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ESTIMATING APPARENT SURVIVAL IN BLACK-HEADED GULLS *Chroicocephalus ridibundus*: EFFECTS OF SEX, AGE, AND OBSERVER DISTRIBUTION BIAS

Procjena preživljavanja riječnih galeba Chroicocephalus ridibundus: utjecaj spola, dobi i neravnomjerne raspodjele opažača

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ABSTRACT

The Black-headed Gull *Chroicocephalus ridibundus* is one of the most widespread gull species in Europe and has been the focus of extensive ringing programs for decades. Black-headed Gulls provide an excellent model system for studying survival patterns over large spatial and temporal scales because large numbers of colour-ringed individuals are regularly reported throughout Europe. We ringed 12,721 Black-headed Gulls in Zagreb, Croatia landfill between 2011 and 2025, and received 31,792 recoveries. We estimated apparent survival of ringed individuals using Cormack–Jolly–Seber and Bayesian survival models. Candidate models examined the influence of sex, age at ringing, calendar year, and number of observations within countries on the apparent survival probability. Country-related variations were the strongest predictors of apparent survival. Apparent survival ranged between 0.88 and 0.97 for selected countries (Poland, Italy, and Hungary), countries with the highest number of observers, and between 0.62 and 0.87 for other countries. The age effect was moderate, and the sex effect was negligible. Strong transient effects and seasonal variations in detection probability demonstrate the importance of considering movement behaviour and observer-distribution bias

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when interpreting survival estimates of highly mobile species, such as the Black-headed Gull.

Keywords: Apparent survival, capture–mark–recapture, detection probability, observer bias, Black-headed Gull

INTRODUCTION

Survival is one of the most important demographic parameters determining population dynamics, particularly in long-lived species, where population growth is often more sensitive to changes in survival than to variation in reproductive output (Lebreton & Clobert 1991, Lebreton *et al.* 1992). A key parameter affecting population trends among long-lived species is the adult annual survival (Harris 1970, Perrins 1991). Capture–mark–recapture (CMR) methods provide powerful tools for estimating survival while accounting for imperfect detection, allowing for the separation of demographic processes from observational uncertainty (Lebreton *et al.* 1992). Therefore, accurate survival estimates are essential for understanding population trends and fitness and for informing conservation and management decisions in wild populations (Morris & Doak 2002, Fletcher *et al.* 2012, Abadi *et al.* 2013).

The Black-headed Gull *Chroicocephalus ridibundus* is one of the most widespread gull species in Europe and has been the focus of extensive ringing programs for several decades (Prévot-Julliard *et al.* 1998, Cramp & Simmons 2006). This species is relatively long-lived, with recorded lifespans exceeding 30 years in the wild (van Dijk *et al.* 2012). Because large numbers of colour-ringed individuals are regularly reported throughout Europe, Black-headed Gulls provide an excellent model system for studying survival patterns over large spatial and temporal scales. Previous studies have demonstrated the usefulness of ringing and resighting data for estimating demographic parameters in gulls and other long-lived seabirds (Prévot-Julliard *et al.* 1998, Rock & Vaughan 2013, Robertson *et al.* 2016, Kralj *et al.* 2018).

Age- and sex-specific variations in survival are key components of population dynamics (Cam *et al.* 2002, Oro *et al.* 2010). In many bird species, juveniles experience lower survival rates than adults because the first year of life includes several demanding life-history stages, including independence from parental care, moult, competition with experienced adults, and their first migration and wintering periods (Kralj *et al.* 2018, Indykiewicz *et al.* 2026). Sex-specific differences may also occur due to variations in migration strategies, habitat use, behaviour, or reproductive investment, although evidence from gulls remains inconsistent (Andersson 1994, Lindström 1999, Camphuysen & Gronert 2012). Furthermore, individual heterogeneity may generate apparent age-related survival patterns that differ from true demographic processes, making careful modelling necessary (Vaupel & Yashin 1985, Service 2000, Cam *et al.* 2002).

