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Exploring Bird Demographics: Unraveling the Impact of Fitness, Species Interactions, and Climate Change

by

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Executive Summary

The main objective of this study is to investigate the survival patterns of various passerine bird species in different age groups during the inter-winter period, spanning from October to April, over the years 2007 to 2018. Survival can give us insights into the overall health of the concerned species population.

Data: Data for the three concerned species of the passerine birds- blackcap, chiffchaff, and robin are collected through the capture-recapture method. The capture-recapture method involves capturing the birds, marking or tagging them in a unique way, and releasing them back into the wild. These marked birds are categorised into juveniles and adults based on whether their age is less than 1 year(juvenile) or older than 1 year(adult). However, in some cases, the age determination process is inconclusive, resulting in observations with unknown ages. Out of a total of 704 blackcap birds, the age of 13 birds is unknown. Similarly, among the 573 chiffchaff birds, the age of 128 birds is unknown. Lastly, out of the 439 robin birds, there are 4 birds of unknown age. Due to the exact cause hindering the age-determining process, these observations are removed from the analysis.

Methodology: In open environments, birds are subject to a variety of factors that can affect their survival, including births, deaths, migrations, and emigrations. To estimate the survival estimates of birds in these environments, a model named Cormack-Jolly-Seber(CJS) is often used. Our considered model is based on the assumption that the probability of survival for a bird depends on age. This model only takes the time period between the initial and final capture occasion. Furthermore, in each of the three species, it is assumed that chances of recapturing a bird remain the same regardless of age or capture occasion.

Main findings:

- The study reveals a consistent trend across all bird species, indicating that adults generally exhibit higher survival rates during the inter-winter periods compared to juveniles. This may indicate low survival chances during the early years during the winter season as compared to adult birds.
- Among all the species, chiffchaffs show slightly higher chances of being recaptured again, in contrast to blackcaps, which exhibit comparatively lower chances of being recaptured. In the case of the robins, it appears that there are some other factors that we have not taken into account in the considered model.
- The research results also indicate that certain bird species like blackcaps have significantly lower survival, notably during the winter seasons between 2011 and 2013. This phenomenon might be attributed to various factors, including natural elements such as increased predation by other animals, or anthropogenic influences like climate shifts due to global warming. To precisely identify the underlying cause, additional information regarding the average temperatures during those inter-winter periods is required.

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1 Introduction

1.1 Background

Birds can be observed in our daily lives, but they frequently go overlooked in our fast-paced world. However, these creatures are facing potential extinction due to various threats such as pollution, climate change and hunting, among many other factors ([1], [2]). These factors may have a global impact on the ecosystem. For example, many organisms may alter their seasonal behaviours such as the early emergence of insects from hibernation might disrupt the primary food source of the birds, which in turn disrupts their reproductive cycle [15]. The demography of the birds can give us significant insight into how these factors are influencing the birds, which can help us to mitigate serious threats and promote the conservation of these species. A vital position in the food chain and ecosystem is held by the birds. Ecological processes cannot function properly without their existence. But the extinction of these species would cause serious disruptions in ecological dynamics, upsetting the complex web of life. Ecological data can be collected in order to obtain insights about the survival of the birds. Survival can be considered as a key demographic feature for the population of birds in ecology. It helps in determining the population growth or decline over a specific period of time. There are various ways to gather the data including remote sensing and satellite imagery by taking snapshots of the birds in a given area which is a type of digital marking. Furthermore, traps can be used to capture the birds physically, and mark them using a tag. But due to time and financial constraints, a complete survey of the population is not always feasible [6]. So typically multiple surveys are conducted in the given area to gather the data. The data considered in this study is based on the capture-recapture process. This capture-recapture data is collected by the researchers going into the field periodically to mark the captured birds and release them. This can be used to estimate the size of the population and to track changes in the population over time. Further elaboration concerning the data can be found in section 2.

1.2 Objective

Passerine bird species are of primary interest in this project. More than half of the bird species in the world are passerines [3]. The main objective of this study is to estimate the survival probability and recapture probability of different species across inter-winter(i.e. across years) periods, which are defined as the time between October and April in consecutive years. For example, the inter-winter period for the year 2007 would be from October 2007 to April 2008. The study primarily focuses on the inter-winter periods from 2007 to 2018. Furthermore, the main focus is on open population models where it is assumed that there are births, deaths, emigration or migration in the population within the study period. Additionally, the limitations of the considered model are also discussed.

2 Data

The main focus of this report is on the data collected over an 11-year period, from 2007 to 2018. The data is collected on a monthly basis between October and April by researchers from the University of Valencia. This data is gathered through the capture-recapture method, which provides insights into the winter nesting patterns of some passerine bird sub-species in Valencia. Moreover, it is assumed that the birds are uniquely identifiable during each distinct capture occasion. Additionally, in order to uniquely identify a bird, rings are attached to an individual the first time they are observed and assumed that the ring will not get lost during the study period.

Let us assume that data is in the form of $n \times T$ dataframe named x, where n is the number of distinct birds caught, and T is the individual capture history ranging from the $t = 1, 2, ..., 77$.

$$x_{i,t} = \begin{cases} 0, & \text{if bird } i \text{ is not unobserved at time } t \\ 1, & \text{if bird } i \text{ is observed at time } t \end{cases}$$

Initially there are 77 capture monthly occasions, which are collapsed into 11 yearly capture occasions depending on the inter-winter sessions. For example, for an individual i if the capture histories for the first seven inter-winter months are $0, 1, 0, 1, 0, 0, 0$; then it can be marked as seen(i.e "1") for that period in the yearly capture occasion. If an individual i is not seen even once throughout those inter-winter months, then it can be marked as not seen(i.e. "0"). A similar operation could be performed on subsequent months till the end of the monthly capture sessions to convert the data to yearly capture occasions.

