

## Survival, dispersal, and capture probability of male and female birds

Lilla Lovász<sup>a</sup>, Tobias Roth<sup>a</sup>, Zsolt Karcza<sup>b</sup>, Katalin Odett Lukács<sup>b</sup>, József Gyurácz<sup>c</sup>, Valentin Amrhein<sup>a,d</sup>

<sup>a</sup>Zoological Institute, University of Basel, Switzerland

<sup>b</sup>Ringling Centre, BirdLife Hungary, Budapest, Hungary

<sup>c</sup>Savaria Department of Biology, Eötvös Loránd University, Szombathely, Hungary

<sup>d</sup>Swiss Ornithological Institute, Sempach, Switzerland

\*Author for correspondence (lilla.lovasz@unibas.ch)

## Abstract

**In birds, observed adult sex ratios often are biased towards males. This bias could arise due to differences between sexes in dispersal or in detectability / catchability, but a preferred explanation has been sex differences in survival. However, most studies investigated apparent survival, in which differences in dispersal were not accounted for. Here, we used data from 24'830 captures of 11 bird species, collected at 40 Hungarian constant effort ringing sites, to estimate true survival, dispersal, and capture probability. On average, dispersal and capture probabilities were similar between sexes. However, the probability to survive from one year to the next was 0.46 in males but only 0.37 in females, suggesting that higher female mortality may indeed be the most important predictor of male-biased adult sex ratios.**

## 1. Introduction

In many bird species, males seem to outnumber females, resulting in male-biased adult sex ratios [1, 2]. If the proportion of adult males in a population is higher than that of females, this has implications for the evolution of life history strategies, population dynamics and sex roles, as well as for wildlife conservation [2-4].

One of the most likely causes of biased adult sex ratios are differences in survival between sexes [2, 5, 6], which may arise, for example, because of sex differences in parental investment [7], in mating competition [8], or predation [9].

Studies on adult sex ratios in birds are often based on capture-recapture data from bird ringing schemes [1], in which differences between sexes in catchability, i.e., in probability of capture, can be accounted for [10]. However, accounting for catchability might not be sufficient because

there are still two possibilities for the fate of a non-recaptured bird: it may either have dispersed or died [11, 12]. Apparent survival, which is the probability that an individual survives from one year to the next and returns to the same study site [13-15], may thus not equal true survival, which is the probability that a bird survives, wherever it is located [11]. Unless dispersal is zero and its complement, site fidelity, equals one, apparent survival will be lower than true survival [15]. In a recent review, Ancona et al [16] therefore argued that studies on adult sex ratios need to take dispersal into account.

Here, we used capture-recapture data from 11 bird species and from 40 Hungarian constant effort ringing sites to investigate possible predictors of observed adult sex ratios in European breeding birds. We applied a multi-state capture-recapture model in a Bayesian framework to estimate capture probability (the probability that an already ringed bird is captured again), site fidelity (the probability that a bird stayed at the site of capture from one year to the next), and true survival (the probability that a bird survived, regardless of its location).

## **2. Materials and methods**

### **2.1. Data and observed sex ratios**

Data are from a constant effort ringing scheme on passerine and near passerine bird species, using 40 ringing sites spread over Hungary, spanning 12 years (2004 to 2015). Sites were merged when they were closer than 1 km to each other; in four cases, two sites were thus merged, resulting in a final sample of 36 sites (figure 1).

