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Estimating adult sex ratios from bird mist netting data

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Summary

1. It is increasingly acknowledged that skewed adult sex ratios (ASRs) may play an important role in ecology, evolution and conservation of animals.

2. In birds, published estimates on ASRs mostly rely on mist netting data. However, previous studies suggested that mist nets or other trap types provide biased estimates on sex ratios, with males being more susceptible to capture than females.

3. We used data from a Constant Effort Site ringing scheme to show how sex ratios that are corrected for sex- and year-specific capture probabilities can be directly estimated by applying capture–recapture analysis, for example, in a Bayesian framework.

4. When capture data were pooled from the 19 years of study, we found that in the blackbird (*Turdus merula*) and the blackcap (*Sylvia atricapilla*), the observed proportions of males were 57% and 55%, respectively. However, when the observed annual proportions of males were corrected for the sex-specific capture probabilities, the proportions of males did not clearly differ from 50% in most study years, and thus, the apparent male-bias in the ASRs almost completely disappeared.

5. We propose that published estimates on ASRs in birds should be re-evaluated if based solely on observed sex ratios from mist netting studies.

6. We further propose that data from national bird ringing schemes and in particular from Constant Effort Site ringing programs can provide valuable information on ASRs, if analysed using capture–recapture models. We discuss important assumptions of those models; for example, movements that may differ between sexes should be taken into account, as well as the occurrence of transient individuals that do not hold breeding territories within a study site.

Key-words: Adult sex ratio, Bayesian analysis, capture probability, detectability, mark-recapture

Introduction

Skewed adult sex ratios (ASRs) have important consequences for ecology, evolution and conservation of animals. The ASR is defined as the proportion of adults in a population that are male (Wilson & Hardy 2002) and is one of the key parameters responsible for the control of sexual selection (Parker & Simmons 1996). Via its effect on the operational sex ratio (the ratio of sexually active males to fertilisable females), the ASR is thought to influence mating systems and arrival time from migration in birds (Kokko *et al.* 2006; Kokko & Jennions 2008; Veran & Beissinger 2009). A male-biased ASR should be taken into account in conservation actions; for example, in bird populations with many unpaired males, the effective population sizes are likely over-estimated because the number of breeding pairs is lower than the number of singing males recorded during breeding bird surveys (Newson *et al.* 2005; Amrhein *et al.* 2007). Furthermore, a shortage of females can have vital consequences for endangered bird populations (Lawrence *et al.* 2008; Dale 2011). In globally threatened species, the sex ratio distortion seems to be often larger than in non-threatened species, suggesting that their extinction risk could be higher than currently estimated (Donald 2007).

However, as Kosztolányi *et al.* (2011) put it, the ASR is notoriously difficult to estimate in the wild, except in population studies where all or most animals are individually marked. When the ASR is obtained from simple counts of males and females, estimates are often biased owing to differences in detectability between the sexes (Donald 2011). Evidently, the

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males of most temperate zone songbirds are much easier heard or seen than the females because of their song and of other territorial displays, because of their often brighter plumage colours, because females take the bulk of incubation duties, or because of sex differences in habitat preferences.

Capturing birds using mist nets usually has some advantages over visual and aural population monitoring techniques: counts are not subject to a strong observer bias, netting effort is easily standardised, and the sex of many species is clearly recognised in the hand (Dunn & Ralph 2004). Many of the studies on ASR that were reviewed, for example, in Donald (2007) are making inferences on sex ratio based on mist netting results. At least four different studies, however, suggested that mist nets or other trap types provide biased estimates on sex ratios, with males being more susceptible to capture than females (Domènech & Senar 1998; Greene & Fraser 1998; Vanderkist *et al.* 1999; Humple *et al.* 2001). None of those studies, however, directly estimated sex ratios while accounting for sex-specific capture probabilities by use of capture–recapture models (Casula & Nichols 2003; Kéry & Juillerat 2004). Such models were successfully used in population studies from which demographic data for ringed breeding birds were available (Townsend & Anderson 2007; Veran & Beissinger 2009).

