

SMALL POND, BIG INSIGHT: ASSESSMENT OF RECAPTURE PROBABILITIES AND MIGRATION DYNAMICS OF PASSERINES IN THE NORTHERN ADRIATIC KARST LANDSCAPE

Mala lokva, veliki uvidi: procjena vjerojatnosti ponovnog hvatanja i dinamike selidbe pjevnica u krškom području sjevernog Jadrana

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ABSTRACT

Stopover sites are important for migratory birds to rest and restore their fat reserves. In this study, we analysed the autumn stopover period and recapture probability of the most commonly captured bird species that migrate through and reside around the Rovozna pond in Učka Nature Park. Between 2015 and 2024, 12,943 individuals of the target species were ringed at the ringing camp in Učka, Croatia. The most frequently captured species were the European Robin *Erithacus rubecula*, Eurasian Blackcap *Sylvia atricapilla*, and Eurasian Blackbird *Turdus merula*. Analyses also included Common Chiffchaff *Phylloscopus collybita*, early long-distance migrants, and locally breeding tit species. Robins, Blackcaps, and Chiffchaffs captured earlier in the season exhibited prolonged stopover durations, indicating that the site could be an important stopover or possibly an early wintering area for these species. However, these species also showed low apparent recapture probabilities in the years following ringing. Early long-distance migrants were caught in high numbers until the beginning of September, exhibited higher fat scores, and remained in the area for shorter periods. In contrast, resident species remained in the area throughout the entire period and showed the highest recapture probabilities among all species analysed.

Keywords: bird ringing, fat score, capture-recapture, stopover duration

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INTRODUCTION

The accumulation and replenishment of fat stores prior to migration are critical for the successful crossing of major ecological barriers, such as oceans and deserts, as migration imposes extremely high energy demands (BAIRLEIN & SCHAUB 2009). During migration, some birds spend most of their time at stopover sites (HEDENSTRÖM & ALERSTAM 1997). Small passerines rely primarily on fat as their main energy source during migration (BLEM 1980), and stopover sites provide essential opportunities for rest and refuelling (BAIRLEIN & SCHAUB 2009).

Several factors can influence the quality and suitability of stopover sites, including geographical location (FITZGERALD & TAYLOR 2008, RUBOLINI *et al.* 2002), habitat type (KITTOROV *et al.* 2008), food availability (DIERSCHKE 2003), competition (DIERSCHKE *et al.* 2005), and predation risk (DIERSCHKE 2003, SCHMALJOHANN & DIERSCHKE 2005). The northern Mediterranean region hosts several important stopover sites for European migratory bird populations (BIBBY & GREEN 1983). Small wetlands and water bodies in the Mediterranean are also critical stopover habitats and biodiversity hotspots, underscoring their importance for conservation (HAIG *et al.* 1998, SEBASTIÁN-GONZÁLEZ & GREEN 2014, SEMLITSCH & BODIE 1998).

Understanding how different species use stopover sites is essential for informing conservation efforts and identifying key habitats for their protection. One approach to studying stopover use involves marking individual birds and applying capture–recapture or capture–resighting methods (BAIRLEIN & SCHAUB 2009, HOCHACHKA & FIEDLER 2008). Through capture–recapture analysis of variation in the numbers of ringed and recaptured individuals, insights can be gained into survival rates and migratory behaviour (FAUSTINO *et al.* 2004, SCHAUB *et al.* 2001).

To make such comparisons meaningful, ringing stations must apply a constant-effort methodology that involves using the same trapping devices for the same duration each day and across a consistent number of days every year (HOCHACHKA & FIEDLER 2008). Many analyses of constant-effort ringing data assume that capture probability is directly proportional to trapping effort and that this relationship remains stable over time without introducing systematic bias in the apparent bird numbers (HOCHACHKA & FIEDLER 2008).

In this study, we analysed the stopover period of the most numerous bird species that migrated through and resided in the area of the Učka Nature Park around the Rovozna pond. We analysed how long our target species remained in our research area and their fat reserves. The length of stay and fat reserves could indicate the importance of our research site for migrating birds. We also examined the recapture probabilities of ringed birds to determine the probability of re-encountering individuals and how often do individuals use our research area in the following years.

MATERIALS AND METHODS

Nature Park Učka is an important area for birds in Croatia (RADOVIĆ *et al.* 2005). It encompasses the coastal Dinaric mountain range, which separates the Istrian Peninsula from the Gulf of Kvarner in the northern Adriatic region. The area is characterised by a mountainous karst landscape with prominent ridges, parallel terraces, and steep vertical cliffs. The highest zones consist of bare peaks and cliffs that transition into forested slopes and open pastures. The eastern and coastal sides of the park are dominated by forests of Hornbeam *Carpinus* spp., Downy Oak *Quercus pubescens*, and European Chestnut *Castanea sativa*, whereas Common Beech *Fagus sylvatica* forests prevail at elevations above 700 m above sea level. Located within the park, Rovozna Pond is among the largest water bodies in the area, with an area of approximately 0.15 ha (JAVNA USTANOVA PARK PRIRODE UČKA 2023).