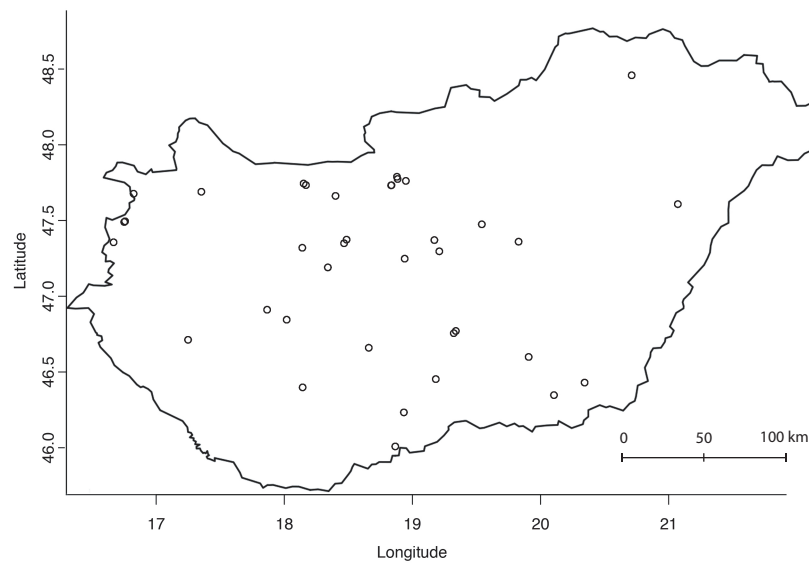


Figure 1. Locations of the 40 investigated constant effort bird ringing sites in Hungary. In four cases, two sites were merged because they were closer than 1 km to each other, resulting in a final sample of 36 sites (circles).

According to the Hungarian protocol, birds were ringed during about 9 sessions that were separated by at least five days, covering the breeding period (mid-April to early July). Ringing sessions lasted from sunrise to noon, and numbers, locations, types, and lengths of mist nets were held constant.

From the 26 species with more than 100 recaptured individuals, we selected 11 species (figure 2) in which the sex is most easily determined by plumage. We thus excluded species in which sex determination is only possible by examining broodpatch or cloacal protuberance. The data comprise 24'830 events of capture, from which 1.24% did not include information on sex determination. Our final data set comprises 19'349 captured adult individuals (EURING age code 2, 4, 5 or 6; [17]), of which 16.6% were recaptured at least once; 63 individuals dispersed and were recaptured at sites other than the site of capture. Numbers of capture events (including recaptures) / of captured individuals per species were the following: European greenfinch (*Chloris*

*chloris*): 2097 / 2004; Hawfinch (*Coccothraustes coccothraustes*): 1113 / 1061; Great spotted woodpecker (*Dendrocopos major*): 372 / 267; Yellowhammer (*Emberiza citrinella*): 530 / 463; Common reed bunting (*Emberiza schoeniclus*): 1086 / 879; Common chaffinch (*Fringilla coelebs*): 1334 / 1145; Red-backed shrike (*Lanius collurio*): 1089 / 859; Bearded reedling (*Panurus biarmicus*): 2833 / 2333; Great tit (*Parus major*): 2200 / 1657; Eurasian blackcap (*Sylvia atricapilla*): 9027 / 6766; Common blackbird (*Turdus merula*): 2840 / 1915.

We defined observed adult sex ratios as the number of capture events of adult males divided by number of total capture events of both adult males and females (see, e.g., [2]).

## 2.2. Model description

To estimate survival, dispersal, and capture probability, we took the multi-event model by Lagrange et al [18] as a starting point and reformulated it as a state-space model in a Bayesian framework [19], slightly changing the parametrization as we describe below. One of the advantages of state-space models in a Bayesian framework is that latent states (unobserved states of an animal such as "alive but dispersed from the study site" or "dead") can be directly estimated without the need to define how the visible layer (the events, e.g., the events of capture) relates to the hidden layer (the unobserved states). See Gimenez et al [20] for an explanation of the differences between the multi-event approach sensu Pradel [21], which is usually applied in a frequentist framework, and the state-space approach that is usually applied in a Bayesian framework. We call our model a multi-state model for the sake of simplicity, although other names might be used as well: it is a multi-event model [21], because not all states can be observed; it is a Hidden Markov model [21], because the next state depends only on the current state; it is a state-space model, as mentioned above; it is essentially a capture-recapture

model; and it is an extension of a Cormack–Jolly–Seber [22-24] model that allows estimation of transition between states, i.e., it is a multi-state model.