A major challenge in survival estimation is imperfect detection. Capture–mark–recapture models estimate apparent survival rather than true survival because permanent emigration cannot be distinguished from mortality (Lebreton *et al.* 1992). True survival refers to the probability that an individual remains alive between two sampling occasions, regardless of its location. In contrast, apparent survival combines true survival with site fidelity and therefore reflects the probability that an individual remains alive and does not permanently leave the monitored population. Consequently, apparent survival may underestimate true survival in highly mobile species, particularly when permanent emigration is common. Differences in detection probability among years, age classes, sexes, or individuals can bias survival estimates if they are not properly accounted for (Prévot-Julliard *et al.* 1998, Abadi *et al.* 2013). In particular, transients and individuals with consistently low detection probabilities may generate substantial downward biases in the estimated survival rates (Prévot-Julliard *et al.* 1998, Abadi *et al.* 2013). Transient individuals due to differences in their wintering areas may influence survival rates (Lok *et al.* 2011, Alves *et al.* 2013). In long-lived species, changes in wintering areas occur mostly between the first and second winters, whereas adults usually show high site fidelity (Lok *et al.* 2011, Sanz-Aguilar *et al.* 2012). When the capture or observation probability is high, the effects of heterogeneity on survival estimates are limited (Loery *et al.* 1987, Lebreton 1995).

The increasing availability of citizen-science observations and international ringing databases has greatly expanded the opportunities for large-scale survival studies. However, observer effort is often unevenly distributed across space, creating spatial biases in the monitoring data (Buckland & Johnston 2017, Bowler *et al.* 2022, Rieger *et al.* 2024). Some regions attract disproportionately high observer activity, whereas others are poorly covered. Consequently, geographic differences in resighting probability may influence apparent survival estimates independently of the true biological differences among individuals (Bowler *et al.* 2022, Morrison *et al.* 2022, Rieger *et al.* 2024). Because Black-headed Gulls are highly mobile, differences in apparent survival may reflect not only mortality but also variation in dispersal, migration behaviour, and observation probability.

Using a long-term colour-ringing dataset of Black-headed Gulls ringed in Zagreb between 2011 and 2025, we estimated apparent survival using Cormack–Jolly–Seber and Bayesian survival models. Specifically, we tested whether apparent survival varied according to sex, age at ringing, and observations in selected countries. We further evaluated how seasonal variations in detection probability and potential observer-distribution bias may influence apparent survival estimates. We predicted that age would influence survival, with juveniles showing lower survival than adults, and that sex effects would be weak. We also expected spatial variation in observation effort to contribute to differences in apparent survival among country groups.

MATERIALS AND METHODS

Between November and March, from 2011 to 2025, 12,721 Black-headed Gulls were captured at a landfill in Zagreb, Croatia (45.765 N, 16.024 E) using cannon and clap nets. All individuals were ringed with a metal and a plastic colour ring. Birds were aged as first-winter (juvenile) or adult according to plumage characteristics and sexed using the linear discriminant model described by Taylor *et al.* (2025).

The ringed individuals generated 31,792 resightings up to 1st of April 2026 (Fig. 1), which was used as the cutoff date for all analyses. As most Black-headed Gulls leave the study area by 1st of April, April was considered the beginning of a new research year.

Capture histories were constructed for each individual based on the annual encounter data. For each research year, individuals were classified as detected (1) or not detected (0), generating 25,438 annual observations. Of the ringed individuals, 6644 (52.2%) were never observed again after the year of ringing.

