Detection probability of the Collared Flycatcher *Ficedula albicollis* during quick, multiple surveys: a case study in an isolated population in northern Poland

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We investigated factors affecting the detection probability of the Collared Flycatcher *Ficedula albicollis*, a secretive forest passerine, whose range is confined to central and eastern Europe. With a robust design sampling protocol, 78 sites were surveyed four times in spring 2012 for the presence of singing males in the Las Warmiński nature reserve (northern Poland). Multi-season occupancy models fitted to the data showed that detection probability varied considerably as a function of habitat quality. Probabilities of detection of at least one singing male during a single survey were very similar under various models: 0.383–0.419 at sites with single males, 0.815–0.837 at sites with two males, 0.970–0.974 and 0.999 at sites with three and four males. Detection probability did not depend on time of day, indicating no decline in singing activity as the day progresses. The local extinction probability was zero, suggesting that sites occupied early in the season are unlikely to be deserted – males were actively singing several days after arrival. Since mated males reduce their singing activity very much, these results may suggest low mating success. If this holds true, the colonization probability invariably estimated at 1.0 is best explained by the late arrival of some males rather, than by within-season movements of males already present. This study emphasizes that occupancy models are useful for the simultaneous investigation of the effects of multiple covariates not only on detection but also on other, biologically important parameters.

1. Introduction

The detection probability of any species is rarely equal to 1 (all presences detected). This is particularly true of species that are rare, shy and difficult to detect or that live in habitats difficult to survey. This is mainly because recorded absences may be non-detections – the species may nonetheless be present. Using naive estimates of occupancy results in underestimating the proportion of sites occupied. Detection error must therefore be taken into account when estimating occupancy and related parameters. The probability of detection, its temporal and spatial variation, and its relationships to various factors are interesting in themselves, for instance, when designing an optimal

survey. In almost all species, activity (e.g., singing or other displays) is shaped by multiple factors, including weather conditions, individual condition or interactions with neighbours, so that audibility also varies.

Occupancy models provide a useful framework for deriving occupancy corrected for imperfect detection (MacKenzie *et al*. 2002). Among the variety of models developed so far, perhaps the simplest is the single season model, which assumes demographic closure of the population between surveys: the "empty" site cannot be colonized between surveys and the occupied site cannot become extinct (MacKenzie *et al*. 2006). In contrast, multi-season models (or dynamic occupancy models) assume that empty sites can be colonized and that an occupied site can be deserted. The latter models provide a useful tool for measuring changes in demographic parameters (such as occupancy) and are used to estimate probabilities of extinction or colonization (MacKenzie *et al*. 2003). Rota *et al*. (2009) have shown that many sites are open to changes over time-scales usually used in occupancy studies (that is, within a single season); in this case the use of models assuming closure can lead to biased parameter estimates. Yet one of the assumptions underlying the modelling of occupancy and related parameters using standard models is that parameters are the same across surveyed sites (no heterogeneity) unless covariates are included. In reality, however, it is unwise to assume such a situation; one can use covariates related to site characteristics (site-specific covariates, like patch size or habitat quality) or surveys (survey-specific covariates, like weather conditions or the observer) in order to incorporate some among-site heterogeneity. The use of covariates enables their influence on target parameters to be investigated. In this way one may achieve results which, apart from the numerical estimation of occupancy and detection probability, bear important biological information about the processes or species studied. Alternatively, random effect models can also account for unstructured heterogeneity.