Our general aim was to describe whether, from one year to the next, a bird stayed at the site where it was marked or dispersed, and whether it survived or died. Our model allowed assigning estimated probabilities to such changes of states, e.g., for changing from the state "alive and at the site of capture" or "alive but dispersed" to "dead".

The model was applied to each of the eleven bird species separately, taking into account only ringed birds, i.e., birds that have already been captured (birds that were not ringed were not considered in our model; to make general conclusions including unmarked birds we need to assume that marked birds had the same survival probability and site fidelity as unmarked birds). Thus, the model described the state of an individual for each year after the year it has been captured the first time and has been marked: An individual could be alive at the site where it was marked (state 1), it could be alive at another site (i.e., it dispersed from the site where it was marked; state 2), or it could be dead (state 3). By definition, the state of an individual in the year it has been captured the first time was set to 1.

We used a Bernoulli distribution to describe whether a bird was captured or not captured in a given year, and capture probability could differ between the sexes, states, years and sites of capture; we thus assumed that all other factors such as wind, rain, time of the season had no effect on capture probability. However, even by making this strong assumption we would still have to estimate 2592 different capture probabilities, i.e., for 2 different sexes \* 3 different states \* 12 years of study \* 36 study sites.

We thus had to make further assumptions to reduce the number of parameters: For individuals in state 1 (alive and at the site where it was marked), we assumed that capture probability was the same across sites and years and only varied according to sex and to the number of ringing sessions per year and per site (thus depending on capturing effort). This is our definition of "capture probability of state 1 individuals". For individuals in state 2 (alive but dispersed from the site where they were marked), we assumed that capture probability was the same across sites, years and between sexes, and depended only on the probability that the birds had settled at a part of the country where there was another constant effort ringing site (and not at a place where birds are not captured and ringed. This is our definition of "capture probability of state 2 individuals", which we call "availability". For individuals in state 3 (dead), we assumed that the individual could not be captured. Thus, the capture probability of state 3 individuals was set to 0, and no additional parameter was needed. An additional assumption was that dispersed birds had the same survival probability as birds that remained at the site where they were first ringed.

With the above explained states (1: alive at the site where a bird was marked; 2: dispersed from the site where it was marked; 3: dead) we defined state-histories for each individual per year, during the study period of 12 years (e.g., 1,1,1,3,3,3,3,3,3,3,3,3; state-histories were defined from the year an individual was captured the first time, thus for most individuals the histories did not contain 12 numbers). Note that we thus assumed that states did not change within the season. This means for example that we assumed that birds do not die within a breeding season. To describe how the states changed from year to year we used a categorical distribution with one probability for each of the three states that summed to 1 (because all

individuals needed to be in one of the three states). This means that we assumed that no other state was possible. A potentially important state that is thus not considered in our model are individuals during migration (transients); we assume such transients did not occur (see discussion).

We described whether and how individuals changed states from year to year considering only the two parameters survival and site fidelity that could however differ between males and females. A state 1 individual retained state 1 if it survived from one year to the next and remained at the same site at which it was first captured (= survival probability \* site fidelity; note that the product of these two parameters is often considered as a single parameter called "apparent survival"); an individual changed from state 1 to state 2 if it survived and changed to a different site (= survival probability \* (1 – site fidelity)); and an individual changed from state 1 to state 3 if it died (= 1 – survival probability). A state 2 individual either retained state 2 if it survived from one year to the next (survival probability) or it died (1 – survival probability). We thus assumed that dispersed individuals did not disperse back to the original site where they were captured (i.e., a change from state 2 to state 1 had a probability of 0). Finally, state 3 individuals remained in state 3 with probability of 1.