2.1 Data analysis

Three different datasets consist of data about the species three passerine species namely blackcap, chiffchaff, and robin. Since the period of the study starts in October 2007, observations from the first four months(January 2007 to April 2007) are removed from the data because some of the birds are only captured in those months and are never recaptured again. There are around 157 blackcap, 8 chiffchaff, and 8 robin birds that are never sighted after the first four months and are thus eliminated from the respective datasets. This absence might be attributed to factors such as mortality(death) or permanent migration.

The age of birds in all of the three species is determined at the first time of ringing. Juveniles are less than 1 year old, while adults are greater than 1 year old. Passerine birds' age can be determined by examining their feathers and skull area [11]. However, damage to these areas can make this process more challenging. Hence, some of the observations have unknown ages. The age missingness in the data cannot be directly classified as MNAR(missing not at random) due to various external factors impacting the age information. In order to address this, it can be assumed that the missing age observations are unrelated to age itself. As a result, these observations are removed from the dataset. The detailed number of birds for three species in each category is presented in Table 1.

Table 1: Populations of different species

Species	**Juveniles**	**Adults**	**Unknown age**	**Total**
Blackcap	513	178	13	704
Chiffchaff	299	146	128	573
Robin	325	110	4	439
Total	1,137	434	145	1,716

From Table 1, it can be observed that the juvenile population is in abundance than the adult population in all of the captured species. This is because age is determined at the time of initial capture of the bird, and this is not updated after the same bird is recaptured again in the next yearly capture occasion; which should be considered as an adult.

Figure 1 depicts the total number of birds captured across different species in distinct capture sessions. The birds that have already been marked and captured again are also included in the figure.

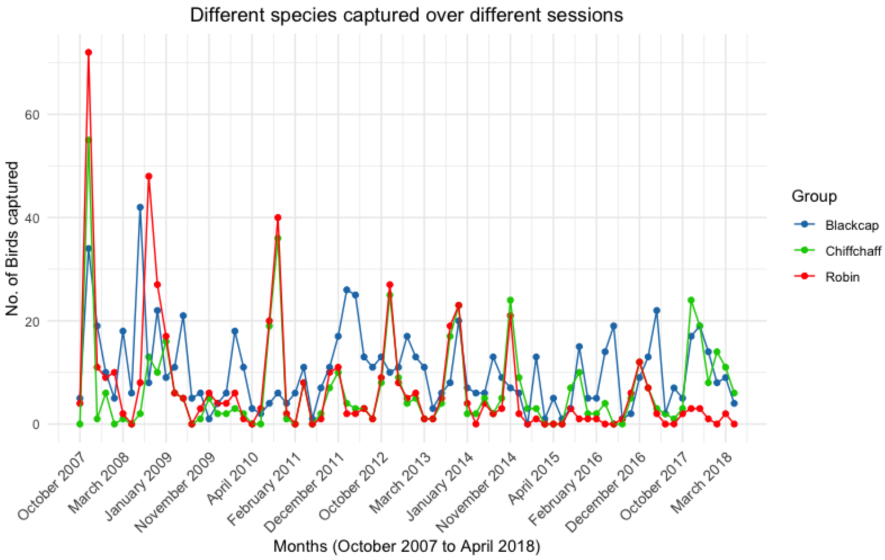


Figure 1: Total birds captured over different sessions

It is evident that most of the birds are captured during mid-winter capture sessions in most of the cases. This may indicate that the birds have become familiar with their respective surrounding, and are exploring(e.g. searching for food) the specific areas where capturing process is done. Also, it can be observed that between January 2009 and April 2010, very few chiffchaffs are captured. Moreover, after November 2014 there is a sharp decline in the number of robin birds captured in each session. Since robins are territorial birds and the capturing is being done in a specific location, it may be a sign of temporary migration or, if not, cause for concern [9]. It can be a sign that the local robin population is gravely in distress, and require immediate conservation efforts to investigate the potential factors.

Table 2 shows the data about capture-recaptured individuals during different inter-winter sessions. This is obtained by changing the data collection intervals from monthly to yearly(inter-winter). In the table below, the session labelled as ”2007-2008” corresponds to the inter-winter period from October 2007 to April 2008. Similarly, sessions are labelled in accordance with their respective yearly inter-winter periods, such as ”2008-2009,” ”2009-2010,” and so forth, up to the session of ”2017-2018.”

Table 2: Different birds captured during different sessions

Session	**Blackcap**	**Chiffchaff**	**Robin**	**Total**
2007-2008	96	63	108	267
2008-2009	110	51	109	270
2009-2010	48	13	22	83
2010-2011	30	61	70	161
2011-2012	102	26	26	154
2012-2013	68	49	54	171
2013-2014	57	53	53	163
2014-2015	34	35	24	93
2015-2016	58	22	5	85
2016-2017	51	28	26	105
2017-2018	67	73	6	146
Total	721	474	503	1,698

Table 2 shows that a total of 1,698 birds are sighted during the different yearly capture sessions. The birds that are captured once or more across various sessions are also included in this total. The overall number of birds observed is highest in the inter-winter session of 2008–2009 and lowest in 2009–2010.

