

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

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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 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 in both 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.

Keywords: true survival, site fidelity, dispersal, capture probability, constant effort site (CES)

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, 3]. One of the most likely causes of biased adult sex ratios is differences in survival between sexes [2, 4, 5], which may arise, for example, because of sex differences in parental investment [6], in mating competition [7], or predation [8].

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 [9]. After correcting for catchability, there are two possibilities for the fate of a non-recaptured bird: it may either have dispersed or died [10]. Apparent survival, which is the probability that an individual survives from one year to the next and returns to the same study site [11-13], may thus not equal true survival, which is the probability that a bird survives, wherever it is located [10].

Unless dispersal is zero and its complement, site fidelity, equals one, apparent survival will be lower than true survival [13]. In a recent review, Ancona et al. [14] therefore argued that studies on adult sex ratios need to take dispersal into account. Based on capture-recapture data from 11 bird species and from 40 Hungarian constant effort ringing sites, we estimated capture probability, site fidelity, and true survival as possible predictors of observed adult sex ratios in European breeding birds.

2. Materials and methods

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 study sites.

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 26 species with more than 100 recaptured individuals, we selected 11 species (Fig. 1) 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; [15]), of which 16.6% were recaptured at least once; 63 individuals dispersed and were recaptured at sites other than the site of capture.

We adapted a multi-state capture-recapture model by Lagrange et al. [16], describing the fate of an individual for each year after the year it has been captured the first time. An individual can be alive at the site of capture (state 1), alive at another site after dispersal (state 2), or dead (state 3). To describe how individuals change states, the following parameters were defined: the probability that an individual survived from year $t-1$ to t , regardless of whether it has dispersed or not, was true survival (S); the probability that from year $t-1$ to t , an individual remained at the site of capture was site fidelity (λ); the probability that after dispersal, an individual has settled at one of our study sites was availability (ψ); and the probability that an individual that was alive and present at a study site was captured during a ringing session was capture probability (p).

Transition probabilities between states were described as follows: An individual retained state 1 if it survived from year $t-1$ to t and remained at the same site at which it was first captured, with probability $S\lambda$. It changed from state 1 to state 2 if it survived and changed to a different site, with probability $S(1-\lambda)$. It changed from state 1 to state 3 if it did not survive, with probability $1-S$. We assumed that dispersed individuals (state 2) did not return to the site of capture, meaning that transition probability from state 2 to state 1 was set to zero. An individual in state 2 (dispersed) therefore retained state 2 if it survived with probability S , while an individual with state 2 changed to state 3 if it died (with probability $1-S$). Finally, dead individuals were assumed to remain dead, thus the probability that an individual changed from state 3 to 1 or 2 was set to zero, and the probability that an individual with state 3 remained at state 3 was set to one.

Model parameters were estimated in a Bayesian framework, based on Markov Chain Monte Carlo (MCMC) algorithms applied in JAGS 3.3.0, using R [17] via the R package rjags [18]. We used priors with uniform distribution (0, 1) for true survival (S), site fidelity (λ), availability (ψ) and capture probability (p). 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 30th value. Convergence was assessed using the Gelman-Rubin diagnostic [19]. 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.

3. Results

The observed adult sex ratio was 0.58 ± 0.065 (average of 11 bird species \pm SD) and was male-biased in 9 and slightly female-biased in 2 species (Fig. 1).

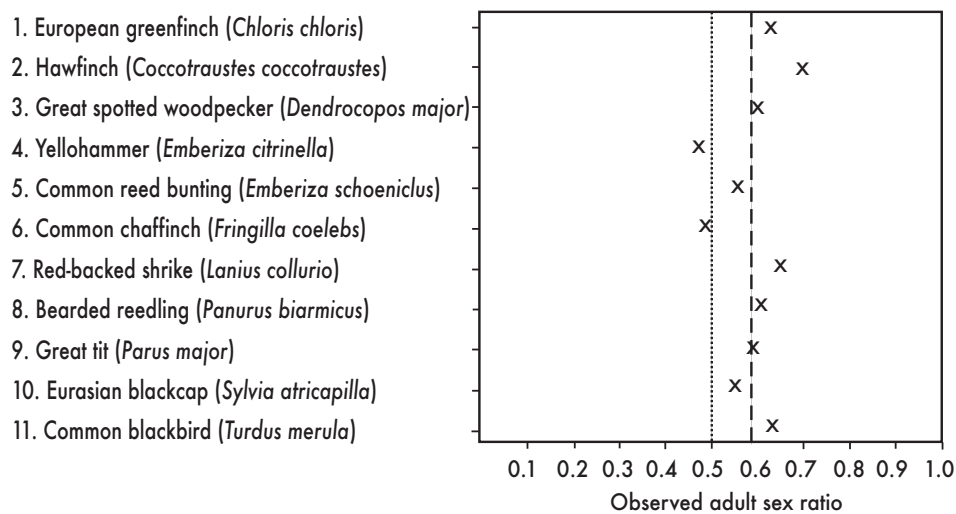


Figure 1. Observed adult sex ratio (proportion of males) in 11 European bird species. Dotted line: sex ratio of 0.5. Dashed line: average sex ratio of the 11 species.

We found an average capture probability (Fig. 2a) 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. The average posterior probability that capture probability of males is higher than that of females was 0.51 ± 0.36 (and thus the probability that capture probability is higher in females was 0.49), suggesting that overall capture probability was similar in the sexes of the 11 species.