However, a huge body of ringing data is collected in the national bird ringing schemes, in which usually no demographic data on individual breeding pairs are obtained. For example, in Constant Effort Site (CES) mist netting programs in the UK (Peach, Buckland & Baillie 1996), in the USA (DeSante, O'Grady & Pyle 1999) and in France (Julliard, Jiguet & Couvet 2004a), birds are captured and ringed during the breeding season at hundreds of different sites, and the number and placement of mist nets as well as the number and dates of trapping sessions per year are fixed within a site. Because these programs are often applied over many years and because capture sessions take place between three and 12 times per year, the data were used to study changes in abundance (Silkey, Nur & Geupel 1999), productivity (Bart *et al.* 1999) and survival (DeSante, O'Grady & Pyle 1999; Nur, Geupel & Ballard 2004), as well as to investigate the responses to climate change (Julliard, Jiguet & Couvet 2004b; Moussus *et al.* 2011).

Here, we used data collected over 19 years from one study plot from the French constant effort ringing scheme, to show how an observed male-bias in mist netting sex ratios can be caused by a male-biased capture probability in two of the most commonly trapped European songbirds, the blackbird (*Turdus merula*) and the blackcap (*Sylvia atricapilla*). We used a state-space formulation of the robust design (Pollock 1982) version of the Cormack–Jolly–Seber model (Cormack 1964; Jolly 1965; Seber 1965) for capture–recapture analysis in a Bayesian framework, to directly estimate sex ratios that are corrected for the sex- and year-specific capture probability. We also discuss two further factors that will affect capture rates and the results of capture–recapture analyses, namely the type and height of mist nets (Jenni, Leuenberger & Rampazzi 1996) and the occurrence of transient individuals that do not hold local breeding territories (Pradel *et al.* 1997; Hines, Kendall & Nichols 2003; Nur, Geupel & Ballard 2004).

Material and methods

STUDY SITE

The study was conducted at the Petite Camargue Alsacienne in the Upper Rhine Valley, France, from 1990 to 2008. The study site (47°37·577′N, 7°33·692′E) was a relatively isolated piece of woods in open landscape that had the form of a rectangular triangle, with lengths of the legs of 300 and 450 m, and a total surface of 6·75 ha. On one side, the study site was aligned to the Grand Canal d'Alsace, which is a 160-m-wide channel of the river Rhine. On the two other sides of the triangle, there was arable land. On the same side of the channel, the closest other woods were 800 m to the north and 400 m to the south.

The study site was covered with open forest, interspersed with bushes. 35% of all trees were oaks (*Quercus robur*). Further common tree species were black poplar (*Populus nigra*, 29%), European ash (*Fraxinus excelsior*, 18%) and white willow (*Salix alba*, 15%). The bush layer was characterised by elder (*Sambucus nigra*, 51%), common hawthorn (*Crataegus monogyna*, 22%) and common hazel (*Corylus avellana*, 9%). The vegetation at the study site was subject to natural succession, and throughout the study period, the only human interference was that during the week before the capture sessions, the herbs were cut around the paths and at the places used for mist netting. In the herbaceous layer, the nettle (*Urtica dioica*) was the predominating plant species; starting in about the year 2000, the nettles around the paths and capturing places became replaced by Himalayan balsam (*Impatiens glandulifera*).

CAPTURING METHODS

The study was part of a nation-wide Constant Effort Site ringing scheme on common bird species in France (Julliard, Jiguet & Couvet 2004a). Over a period of 19 years, we captured in 32 mist nets that were always at the same locations and were homogenously distributed over the entire study plot on a grid with *c*. 50-m intervals. The total length of the nets was 384 m. During the breeding season, we made three capture sessions per year, each of 6 h duration. The first session was between 2 and 26 May (mean ± SD = 13 May ± 7 days), the second session was between 23 May and 19 June (6 June ± 9 days), and the third session was between 20 June and 11 July (29 June ± 6 days). The particular days of capture were chosen to avoid rainy days as predicted by the weather forecast. During the days of capture, the nets were opened at 05:00 and closed at 11:00. Nets were checked every 30–45 min. Birds were ringed at the site of capture, and we noted the species name, the sex and the age. To avoid lengthy handling times during the breeding season, no other measures were taken.

The nets were 12 m long; they had a mesh size of 16 mm and four mesh pockets. During the years 2000–2003, we changed the type of nets (eight old nets were replaced by new nets per year). The 'old' nets had a height of 160 cm, the mesh pocket depth was 20 cm, and the vertical distance between two pockets was 40 cm. The 'new' nets had a height of 240 cm, the mesh pocket depth was 30 cm, and the vertical distance between two pockets was 60 cm.

SAMPLE SIZES

For analysis, we selected the blackbird and the blackcap, because they had relatively large capture and recapture rates (Table 1), and the sexes were easily distinguished in the field. In the analyses, we only included adult birds.