3 Methodology

The assumption in open population models is that the population varies over time during the study period. This could be due to the birds arriving(through birth or emigration) or departing(by death or migration). The basic model for modelling the survival probabilities in an open population is Cormack-jolly-seber(CJS) model [8].

3.1 Cormack-Jolly-Seber model

The CJS model makes the assumption of a multinomial likelihood that is dependent on the first time the birds are captured. Let, θ denote the set of model parameters and are given as $\theta = \{\phi_t, p_t\}$.

$$\phi_t = P(\text{individual is alive at time } t+1 \,|\, \text{alive at time } t) \quad \text{for } t = 1, \dots, T-1;$$

$$p_t = P(\text{individual is recaptured at time } t \,|\, \text{alive at time } t) \quad \text{for } t = 2, \dots, T.$$

Assuming an individual bird denoted as i with a known capture history of x_i, a first capture time of f_i, and a last capture time of l_i, has an unknown emigration or death time(i.e. $\geq l_i$). Therefore, the likelihood of the observed capture history conditioned on the first capture can be written as

$$f(x_{i,t}|\theta) = \prod_{t=f(i)}^{l(i)-1} \phi_t p_t^{x_{i,t+1}} (1-p_t)^{x_{i,t+1}} \chi_{l(i)}, \tag{3.1}$$

It is also assumed that the individuals behave independently of each other. Then equation 3.1 can be written as:

$$f(x|\theta) = \prod_{i=1}^{n} \prod_{t=f(i)}^{l(i)-1} \phi_t p_t^{x_{i,t+1}} (1-p_t)^{x_{i,t+1}} \chi_{l(i)}, \tag{3.2}$$

where χ_t in equation 3.2 denotes the probability of not being observed again within the study period, given that individual is observed at time t and can be calculated recursively using

$$\chi_t = (1-\phi_t) + \phi_t(1-p_{t+1})\chi_{t+1}, \tag{3.3}$$

where $(1-\phi_t)$ is the probability of an individual dying(mortality rate), and the second term represents the probability that an individual will survive at time t, not be seen at time $t+1$, and also not be seen at any time after $t+1$.

In the above likelihood(equation 3.2) only the time between the initial capture $f(i)$ and the final $l(i)$ for an individual is considered because the model is designed to focus only the times during which an individual is at risk of being captured and marked again. if an individual is only seen once during the study period i.e. $l(i) = f(i)$, then the model cannot provide any survival estimates for those observations. Because there is no information about the individual being seen again, and this lack of recapture hinders the estimation of the parameters for that individual.

3.1.1 Assumptions

The following presumptions are taken into account when constructing the likelihood:

- The likelihood is conditioned on the first time a bird is observed. This suggests that the likelihood contains no information about the initial capture probability.
- Since it is impossible to tell whether a loss of the bird is the result of death or permanent emigration, only the apparent survival probability is estimated.
- It is assumed that the age remains static throughout the study period; which mean if a birds is identifies as a juvenile during the initial it remains juvenile during the entire study period. and is independent of the survival probabilities, therefore no age variation in the model parameters.

- Due to the joint time dependence of the model on the survival(ϕ_t), and recapture(p_t) are parameter redundant, and cannot be estimated separately. Only their product($\phi_{T-1}p_t$) can be estimated.

3.2 Age-dependent CJS model

The age-dependent CJS [14] model allows the survival probability to vary with age. Hence, the likelihood defined in equation 3.2 can be extended to include age-dependent survival probabilities, and can be rewritten as

$$f(x|\theta) = \prod_{i=1}^{n} \prod_{t=f(i)}^{l(i)-1} \phi_{it}(age) p_t^{x_{i,t+1}} (1-p_t)^{x_{i,t+1}} \chi_{i,l(i)}, \tag{3.4}$$

where $\phi_{it}(age)$ represents the survival probability of an individual i at time t, given their age. Similarly, χ_{it} in equation 3.4 denotes the probability of an individual i not being observed at time t given their age and can be defined as

$$\chi_{it} = (1 - \phi_{it}(age) + \phi_{it}(age)(1 - p_{t+1})\chi_{i,t+1}, \tag{3.5}$$

In order to make the ϕ as a function of age, let α_t represent the weight for the juvenile population for time $t = 1, \ldots, T-1$. It determines the baseline survival probability for individuals when they are juveniles. Moreover, let β represent the weight representing the change in the odds of survival when an individual transitions from being a juvenile to an adult. According to this, the ϕ can be modified as

$$\mathrm{logit}(\phi_{it}(age)) = \alpha_t + \beta.I(age_{it}), \tag{3.6}$$

where I is an indicator function that take values of 1 if the individual is considered as adult and 0 if juvenile.

$$I(age_{it}) = \begin{cases} 1, & \text{if age of an individual } i \text{ at time } t \text{ is adult} \\ 0, & \text{if age of an individual } i \text{ at time } t \text{ is juvenile} \end{cases} \tag{3.7}$$

