizes corrected Akaike values; Delta AICc = difference of models' AICc values in relation to the top model; AICc weights = indicating model probabilities; No. Par. = Number of parameters. ĉ = variance inflation factor. Only the top models (Delta AICc<3) are shown.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	No. Par	Deviance
Eurasian Blackcap *(Sylvia atricapilla)* - Sex and age dependent model, p=0.28, ĉ=1.44						
Phi1yA1(.)Phi1yA2(.)PhiM(.)PhiF(.)p1yA1(.)p1yA2(.)pM(.)pF(.)	3439.64	0.00	0.54	1.00	8	392.19
Phi1yA1(.)Phi1yA2F(.)PhiM(.)p1yA1(.)p1yA2(.)pM(.)pF(.)	3440.99	1.35	0.27	0.51	7	395.55
Phi1yA1(.)Phi1yA2MF(.)p1yA1(.)p1yA2(.)pM(.)pF(.)	3441.77	2.14	0.19	0.34	6	398.33
Barred Warbler *(Sylvia nisoria)* - Sex dependent model, p=0.66, ĉ=1.40						
PhiM(.)PhiF(.)pMF(.)	113.41	0.00	0.50	1.00	3	52.84
PhiMF(.)pMF(.)	114.35	0.94	0.31	0.63	2	55.83
PhiMF(.)pM(.)pF(.)	115.37	1.96	0.19	0.38	3	54.80
Lesser Whitethroat *(Sylvia curruca)* - Sex and age dependent model, p=0.13, ĉ=1.56						
Phi1y(.)PhiMF(.)p1yMF(.)	113.78	0.00	0.74	1.00	3	48.30
Phi1y(.)PhiM(.)PhiF(.)p1yMF(.)	115.85	2.07	0.26	0.35	4	48.29
Common Chiffchaff *(Phylloscopus collybita)* - Sex and age dependent model, p=0.61, ĉ=1						
Phi1yA1(.)Phi1yA2(.)PhiM(.)PhiF(.)p1yA1(.)p1yA2(.)pMF(.)	1167.98	0.00	0.39	1.00	7	204.54
Phi1yA1(.)Phi1yA2(.)PhiM(.)PhiF(.)p1yA1(.)p1yA2(.)pM(.)pF(.)	1168.62	0.64	0.29	0.73	8	203.15
Phi1yA1(.)Phi1yA2(.)PhiM(.)PhiF(.)p1yA1(.)p1yA2M(.)pF(.)	1169.74	1.76	0.16	0.41	7	206.30
Phi1yA1(.)Phi1yA2(.)PhiMF(.)p1yA1(.)p1yA2(.)pMF(.)	1169.78	1.80	0.16	0.41	6	208.35
Red-backed Shrike *(Lanius collurio)* - Sex dependent model, p=0.06, ĉ=1.82						
PhiMF(.)pM(.)pF(.)	192.14	0.00	0.73	1.00	3	52.79
PhiM(.)PhiF(.)pM(.)pF(.)	194.14	2.00	0.27	0.37	4	52.76

Common features of the most probable models (Table 2.) were that both apparent survival and capture probabilities differed between the first and consecutive captures of juvenile birds. Also, capture probabilities of adult male and female Blackcaps differed in all of the best fit models. The apparent survival rate of first-year birds was very low: only 13.6% of the birds survived and were recaptured in their second year. This means that an unknown proportion of the remaining 86.4% of birds died and an unknown proportion did not return to their natal site. The apparent survival probability of second-year birds was significantly higher: more than 48% of them survived the following year. Within the adults, the survival probabilities of the sexes were very similar: 40.3% of males and 42.0% of females. Adult and juvenile capture probabilities were similar, but the capture probability of adult males was much higher than that of adult females (Table 3).

At the ringing sites, 16 (6.02%) Barred Warblers were recaptured, but all were first ringed as adults (Table 1). Therefore, the three best-fit models (Table 2) could only compare the two sexes. The apparent survival and capture probability of males was slightly higher than that of females, but the difference was not significant (Table 3).

With respect to Lesser Whitethroats, 47 (9.55%) individuals were recaptured at the ringing sites. The Goodness of Fit test suggested that the standard CJS model fits well with the data. According to the highest probability models (Table 2), the survival and capture probabilities of age and sex groups were very similar, although the first-year bird survival probability was slightly lower than that of adults (Table 3).