Rovozna is the largest permanent pond within the Nature Park, which serves as a reliable source of water for animals that live nearby and for those that pass through the area during migration. Around the camp, there is a forest of Black Pine *Pinus nigra* with European Hop-hornbeam *Ostrya carpinifolia*, while around the pond there is dense vegetation composed of Common Dogwood *Cornus sanguinea*, European Cornel *Cornus mas*, and Blackthorn *Prunus spinosa*.

The ringing camp is located next to Rovozna Pond in the southern part of the Nature Park Učka (Fig. 1). Ringing at this location has been conducted since 2006, but constant efforts have been made since 2015. Constant effort included the same number and type of nets set up in the same positions, same net checking time, and time period in which the camp was active, with no tape lure used. Fourteen vertical ornithological nets (16×16 mm mesh, 12×2.7 m, 5 shelves) were set up throughout the forest and on one side of the Rovozna pond. Nets were raised half an hour before sunrise, closed at 11h, and opened at 16h until half an hour after sunset. The camp started between mid-August (15th–20th) and lasted until the first week of October (3rd–9th). From 2021 to 2024, the ringing camp was shortened and lasted until September 11th–16th. The fat score of all caught individuals was assessed as described by BUSSE (2015). In our analysis, we used the ringing data collected between 2015 and 2024.

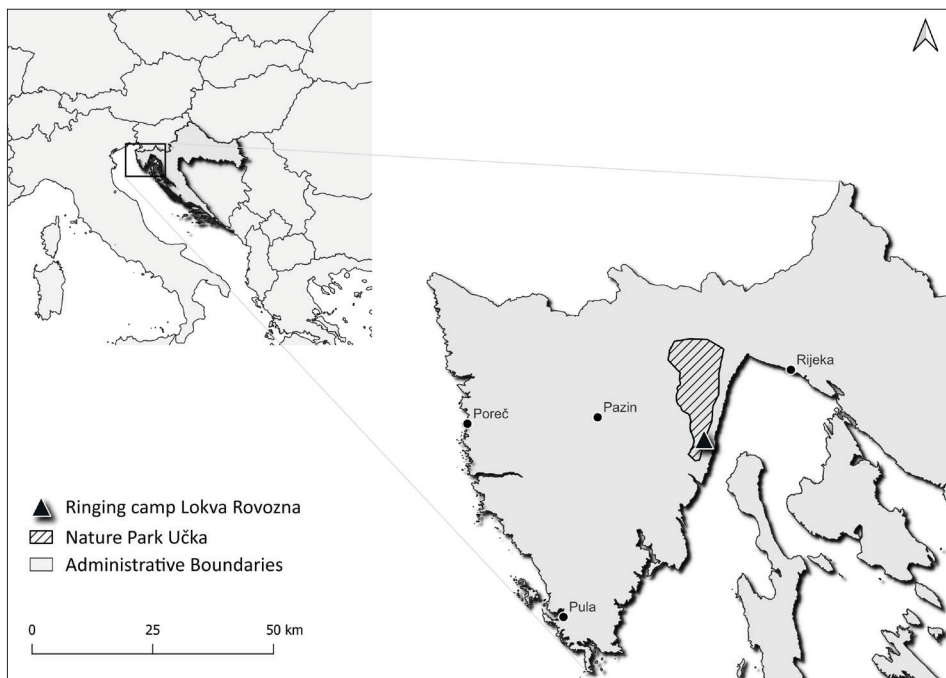


Figure 1. Location of the ringing camp Učka

Slika 1. Lokacija prstenovačkog kampa Učka

We analysed stopover patterns based on the duration of individual stays within the area and recapture probabilities of the most numerous species caught. We analysed the stopover patterns of partly migratory species: European Robins *Erithacus rubecula*, Eurasian Blackcaps *Sylvia atricapilla* and Common Chiffchaffs *Phylloscopus collybita*, early long-distance migrants (later referred as early migrants) that we grouped (Icterine Warbler *Hippolais icterina*, Garden Warbler *Sylvia borin*, Common Redstart *Phoenicurus phoenicurus*, European Pied Flycatcher *Ficedula hypoleuca*, Wood Warbler *Phylloscopus sibilatrix*, Spotted Flycatcher *Muscicapa striata*, and Common Whitethroat *Curruc communis*) and mostly resident species: Eurasian Blackbirds *Turdus merula* and tits (Great Tit *Parus major*, Blue Tit *Cyanistes caeruleus*, Coal Tit *Parus ater*, Crested Tit *Lophophanes cristatus*, Marsh Tit *Poecile palustris* and Long-tailed Tit *Aegithalos caudatus*) that had 50 or more ringed individuals. Some ringed individuals of Robins, Blackcaps, and Chiffchaffs likely remained in the area during winter, although the ringing camp was concluded in October. Stopover patterns were graphically presented using the R package ringR for previously described groups (HARNOS *et al.* 2015). Fat scores for each species or group are shown graphically. The length of stay and fat score