In order to encode this age information, let us assume that we have captured a bird on the first capture occasion and is identified as a juvenile. However, if the ringed bird is still alive and recovered on the next capture session, then it will be classified as an adult. A time-based age data can therefore be created in order accurately represent age across different capture sessions in the form of age_{it} dataframe. Assuming a juvenile has a capture history of 0,1,0,1,0,1 in 6 distinct capture events, then it can be represented as 0,1,2,2,2,2 in the age data, where '1' represents the age at initial capture, indicating that the bird was juvenile at the time, and '2' indicates that the bird is now considered as an adult. If the bird is already an adult at the time of initial capture, the capture history is represented in the age matrix as 0,2,2,2,2,2. Hence, this age data can be considered as an indicator function for the survival probabilities by subtracting 1 from age_{it} of an individual i for indicating their age at time t. Therefore, equation 3.6 can be written as

$$\mathrm{logit}(\phi_{it}(age)) = \begin{cases} \alpha_t, & \text{if } I(\mathrm{age}_{it}) = 0 \\ \alpha_t + \beta, & \text{if } I(\mathrm{age}_{it}) = 1 \end{cases} \tag{3.8}$$

Hence, the survival probability for juveniles can be defined as $\mathrm{logit}(\phi_t(juveniles)) = \alpha_t$ and for adults it becomes $\mathrm{logit}(\phi_t(adults)) = \alpha_t + \beta$. Therefore, the model parameters can be defined as $\theta = \{\alpha_t, \beta, p_t\}$.

The primary distinction in the currently defined model lies in the assumption that an individual's survival probability is influenced by their age at each occasion while retaining the other assumptions similar to the age-independent CJS model. Moreover, the CJS model can be extended to include various heterogeneity factors such as time-varying recapture probability or annual constant survival ([12], [6]).

4 Experimental results and discussions

4.1 Model fitting

We have used the *optim* function, which is part of the *R* programming language, to find the parameter values that maximises the likelihood of the considered CJS models. Due to the sensitivity of the *optim* to the starting value, SA(Simulated annealing) [4] optimisation algorithm is used in order to make the results more stable. The SA method is a stochastic approach that effectively searches the solution space by acknowledging probabilistic modifications similar to the annealing process in order to find the global optima. The obtained MLEs(maximum likelihood estimates) for the parameters are then converted back to the real line using the inverse of the logit function, which is also known as the sigmoid function. It maps any real number to a value between 0 and 1, which is the desired range of probabilities and can be defined as:

$$\text{logistic}(\hat{\theta}_{\text{MLE}}) = \frac{1}{1 + e^{-\hat{\theta}_{\text{MLE}}}}, \tag{4.1}$$

where $\hat{\theta}_{\text{MLE}}$ represent the maximum likelihood estimate for the model parameters θ. The corresponding 95% confidence intervals(CI) for the estimated parameters are obtained using a non-parametric bootstrapping approach. The non-parametric bootstrap approach does make any assumption about the underlying data distribution. Hence, can provide robust and reliable estimates of confidence intervals by re-sampling from the observed data with replacement and estimating the MLE(maximum likelihood estimates) of the model parameters for each re-sampled data. Due to the limited computational resources only 500 bootstrap samples are taken to estimate 95% CI by using the lower and upper 2.5% quantiles of the related MLEs produced from bootstrapping.

4.2 Model checking

AIC(Akaike's Information Criterion)[13] and BIC(Bayesian Information Criterion) both be used to compare the relative goodness of fit of the considered models In comparison to AIC, BIC penalises the model more for its complexity, resulting in more complex models being less favoured in the model selection process [7]. Only the multinomial combinatorial terms varying with time are used to penalise the models. The detailed information about the AIC and BIC criterion can be found in Appendix A.1.

To assess the absolute goodness-of-fit test, m-arrays are constructed to summarise the data for each species. In m-arrays, m_{ij} denotes the number of marked birds of species released on occasion i and first recaptured on occasion j. This summary statistic is done due to the multinomial assumption of the CJS model. Each row of the m-array represents an independent multinomial distribution. As a result of this method, the associated probability of the capture histories can be created as (T-1)(T+2)/2 multinomial probabilities, where T is the total number of capture occasions [10]. However, due to age dependence separate m-arrays should be constructed according to the different age classes of the individuals but instead of doing that expected arrays can be pooled to incorporate the age-dependent information. Furthermore, the expected values are constructed based on the survival and recapture probabilities. More Detailed information about the construction of observed and expected m-arrays can be found in Appendix A.2).

4.3 Results

4.3.1 Blackcap

Model comparison

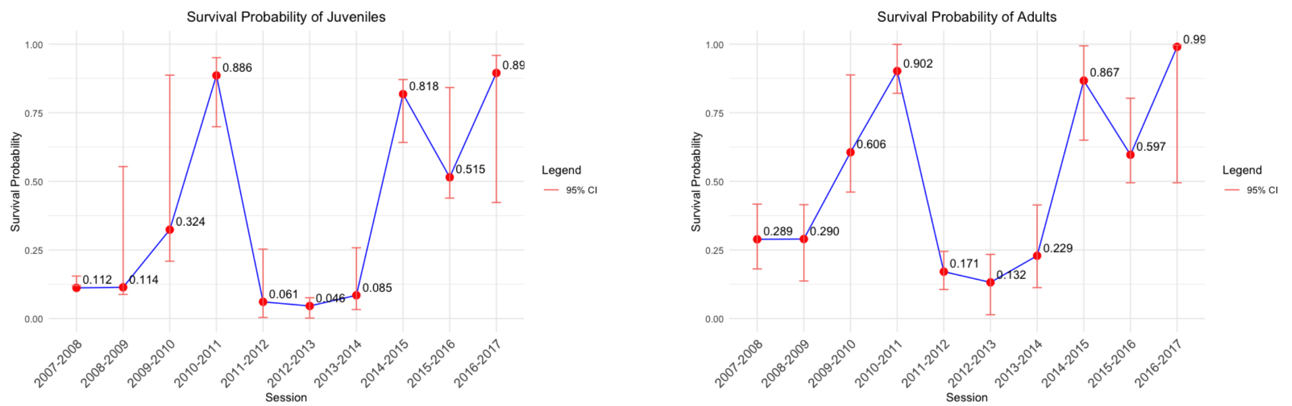
Table 3 shows the different variations of the Cormack-Jolly-Seber(CJS) model applied to blackcap bird data and their associated AIC and BIC values. Each model is characterised by its parameterisation, including whether survival probabilities are age-dependent and whether recapture probabilities are constant or vary over time.