To summarize, the following parameters were defined in our model: capture probability of state 1 individuals ( $p$ , sex-specific): the probability that an already ringed individual that was alive and present at the site where it was ringed was captured during a ringing session; capture probability of state 2 individuals or availability ( $\psi$ , same for both sexes): the probability that a dispersing individual settles again at a constant effort ringing site and will be captured again at this site; site fidelity ( $\lambda$ , sex-specific): the probability that an individual that survived from year  $t$ -



1 to  $t$  remained at the site of capture; and true survival ( $S$ , sex-specific): the probability that an individual survived from year  $t-1$  to  $t$ , regardless of whether it has dispersed or not.

Model parameters were estimated based on Markov Chain Monte Carlo (MCMC) algorithms applied in JAGS 3.3.0, using R [25] via the R package rjags [26]. We used priors with uniform distribution (0, 1) for capture probability ( $p$ ), site fidelity ( $\lambda$ ), availability ( $\psi$ ), and true survival ( $S$ ). Posterior distributions of the parameters were obtained using MCMC simulations, based on two parallel chains with 60'000 iterations each; we discarded the first 30'000 values and thinned the remainder by using every 30<sup>th</sup> value. Convergence was assessed using the Gelman-Rubin diagnostic [27]. We used the means of the simulated values of the posterior distributions as point estimates of the parameters, and 2.5% and 97.5% quantiles as 95% Bayesian credible intervals. We interpreted credible intervals as compatibility intervals [28, 29].

### **2.3. Declaration of reporting decisions**

When starting to develop our model, we initially aimed to estimate the local population sizes at the study sites following Amrhein et al [10], which would be necessary to directly estimate sex ratios (i.e., to estimate the proportion of males in the populations). For that we would need to account for individuals that were never captured; and because spatial behaviour and thus the effective sample areas probably vary between females and males, we would need to account for the spatial distribution of captures using spatially explicit models [30, 31]. This was not feasible for this study because the precise coordinates of every single mist net could not be determined.

We thus decided to abandon the aim of estimating local population sizes and instead aimed for improving the estimates of sex-specific survival by accounting for dispersal. Using our approach, we thus avoided the problems with estimating accurate sex-specific population sizes.

Other than that, there was no model selection, and we developed the model as described above.

Because conventional model selection based on threshold criteria like p-values, Bayes factors, or AIC, and selection of results for interpretation based on p-values usually leads to inflated point estimates or to questionable "proofs of the null hypothesis" [28, 32], we present no tests for statistical "significance". All effect sizes that were calculated are also presented in this paper, and thus there was little or no selective reporting of results based on study outcomes.

### 3. Results

We here summarize the results across the 11 species. For details on single species, see figures 2 and 3, and <https://github.com/TobiasRoth/CES-Hungary>.

The observed adult sex ratio was  $0.58 \pm 0.065$  (average of 11 bird species  $\pm$  SD) and was male-biased in 9 and female-biased in 2 species (figure 2).

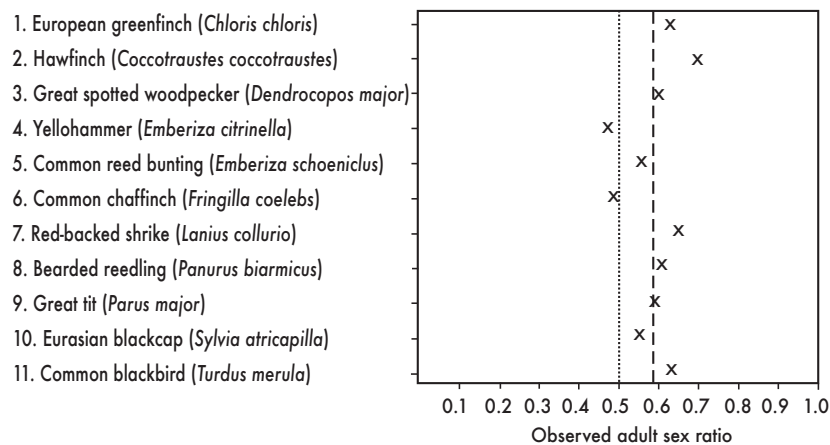


Figure 2. Observed adult sex ratio (proportion of males) in 11 European bird species. Dotted line: sex ratio of 0.5. Dashed line: average sex ratio among the 11 species.