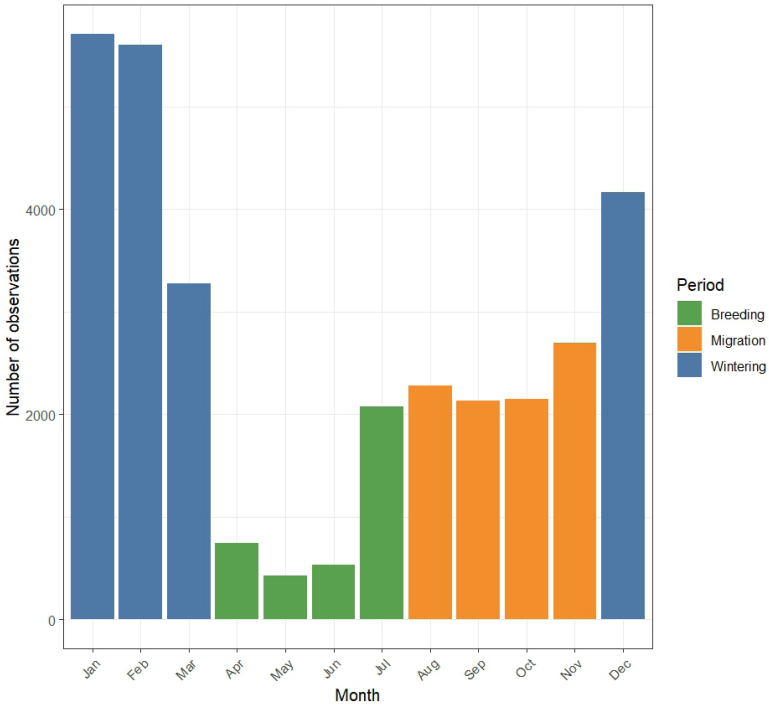


Figure 1. The number of observations of Black-headed Gull *Chroicocephalus ridibundus* ringed in Zagreb, Croatia, from 2011 until 2026, n = 31,792.

Slika 1. *Broj opažanja riječnih galeba Chroicocephalus ridibundus prstenovanih u Zagrebu, Hrvatska, od 2011 do 2026. godine, n = 31,792.*

Apparent survival was analysed using Cormack–Jolly–Seber (CJS) models implemented in the R package RMark (White & Burnham 1999, Laake 2013). Candidate models examined the influence of sex (female, male, or unknown), age at ringing (juvenile or adult), calendar year, and number of observations within countries on the apparent survival probability (Φ). We included the three countries with the highest number of resightings of our gulls (later referred to as selected countries) to examine whether there was potential bias within our dataset: Poland (7572 observations), Hungary (5564 observations), and Italy (4370 observations). Together, these countries accounted for 55% of all the observations. Detection probability (p) was modelled as either a constant or a function of season, depending on the candidate model. Model selection was performed using Akaike's Information Criterion corrected for small sample sizes (AICc; Anderson *et al.* 1998, Burnham & Anderson 2002), and competing models were compared using ΔAICc values and AICc weights. Seasonal CJS analyses were performed using the same individuals, generating 28,555 seasonal observations. Seasonal Cormack–Jolly–Seber models included a transient effect to account for potential differences in apparent survival between newly ringed individuals and birds observed in subsequent intervals. Detection probability (p), representing the probability of observing a marked individual that was alive and present in the population, was modelled as a function of season. This allowed survival probability (Φ) and detection probability (p) to be estimated separately, following the Cormack–Jolly–Seber framework.

The goodness-of-fit of the global Cormack–Jolly–Seber model was evaluated using the RELEASE tests implemented in RMark. Model overdispersion was assessed using the variance inflation factor (ĉ), which was calculated as the ratio between the overall chi-square statistic and its degrees of freedom. Values of ĉ greater than 1 indicate departures from the assumptions of the Cormack–Jolly–Seber model (Lebreton *et al.* 1992).

To complement the CJS analyses, age-specific survival trajectories were estimated using the Bayesian Survival Trajectory Analysis (BaSTA) (Colchero *et al.* 2012). Gompertz ("GO") models with a simple hazard structure were fitted separately for sex, age, and country groups. Analyses were conducted using minimum ages of 0 (all individuals) and 1 year (individuals that were observed at least once after the year they were ringed) to evaluate the sensitivity of age-specific survival estimates to the inclusion of the first year of life in the model. Model support was evaluated using the Deviance Information Criterion (DIC). Posterior survival curves were generated for all individuals and for individuals observed for at least one research year after ringing.