Table 3: Relative goodness-of-fit test results (for Blackcap data)

Model	No. of Parameters	AIC	BIC
$\phi_t, p(\text{constant})$	10	292.919	338.300
$\phi_t(age), p(\text{constant})$	10	284.43	329.818
$\phi_t(age), p_t$	20	308.212	398.97

As it is known that the AIC and BIC favour the model with lower values, hence the model with constant recapture probability and time-varying survival as a function of age model($\phi_t(age), p(\text{constant})$) is considered to estimate the survival probabilities for both juveniles and adults.

Figure 2 shows the estimated MLEs and 95% non-parametric bootstrap confidence intervals(CI) of the survival probabilities for both juveniles and adult blackcap.



(a) Survival Probability Estimates for Juveniles

(b) Survival Probability Estimates for Adults

Figure 2: Survival Probability Estimates for Blackcap birds

The constant recapture probability for the blackcap birds is $p = 0.089$, with a 95% Confidence interval(CI) of (0.045, 0.111). From Figure 2a, it is evident that for the inter-winter periods between the 2011-2012 and 2013-2014 sessions, the juveniles have very low survival probabilities. Survival in between those years can be affected by many factors such as harsh temperatures during the winter season. A similar trend can be seen with adults(fig. 2b) but have a high survival probability as compared to adults. Furthermore, it can also be noted that the estimated MLEs for the survival probabilities have wide confidence intervals(i.e. high uncertainty) for both juveniles and adults. This may be due to the small sample size of the bootstrap replicates(i.e. 500) or sparsity in the data of the blackcap species.

It can also be observed that the apparent survival probabilities of the juvenile are lower than adults in each capture session. This may indicate that the mortality rate for the birds in their first year(i.e. juvenile) is higher as compared to the birds older than a year. This is due to many factors including the predators targeting the juvenile population because of their smaller size and lack of experience. Moreover, juveniles may also try to migrate with the older population, which may expose them to unfamiliar locations and potentially dangerous environments. Furthermore, human-induced threats such as pollution and habitat destruction can also affect the survival of the birds in the early years.

Model checking

In order to check the absolute goodness-of-fit of the age-dependent model for the blackcap data, it is possible to compare the observed and expected number of first captures following release values. But the expected values are smaller than 5 in some cells, hence do not meet the requirements of Pearson's chi-square test. Instead Hosmer-Lemeshow(HL) [5] goodness-of-fit test is used to check the difference between observed and expected frequencies. In this test, the predicted frequencies are ranked and divided into g groups of equal sizes for creating the groups. These g different groups or bins can be considered as distinct categories representing various independent multinomial outcomes. Hence, HL test then evaluates how well the model fits these observed and expected frequencies within each group, providing an assessment of the model's overall goodness of fit across the entire range of expected frequencies. More information about this test can be found in Appendix A.2.3.

Likewise, in other goodness-of-fit tests, the **null hypothesis** for Hosmer-lemeshow test states that observed and expected frequencies are the same across different groups and the data fits well to the considered model(i.e. p-value > 0.05). Furthermore, **alternative hypothesis** states that there is a significant difference between the observed and expected frequencies such that the data doesn't fit well(p-value < 0.05). Applying hosmer-lemeshow goodness-of-fit test to the considered model, we obtained a HL statistic of 1.383 with an associated p-value of 0.99. Hence, the null hypothesis cannot be rejected and may indicate that the data does fit well to the model.

4.3.2 Chiffchaff

Model comparison

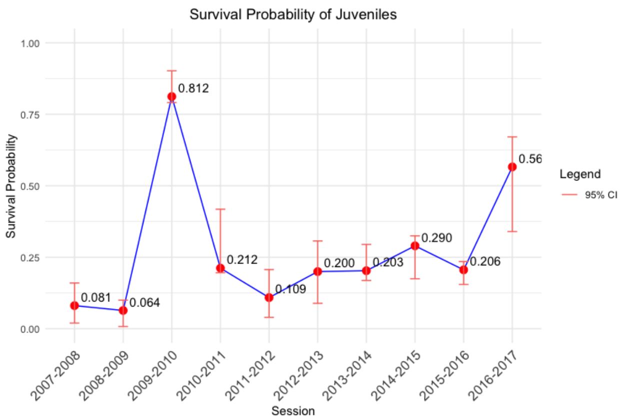
Table 4 shows the different variations of the CJS model applied to chiffchaff bird data. The detailed information about the AIC and BIC statistics for the fitted models can also be found in the Table.