In the present study, we investigated the probability of detecting the Collared Flycatcher *Ficedula albicollis*, a species considered difficult to detect unless a large amount of time is spent in the field (Walankiewicz *et al*. 1997). We performed our study in a population of Collared Flycatchers nesting only in natural tree-holes, in contrast to most other studied populations of this species, which bred in nest boxes (e.g., Lundberg & Alatalo 1992, Walankiewicz et al. 1997). We were primarily interested in checking whether detectability differs between early (just after arrival) and late (three weeks later) periods of the breeding season; in this way we intended to delimit the optimal survey period. Because our experience suggested that males do not reduce their singing activity until late afternoon (AS and GN, personal observations), we also tested whether this was related to the time of day when the survey was being conducted. As activity (and thus audibility) could be related to habitat quality (e.g., patch size, number of singing neighbours or food abundance), we included a "habitat" covariate. We assumed that detectability might be higher and/or might decline with time of day at a slower rate in better habitats, occupied by more territorial males, in contrast to poorer ones. To address these questions, we conducted four surveys following a robust design sampling protocol (two secondary sampling surveys within each of the two primary periods) in an isolated Collared Flycatcher population in northern Poland. We modelled occupancy, probability of colonization, probability of local extinction and probability of detection using multi-season models (MacKenzie *et al*. 2003, 2006).

2. Material and methods

2.2. Study area

The Las Warmiński reserve (1803 ha, including forests – 1550 ha, a few lakes – 147 ha and other open areas – 106 ha) lies in northern Poland (the Warmia-Mazuria Lowland) and is an old-grown deciduous forest, protected as a nature reserve since 1982. Since the 1950s it was less formally protected as a hunting area for VIPs of the former regime (Rancew-Sikora 2009). Forestry practices were far less intensive than in typical managed stands, which allowed effective protection of the oldest parts, including over 230-year old oak stands and a 200-year old pine stand. Most of the area is covered by coniferous tree stands (Scots Pine *Pinus sylvestris*, Norway Spruce *Picea abies*

and European Larch *Larix decidua*). The few deciduous stands are scattered mostly along lake shores and along the River Łyna in the central parts of the reserve. They consist mainly of Pedunculate Oak *Quercus robur*, European Hornbeam *Carpinus betulus*, European Ash *Fraxinus excelsior*, Black Alder *Alnus glutinosa* near water, and the rarely planted European Beech *Fagus sylvatica*. There are only a few nest-boxes, so almost all the Collared Flycatchers nest here in natural tree-holes. A small area outside the reserve with a few males regularly seen in previous years, was also surveyed.

2.3. Study species

The Collared Flycatcher is mostly a central- and east-European species with a total population estimated at 1.4–2.4 million pairs, but only 0.15–0.36 million in the EU. The largest populations are in Romania, Ukraine and Russia (BirdLife International 2004a, b). This species is listed in the EU Birds Directive (BirdLife International 2004b). Its discontinuous core range is bordered by numerous, small, isolated populations far from the main range (e.g., on the Baltic island of Gotland, Sweden, Hagemeijer & Blair 1997). In Poland, the species is widespread in the south, but local elsewhere (Mielczarek & Walankiewicz 2007). The population size has been roughly estimated at 5 (2.5–10) thousand pairs (Chylarecki & Sikora 2007), but more precise data on numbers and information on trends are lacking. The Collared Flycatcher prefers mature deciduous forests across its range and is fully insectivorous (Cramp & Perrins 1993). In Poland, it arrives in late April, while departures are thought to occur mainly in summer (Tomiałojć & Stawarczyk 2003). The wintering range includes central Africa (Lundberg & Alatalo 1992).

2.4. Field protocol

In this work, we define 'site' as a patch of suitable habitat that could potentially be occupied by Collared Flycatchers. The sites were selected primarily on the basis of habitat, which was classified as suitable or not prior to the study. A suitable habitat was defined as a forest, at least 100 years old, with