All analyses and graphical representations were performed using R Statistical Software (v4.4.0, R Core Team 2024) and the statistical package ggplot2 v. 3.4.0 (Wickham 2016).

RESULTS

Model selection strongly supported the variation in apparent survival among years, countries, and age classes (Table 1). The model Φ(time + country + age) p(.) received overwhelming support (AICc = 61521.82), outperforming the next-best model Φ(time + country) p(.) by 14.31 AICc units.

Country had the strongest effect on the apparent survival. Individuals classified within the selected country group exhibited substantially higher apparent survival than those in the reference group (β = 1.37 ± 0.03 SE), corresponding to a 3.9-fold increase in the odds of apparent survival. Juveniles showed slightly lower apparent survival than adults (β = -0.11 ± 0.03 SE). Sex had little influence on apparent survival, with both female (β = -0.01 ± 0.01 SE) and unknown sex individuals (β = -0.05 ± 0.02 SE) showing survival estimates similar to those of males.

Table 1. Models and selection criteria used to determine the year effects on Black-headed Gulls *Chroicocephalus ridibundus*. The number of parameters in the models is indicated by NP.

Tablica 1. *Modeli i kriteriji odabira korišteni za određivanje njihovog utjecaja godine na riječne galebove Chroicocephalus ridibundus. Broj parametara u modelima označen sa NP.*

Model (Φ)	NP	AICc	ΔAICc	AICc weight	Model likelihood	Deviance
Time + country + age	22	**61521.82**	**0.00**	0.9992	1	61477.78
Time + country	21	61536.13	14.31	0.0008	8e-04	61494.09
Country	3	61795.67	273.86	0	0	61789.67
Time + age	21	63859.43	2337.61	0	0	63817.39
Time	20	63866.43	2344.61	0	0	6696.30
Sex	4	64153.31	2631.49	0	0	64145.31
Age	3	64156.33	2634.51	0	0	64150.33
Null	2	64162.58	2640.76	0	0	7028.49

All seasonal models strongly supported the inclusion of transient effects (Table 2). The best-supported seasonal model was Φ(transient + country) p(season). Apparent survival during the first interval following ringing was estimated at 0.73, whereas apparent survival in subsequent intervals increased to 0.92. Mean annual apparent survival was 0.74 and varied from 0.41 to 0.90 among years.

Detection probability differed markedly between annual and seasonal analyses. In annual models, detection probability was estimated as 0.40 and remained constant among years. In seasonal models, detection probability varied substantially among seasons, with estimated values of 0.07 during the breeding period, 0.13 during migration, and 0.24 during wintering.

Table 2. Models and selection criteria used to determine the seasonal effects on Black-headed Gulls *Chroicocephalus ridibundus*. The number of parameters in the models is indicated by NP.

Tablica 2. *Modeli i kriteriji odabira korišteni za određivanje njihovog utjecaja sezona ne na riječne galebove Chroicocephalus ridibundus. Broj parametara u modelima označen sa NP.*

Model (Φ)	NP	AICc	ΔAICc	AICc weight	Model likelihood	Deviance
Transient + country	6	104574.38	0.00	0.49	1.00	104562.38
Transient + country + sex	8	104575.81	1.43	0.24	0.50	104559.80
Transient + country + age	7	104576.37	1.99	0.18	0.37	104562.37
Transient + country + age + sex	9	104577.81	3.43	0.09	0.18	104559.80
Transient + season	7	107873.90	3299.52	0	0	35286.89
Transient + age	6	107971.48	3397.10	0	0	107959.48
Transient	5	107973.20	3398.82	0	0	35390.19
Transient + age + sex	8	107973.80	3399.42	0	0	107957.80
Transient + sex	7	107975.65	3401.27	0	0	107961.65

As in the annual analyses, country effects strongly influenced apparent survival. Apparent survival ranged between 0.62 and 0.87 for the non-selected country group and between 0.88 and 0.97 for the selected country group. In contrast, sex effects were negligible, and adding age provided little improvement once the country was included in the model.