Table 4: Relative goodness-of-fit test results (for Chiffchaff data)

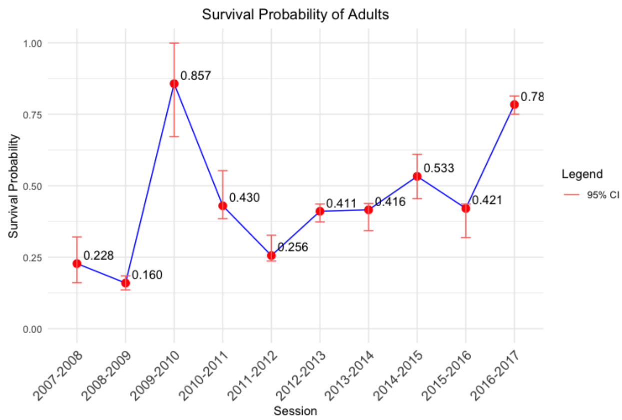
Model	No. of Parameters	AIC	BIC
$\phi_t, p(\text{constant})$	10	266.804	307.7849
$\phi_t(age), p(\text{constant})$	10	254.2895	295.2702
$\phi_t(age), p_t$	20	279.3091	361.2706

Among all of the three fitted models, the model with constant recapture probability and time-varying survival as a function of the age model($\phi_t(age), p(\text{constant})$) has the lowest AIC and BIC score and is considered to estimate the survival probabilities for both juvenile and adult chiffchaffs.

Figure 3 shows the estimated MLEs and 95% non-parametric bootstrap confidence intervals(CI) of the survival probabilities of both juveniles and adult chiffchaffs.



(a) Survival Probability Estimates for Juveniles



(b) Survival Probability Estimates for Adults

Figure 3: Survival Probability Estimates for Chiffchaff birds

The constant recapture probability for the chiffchaffs regardless of their age is $p = 0.192$, with a 95% Confidence interval(CI) of (0.116, 0.275).

The narrow confidence intervals in Figure 3 may indicate the low uncertainty in estimates MLEs for survival probabilities as compared to blackcaps. It is also evident that during the inter-winter period between the 2007-2008 and 2008-2009 sessions, chiffchaffs have a very low survival as compared to blackcap birds. Moreover, after the 2008-2009 inter-winter session there is a sudden increase in the survival probability for chiffchaffs. This may be due to changes in the habitat condition of the concerned species. Further investigation is needed to determine the cause of the survival during those periods. However, it is important to acknowledge that the chiffchaff data contains a relatively larger number of birds with unknown ages(i.e. 128) compared to other species, and these cases were subsequently excluded. As a result, the estimation of survival probabilities for chiffchaffs might be impacted by the bias introduced due to the exclusion of cases with unknown ages.

Model checking

Similarly, like the blackcap data, the chiffchaff dataset is converted to m-array by following the multinomial assumption in order to assess the absolute goodness-of-fit of the model. However, due to low expected values in some cells (i.e. < 5); the Pearson chi-square test cannot be applied. Hence, hosmer-lemeshow test is used, which gave a hosmer-lemeshow statistic of 0.652, with an associated p-value of

0.99. It suggests that the observed and expected frequencies are not significantly different from each other in each group. Hence, the null hypothesis cannot be rejected, and the considered model is a good fit for the chiffchaffs data.

4.3.3 Robin

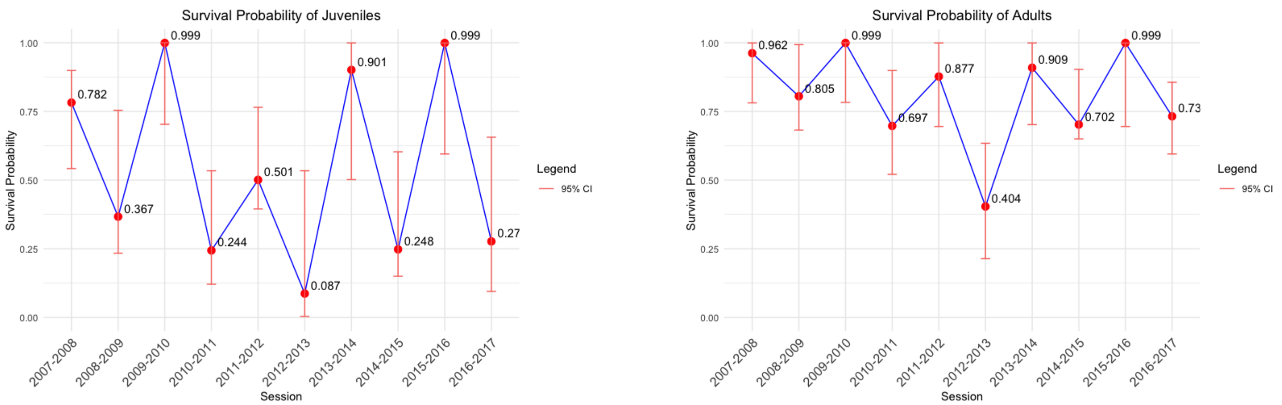
Table 5 displays various variations of the CJS model applied to robin bird data. The table also includes the associated AIC and BIC values for each model variation.

Table 5: Relative goodness-of-fit test results (for Robin data)

Model	No. of Parameters	AIC	BIC
$\phi_t, p(\text{constant})$	10	634.35	675.10
$\phi_t(age), p(\text{constant})$	10	624.82	665.58
$\phi_t(age), p_t$	20	631.77	713.28

From Table 5, it is evident that the model with survival as a function of age and constant recapture probability parameters has low AIC as well as BIC values. Hence, this model is used to estimate the survival probabilities for both adult and juvenile robin birds.