deciduous trees (Pedunculate Oak, European Hornbeam, European Ash, Black Alder, European Beech) predominating over coniferous ones (Scots Pine, Red Spruce and European Larch). Sites were variable in size and shape, as some were well-defined sections planted by foresters (up to 200 years ago), while others were natural formations, e.g., riparian alder forests growing along the River Łyna (thus more or less continuous). Their areas (in ha) were read off from digital forest maps (available at http://rdlpol.gis-net.pl/) for 73 sites (remaining 5 sites were located on private grounds and their exact size was unknown; they were similar in size to measured ones). Mean site area was 4.4 ha (SD = 2.9 ha, range 0.49–11.11 ha). 78 sites distributed across suitable habitats in the reserve were visited four times in spring 2012. Additional sites which did not satisfy these criteria were surveyed only if Collared Flycatchers had been recorded there in previous years. Observers conducted four surveys at each site, following a robust design protocol: primary sampling period I ("season" one) included two surveys (survey 1: 27–30 April and survey 2: 30 April–3 May) as did primary sampling period II ("season" two, survey 3: 18–20 May and survey 4: 20–23 May). During both sampling periods, the two visits at each site were separated by an interval of 2–3 days. Observers surveyed the sites with the average speed of 6–8 minutes per 10 ha of forest (which is roughly the speed recommended for the territory mapping censuses, Walankiewicz & Czeszczewik 2009). Surveys were conducted from sunrise (approx. 05:00 hrs during surveys 1–2 and approx. 04:30 during surveys 3–4) until about 16:00, but were frequently over by around 13:00–14:00 hrs. Surveys were conducted only in good weather (no rain, no strong wind).

2.5. Modelling detection probability: models and covariates

The field protocol described above enabled the dataset to be treated as having been collected during two "seasons", where the primary sampling period I with two surveys represented the first season, and the primary sampling period II with two surveys represented the second season. We therefore used single-species, multi-season models,

Table 1. Candidate models for occupancy (ψ), colonization (δ), local extinction (ε) and detection probabilities for Collared Flycatcher in the Las Warmiński nature reserve, northern Poland. Models are ranked according to QAICc, and the best-supported model is given in bold. ψ(I) – initial occupancy (i.e., occupancy estimated for the first primary sampling period), δ – probability of colonization, ε – probability of local extinction, p – probability of detection. Δ QAICc – difference in AIC units between the best model and a given model, ω AICc – Akaike weight (strength of support for a given model). Parameter counts (k) include $\hat{c}$.

Model	QAICc	Δ QAICc	ω AICc	Likelihood	k
ψ(I), δ(), ε(), p(Habitat)	**219.09**	**0.00**	**0.4506**	**1.0000**	**6**
ψ(I), δ(), ε(), p(Survey+Habitat)	220.47	1.38	0.2260	0.5016	7
ψ(I), δ(), ε(), p(Habitat+Time)	221.32	2.23	0.1478	0.3279	7
ψ(I), δ(), ε(), p(Survey+Habitat+Time)	222.79	3.70	0.0709	0.1572	8
ψ(I), δ(), ε(), p(Obs+Habitat)	223.26	4.16	0.0563	0.1249	8
ψ(I), δ(), ε(), p(Survey+Obs+Habitat)	224.90	5.81	0.0247	0.0547	9
ψ(I), δ(), ε(), p(Obs+Habitat+Time)	225.67	6.58	0.0168	0.0373	9
ψ(I), δ(), ε(), p(Survey+Obs+Habitat+Time)	227.41	8.32	0.0070	0.0156	10
ψ(I), δ(), ε(), p(Survey)	253.28	34.19	0.0000	0.0000	6
ψ(I), δ(), ε(), p(Survey+Time)	253.35	34.26	0.0000	0.0000	7
ψ(I), δ(), ε(), p()	256.17	37.08	0.0000	0.0000	5
ψ(I), δ(), ε(), p(Time)	256.29	37.20	0.0000	0.0000	6
ψ(I), δ(), ε(), p(Survey+Obs)	257.44	38.35	0.0000	0.0000	8
ψ(I), δ(), ε(), p(Survey+Obs+Time)	257.70	38.61	0.0000	0.0000	9
ψ(I), δ(), ε(), p(Obs)	259.75	40.66	0.0000	0.0000	7
ψ(I), δ(), ε(), p(Obs+Time)	260.21	41.12	0.0000	0.0000	8

which assume that the population is open between the primary sampling sessions. With these models four types of parameters are estimated: occupancy probability ψ, colonization δ, local extinction ε probabilities, and probability of detection p. The occupancy parameter is the occupancy corrected for imperfect detection. We used the parameterization that estimates "initial" occupancy (i.e., occupancy for the primary sampling period I). Occupancy for the primary sampling period II is best achieved by fitting a model with parameterization that includes "seasonal" occupancy (i.e., occupancy for each season) and lacks either colonization or the extinction parameter.