We found an average capture probability (figure 3a) of 0.023 ( $\pm$  0.013) in males and of 0.029 ( $\pm$  0.023) in females. In three species, the probability to capture a male was higher than to capture

a female, while in six species, it was more likely to capture a female; note that in five of those six species, the credible intervals indicate that also male-biased capture probabilities are compatible with the data, given our model. The average posterior probability that capture probability of males is higher than that of females was  $0.51 \pm 0.36$  (and thus the probability that capture probability is higher in females was  $0.49 \pm 0.36$ ), suggesting that overall capture probability was similar in the sexes of the 11 species.

Average site fidelities (figure 3b) were  $0.79 (\pm 0.04)$  in males and  $0.74 (\pm 0.086)$  in females but could be as low as 0.2 in some species, according to the wide credible intervals. Overall, the posterior probability that site fidelity of males is higher than of females was  $0.55 (\pm 0.21)$  (and  $0.45 \pm 0.21$  vice versa), suggesting that on average, site fidelity was rather similar in both sexes.

Survival (figure 3c), corrected for capture probability and site fidelity, was higher in males than in females in 9 species, and the credible intervals indicate generally higher values for male survival than for female survival. Average probabilities that birds survive from one year to the next were  $0.46 (\pm 0.11)$  in males and of  $0.37 (\pm 0.11)$  in females. Accordingly, the probability that true survival of males is higher than of females was  $0.71 (\pm 0.21)$  (and  $0.29 \pm 0.21$  vice versa), suggesting that average true survival was higher in males than in females in the 11 species.

In the  $n = 11$  species, the correlations with the observed adult sex ratio were  $r = -0.38$  ( $p = 0.24$ ) for capture probability (meaning that observed sex ratio was slightly male-biased when capture probability was female-biased),  $r = 0.08$  ( $p = 0.80$ ) for site fidelity, and  $r = 0.12$  ( $p = 0.72$ ) for true survival (meaning that site fidelity and true survival were slightly male-biased when observed sex ratio was male-biased).