Table 1. Sample sizes

	Number ringed			Number recaptured		
Species	Males	Females	Total	Males	Females	Total
Blackbird	164	125	289	82	48	130
Blackcap	652	524	1176	203	87	290

DATA ANALYSIS

Data of each species were analysed separately. The data were arranged so that $y_{i,j,v}$ was a binary variable being 1 if the individual *i* was captured in year *j* during session *v* and 0 otherwise.

We used a state-space formulation of the robust design (Pollock 1982) version of the Cormack–Jolly–Seber model (Cormack 1964; Jolly 1965; Seber 1965). The latent state variable $z_{i,j}$ described whether individual *i* was alive and present at the study site in year *j*. We assumed that the state of an individual did not change between the 3 capture sessions of the same breeding season, whereas between breeding seasons, individuals could either die or emigrate from the study area; that is, they could change their state from $z_{i,j} = 1$ to $z_{i,j+1} = 0$ with probability $1-\Phi_{i,j}$ (see below). This approach is the main characteristics of the robust design (Pollock 1982) and allows a robust estimation of capture probability because of replicated capturing of the same individuals within the same breeding season. We conditioned our model on first capture: the latent state variable *z* was set to 1 for each individual *i* in its year of first capture (first_i) $z_{i,\text{first}_i} = 1$ and then modelled as a Bernoulli process. The probability that an individual in state 1 in year *j* has again state 1 in year $j + 1$ was defined as apparent survival probability $\Phi_{i,j}$. If an individual had state 0 (i.e. dead or emigrated), it maintained state 0 by defining the success probability of the Bernoulli process as the product of the state $z_{i,j}$ and the apparent survival probability:

$$z_{i,j+1} \sim \text{Bern}(z_{i,j}\Phi_{i,j})$$

The observations $y_{i,j,v}$ were modelled as a second Bernoulli process:

$$y_{i,j,v} \sim \text{Bern}(z_{i,j}p_{i,j,v})$$

with $p_{i,j,v}$ being the capture probability of individual *i* in year *j* during session *v*. The logit of the capture probability $p_{i,j,v}$ was constrained to be linearly dependent on four predictor variables and on one interaction: (i) year (linear time trend), (ii) an indicator being 1 for the years starting with 2002 when at least half or all of the 'old' mist nets were replaced by the 'new' mist nets, (iii) sex of the bird, (iv) session number (two dummy variables that indicate session 2 and 3), and the interaction between sex and session number to allow for sex-specific seasonal patterns of capture probability. The logit of the apparent survival probability $\Phi_{i,j}$ was modelled as a linear function of (i) year (linear time trend) and (ii) sex. Because only data from adult birds were used, no age effect was included.

For fitting the model, we used Bayesian methods. Reversible jump Markov chain Monte Carlo simulation (RJ-MCMC) was used to estimate the posterior inclusion probability of each predictor variable. For estimating the posterior distributions of the parameters in the full model, we used Markov chain Monte Carlo simulation (MCMC), because convergence can be more reliably assessed in MCMC compared to RJ-MCMC. The posterior distribution of the parameters was described using every 100th of the last 10 000 values of two Markov chains, each of total length 20 000 (burnin was set to 10 000). For the RJ-MCMC, burnin was set to 20 000, and 50 000 simulations were carried out in total. We assessed convergence of the Markov chains by visually inspecting the chains, and we accepted R-hat values smaller than 1·005 (Brooks & Gelman 1998). The MCMC model fits and the RJ-MCMC simulations were done using WinBUGS (Spiegelhalter, Thomas & Best 2003) and the R-interface R2WinBUGS (Sturtz, Ligges & Gelman 2005). See Appendix S1 (Supporting information) for the WinBUGS implementation of our model.

Throughout, we speak of a 'clear' effect (which, in a frequentist terminology, may be similar to a significant effect) if zero is not included in the 95% Bayesian credible interval of an estimate. The limits of a 95% credible interval were obtained as the 2·5% and 97·5% quantiles of the posterior distribution of a parameter in the full model containing all predictor variables. Thus, all reported estimates are partial effects, which are the respective effects after having corrected for all the other effects. Note that these estimates and credible intervals are conditional on one model, which in our case is the full model containing all predictor variables (we chose the full model for making inference because this usually leads to the most conservative results). In contrast, the inclusion probability gives the posterior probability that a variable is included in the model, given an array of different models; more exactly, our inclusion probability is the sum of the posterior model probabilities of the models containing a specific variable. The inclusion probability is thus the probability that the effect is actually there, which we call the 'reliability' of an effect. It may happen that based on the inclusion probability, there is strong evidence that the effect is actually there, but still its partial effect, that is, the additional effect of the variable after having corrected for all the other variables in the full model is weak; this would lead to a high inclusion probability but to a large credible interval that could also include zero.