differences were tested using the Kruskal-Wallis test, and for post-hoc we used Dunn's test to test the difference in length of stay and fat scores. We excluded all birds that were not recaptured from the analyses.

We analysed the recapture probability of Robins, Blackcaps, and Blackbirds separately, and pooled the tits. Results of Robins and Blackcaps are shown together because the individual analyses were almost identical, and the individual species are shown in Supplementary fig. 1 and 2. Both species were caught in high numbers, with a small number of recaptures between years. Tits were analysed together because they were mostly residents and were individually captured in small numbers. The recapture probability for Chiffchaffs was not analysed because of the low number of recaptured birds in the years following ringing and for early migrants because of the lack of recaptures in the years following ringing. Analyses were performed using BaSTA: Age-Specific Bayesian Survival Trajectory Analysis from Incomplete Census or Capture-Recapture/Recovery Data (COLCHERO *et al.* 2012). Analyses were performed for all individuals that were recaptured at least once in the same year and for those that were recaptured in subsequent years.

RESULTS

Between 2015 and 2024, we ringed 14,768 individuals and had 2,566 recaptures of 65 species, with 12,943 individuals of our target species (Table 1). A total of 1669 individuals were recaptured, of which 686 were recaptured in different months after the first capture, and 196 were recaptured at least one year later.

Table 1. Number of ringed individuals per species and number of recaptured individuals caught at the ringing camp Učka.**Tablica 1.** Broj prstenovanih jedinki po vrsti te broj ponovno uhvaćenih jedinka, uhvaćenih na prstenovačkom kampu Učka.

Species	n of ringed individuals	n of recaptured individuals	n of individuals recaptured in following month	n of individuals recaptured in following years
<i>Erithacus rubecula</i>	5420	734	311	66
<i>Sylvia atricapilla</i>	2469	179	88	25
<i>Turdus merula</i>	922	82	76	36
<i>Phylloscopus collybita</i>	506	41	25	7
Early long-distance migrants	2268	151	31	0
<i>Sylvia borin</i>	704	48	8	0
<i>Phylloscopus sibilatrix</i>	571	57	14	0
<i>Ficedula hypoleuca</i>	474	10	0	0
<i>Hippolais icterina</i>	280	28	8	0
<i>Muscicapa striata</i>	89	2	0	0
<i>Phoenicurus phoenicurus</i>	82	1	0	0
<i>Sylvia communis</i>	68	5	1	0
Tits	1358	218	155	62
<i>Aegithalos caudatus</i>	371	77	56	22
<i>Cyanistes caeruleus</i>	368	52	38	18
<i>Parus major</i>	258	43	31	11
<i>Periparus ater</i>	189	14	7	2
<i>Poecile palustris</i>	95	25	18	7
<i>Lophophanes cristatus</i>	77	7	5	2

The most abundant species, Robins and Blackcaps, showed similar stopover patterns (Fig. 2). However, more Robins stayed in the area during autumn migration, but on average for a shorter period than Blackcaps, while some individuals of Robins stayed longer (Table 2, $p > 0.05$). Most Robins had a fat score of 0 (40.6%), and 46% of individuals had a fat score of 2 or higher (Supplementary fig. 3). Blackcaps had fat scores similar to those of Robins ($p = 1$), with 39.4% having a score of 0 and 44.2% having a score of 2 or higher (Supplementary fig. 4). However, individuals caught until the beginning of September had a predominant fat score of 0, while after, there was an almost equal part score of 0 and 2 (Supplementary fig. 5 and 6), most similar to Chiffchafs caught later in the season ($p = 1$).

Table 2. The length of stay within the ringing camp Učka within the same season. The standard deviation is shown in parentheses.

Tablica 2. Duljina ostanka na prstenovačkom kampu Učka unutar iste sezone. Standardna devijacija prikazana je unutar zagrada.