Figure 4 shows the MLEs and 95% non-parametric bootstrap confidence intervals for the estimated survival probabilities.



(a) Survival Probability Estimates for Juveniles

(b) Survival Probability Estimates for Adults

Figure 4: Survival Probability Estimates for Robin birds

The constant recapture probability for the robin birds regardless of the age is $p = 0.0759$ with a 95% Confidence interval(CI) of (0.033, 0.128). Furthermore, it can also be observed that during the inter-winter session of 2012-2013 both juveniles and adult robin birds have a very low survival probability as compared to other sessions. Moreover, the estimated MLEs for the survival probabilities of juveniles as well as adults have very wide confidence intervals(i.e. very high uncertainty). Although the data for robins is less sparse as compared to other datasets, this may indicate that there maybe other factors that are not being accounted for in the considered model. The unaccounted factors might encompass variations in behaviour, habitat preferences, or migration patterns that could impact the recapture rates of different age groups among robins.

Model checking

Similarly, as other datasets the observed and expected values do not follow the requirements of Pearson chi-square test. Hence, following the same reasoning hosmer-lemeshow test is applied to observed and expected frequencies; which gave a hosmer-lemeshow test statistic of 44.714 with a p-value of 1.042×10^{-6}. Therefore, the null hypothesis can be rejected and the considered model is not a good fit for the robin dataset. As a result, we can conclude that there appear to be other factors that are not being accounted for in the considered model.

4.4 Limitations

Several assumptions are considered when estimating survival probabilities using the CJS model. However, it's important to recognise that these assumptions may not always be valid in practical, real-world situations. The limitations of the study are outlined as follows:

- The considered models do not take into account the dead or permanently emigrated birds, hence can lead to biased survival estimates.

- It is also assumed that birds have a constant recapture probability during each session, regardless of their ages in each species, which is not always the case. Different age groups may have different behaviours, and habitat preferences, which can increase or hinder their recaptures during subsequent capture sessions.

- The study involves tagging individuals, with the assumption that tags are not lost during the study period. In practice, however, tags can be lost and individuals might go undetected during successive captures. Furthermore, if the bird gets injured during the tagging process, it will alter its mortality and can lead to biased survival estimates.

- There may be many unaccounted factors that affect survival such as average temperatures or disease prevalence during the winter seasons. Hence, the inclusion of these covariates might be helpful to estimate the accurate survival probabilities.

- It may be noted that the birds with unknown ages are removed from the analysis which might lead to biased survival estimates for the juveniles as well as adult birds.

5 Conclusion

In this report, we have estimated the survival probabilities for both juveniles and adults of three species of passerine birds: blackcap, chiffchaff, and robin. From the analysis, it is evident that across various species, the chances of survival during the early years are consistently lower when contrasted with the survival rates of the adult population. However, due to the absence of data related to average temperatures during the winter seasons between 2011 and 2013, the precise reason behind the decreased survival of blackcaps during that period could not be determined. Additionally, chiffchaffs showed a higher constant recapture probability as compared to blackcaps. Furthermore, except for the winter period between 2007 and 2008, chiffchaffs exhibited a consistent trend in their survival probabilities throughout the studied period. But in the case of robins, there may be some factors that have not been accounted for in the considered CJS models.

Further research is needed to understand how distinct age groups or genders might exhibit different behaviours in response to the capturing process in each species. Hence, it may be interesting to consider recapture probabilities as the function of age or gender. Additionally, further research can be done to include the unknown aged observed to see how they will affect the survival of the concerned species.

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Appendices

A More about Goodness-of-fit test Methods

A.1 Relative goodness-of-fit tests

A.1.1 AIC: Akaike's Information Criterion

For the relative goodness of fit check, AIC(Akaike's Information Criterion) is considered. AIC can be defined as

$$\text{AIC} = -2 \log L(\hat{\theta}_{\text{MLE}}) + \gamma \times \text{K}, \tag{A.1}$$

where $\log L(\hat{\theta}_{\text{MLE}})$ is the log likelihood evaluated at MLE of the parameter θ, and K represents the number of estimated parameters. Moreover, γ is the weight given to the complexity of the model. For our models, the value of γ is taken as 2.

A.1.2 BIC: Bayesian information criterion

BIC is also used to assess the relative goodness of fit test. BIC statistics can be calculated as follows:

$$\text{BIC} = -2 \log L(\hat{\theta}_{\text{MLE}}) + K \times \log(n), \tag{A.2}$$

where $\log L(\hat{\theta}_{\text{MLE}})$ is the log likelihood evaluated at MLE of the parameter θ, and K represents the number of estimated parameters. Moreover, n is the number of observations present in the data. The BIC's penalty term i.e. $K \times \log(n)$, discourages overly complex models by accounting for the number of parameters relative to the sample size.