A total of 142 (7.38%) Common Chiffchaffs were recaptured at the ringing sites. GOF test showed that for juvenile birds, an age-dependent model was appropriate. In the most probable models, both apparent survival and capture probabilities differed between the first and consecutive captures of juvenile birds (Table 2). The apparent survival rate of the first-year birds was very small: only 15.1% of the birds living to their second year. The survival probability of second-year birds was significantly higher than that of the first-year ones: more than 60% survived to the following year. There was no significant difference between the capture probability of adults and juveniles, nor between the survival probability of adult males and females (Table 3).

The number of recaptured Red-backed Shrikes was 33 (4.26%). Due to the low sample size, the two highest probability standard CJS models (Table 2) gave a significant result only for sex dependence. The apparent survival probability of adult males and females did not differ significantly, and about 50% of both sexes survived and were recaptured in the following year. However, the capture probability of adult males was significantly higher than that of adult females (Table 3).

Discussion

Apparent survival rate is one of the most important factors affecting the temporal changes of small passerine species (Peach & Baillie 2004). Salewski et al. (2013) showed that weather, experienced during the breeding season, did not affect the apparent survival of some frequent European passerines. Maness and Anderson (2013) reviewed the literature on the predictors of juvenile survival in birds. Factors other

Table 3. Summary of average values for the different parameters (Phi = apparent survival rate, p = capture probability, 1y = constant parameter for juveniles across study years, M = constant parameter for adult males across study years, F = constant parameter for adult females across study years, 1yA1 = juveniles in their first year, 1yA2 = juveniles in their second and following years) for bird species, according to the best models from CJS model. SE = unconditional standard error, CI = confidence interval, MV = percentage of variation attributable to model variation. Significant differences in bold.

Parameters	Weighted average	SE	95% CI		MV%
Eurasian Blackcap *(Sylvia atricapilla)*					
Phi1yA1	0.136	0.020	**0.100**	**0.181**	10.9
Phi1yA2	0.488	0.050	**0.392**	**0.548**	48.2
PhiM	0.403	0.030	0.346	0.464	18.27
PhiF	0.420	0.055	0.317	0.531	43.66
p1yA1	0.279	0.047	0.196	0.379	8.13
p1yA2	0.354	0.055	0.256	0.467	7.1
pM	0.211	0.027	**0.163**	**0.269**	11.05
pF	0.073	0.018	**0.044**	**0.118**	29.26
Barred Warbler *(Sylvia nisoria)*					
PhiM	0.382	0.112	0.196	0.611	6.45
PhiF	0.280	0.129	0.100	0.576	33.94
pM	0.183	0.091	0.064	0.424	2.26
pF	0.166	0.090	0.053	0.416	11.46
Lesser Whitethroat *(Sylvia curruca)*					
Phi1y	0.125	0.076	0.036	0.358	0
PhiM	0.354	0.113	0.172	0.591	1.5
PhiF	0.352	0.108	0.177	0.578	0.32
p1y	0.324	0.145	0.116	0.636	0
pM	0.324	0.145	0.116	0.636	0
pF	0.324	0.143	0.116	0.636	0
Common Chiffchaff *(Phylloscopus collybita)*					
Phi1yA1	0.151	0.035	**0.094**	**0.234**	4.4
Phi1yA2	0.635	0.073	**0.484**	**0.763**	5.53
PhiM	0.360	0.071	0.235	0.508	30.53
PhiF	0.202	0.083	0.084	0.411	47.69
p1yA1	0.355	0.087	0.208	0.537	3.81
p1yA2	0.130	0.045	0.065	0.245	22.32
pM	0.264	0.080	0.139	0.445	29.42
pF	0.400	0.221	0.100	0.802	48.24
Red-backed Shrike *(Lanius collurio)*					
PhiM	0.485	0.087	0.323	0.651	0.04
PhiF	0.501	0.204	0.169	0.832	37.75
pM	0.098	0.037	**0.045**	**0.200**	0.03
pF	0.009	0.010	**-0.010**	**0.029**	2.32