The model's deviance and AIC values are the same regardless of the parameterization. Colonization probability is the probability that a site unoccupied during primary sampling period I is occupied during primary sampling period II (i.e., has been colonized); local extinction probability is the probability that a site that was occupied during primary sampling session I is unoccupied during primary sampling period II (i.e., has been deserted). These two parameters are useful for describing the dynamics of the system. Detection probability is the probability of detecting one or at least one indi-

vidual of a species at a surveyed site, assuming it is occupied.

Sixteen logistic-linear additive models were constructed, differing in the constant (.) or survey-dependent (Survey) structure of the detection probability parameter and the absence/presence of covariates: habitat, observer and time of day.

(a) Habitat. A site-specific covariate, indicating the quality of the habitat at the site. Expressed as the number of territorial males recorded within the given patch plus one. This covariate is likely to measure both patch size and patch quality (e.g., the amount of food or availability of nest-holes), which affect the parameters of interest.

(b) Time. A survey-specific covariate, stating at what time a visit has been made at a given site during a given survey. Expressed in minutes since sunrise and calculated separately for each day.

(c) Observer. A survey-specific, dummy variable, indicating whether a survey was conducted by AS or GN.

Observer effect was measured as well, because we could not reasonably assume that both observers

had the same detection probabilities (AS has much greater experience with both the species and the area).

All the covariates were included as being likely to affect detection probability p. For instance, in the model $\{\psi(), \delta(), \epsilon(), p(\text{Obs})\}$, detection probability (p) was allowed to vary as a function of observer only, whereas in the model $\{\psi(), \delta(), \epsilon(), p(\text{Obs} + \text{Time})\}$ it could include the additive effects of both observer and time. To ensure easy and clear interpretation and to avoid evaluating every possible combination of variables (Burnham & Anderson 2002), we reduced the number of models considered by keeping occupancy, colonization and extinction parameters unaffected by any of the covariates. Similarly, instead of fitting models with a fully survey-dependent detection probability (4 parameters of detection estimated), we fitted a reduced version with only two detection parameters: one parameter shared for the early surveys 1–2 and another one shared for the late surveys 3–4; these models are treated here so as to reflect survey-dependence. In this way, we reduced both the number of models considered and the number of parameters, with the global model having $K = 9$ parameters. All the remaining models (Table 1) were simpler in that they lacked one or more covariates; the total number of models considered in the model set was $R = 16$, thus keeping the ratio of effective sample size to the number of models high enough ($78 / 16 \approx 4.9$) (see Burnham & Anderson 2002).

All quantitative covariates were standardized before analysis (mean = 0, standard deviation = 1). Goodness-of-fit was assessed with the Pearson chi-square statistic (MacKenzie *et al.* 2003). The resulting value was insignificant ($\chi^2 = 14.33$, df = 9, $P = 0.11$) and indicated a good fit. Models were ranked according to the Akaike Information Criterion corrected for small sample size and a lack-of-fit (QAICc). We corrected model ranking by adjusting both c-hat ($\hat{c} = 1.58$, calculated as model deviance divided by the model df) and effective sample size ($K = 78$). This modified the ranking in favour of models with fewer parameters. Because support for several models was rather balanced without a clear leader (the first two models had Δ QAIC < 2), we reported model-averaged estimates unless stated otherwise. Variance and standard errors were calculated following Burnham and An-
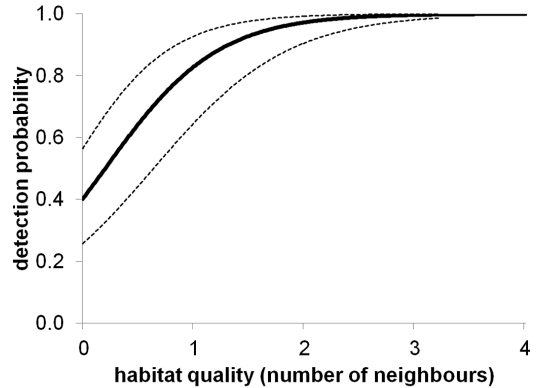