The goodness of fit of the model was assessed by plotting the observed frequencies of capture histories against the predicted frequencies (see Appendix S2, Supporting information). In particular, we checked whether the proportion of individuals that were captured only once and thus could be so-called transients that do not settle at the study site (Pradel *et al.* 1997) exceeded the model expectations. This was apparently not the case for the blackbird, and only weakly for the blackcap. In both sexes of the blackcap, the proportion of individuals captured only once was slightly higher compared to the model predictions during the first capture session, that is, early in the breeding season. However, as this was largely consistent between sexes, we judged the influence on sex ratio estimation as weak (see Discussion).

To estimate the proportion of males in the population at the study site from the observed numbers of males and females captured per year, $n_{\text{sex},j}$, we took the sex- and year-specific capture probability into account. We calculated the probability that an individual is captured at least once in year *j* (which is 1 minus the probability that it is not recaptured during any of the three capture sessions) using $p_{\text{sex},j} = 1-(1-p_{\text{sex},j,1})(1-p_{\text{sex},j,2})(1-p_{\text{sex},j,3})$ for each sex and year. Then, the number of captured individuals was divided by this probability: $n_{\text{sex},j}/p_{\text{sex},j}$. We thus obtained an estimate for the true number of individuals per sex within the study site. The estimated sex ratio was then obtained from WinBUGS as a derived parameter so that the uncertainty of the estimates for capture probability propagated into the uncertainty of the estimated sex ratio (Gelman *et al.* 2004; Link & Barker 2010). Similarly, the yearly population size was estimated as a derived parameter as the sum of the estimated numbers of individuals per sex.

To compare the spatial activity between males and females, we used the distances (in metres) between the locations of two catches of the same individual within the same capture session or within the same season. For the blackbird, we had data on 174 distances from 113 individuals, and for the blackcap, on 318 distances from 245 individuals. These differences were transformed by adding 1 and taking the natural logarithm before they were analysed with a linear mixed model. The individual bird was used as random factor to account for dependency of measurements of the same individuals. Sex entered the model as fixed effect. We used the function lmer from the package lme4 (Bates 2005) to fit the models, and the function sim from the package arm to simulate values from the posterior distributions of the model parameters (Gelman & Hill 2007).

Results

The capture probability as predicted by the model was higher in males compared to females in both the blackbird and the blackcap (Table 2, Fig. 1). This difference was largely constant over the season in the blackcap (clear effect of sex but no clear evidence for interaction between sex and capture session), whereas in the blackbird, the difference decreased in the course of the season (clear and, according to the inclusion probability of the parameter, also reliable interaction between sex and capture session). The 'new' mist nets appeared to be more efficient than 'old' mist nets in capturing blackbirds, but less efficient in capturing blackcaps; however, the differences in capture probability between types of nets were smaller than between the sexes. Inclusion probability of the parameter indicating types of nets was higher in blackbirds compared to blackcaps, indicating a more reliable effect in the blackbird. Among the years of the study, no clear linear trend in capture probability was found in the blackbird, while a slight but, according to the inclusion probability, reliable linear increase in capture probability was found in the blackcap.

In blackbirds, the probability of being captured at least once during one breeding season was 0·62 for males and 0·33 for females (based on the estimated session-specific capture probabilities for new nets for the arbitrarily selected year 2005). This would lead to a proportion of males of 0·62/(0·62 + 0·33) = 0·65 in the captured birds when in the population there is actually a balanced ASR with 50% males.

In blackcaps, the same probability was 0·35 for males and 0·22 for females. This would lead to a proportion of males of 0·35/(0·35 + 0·22) = 0·61 in the captured birds when the ASR in the population is actually balanced.

Over the entire study period, the observed annual proportions of males among the captured individuals were substantially higher than 50% (Fig. 2). Among the total of the ringed birds, 57% of blackbirds and 55% of blackcaps were males (Table 1). The average of the observed annual proportions of males (Fig. 2) was 63% for the blackbird and 59% for the blackcap. However, when the observed annual proportions of males were corrected for the sex-specific capture probabilities, the proportions of males did not clearly differ from 50% in most study years, and thus, the apparent male-bias in the ASRs almost completely disappeared (Fig. 2).