Average site fidelities (Fig. 2b) 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. On average, the posterior probability that site fidelity of males is higher than that of females was $0.55 (\pm 0.21)$ (and 0.45 vice versa), suggesting that overall site fidelity was rather similar in both sexes.

Survival (Fig. 2c), 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 $0.37 (\pm 0.11)$ in females. Accordingly, the average probability that true survival of males is higher than that of females was $0.71 (\pm 0.21)$ (and 0.29 vice versa), suggesting that overall 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 the 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 the observed sex ratio was slightly male-biased when site fidelity and true survival were male-biased).

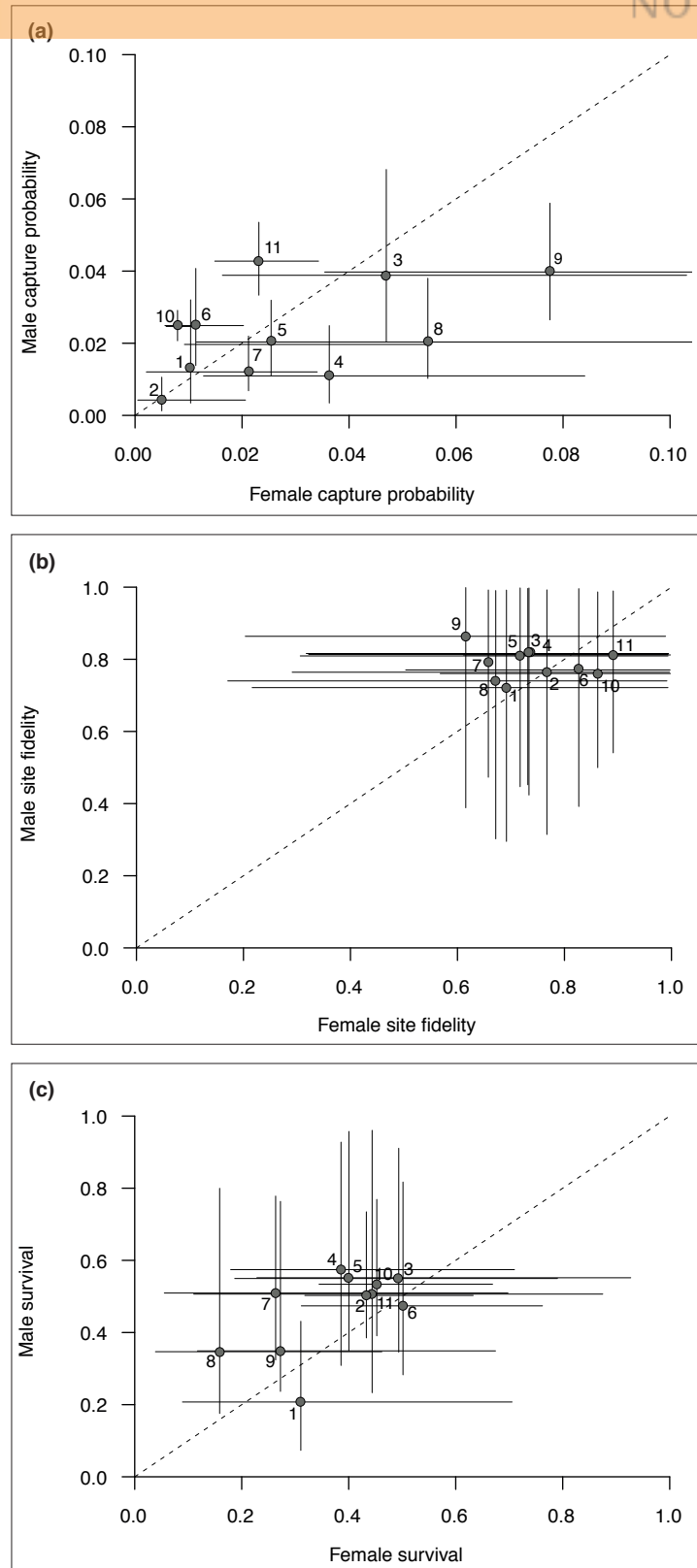


Figure 2. Probabilities of (a) capture (per ringing session), (b) site fidelity, and (c) true survival of males and females in 11 European bird species. Horizontal and vertical lines are 95% Bayesian credible intervals, and dashed lines indicate equal probability of the sexes. For numbers and species names, see Fig.1.

4. Discussion

Among 19'349 adult birds captured at 40 Hungarian study sites, 58% were males. Our overall observed adult sex ratio was thus similar to the 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 [9]. 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 [5, 20], 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 true survival would therefore need to take dispersal into account. However, we found little evidence that dispersal, or its complement, site fidelity, differs between sexes in the investigated species.

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 [2, 4, 6]. While those earlier studies investigated apparent survival, we showed that at least in our 11 investigated bird species, also true survival that is corrected for differences between sexes in capture probability and dispersal was higher in males than in females.

Our model could be applied to data from constant effort ringing sites from other countries and on other species. 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 catchability 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 analyses are available as supplementary material:

<https://github.com/TobiasRoth/CES-Hungary>.

Authors' contributions

L.L., T.R. and V.A. designed the research; L.L., Zs.K., K.O.D. and J.Gy. helped in data collection and prepared the dataset; T.R. performed statistical analyses; L.L., T.R. and V.A. contributed to the writing of the original manuscript and revisions. All authors gave final approval for publication and agreed to be held accountable for the content of this article.

Competing interests

The authors have no competing interests.

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Permission to carry out fieldwork

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