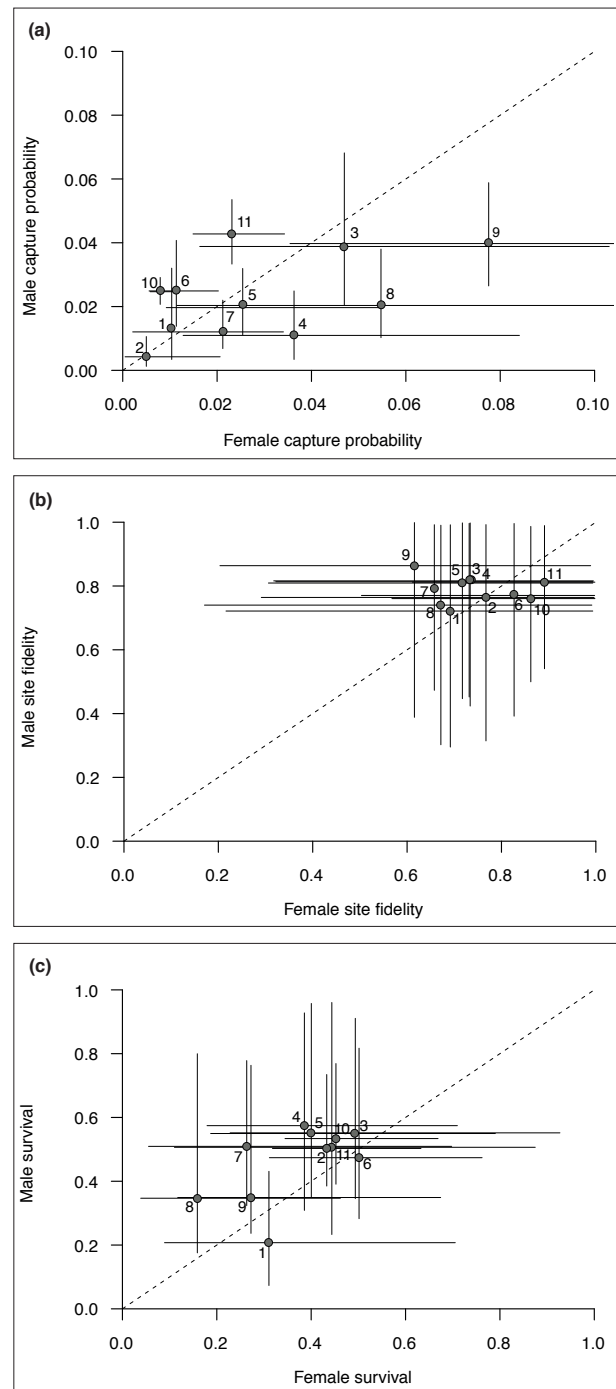


Figure 3. Probabilities of (a) capture (per ringing session), (b) site fidelity, and (c) true survival of males and females in 11 European bird species. Horizontal and vertical lines are 95% Bayesian credible intervals, and dashed lines indicate equal probabilities in the sexes. For numbers of species names, see figure 2.

#### 4. Discussion

Among 19'349 adult birds captured at 36 Hungarian study sites, 58% were males. Our overall observed adult sex ratio was thus similar to observed sex ratios in literature reviews by Donald (57%) and Szekely (55%) [1, 2]. We estimated sex differences in three factors that could potentially influence observed adult sex ratios: capture probability (catchability), dispersal, and true survival.

With an average of about 3%, capture probability was generally low in the 11 investigated species. We found clear male bias in capture probabilities of three species, among them Blackbirds and Blackcaps, which also had male-biased capture probabilities in a French constant effort ringing site [10]. The other species either showed relatively balanced capture probabilities or a moderate female bias, so that over all 11 species, capture probability was similar in both sexes. While this contradicts earlier notions that male birds are generally more likely to be captured than females [6, 33], our findings suggest that in the investigated 11 species, differences in capture probability do not sufficiently explain why the observed adult sex ratio was male-biased.

We estimated that on average, about one quarter of adult individuals dispersed from the site of first capture. An accurate estimate of survival would therefore need to take dispersal into account. In birds, females are usually the more dispersing sex [34, 35]. If females disperse outside the range of the local males, they become lost for the particular population, leading to male-biased adult sex ratios [36, 37]. However, Dale [36] and Szekely et al [2] argue that if emigrating females find other habitat patches occupied by the species, emigration from one site and immigration to another site should cancel out on a meta-population level. This effect will possibly

act on the local population level as well, since some individuals of the dispersing sex will emigrate from the sampling area, while others will immigrate into it [10]. Thus, sex-specific emigration would probably affect small and isolated populations most severely [36]. We found little evidence that dispersal, or its complement, site fidelity, differs between sexes in the investigated species. In our study, it therefore seems likely that dispersal is either similar between sexes or that sex-specific emigration and immigration rates do indeed cancel out on the larger scale.

Among the three examined factors, only true survival showed, on average, remarkable differences between sexes, and in all but two species (Greenfinch and Chaffinch), point estimates on true survival were male-biased. Our study thus supports previous suggestions that female-biased mortality may be the most important explanation for male-biased adult sex ratios in birds [e.g. 2, 5, 7]. While those earlier studies investigated apparent survival (i.e., the product of survival and dispersal), we showed that in our 11 investigated bird species, true survival was higher in males than in females.

A potentially important factor that could bias the results of sex ratio estimations is the occurrence of individuals during migration, i.e. transients [discussed in 10]. However, transients are unlikely to be captured during more than one ringing session, and since we took into account only those birds that were captured more than once, we do not expect that transients would bias our results.