The apparent survival probability is defined as the probability to survive and to return to the study area from one year to the next. Females had a lower apparent survival probability than males in both species, but this difference was only clear in the blackcap (Table 3). Among the years of the study, no clear linear trend in apparent survival probability was found in the blackbird, while a slight but reliable linear decrease in apparent survival probability was found in the blackcap.

For blackbirds, our model estimated total population sizes that varied from 33 to 93 individuals per year (mean ± SD = 51·2 ± 15·8). The estimated population size was not found to correlate with the estimated sex ratio in a given year (correlation coefficient r = −0·19; 95% credible interval: −0·71 to 0·30).

In blackcaps, population sizes were estimated to vary from 173 to 511 individuals per year (mean ± SD = 283·4 ± 76·5). As in blackbirds, the estimated population size was not found to correlate with the estimated sex ratio (r = 0·12; 95% credible interval: −0·36 to 0·62).

In blackbirds, the average distance between two nets in which the same individual was captured within the same capture session or within the same season tended to be larger in males (52 m; 95% credible interval: 38–69 m) than in females (34 m; 95% credible interval: 23–50 m). The posterior probability for the hypothesis that males have a greater distance between two capture sites than females was 0·95 (proportion of pairs of simulated mean distances for males and females from their joint posterior distribution for which the means of males were larger than the means of females).

Table 2. Estimated effect sizes and reliability of the predictors of capture probability

	Blackbird				Blackcap			
Predictor variable	$\hat{\beta}$	$q_{2·5\%}$	$q_{97·5\%}$	$p_{(\mathrm{incl})}$	$\hat{\beta}$	$q_{2·5\%}$	$q_{97·5\%}$	$p_{(\mathrm{incl})}$
Year	−0·06	−0·15	0·03	0·01	0·06	0	0·11	1
Indicator new nets	0·74	−0·06	1·53	0·54	−0·51	−1·02	0·02	0·30
Sex (indicator females)	−1·43	−2·23	−0·69	0·75	−0·78	−1·41	−0·17	0·30
Indicator session 2	−0·77	−1·26	−0·27	0·26	0·33	−0·01	0·68	0·64
Indicator session 3	−1·88	−2·49	−1·28	1	−0·05	−0·41	0·31	0·19
Indicator session 2 × sex	0·16	−0·88	1·16	0·77	0·25	−0·41	0·91	0·13
Indicator session 3 × sex	1·72	0·69	2·75	0·38	−0·31	−0·40	0·98	0·21

$\hat{\beta}$ = estimated coefficient (mean of posterior distribution), $q_{2·5\%}$ and $q_{97·5\%}$ = 2·5% and 97·5% quantiles of the posterior distribution (95% credible intervals), $p_{(\mathrm{incl})}$ = posterior inclusion probability of the parameter. Effects with credible intervals that do not include zero are judged as clear. Predictors with large posterior inclusion probabilities are judged as reliable (see text).