Fig. 1. Detection probability of at least one Collared Flycatcher at sites in the Las Warmiński nature reserve, northern Poland, in relation to habitat quality (expressed as the number of neighbours at a site, see Methods). Zero means no neighbours and detection probability refers to single males at a site. The bold line shows the detection probability estimate from the best model; dashed lines show ± 1 standard error.

derson (2002) to include both variance conditional on model M_i and variance due to model selection uncertainty. The Relative Importance of Variables (RVI) was assessed by summing Akaike weights across all models including a given variable (Burnham & Anderson 2002). Model construction and fitting was performed in Presence 5.2 (Hines 2006).

Because some sites could be occupied by more than one male, the probability of detection reported here is the probability of detecting at least one singing male at a site.

3. Results

The best two of the sixteen models fitted to the data were equally good (Δ QAICc < 2 for the second ranked model) with a cumulative weight of ~0.67 (Table 1). Both included the effect of habitat quality, but differed with respect to whether detection probability was modelled as survey-dependent or constant. In general, there was overwhelming evidence for the effect of habitat quality on detection probability (Fig. 1), as eight models containing this covariate had a cumulative weight of 1.0, whereas models excluding this effect had no sup-
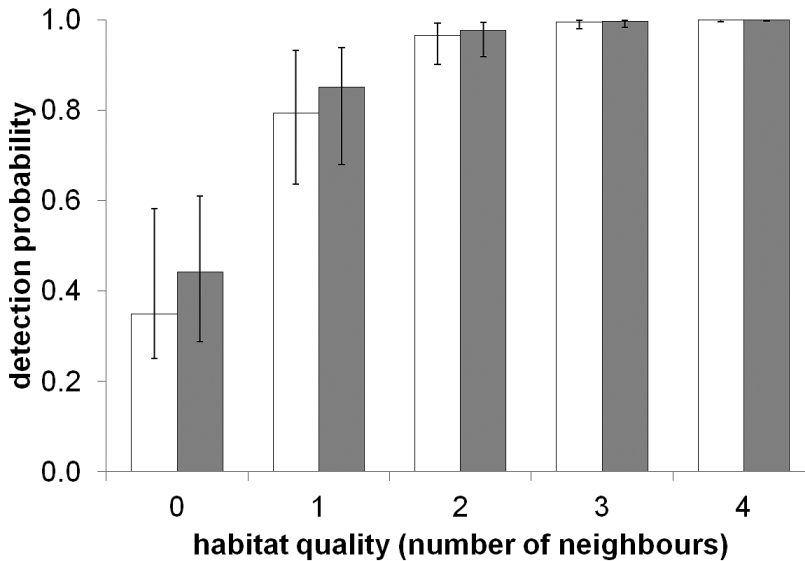
Fig. 2. Model-averaged estimates of detection probability of the Collared Flycatcher during early (white bars) and late (grey bars) surveys in relation to habitat quality (expressed by the number of males at a site, see Methods) in the Las Warmiński nature reserve, northern Poland. Error bars show ± 1 standard error.