Species	Average length of stay	Median	Max n of days	n
<i>Erithacus rubecula</i>	8.49 (9.47)	5	50	734
<i>Sylvia atricapilla</i>	11.21 (11.98)	5	48	179
<i>Turdus merula</i>	16.88 (11.65)	15	48	82
<i>Phylloscopus collybita</i>	13.90 (10.74)	11	38	41
Early long-distance migrants	5.28 (4.72)	4	22	151
<i>Sylvia borin</i>	4.40 (3.15)	4	15	48
<i>Phylloscopus sibilatrix</i>	5.86 (5.91)	3	22	57
<i>Ficedula hypoleuca</i>	1.90 (1.2)	1.5	4	10
<i>Hippolais icterina</i>	6.18 (4.74)	5.5	21	28
<i>Muscicapa striata</i>	7.50 (3.54)	7.5	10	2
<i>Phoenicurus phoenicurus</i>	8.00 (0)	8	8	1
<i>Sylvia communis</i>	7.60 (3.78)	9	12	5
Tits	17.26 (12.63)	16	50	218
<i>Aegithalos caudatus</i>	19.47 (12.8)	20	49	77
<i>Cyanistes caeruleus</i>	15.23 (12.33)	14	44	52
<i>Parus major</i>	18.74 (13.35)	16	50	43
<i>Periparus ater</i>	11.86 (12.35)	9	40	14
<i>Poecile palustris</i>	15.24 (11.25)	11	43	25
<i>Lophophanes cristatus</i>	17.00 (10.98)	15	38	7

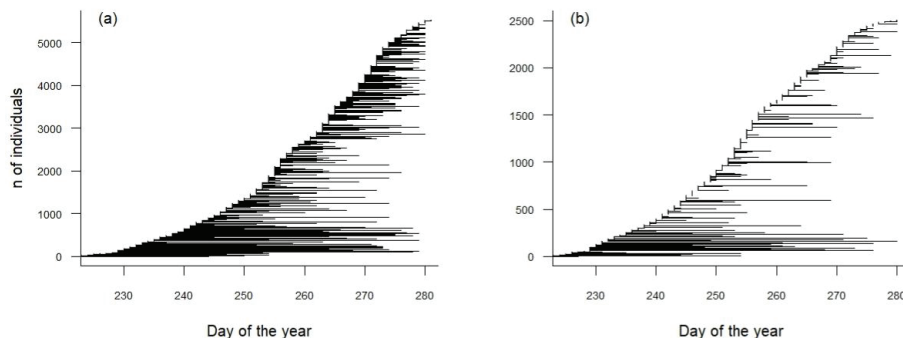


Figure 2. Cumulative distribution of the dates of the first capture depicted together with the last recapture dates of individual Robins (a) and Blackcaps (b) caught in the ringing camp Učka. The steepness of the curve indicates an increase in the number of individuals captured during that period.

Slika 2. Kumulativna distribucija datuma prvog hvatanja prikazana zajedno s datumom posljednjeg hvatanja jedinki crvendača (a) i crnoglavih grmuša (b) na prstenovačkom kampu Učka. Strmina krivulje ukazuje na porast broja jedinki u tom razdoblju.

Early migrants were ringed in high numbers at the beginning of the autumn migration, and their numbers declined in September. Recaptured individuals mostly spent only a brief time within the area, and only a small number of individuals were recaptured in the following month (Fig. 3, Table 2). Among early migrants, 27.2% had a fat score of 0, and 56.5% had a fat score of 2 or higher (Supplementary fig. 7), which differed from all other groups, except Chiffchaffs caught after mid-September ($p < 0.05$). Early migrants stayed significantly shorter than the other groups ($p < 0.05$).

Chiffchaffs were regularly caught during the ringing period. Chiffchaffs caught until early September were recaptured almost until the end of the camp in the first week of October, whereas only one individual ringed after the beginning of September was recaptured in the same year (Fig. 3, Table 2). The fat scores of individuals caught from the beginning of the camp until mid-September (17th of September) were predominantly 0 (78.4%), similar to those of resident species, Blackbirds, and tits ($p > 0.9$). Individuals, including recaptures caught later, predominantly had a fat score of 2 (41.5%; Supplementary fig. 8 and 9). Chiffchaffs showed a stay length similar to that of Blackcaps, Blackbirds, and tits ($p > 0.05$) and significantly different from other groups.