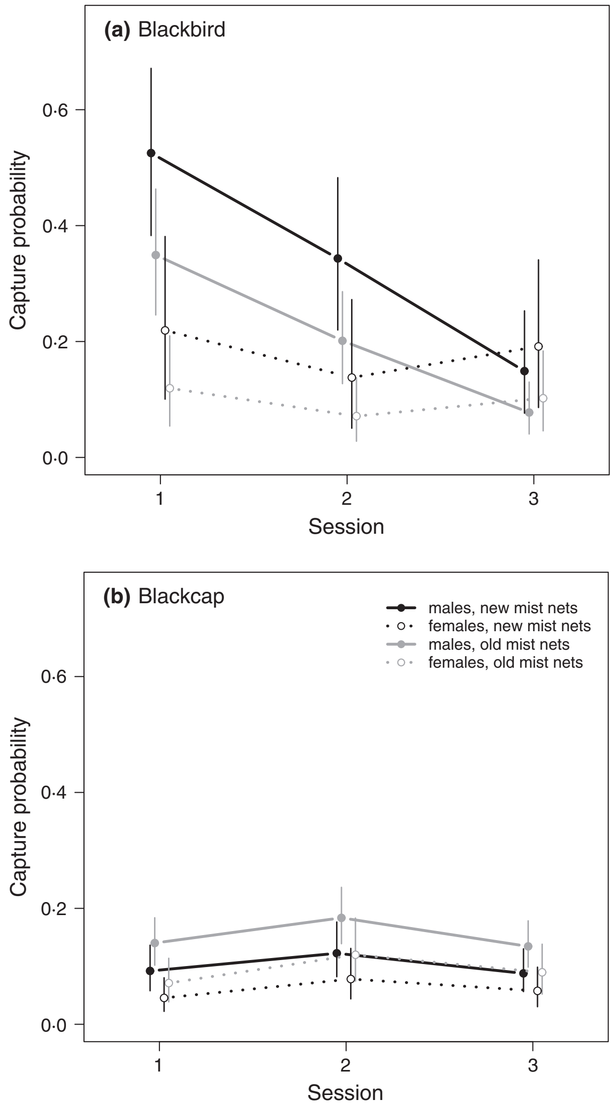

Fig. 1. Capture probability per sex and capture session as predicted by the model for the study years 1990–2001 (using 'old' mist nets) and for 2002–2008 (using 'new' mist nets). The three capture sessions were on average on 13 May, 6 and 29 June (see text). Vertical lines are 95% credible intervals (based on the quantiles of the posterior distribution).

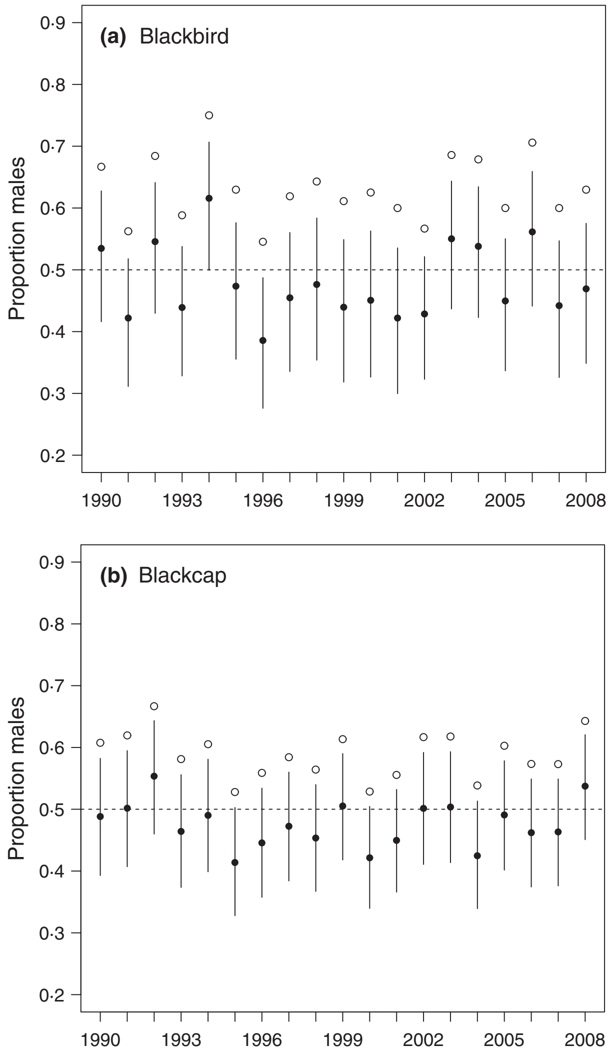

Fig. 2. Observed (empty circles) and estimated (black dots with 95% credible intervals) proportions of males in the populations of blackbirds and blackcaps at the study site. Estimates with credible intervals that do not cross the hatched line are judged as being clearly different from a balanced adult sex ratio.

Also in blackcaps, the average distance between two nets in which an individual was captured tended to be larger in males (15·8 m; 95% credible interval: 11·5–21·9 m) than in females (10·1 m; 95% credible interval: 6·7–15·2 m). Also here, the posterior probability for the hypothesis that males have a greater distance between two capture sites was 0·95.

Discussion

Skewed ASRs certainly have important consequences for ecology, evolution and conservation of birds. However, our study implies that published estimates on ASRs should be re-evaluated if based solely on observed sex ratios from mist netting studies. After correcting for sex- and year-specific capture probabilities, we did not find that ASRs as estimated from capture–recapture models clearly differed from parity in two species of common European songbirds. From the total of captured individuals per species, however, we observed an uncorrected proportion of 57% males in blackbirds and of 55% males in blackcaps.