port. The evidence for the survey-dependent detection probability was slightly better (0.736) than that for the constant detection probability (0.672). Detection probabilities were very similar during the early and late surveys and varied enormously as a function of habitat quality (Fig. 2). Model-averaged probabilities of detection of at least one singing male during a single survey were very similar in all models: 0.383–0.419 at sites with no neighbours (single males present), 0.815–0.837 at sites with two males, 0.970–0.974 and 0.999 at sites with three and four males. The relative importance of Time (RVI = 0.236) and Observer (RVI = 0.105) effects were much lower. The effect of time was not significant: in all models betas were extremely low with confidence intervals including zero; the highest-ranked model that included this effect had a weight of ~0.15 (Table 1: model 3). This indicates that Collared Flycatchers do not reduce their singing activity until at least the afternoon (14:00–16:00 hrs). Overall, detection probabilities varied mostly as a result of the habitat quality effect – Collared Flycatchers were more likely to be detected at sites with more neighbours. The colonization probability, invariably estimated at 1 (parameter on a boundary, no standard errors available), indicated that all sites unoccupied during primary sampling period I were occupied during primary sampling period II. This can be interpreted in terms of the second wave of later arrivals – perhaps young males occupying sites that were

previously unoccupied. In line with this, true occupancy was higher later in the season (model averaged estimate: 1.0, parameter on a boundary, no standard error) compared to the initial occupancy early in the season (0.861 ± 0.072). Such a high occupancy estimates are a consequence of the study design, in which only sites of preferred habitat, likely to be occupied, were chosen (see Discussion). The probability of local extinction was estimated at zero in all models (parameter on a boundary, no standard error) and suggested that sites occupied early in the season were unlikely to be deserted within two to three weeks of arrival.

From none to five singing males were detected at the surveyed sites (mean 1.12 male per site, 95% confidence intervals 0.88–1.35). Using estimates of detection probability from the best model, the population size was estimated at 55–60 males during surveys 1–2 and at 76–88 males during surveys 3–4 (Fig. 3). Numbers of males recorded during consecutive surveys (i.e., naive estimates of population size) were 24, 26, 38 and 33.

With four surveys following the protocol described in this paper, and assuming similar observer detection abilities, the probability of detecting at least one Collared Flycatcher male depends mostly on the number of males present and on the number of surveys (Fig. 4). When sites are occupied by single males (no neighbours), one needs to undertake four surveys to obtain a detection probability close to 90%. With two males at a site, the
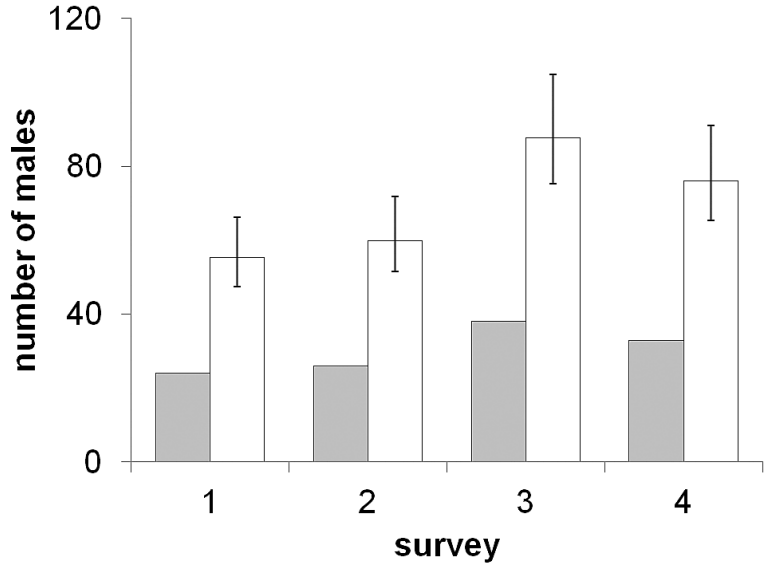
Fig. 3. Population size estimates of the Collared Flycatcher in the Las Warmiński nature reserve, northern Poland, 2012. Grey bars – number of males recorded during consecutive surveys 1, 2, 3 and 4, white bars – estimated number of males corrected for imperfect detectability. Whiskers denote 95% confidence intervals.

probability of detecting at least one of them exceeds 95% in the second survey; with three and more males one survey is enough to detect at least one of them with a probability of 95% or higher.