Goodness-of-fit testing revealed significant departures from the standard Cormack–Jolly–Seber assumptions in both annual and seasonal encounter histories. The annual dataset produced an overall RELEASE statistic of $\chi^2 = 1086.0$ (df = 137, $P < 0.001$; $\hat{c} = 7.93$), whereas the seasonal dataset produced $\chi^2 = 4177.7$ (df = 694, $P < 0.001$; $\hat{c} = 6.02$). Significant TEST2 and TEST3 components in both analyses indicated substantial heterogeneity among individuals and encounter histories.

BaSTA analyses supported the results obtained from the Cormack–Jolly–Seber models (Table S1). Country-based models consistently received the strongest support, yielding the lowest DIC values under both minimum age assumptions (minimum age = 1: DIC = 33 506.9; minimum age = 0: DIC = 53 445.6). Age models received intermediate support, whereas sex-based models consistently performed poorly.

Survival trajectories differed substantially between the country groups (Fig. 2, Supplementary Table S2). In contrast, survival trajectories were largely similar

among sex categories, indicating only minor differences in survival between males, females, and individuals of unknown sex (Fig. 2, Supplementary Table S3).

Age-specific survival trajectories depended on the inclusion of all individuals or the exclusion of transient individuals (Fig. 2, Supplementary Table S4). When all individuals were included, adult survival exceeded juvenile survival during the early life stage. However, when the analyses were restricted to individuals observed at least after the first year, juveniles exhibited higher survival rates than adults. The survival curves for both age classes converged at older ages.

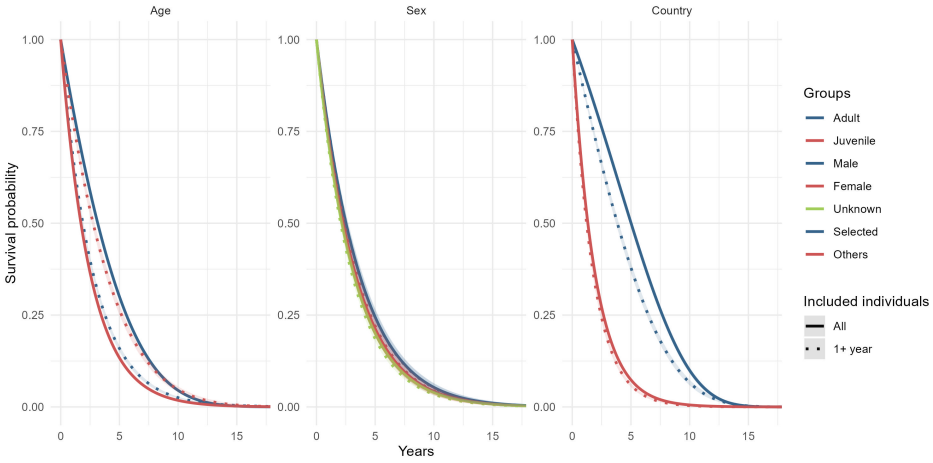


Figure 2. Survivability trajectory for Black-headed gulls *Chroicocephalus ridibundus* obtained with Bayesian survival models for groups, all individuals, and individuals that were observed at least after the first year after ringing (1+ year).

Slika 2. *Krivulje preživljavanja riječnih galebova Chroicocephalus ridibundus dobivene koristeći Bayesovih modela preživljavanja za grupe, sve jedinke te jedinke koje su bile viđene barem godinu dana nakon prstenovanja (1+ year).*