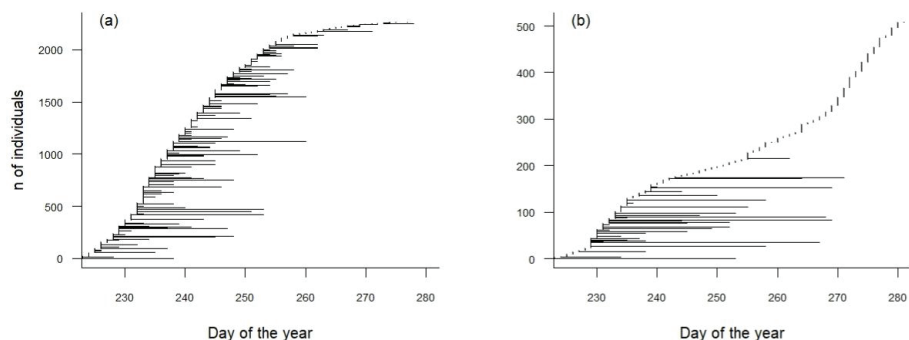


Figure 3. Cumulative distribution of the dates of the first capture depicted together with the last recapture dates of individual early long-distance migrants (a) and Chiffchaffs (b) caught in the ringing camp Učka. The steepness of the curve indicates an increase in the number of individuals captured during that period.

Slika 3. Kumulativna distribucija datuma prvog hvatanja prikazana zajedno s datumom posljednjeg hvatanja jedinki ranih selica (a) i zviška (b) uhvaćenih na prstenovačkom kampu Učka. Strmina krivulje ukazuje na porast broja jedinki u tom razdoblju.

The resident species were recaptured throughout the entire period of the camp and had similar lengths of stay (Fig. 4, Table 2, $p > 0.05$). They were caught in uniform numbers during the camp. Blackbirds captured from mid-September onwards were rarely recaptured compared to individuals captured earlier. The fat scores of both Blackbirds and tits were predominantly 0, at 91.7% and 68.9%, respectively (Supplementary fig. 10 and 11).

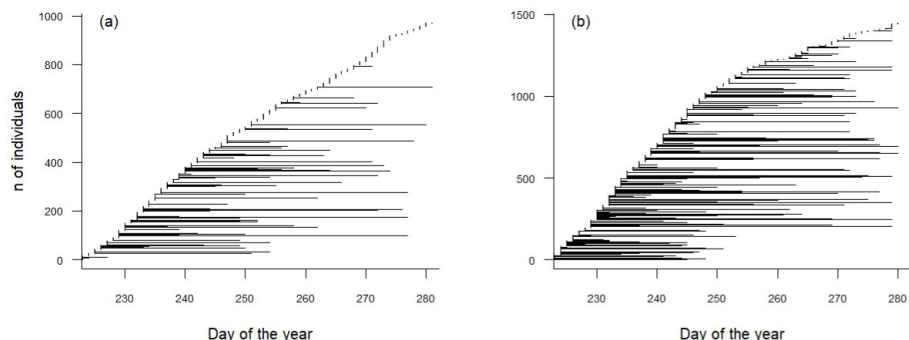


Figure 4. Cumulative distribution of the dates of the first capture depicted together with the last recapture dates of individual Blackbirds (a) and tits (b) caught in the ringing camp Učka. The steepness of the curve indicates an increase in the number of individuals captured during that period.

Slika 4. Kumulativna distribucija datuma prvog hvatanja prikazana zajedno s datumom posljednjeg hvatanja jedinki koseva (a) i sjenica (b) uhvaćenih na prstenovačkom kampu Učka. Strmina krivulje ukazuje na porast broja jedinki u tom razdoblju.

The recapture probability of all ringed individuals of Robins and Blackcaps in the following year was almost 0% (Fig. 5), compared to the resident species Blackbird and tits, for which all individuals had some probability of being recaptured again (Fig. 6 and 7). Individuals that were recaptured in subsequent years across all species had a higher likelihood of being recaptured again in later years than the overall recapture probability for all individuals (Fig. 5, 6, and 7).