4. Discussion

In general, if detection is imperfect, the expectation of a count or analogous measures of abundance (such as the number of occupied sites) follows the relationship $E(n) = N \times a \times p$, where N is the true population size, a is the availability probability and p is the detection probability for given a (Kéry & Schmidt 2008). In our case, a represents the probability that a Collared Flycatcher male is present at the site and can be detected (i.e., it sings). In the modelling we performed, the estimated p is in fact the product of $a \times p$ (or, in other words, the estimated p is "true" p only if $a = 1$). The need to model a and p explicitly was stated by Kéry and Schmidt (2008). In the present study, we assume that a is close to 1 for the sake of simplifying the interpretation and thus that p refers to "true" p.

Only a small number of models were evaluated in this study. The number of possible models increases rapidly with the number of covariates considered. We used a rather simplified approach for our small dataset, with covariates allowed to have effects on detection probability only. Many more

models could be fitted, but evaluation of every possible combination is not recommended (Burnham & Anderson 2002). Secondly, more complex models may have problems in reaching numerical convergence on small datasets. The lack of one or two leaders among the models indicates that none of them was clearly superior. The overwhelming evidence for habitat quality (i.e., the number of neighbours) suggests that the probability of conducting effective surveys increases in
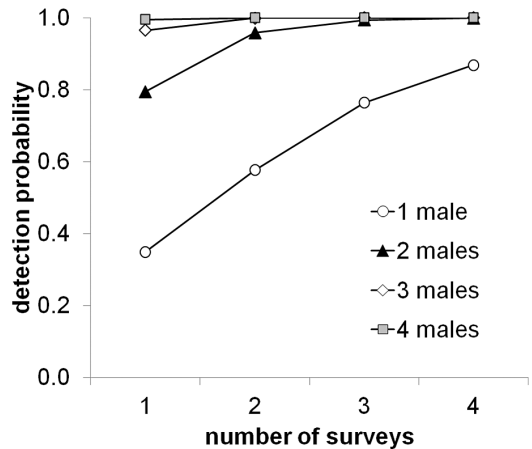

Fig. 4. Cumulative detection probability of Collared Flycatcher at sites occupied by 1, 2, 3 and 4 males in relation to the number of surveys in the Las Warmiński nature reserve, northern Poland. Model-averaged estimates are presented.

high-density populations. The observer effect was negligible: the difference between AS and GN appeared to be small and insignificant, contrary to what was expected. Perhaps the most surprising was the lack of a time effect, which indicates that singing activity does not decline as the day progresses. One of the reasons for there being no decline in detectability during the day (i.e., no decline in singing activity) is that in a low-density population males have to sing longer to compensate for the generally fewer mating opportunities (fewer females available). A similar study conducted in a high-density population would enable this hypothesis to be tested. Such a result may also suggest that many males that sing loudly and actively during the day (as we observed in the Las Warmiński reserve) are unmated and that this is the fraction of the population recorded most frequently. On a 36 ha study plot in the Białowieża primeval forest, 22%–48% males defending tree holes were non-breeders, while males that were already paired sang only for a short time close to the nest very early in the morning (Walankiewicz 2002).

The increase in the number of males between the early (late April–beginning of May) and late (18–23 May) surveys was evident and visible even in the naive estimates (numbers of males recorded during consecutive surveys), in occupancy estimates corrected for imperfect detection and in high colonization probability estimates. This favours the use of multi-season models for analysing data collected in a robust design fashion, mainly because a population of a migrant bird is unlikely to be demographically closed when the intervals between the primary sampling periods are longer than one to a few days (15 days in our case). The openness of the population can be due to the variation in arrival dates, which may be age-dependent, condition-dependent, or merely exhibit an individual variation not attributable to these factors (Cramp & Perrins 1993, Newton 2008). Previous studies have shown that Collared Flycatchers arrive during a period of approximately three weeks (Mitrus *et al.* 1996). Additionally, some migrant, singing males may be present in any population, which also leads to a lack of closure.