DISCUSSION

Whether an individual was observed in the selected countries had the most significant effect on apparent survival in both the Cormack–Jolly–Seber and BaSTA analyses. Both analyses identified the country as the most important predictor of survival, substantially outperforming the age- and sex-based models. Similar spatial differences have been reported in other gull species, where wintering locations and movement behaviours influenced apparent survival estimates (Kralj *et al.* 2018). The magnitude of this effect suggests that variations among countries are a major determinant of the encounter histories observed in this population. Individuals using different wintering areas may experience different environmental

conditions, food availability, anthropogenic pressures and migration costs. Alternatively, the observed pattern may partly result from differences in the observer effort and reporting rates among countries. Regions with a greater number of active observers may generate higher resighting probabilities, leading to elevated estimates of apparent survival. Consequently, the strong country effect identified in this study likely reflects a combination of biological and observational processes (Lebreton *et al.* 1992, Rieger *et al.* 2024). Over and under inflated estimates could also be due to spatial bias caused by using citizen science data, influenced by the observer, number of observers, and biased by its preference (Johnston *et al.* 2020, Bowler *et al.* 2022, Rieger *et al.* 2024).

Seasonal analyses consistently supported the inclusion of transient effects. The strong transient effect observed in seasonal models suggests that a substantial proportion of ringed individuals were encountered only once and subsequently died or changed their wintering, breeding, or migratory areas. This pattern is common in capture–mark–recapture studies and may result from permanent emigration rather than mortality, and has been identified as an important source of bias in survival estimation (Prévot-Julliard *et al.* 1998, Abadi *et al.* 2013). Apparent survival during the interval immediately following ringing was substantially lower than that in subsequent intervals. Prévot-Julliard *et al.* (1998) showed that an excess of individuals resighted only once may result from either mortality or dispersal and that transients can substantially influence apparent survival estimates. Similarly, Abadi *et al.* (2013) demonstrated that heterogeneity in detection and movement behaviour can bias survival estimates when not explicitly modelled in the analysis. Given that Black-headed Gulls are highly mobile and the Zagreb landfill is used as a wintering site by birds from different populations, transient behaviour and permanent emigration are likely contributors to the observed pattern.

Age effects were detected in both modelling approaches, although their magnitude was considerably smaller than that of the country effect. Juveniles generally exhibited lower apparent survival than adults, consistent with the expectations for long-lived birds and previous studies of gulls (Cam *et al.* 2002, Indykiewicz *et al.* 2026). However, BaSTA analyses revealed that age-specific survival trajectories depended on the minimum age assumption. When all individuals were included, the juveniles exhibited lower survival trajectories than the adults during early life. However, when analyses were restricted to individuals observed at least once in the years following ringing, juveniles showed survival trajectories similar to those of all included adults. Adults observed at least once in years after ringing showed a lower survival trajectory, which could be due to senescence (Cam *et al.* 2002, Péron *et al.* 2010) or possibly affected by the loss of plastic rings due to wear (Piper *et al.* 1999, Carboneras *et al.* 2013). Our MARK results showed that apparent survival after the first interval was essentially the

same across all later years, similar to the results from France (Péron *et al.* 2010) and the Netherlands (Majoor *et al.* 2005), which showed little year-to-year variation, and our adult survival estimates were similar to those of other studies, around 0.8 to 0.9 (Prévot-Julliard *et al.* 1998, Horswill & Robinson 2015, Indykiewicz *et al.* 2026). These contrasting patterns suggest that estimates of early life survival are particularly sensitive to model assumptions and to individual heterogeneity. Young gulls experience several demanding life-history stages during their first years which may contribute to reduced apparent survival estimates (Indykiewicz *et al.* 2026), or transient individuals that change between wintering areas, which occurs mostly between the first and second winters (Lok *et al.* 2011, Sanz-Aguilar *et al.* 2012).

Sex explained only a small variation in apparent survival. Both CJS and BaSTA analyses consistently provided weak support for sex-dependent models, and survival trajectories were largely similar among males, females, and birds of unknown sex. These findings agree with several studies on gulls that reported either small or inconsistent sex differences in survival (Camphuysen & Gronert 2012, Rock & Vaughan 2013). Although sex differences may arise through variations in migration strategy, energetic expenditure, or habitat use, the present results suggest that such effects are either absent or too small to be detected relative to other sources of variation.