Our model could be applied to data from constant effort ringing sites from other countries and on other species. However, the validity of any conclusions from our model depends on a large amount of assumptions (see section 2.1.), most of which are debatable to some degree [see, e.g., 28]. Some of the assumptions seemed necessary to simplify our model for the present

study, for example that capture probability, site fidelity, availability, and true survival are constant across sites and years. How such assumptions affect survival estimates could be the starting point for further studies.

Furthermore, with 11 investigated species that were selected because the sex is easily determined by plumage, it was so far not possible to reliably estimate whether differences among species in true survival, dispersal, or capture probability correlate with differences among species in the observed adult sex ratio. Based on our results, however, we predict that a higher true survival in male than in female birds is related to a male-biased adult sex ratio.

#### **Data accessibility**

Data and the R code are available on a public repository: <https://github.com/TobiasRoth/CES-Hungary>.

#### **Authors' contributions**

LL., T.R. and V.A. designed the research; L.L., Zs.K., K.O.L. and J.Gy. helped in data collection and prepared the dataset; T.R. performed statistical analyses; L.L., T.R. and V.A. wrote the first version of the paper [38] and the revisions. All authors gave final approval for publication and agreed to be held accountable for the content of this article.

#### **Competing interests**

Zs.K. and K.O.L. are employed by BirdLife Hungary.

**Funding**

Financial support was provided by the Swiss National Science Foundation (grant no. 156294), the Swiss Association Pro Petite Camargue Alsacienne, the Fondation de bienfaisance Jeanne Lovioz and the MAVA Foundation. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Research and Animal Ethics**

We were not required to complete an ethical assessment prior to conducting our research.

**Permission to carry out fieldwork**

Fieldwork was carried out in the framework of the Constant Effort Site ringing scheme of the Ringing Centre of BirdLife Hungary. Permission was given by the Hungarian National Inspectorate for Environment and Nature under the registration number 14/3858-9/2012.

**Acknowledgements**

We thank the ringers and their helpers who collected the data, and two referees as well as Fränzi Korner-Nievergelt and Jacques Laesser for discussions and comments.



## References

1. Donald PF. Adult sex ratios in wild bird populations. *Ibis*. 2007;149(4):671-92.
2. Szekely T, Liker A, Freckleton RP, Fichtel C, Kappeler PM. Sex-biased survival predicts adult sex ratio variation in wild birds. *Proceedings of the Royal Society -Biological Sciences*. 2014;281(1788):8.
3. Liker A, Freckleton RP, Szekely T. The evolution of sex roles in birds is related to adult sex ratio. *Nat Commun*. 2013;4:6.
4. Kokko H, Jennions MD. Parental investment, sexual selection and sex ratios. *J Evol Biol*. 2008;21(4):919-48.
5. Breitwisch R. Mortality Patterns, Sex Ratios, and Parental Investment in Monogamous Birds. *Current Ornithology*. 6.1989. p. 1-50.
6. Donald PF. Lonely males and low lifetime productivity in small populations. *Ibis*. 2011;153(3):465-7.
7. Liker A, Szekely T. Mortality costs of sexual selection and parental care in natural populations of birds. *Evolution*. 2005;59(4):890-7.
8. Roff D. *Life History Evolution*. Sunderland, Mass.: Sinauer Associates; 2002.
9. Post P, Gotmark F. Foraging behavior and predation risk in male and female Eurasian Blackbirds (*Turdus merula*) during the breeding season. *Auk*. 2006;123(1):162-70.
10. Amrhein V, Scaar B, Baumann M, Minery N, Binnert JP, Korner-Nievergelt F. Estimating adult sex ratios from bird mist netting data. *Methods Ecol Evol*. 2012;3(4):713-20.
11. Sandercock BK. Estimation of demographic parameters from live-encounter data: a summary review. *J Wildl Manage*. 2006;70(6):1504-20.
12. Pakanen VM, Lampila S, Arppe H, Valkama J. Estimating sex specific apparent survival and dispersal of Little Ringed Plovers (*Charadrius dubius*). *Ornis Fenn*. 2015;92(4):172-86.