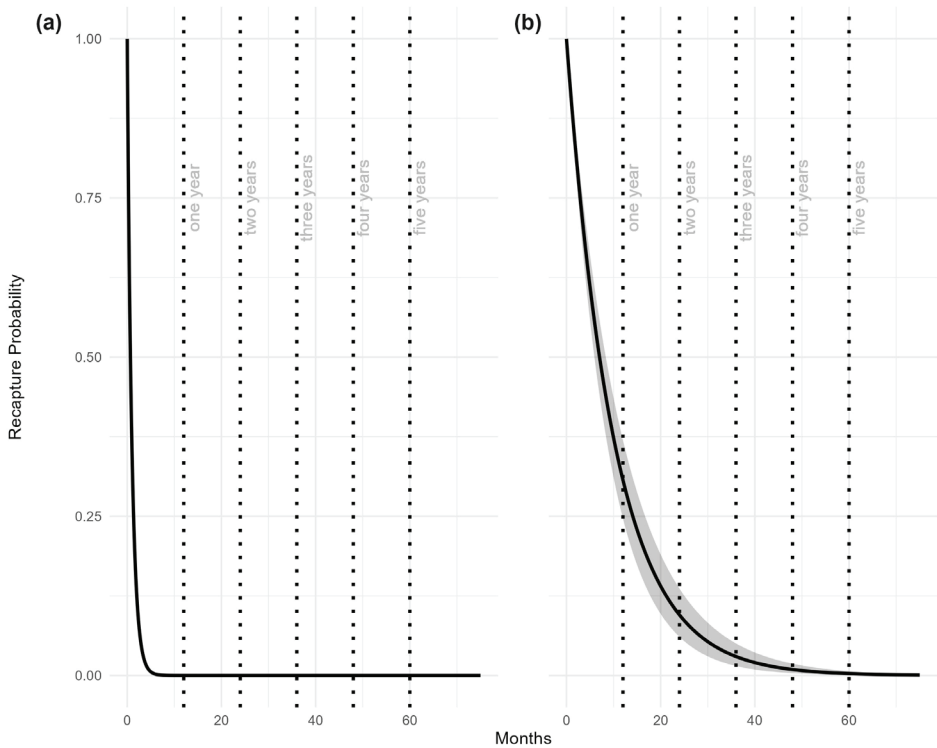


Figure 5. Recapture probability of Robins and Blackcaps; all captured individuals (a) and individuals that were recaptured in one of the following years (b)

Slika 5. Vjerojatnost preživljavanja crvendaća i crnokapih grmuša; sve uhvaćene jedinke (a) i jedinke koje su bile ponovno uhvaćene u jednoj od narednih godina (b)

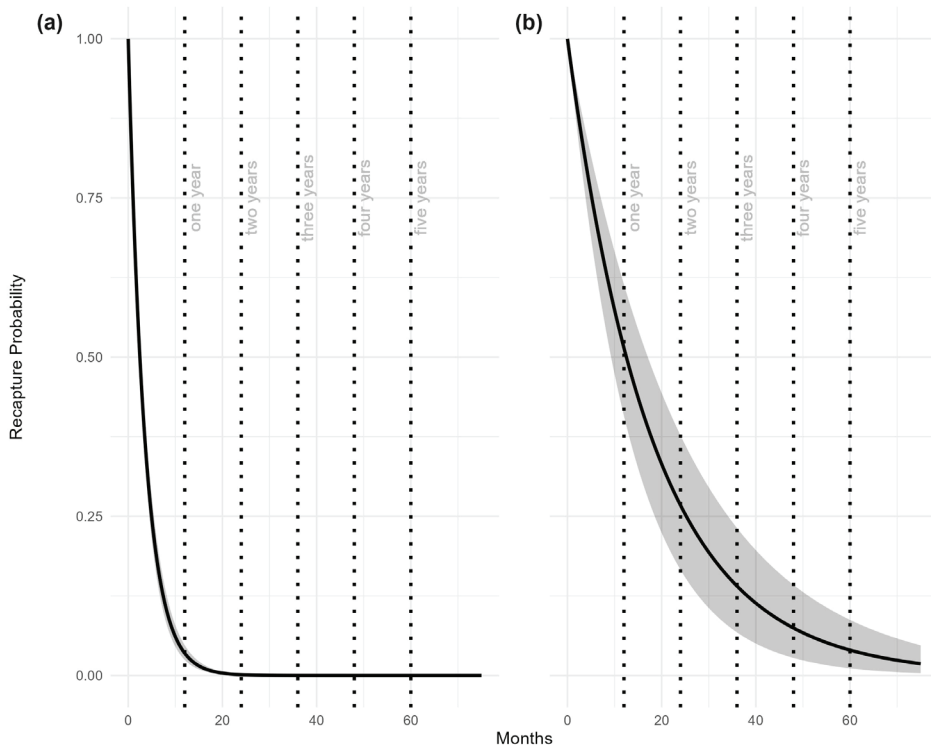


Figure 6. Recapture probability of Blackbirds; all captured individuals (a) and individuals that were recaptured in one of the following years (b)

Slika 6. Vjerojatnost preživljavanja koseva; sve uhvaćene jedinke (a) i jedinke koje su bile ponovno uhvaćene u jednoj od narednih godina (b)