The detection probability varied markedly among seasons, with the highest values occurring during winter and the lowest during the breeding period. This pattern likely reflects seasonal changes in bird distribution and the opportunities for observation. During winter, Black-headed Gulls congregate at feeding or resting sites, usually near anthropogenic structures or food sources, including ports, water reservoirs, landfills, and waste treatment facilities (Cramp & Simmons 2006), increasing the likelihood of resighting marked individuals. During the migration and breeding periods, individuals are more dispersed and consequently less likely to be observed. In their breeding areas, they are less likely to be observed because of vegetation covering the individuals, colonies being unable to be approached, colonies being unsystematically observed, or because the areas are further from anthropogenic areas, and with that, a lower number of people observing them (Buckland & Johnston 2017, Kralj *et al.* 2018, Bowler *et al.* 2022). These differences highlight the importance of explicitly modelling detection probability. Failure to account for temporal variation in detectability can bias survival estimates, particularly when the detection probabilities are low. Therefore, seasonal analyses provide additional evidence that observation processes play a major role in shaping apparent survival estimates (Prévot-Julliard *et al.* 1998, Abadi *et al.* 2013).

A limitation of this study is that capture–mark–recapture analyses estimate apparent rather than true survival. Individuals that permanently emigrate from the monitored population are indistinguishable from mortality events in Cormack–

Jolly–Seber models. Furthermore, variation in observer effort, reporting rates, and detection probability may influence resighting probabilities. Therefore, the estimates presented in this study should be interpreted as apparent survival rather than true survival, since permanent emigration and observer-related processes may contribute to apparent losses from the population. The significant goodness-of-fit tests and elevated ĉ values suggest substantial heterogeneity within the marked population. Such heterogeneity is expected in migratory gulls because apparent survival is influenced by dispersal, transient individuals, and variations in observation probability among regions. Despite these limitations, both CJS and BaSTA analyses produced remarkably consistent results. Country-related variation was the strongest predictor of apparent survival, age effects were moderate, and sex effects were negligible. Furthermore, strong transient effects and seasonal variations in detection probability demonstrate the importance of considering movement behaviour and observer-distribution bias when interpreting survival estimates of highly mobile species such as the Black-headed Gull.

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Supplementary Information

The online version contains supplementary material available at https://hrcak.srce.hr/supplement/975.

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SAŽETAK

Riječni galeb *Chroicocephalus ridibundus* jedna je od najrasprostranjenijih vrsta galebova u Europi te je već nekoliko desetljeća u središtu opsežnih programa prstenovanja. Riječni galebovi predstavljaju izvrstan modelni sustav za proučavanje obrazaca preživljavanja jer se velik broj jedinki označenih prstenovima u boji redovito bilježi diljem Europe. Između 2011. i 2025. godine na odlagalištu otpada u Zagrebu prstenovan je 12.721 riječni galeb, te su ukupno zabilježena 31.792 nalaza. Koristeći podatke o prstenovanju procijenili smo prividno preživljavanje pomoću Cormack–Jolly–Seberovih i Bayesovih modela preživljavanja. Modelima smo ispitali utjecaj spola, starosti pri prstenovanju, kalendarske godine i brojem nalaza u raznim državama na vjerojatnost prividnog preživljavanja. Varijacija povezana s odabranim državama (Poljska, Mađarska i Italija) pokazala se kao najsnažniji prediktor prividnog preživljavanja. Prividno preživljavanje kretalo se između 0,88 i 0,97 za ptice viđene u Poljskoj, Mađarskoj i Italiji, državama s najvećim brojem nalaza, dok je prividno preživljavanje za sve ostale države u kojima su zabilježeni nalazi iznosila između 0,62 i 0,87. Utjecaj starosti jedinki bio je umjeren, dok je utjecaj spola bio zanemariv. Prilikom procjene preživljavanja visoko mobilnih vrsta poput riječnog galeba potrebno je uzeti u obzir veliki udio ptica sa samo jednim nalazom, razlike u sezonskoj varijabilnosti te neravnomjernu raspodjelu promatrača.