13. Pradel R, Hines JE, Lebreton JD, Nichols JD. Capture-recapture survival models taking account of transients. *Biometrics*. 1997;53(1):60-72.
14. Roth T, Amrhein V. Estimating individual survival using territory occupancy data on unmarked animals. *J Appl Ecol*. 2010;47(2):386-92.
15. Taylor CM, Lank DB, Sandercock BK. Using local dispersal data to reduce bias in annual apparent survival and mate fidelity. *Condor*. 2015;117(4):598-608.
16. Ancona S, Denes FV, Kruger O, Szekely T, Beissinger SR. Estimating adult sex ratios in nature. *Philos Trans R Soc B-Biol Sci*. 2017;372(1729):15.
17. Speek G, Clark JA, Rohde Z, Wassenaar RD, Van Noordwijk AJ. The EURING exchange-code 2000. Heteren; 2001.
18. Lagrange P, Pradel R, Belisle M, Gimenez O. Estimating dispersal among numerous sites using capture-recapture data. *Ecology*. 2014;95(8):2316-23.
19. Gimenez OR, V. Choquet, R. Dehais, C. Doris, B. Varella, H. Vila, J.-P. Pradel, R. State-space modelling of data on marked individuals. *Ecol Model*. 2007;206:431-8.
20. Gimenez O, Lebreton, J. D., Gaillard, J. M., Choquet, R., & Pradel, R. . Estimating demographic parameters using hidden process dynamic models. *Theoretical population biology*. 2012;82(4):307-16.
21. Pradel R. Multievent: An Extension of Multistate Capture–Recapture Models to Uncertain States. *Biometrics*. 2005;61:442–7.
22. Cormack RM. Estimates of survival from sighting of marked animals. *Biometrika*. 1964;51(3-4):429-438.
23. Jolly GM. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika*. 1965;52:225-247.
24. Seber GAF. A Note on the Multiple-Recapture Census. *Biometrika*. 1965;52(1/2):249-59.

25. RCoreTeam. A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2016.
26. Plummer M. rjags: Bayesian Graphical Models using MCMC. R package version 4-6. 2016.
27. Brooks SP, Gelman A. General methods for monitoring convergence of iterative simulations. *J Comput Graph Stat.* 1998;7(4):434-55.
28. Amrhein V, Trafimow, D., Greenland, S. Inferential Statistics as Descriptive Statistics: There is No Replication Crisis if We Don't Expect Replication. *The American Statistician*, in press. 2018.
29. Greenland S. Valid P-values behave exactly as they should: Some misleading criticisms of P-values and their resolution with S-values. *The American Statistician*, in press. 2018.
30. Borchers DL, Efford MG. Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics.* 2008;64(2):377-85.
31. Royle JA, Young KV. A hierarchical model for spatial capture-recapture data. *Ecology.* 2008;89(8):2281-9.
32. Amrhein V, Korner-Nievergelt F, Roth T. The earth is flat ( $p > 0.05$ ): significance thresholds and the crisis of unreplicable research. *Peerj.* 2017;5:40.
33. Mayr E. The sex ratio in wild birds. *Am Nat.* 1939;73:156-79.
34. Greenwood PJ. Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav.* 1980;28(NOV):1140-62.
35. Clarke AL, Saether BE, Roskaft E. Sex biases in avian dispersal: A reappraisal. *Oikos.* 1997;79(3):429-38.
36. Dale S. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. *Oikos.* 2001;92(2):344-56.
37. Steifetten O, Dale S. Viability of an endangered population of ortolan buntings: The effect of a skewed operational sex ratio. *Biol Conserv.* 2006;132(1):88-97.

38. Lovász L, Roth T, Karcza Z, Lukács KO, Gyurácz J, Amrhein V. Survival, dispersal, and capture probability of male and female birds. PeerJ Preprints; 2018. Report No.: 2167-9843.