than body mass, 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. According to our results, there were no significant differences in survival probability between sexes, although the capture rates of three species (Eurasian Blackcap, Barred Warbler, Common Chiffchaff) were male-biased in Hungary. The female-biased mortality may be the most important explanation for male-biased adult sex ratios in birds (Breitwisch 1989, Liker & Székely 2005, Székely et al. 2014, Lovász et al. 2018), but other factors such as home range or territorial behavior might also play an important role (Amrhein et al. 2012). The males may be captured more easily during overt territory defense behaviour, while females are less active. In case of species laying multiple clutches, territory defense behaviour by males is continued for longer time periods into the breeding season compared with single-brooded species (Amrhein et al. 2008). Many studies give general support to the early breeding hypothesis for juvenile bird survival. Early breeding means that offspring fledge earlier during seasons of high food abundance. These juveniles which fledge earlier in the breeding season may, therefore, have more time to perfect their foraging skills and gain fat reserves for migration and winter than juveniles which fledge late during breeding season, increasing their survival probability (Lack 1954, Ringsby et al. 1998, Yackel et al. 2006). Hatching order has also been found to influence nestling survival in passerines (Gibbons 1987, Magrath 1989, Forbes et al. 2002) because late-hatched fledglings may not be able to obtain adequate food as a result of competition with larger and older chicks. The growth rate of chicks is expected to influence juvenile survival if fast growth indicates low stress during the breeding period. Offspring that do not receive adequate nutrition during development are expected to grow more slowly than consistently well-fed offspring of the same population (Gebhardt-Henrich & Richner 1998).

Taking a look at our best CJS model, apparent survival rates of first-year Eurasian Blackcap and Common Chiffchaff were found to be significantly lower than for adults. These age-related differences in survival are found in most bird species, mostly because older birds have more experience (Martin 1995, Siriwardena et al. 1998) or hold the best territories. Within the juvenile cohort, low-quality breeders usually occur at a higher rate (Curio 1983, Forslund & Pärt 1995).

The average annual adult survival rate for Eurasian Blackcaps from CES studies in Great Britain and Ireland was similar (44.3%, Peach & Baillie 2004) to Hungarian rates. The average annual survival rate for adult Lesser Whitethroats, estimated from between-year recaptures, was 43.5% in England (Boddy 1994), higher than our result (mean of male and female 35.3%). Returns of juvenile Lesser Whitethroat in subsequent years was very low (0.8% and 3.5%) in England (Norman 1992, Boddy 1994): the latter of these results was very similar to our result (3.56%). Several European studies (Tiainen 1983, Pratt & Peach 1991, Baillie & McCulloch 1993, Peach 1993, Lawn 1994) suggested that an average annual survival rate of more than 40% was realistic for adult Willow Warblers. In our study, the average annual survival rate of male and female Common Chiffchaff was 28.1%, which can also be a realistic proportion. According to the French CES program, the annual survival rate of Eurasian Blackcap and Common Chiffchaff were also similar to Hungarian birds, but statistically significant temporal variation in survival was detected in the French breeding populations (Julliard 2004). According to a Swiss study (Schaub & Royle 2014), the apparent survival of male Red-backed Shrikes (c. 50%) estimated using the CJS model was higher than that for females (c. 40%), although the spatial CJS model suggested that both sexes had similar survival probabilities (c. 60%). In Hungary, both sexes had similar survival probabilities (c. 50%).

Unlike other results (Burton & DeSante 2004, Nur et al. 2004), we observed no significant differences between age classes in capture probability. The most important determinant of capture probability for adults and juveniles was the distance from the net (Ballard et al. 2004). Other factors had no important effect on capture probability of adults, except that those birds that bred earliest were less likely to be caught (Nur et al. 2004). Differences in capture probability between adults and young are most probably related to the greater mobility of young individuals observed in the breeding period (Burton & DeSante 2004). The Eurasian Blackcap and Red-backed Shrike males had significantly higher capture probabilities than females in Hungary. We speculate that differences in territorial behaviour and breeding strategy of the sexes may be responsible (Amrhein et al. 2012), but this needs to be examined directly.

In conclusion, there is evidence that between-year changes in captures at constant effort sites differ between habitats and regions in Great Britain and Ireland for several species, for example, Whitethroats (Peach et al. 1996), so we recommend continuing Hungarian research in this direction. As population dynamics, productivity and sex ratio of birds change over time, particularly in association with ecological factors such as climate change, air, water, light, and other pollutants, continued bird ringing is important even for common species.

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