For the blackbird, the same proportion of 57% males was found among 2534 adults that were ringed between April and June from 1992 to 1999 in the UK (Post & Götmark 2006). However, note that sex ratio estimates as based on first captures of individual birds that are spread over several years are likely biased towards the more dispersing sex. A better estimate should be obtained when calculating sex ratios per year and then taking the average among years. The reason is that from breeding season to breeding season, some individuals of the dispersing sex will not return to a study area, but others will immigrate; so within a study year, sex differences in dispersal should normally not strongly bias sex ratios. If captures are

Table 3. Estimated effect sizes and reliability of the predictors of apparent survival probability. For further explanations, see Table 2

	Blackbird				Blackcap			
Predictor variable	$\hat{\beta}$	$q_{2\cdot5\%}$	$q_{97\cdot5\%}$	$p_{(\mathrm{incl})}$	$\hat{\beta}$	$q_{2\cdot5\%}$	$q_{97\cdot5\%}$	$p_{(\mathrm{incl})}$
Year	−0·02	−0·06	0·03	0·36	−0·03	−0·06	0	1
Sex (indicator female)	−0·19	−0·70	0·34	0·52	−0·40	−0·78	−0·01	0·96

pooled from several years, however, more individuals of the more dispersing sex will be captured. In our case, the average annual proportion of males among the caught birds was 63% for the blackbird and 59% for the blackcap, and was thus even more male-biased than in the pooled capture data from all study years, suggesting that like in many other bird species (Schaub & von Hirschheydt 2009), dispersal was higher in females than in males.

A general prevalence of male-biased ASRs in birds was so far acknowledged in reviews by Mayr (1939), McIlhenny (1940), Breitwisch (1989) and Donald (2007). Among the 201 published estimates summarised by Donald (2007), the ASR differed significantly from equality in 65% of the studies, and both the mean and median ASR were 57%. However, we agree with previous authors that it is difficult to measure ASR in an unbiased way, because the behaviour and detectability of males and females often differ (Donald 2007, 2011; Veran & Beissinger 2009; Kosztolányi *et al.* 2011).

The most reliable sources of data on ASR in birds seem to be population studies in which the presence and identity of ringed males and females in their breeding territories is controlled by a combination of regular mist netting and behavioural observations, while taking account of the potential presence of unpaired floaters (Amrhein, Kunc & Naguib 2004; Amrhein *et al.* 2007; Townsend & Anderson 2007; Veran & Beissinger 2009; Kosztolányi *et al.* 2011). For example, Bairlein (1978) found that in two years of study on a population of blackcaps, one of 20 and two of 25 males remained unpaired, respectively, reflecting an annual ASR of 51% and 52% under the assumption that no polygynous males or floating individuals were missed.

However, we propose that data from national bird ringing schemes and in particular from Constant Effort Site ringing programs can provide valuable information on ASR, if observed sex ratios are corrected for sex-specific capture probabilities using capture–recapture models as applied in the present study. In the following, we discuss general assumptions of those models and their application to our data.

The uncorrected ASR as observed from mist netting data reflects the true population ASR only when the probability to be captured is equal between sexes. This probability is partly influenced by the spatial activity and the home ranges of individuals. Conventional capture–recapture analysis on sex ratios thus relies on the assumption that males and females that may move beyond the boundaries of a capture area do so to a similar extent. Because our study plot was a relatively isolated piece of woods in open landscape, our study may be a case where movements of individuals during the breeding season were largely restricted to the capture area. However, it is still likely that we captured transient individuals that did not hold breeding territories within the study plot (Pradel *et al.* 1997; Hines, Kendall & Nichols 2003; Nur, Geupel & Ballard 2004).

For example, in blackcaps, the number of individuals that we captured only during the first capture session was about 1·3 times higher in males and 1·4 times higher in females than expected based on the predictions by the model (see Appendix S2). Particularly early in the breeding season, we thus probably captured transient blackcaps that did have a low probability of recapture. The inclusion of such transients may have led to underestimated capture probabilities and to overestimated population sizes, and is likely to explain the unrealistically large population sizes that the model estimated for the blackcap. However, as the proportion of such transients was fairly equal between sexes, this should not have caused a strong bias in our estimates of sex ratios. We would further expect that if the proportion of transients were much higher in one sex than in the other, the estimates for population sizes as well as for sex ratios would strongly be influenced by variation in the numbers of birds caught for the particular sex. Thus, estimated population sizes would be correlated with estimated sex ratios. However, we did not find such correlations in our study, which corroborates our assumption that transients should not strongly bias our sex ratio estimates.