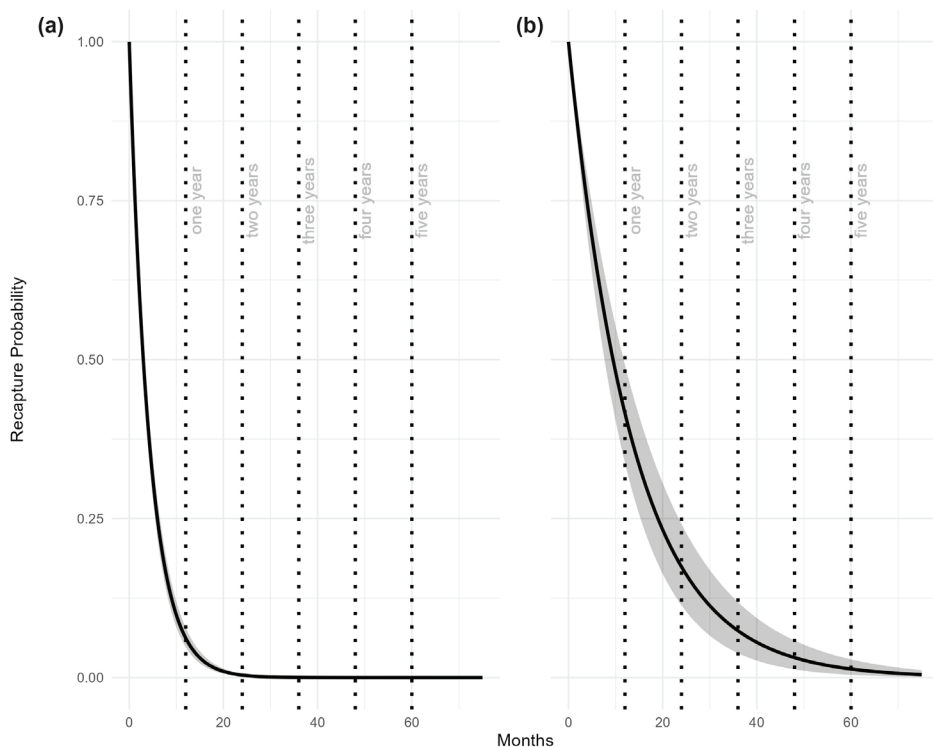


Figure 7. Recapture probability of tits; all captured individuals (a) and individuals that were recaptured in one of the following years (b)

Slika 7. Vjerojatnost preživljavanja sjenica; sve uhvaćene jedinke (a) i jedinke koje su bile ponovno uhvaćene u jednoj od narednih godina (b)

DISCUSSION

Pond Rovozna provides a place of rest and refuelling for birds migrating through the northern Adriatic area. However, early migrants appear to remain in the area for a shorter time and do not use it as a stopover site as extensively. In contrast, species such as the Robin, Blackcap, and Chiffchaff frequently use this area as an important stopover site or even as a breeding site. Some individuals of these species remained in the study area throughout the entire ringing period. As expected, the resident species remained in the area throughout the study and were frequently recaptured.

The differences between these groups may be explained by their migratory strategies, either “energy minimization” or “time minimisation” (ALERSTAM & LINDSTRÖM 1990, HEDENSTRÖM & ALERSTAM 1997, ZHAO *et al.* 2017). Robins, Blackcaps, and Chiffchaffs may use an energy minimisation strategy, refuelling slowly

and departing before reaching their maximum fuel load. Birds using this strategy make multiple stopovers during migration, accounting for up to 90% of the total duration of their journeys (CHERNETSOV *et al.* 2004, WEBER *et al.* 1999). These species typically winter in the Mediterranean region (CRAMP & SIMMONS 2006), and some individuals may even winter within or near our study area.

Among the ringed species, Robins were the most abundant. Robins tend to migrate in short flights and use multiple stopover sites (NOWAKOWSKI *et al.* 2005, POLAK & SZEWCZYK 2007). Some individuals remained in the area throughout the ringing season, whereas others remained only briefly or were not recaptured. Robins defend small territories during stopovers, and individuals unable to establish a territory quickly may leave the site shortly after arrival (SCHAUB *et al.* 2004). This territorial behaviour could explain both the low recapture rate and the prolonged presence of certain individuals. Our nets were set up around the pond in areas with berry-bearing trees and bushes, which are key feeding sites for Robins during autumn migration (BOZÓ & BORBÁTH 2020, COLLAR 2020). Territory-holding individuals may defend these food resources. The generally low fat reserves observed in ringed Robins support the time minimisation strategy typical of the species (BULYUK & TSVEY 2006).

Blackcaps and Chiffchaffs captured in September had higher fat reserves than those captured in August. Birds that migrate later tend to accumulate fat more rapidly and remain at stopover sites for shorter periods (KĘDZIOR 2002, POLAK & SZEWCZYK 2007). Robins, Blackcaps, and Chiffchaffs captured early in the season and present for the entire study period with low fat reserves may have been local breeders or early migrants. Early migrants may benefit from arriving first by securing better wintering sites (TELLERÍA & Pérez-Tris 2004), and some individuals may have overwintered in the area. However, as the ringing camp ended in October, this could not be confirmed.