A.2 Absolute goodness-of-fit test

A.2.1 Creating M-arrays

Open population models such as CJS(Cormack jolly seber) involve reparameterising the multinomial likelihood. Hence, each capture history can be considered as an element of multinomial distribution; which is independent of the different observations across different sessions. In order to assess how well the data fits to model, similar multinomial assumptions can be formulated by using the m-arrays in order to summarise the data. In m-arrays, the m_{ij} corresponds to the number of individuals released on capture occasion i and the next recapture on occasion $j+1$. Consider the capture-recapture data example from Morgan and McCrea's 2006 book Analysis of Capture-Recapture Data[10], section 9.3.1 in Table 6

Individual	**Capture history**				
	T1	**T2**	**T3**	**T4**	**T5**
1	0	1	0	1	1
2	0	1	0	1	0
3	1	1	0	1	1
4	1	1	1	1	1

Table 6: Example Data

In the above data, a total number of 2 birds are released at occasion T_1, out of which both individuals have been recaptured again in session T_2. Hence, cell $m_{1,2}$ in the m-array will be 2. Similarly, after session T_2, in session T_3 and T_4 individual 3 and 4 were recaptured again. But those are already accounted in session T_2, hence in the m-array there will 0 in $m_{1,3}$ and $m_{1,4}$ cells. Following this approach m-array for the above data is shown in Table 7.

The total number of birds that are **never captured** again can be obtained by subtracting the individuals released and recaptured from the total recaptures. Additionally, in order to convert the

Table 7: M-array

	Total captures	T_2	T_3	T_4	T_5	Never captured
T_1	2	2	0	0	0	0
T_2	4		1	3	0	0
T_3	1			1	0	0
T_4	4				3	1

m-arrays to probabilities, one can simply divide each cell with the respective total captures at each session row-wise. However, in age-dependent models, a single m-array might not be sufficient. Instead, it becomes necessary to construct distinct m-arrays based on various age classes.

A.2.2 Creating expected m-arrays

We can obtain the survival and recapture probabilities after maximising the log-likelihood with transformations such as inverse logit (e.g. equation 4.1) to obtain desired probabilities. Hence, the expected m-array can be modelled using these estimated probabilities. Since the considered model has a constant recapture probability(p) and the time-dependent survival probability. Table 8 shows how the detailed expected number of first recaptures following the release for each cell with 5 distinct capture occasions.

Total released	**Expected number of first recaptures following release**			
	j=2	**j=3**	**j=4**	**j=5**
R_1	$R_1\phi_1 p$	$R_1\phi_1(1-p)\phi_2 p$	$R_1\phi_1(1-p)\phi_2(1-p)\phi_3 p$	$R_1\phi_1(1-p)\phi_2(1-p)\phi_3(1-p)\phi_4 p$
R_2		$R_2\phi_2 p$	$R_2\phi_2(1-p)\phi_3 p$	$R_2\phi_2(1-p)\phi_3(1-p)\phi_4 p$
R_3			$R_3\phi_3 p$	$R_3\phi_3(1-p)\phi_4 p$
R_4				$R_4\phi_4 p$

Table 8: Expected m-array

The expected total number of birds that are never recaptured again can be calculated by subtracting the total released from the total expected number of first recaptures following the release. For example, for the first occasion the total of birds never recaptured again can calculated as follows:

$$R_1 - (R_1\phi_1 p + R_1\phi_1(1-p)\phi_2 p + R_1\phi_1(1-p)\phi_2(1-p)\phi_3 p + R_1\phi_1(1-p)\phi_2(1-p)\phi_3(1-p)\phi_4 p)$$

Furthermore, in order to obtain expected probabilities, we can divide each row i by the total number of releases i.e. R_i. Since the survival probabilities are considered a function of age a simple expected array will not full-fill the criterion to do the goodness of fit tests with the observed m-array. In order to account for both juveniles and adults, the expected arrays are pooled based on the survival probability of both age classes of the birds, and a suitable goodness of fit test can then be applied directly.

A.2.3 Hosmer-lemeshow Test

Although Hosmer-lemeshow(HL) is a goodness of fit test for the logistic regression model but can also be extended to multinomial logistic regression [5]. The m-arrays are created using the multinomial assumption such that each column of the m-array corresponds to a category of the multinomial outcome. While each row represents an independent multinomial distribution. Similarly, the expected m-arrays are constructed based on the same assumptions. The comparison between the m-arrays and the expected m-arrays forms the basis of the HL test, which evaluates the fit of the model to the observed data by assessing how closely the expected and observed frequencies align between g different groups. These g different bins can be considered as distinct multinomial outcomes.

Therefore, the Hosmer-Lemeshow test statistic for g different groups or bins can be defined as:

$$HL = \sum_{k=1}^{g} \sum_{j=0}^{c-1} \frac{(O_{kj} - E_{kj})^2}{E_{kj}} \tag{A.3}$$

Where:

- HL is the Hosmer-Lemeshow test statistic,
- g is the number of groups,
- c is the number of distinct categories,
- O_{kj} is the observed frequency in the k-th group and j-th cell,
- E_{kj} is the expected frequency in the k-th group and j-th cell.

The distribution of HL is chi-squared and has $(g - 2) \times (c - 1)$ degrees of freedom under the null hypothesis that the fitted model is the correct model and the sample size is large enough.

B Code and packages used

In this section, we provide a list of R programming language packages that are utilised for conducting the analysis.

Data Preprocessing: The "dplyr" and "tidyr" packages are used for data preprocessing tasks, facilitating data manipulation and organisation.

Visualisations: The "ggplot2" and "gridExtra" packages are utilised to generate graphical representations.

Model checking: The "ResourceSelection" library is used for conducting the Hosmer-Lemeshow goodness of fit test as part of model evaluation.

Code: The code employed for the analysis presented in this report can be accessed here:

https://github.com/kartik481/Birds