It is possible to include the spatial distribution of captures into newly developed so-called spatially explicit or spatially indexed models for capture–recapture studies (Borchers & Efford 2008; Royle & Young 2008). Such models take into account that the effective sample area is often unknown because individuals may partly move outside the capture area, leading to biased density estimates obtained from traditional capture–recapture models. However, because in our case, the surrounding habitat of open landscape was probably not spatially used in the same way as the within-plot habitat, application of such models was not straightforward. Moreover, if as in our study, there is no indication of sex-specific movements outside the study plot because the plot forms an isolated patch of habitat, it is probably not strictly necessary to use spatially explicit capture–recapture models for estimating sex ratios from ringing data.

We showed that within breeding seasons, males had higher capture probabilities than females both in the blackbird and in the blackcap. This finding may partly be explained by a larger home range of males within the study site, as indicated by the about 1·5 times larger average distances between two sites of capture for males than for females in both species. If males are leaving their territories to prospect unfamiliar places within the capture area, they might be easier captured because they show different spatial behaviour in unfamiliar terrain or because they do not know the mist net locations outside their territories.

While the sex difference in capture probability was small but constant in blackcaps, blackbird males had a much higher capture probability than females particularly in mid-May, during our first capture sessions. Possible explanations for the species-specific patterns could be that in the blackbird, only the female is incubating (Glutz von Blotzheim & Bauer 1988), thus leaving the male free to move more often between mist nets early in the breeding season, while in the blackcap, both sexes are incubating (Glutz von Blotzheim & Bauer 1991).

Furthermore, blackbirds usually lay second clutches after a successful first brood (Glutz von Blotzheim & Bauer 1988), while second clutches are rare in blackcaps (Glutz von Blotzheim & Bauer 1991). One possible reason for the generally higher capture probability in males than in females is that the males may be captured more easily during chasing of conspecifics or during other overt territory defence behaviour, while females may behave more covertly. If in species with the potential to lay second clutches, territory defence behaviour by males is continued for longer time periods into the breeding season than in single-brooded species (Amrhein *et al.* 2008), this may explain why in May and early June, blackbirds showed a larger sex difference in capture probability than blackcaps.

Blackcap females had a lower apparent survival probability than males, which is the probability to survive and to return to the study area from one year to the next. This is also found in other migratory species, and the reason is probably higher dispersal in females (Cilimburg *et al.* 2002; Hoover 2003; Schaub & von Hirschheydt 2009). Moreover, in the 19 years of study, blackcaps tended to show generally decreasing apparent survival probabilities, which could indicate either a decrease in survival or an increase in permanent emigration from the study area, perhaps as a response to natural succession of the vegetation at the study site.

We further found that the type of mist nets tended to correlate with capture efficiency: while blackcaps had a slightly higher capture probability with the 'old' nets, blackbirds apparently were easier to capture with the 'new' nets. The main difference between the types of nets was that the new nets were higher and that the vertical distances between mesh pockets were larger. However, because the old nets were used in the first years of our study and the new nets were used starting from the year 2000, it is not possible to fully separate the effects of time and of types of nets on capture probability. Our model accounted for both a linear time trend, that is, for a continuous change in capture probability over time that might be due, for example, to succession of the vegetation, and for a systematic difference between years before 2002, when old mist nets were used, and starting with 2002, when new mist nets were used. Therefore, linear time trends should not confound the effect of mist net type. However, we cannot exclude that because of unknown factors, nonlinear time trends produced differences in capture probability between the two time periods and thus confounded our findings on the effect of mist net type.

In our study, we used a rather ideal study plot in that the nets were homogenously distributed over the entire wooded area, which was fairly isolated in otherwise open landscape. Larger studies integrating data from different sites will have to cope with varying isolation of the sites and thus with study populations that are varying in their extension beyond the boundaries of the capture area. For single plots, we showed how mist netting data can be used to estimate ASRs, taking account of sex-specific capture probabilities using capture–recapture models. Such models should provide access to the huge data sets provided by Constant Effort Site ringing programs, for further investigating the incidence of skewed ASRs in birds.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. WinBUGS implementation of the model.

Appendix S2. Model validation: plots of observed capture history frequencies versus predicted frequencies.