Early migrants adopted a time minimisation strategy, accumulating significant fat reserves to undertake long migratory flights (BAIRLEIN & SCHAUB 2009). These birds must cross large ecological barriers, such as the Mediterranean Sea and the Sahara Desert, in continuous flights lasting 30–40 h (MOREAU 1961). The small number of individuals from these species that were caught, combined with their high-fat reserves and brief stay in the area, suggests that the site is not an important stopover site for refuelling but for rest. If there do not feed in the area, they could use the surrounding vegetation for shelter, or the microclimate of the only waterbody in the area provides them with a better environment. Some species, such as Garden Warblers and Wood Warblers, begin their migration before the start of the ringing camp in early August; therefore, their actual numbers could be higher, and we have no insight into how long they remain in the study area before the start of the camp. In addition, the surrounding vegetation is taller than our nets, meaning that species that feed and fly lower, such as Robins and

Whitethroats, have a higher likelihood of being caught than canopy-dwelling species such as Wood Warblers and Pied Flycatchers. Long-distance migrants must reduce their digestive systems prior to migration and rebuild them before they can resume feeding, a process that takes time (WARNOCK 2010). For example, Garden Warblers may require two to three days for their digestive system to become fully functional again (BIEBACH 1998). This suggests that early migrants with fat reserves observed in the study area may not have fed in the area. These species typically remain at staging sites for extended periods, often several weeks, where they can efficiently refuel their energy reserves (WARNOCK 2010).

As expected, resident species remained in the area throughout the study period and were recaptured more frequently than migratory species, even across years. Birds that remain at the same location for longer periods are more likely to be recaptured when daily trapping is consistent (HOCHACHKA & FIEDLER 2008). Blackbirds captured from mid-September onwards were rarely recaptured, suggesting that they might have been migratory or partially so. Notably, one individual ringed on October 10th was found dead in Italy 16 days after being ringed. It is possible that these individuals shifted to different locations in subsequent years and, given the small size of our study site, they were not recaptured.

Resident species also exhibited the highest recapture probabilities among all the studied species. Many were recaptured in subsequent months and years, unlike early migrants, for whom no long-term recaptures were recorded because of limited data. As no early migrants were recaptured, it is unclear whether they avoided the area in subsequent years or returned in small numbers and evaded the nets. Robins and Blackcaps were recaptured in the months following their initial capture, but only a few individuals were recaptured in later years. Bird trappability and stopover duration can vary due to multiple factors that may have influenced the results of this study (HOCHACHKA & FIEDLER 2008). Capture probability is often the highest at the first encounter, as birds may learn to avoid nets over time. Additionally, adult birds are known to migrate faster and remain at stopover sites for shorter periods than juveniles (FRANSSON 1995, POLAK & SZEWczyk 2007). Thus, returning individuals may have been missed if their stay in the area was short. Other possible explanations include the high mortality rates among young birds in their first year (HAUKIOJA 1969) and the possibility that some birds migrate along a broader front, bypassing the pond.

This analysis highlights the importance of the Rovozna pond and its surrounding area for a number of bird species and provides valuable input for future conservation and research at the site.

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Supplementary Information

The online version contains supplementary material available at <https://hrcak.srce.hr/supplement/788>

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SAŽETAK

Odmorišta su važna mjesta za odmor i za obnavljanje naslaga masti kod ptica selica. U ovom istraživanju analizirali smo razdoblje zadržavanja i vjerojatnost preživljavanja najčešće hvatanih vrsta ptica koje se sele kroz i obitavaju na području lokve Rovožne, Park prirode Učka. U razdoblju od 2015. do 2024. godine na prstenovačkom kampu Učka, Hrvatska, ukupno je prstenovano 12.943 jedinki ciljnih vrsta. Najčešće hvatane vrste bile su crvendać *Erithacus rubecula*, crnokapa grmuša *Sylvia atricapilla* i kos *Turdus merula*. Analize su dodatno uključivale zvištka *Phylloscopus collybita*, kao i rane selice koje sele na velike udaljenosti te lokalno gnijezdeće vrste sjenica grupirane zajedno. Crvendaći, crnokape grmuše i zvištki dulje su se zadržavali na istraživanom području, što ukazuje na to da bi lokacija mogla biti važno odmorište tijekom selidbe ovih vrsta ili potencijalno ranije zauzeta lokacija za zimovanje. Međutim, te su vrste pokazale nisku prividnu stopu preživljavanja u godinama nakon prstenovanja. Rane jesenske selice koje sele na velike udaljenosti hvatane su u većem broju početkom sezone prstenovanja, no kod njih je bilježena veća razina masti te su se kraće zadržavale na području istraživanja. Očekivano, lokalne gnijezdarice su se zadržavale na području tijekom cijelog razdoblja te je kod njih zabilježena najveća vjerojatnost preživljavanja među svim analiziranim vrstama.