Extinction probabilities equal to zero indicate that sites are unlikely to be deserted within two weeks of arrival. Arriving males may first occupy a limited number of the best habitat patches, a familiar pattern in ecology known also as sequential fill of habitats of decreasing quality (Newton 1998) and these remain occupied with high probability, since only worse are available. On the other hand, many males may still be unmated and sing actively (the lack of the time effect is in line with this interpretation), regardless of the quality of the patch they occupy. Mated males reduce singing activity very much (Walankiewicz 2002), but many try to establish a new territory nearby to seek for a second female or possibilities for extra-pair copulations, which is common in this species. The frequency of broods with extra-pair young was 33%, 52% and 35% in Swedish, Czech and south-Polish populations (Sheldon et al. 1997, Krist et al. 2005, Wilk et al. 2008). If this is the case, colonization probabilities should be relatively high (as they are) owing to the appearance of new territories with males holding a territory nearby, but at the same time, extinction probabilities should have non-zero values (as they are not, what suggests that "old" territories are still occupied by unmated, actively singing males). In such a case, colonizations are best explained by establishment of new territories by later arriving males (while "old" territories are still occupied). On the other hand, within-season movements with initial settlement in sub-optimal habitats and subsequent movements to high-quality ones have been detected in Black-throated Blue Warblers (*Dendroica caerulescens*) by Betts *et al.* (2008), who also used dynamic occupancy models. The usefullness of this model type was stressed by Rota *et al.* (2009), who have shown that sites may be open to changes within a single season, that is, over time scales frequently used in occupancy studies.

We obtained very high occupancy estimates, which is a consequence of the study design: the sites surveyed were mostly the ones where Collared Flycatchers had been seen previously, or those in a preferred habitat. Instead of estimating occupancy at randomly selected sites, our aim was to conduct a census (i.e., survey the whole area of preferred habitats) to obtain the abundance measure corrected for imperfect detection. Using a wholly random sample of sites, one would get much lower occupancy estimates owing to the very localized distribution of this species in the reserve. Despite this, sites with no detections (histo-

ries '00 00') occurred in our sample. If only sites known to be occupied by the target species are surveyed, the fit of the data, as judged by the chi-square statistic, may be poor owing to the large difference between the expected and observed numbers of no-detection histories, and the correction factor ($\hat{c}$) must be applied. This, in turn, reorganizes model ranking in favour of models with fewer parameters, particularly if $\hat{c}$ is high, so that more complex models (e.g., those with covariates) have only small support and it becomes difficult to show the effect of any covariate.

An important point that we did not address in this study is predation pressure, which can affect decisions made by individual birds and consequently all the parameters estimated using multi-state models. However, this is rather difficult to measure properly in the field; we were unable to obtain any measure of predation pressure on small forest passerines in our study area.

This study is the first to correct results for imperfect detection via modelling, thereby allowing for the unbiased estimation of population size of Collared Flycatcher. Another formula applied to results obtained using a mapping technique was suggested by Walankiewicz *et al*. (1997); in this case bias was reduced to approximately 14%.

The results of previous censuses in the Las Warmiński reserve were not corrected for imperfect detection, and yielded 35 Collared Flycatcher males in 2000 and 48 in 2001 (AS and B. Brewka, unpublished observations). Small differences in the areas censused during 2000–2001 as compared with 2012 cannot explain this discrepancy; most of it is better attributed to both the single survey performed and the lack of correction for imperfect detection a decade ago. Given this, one can conclude that the population under scrutiny is very probably stable. Studies in the Białowieża primeval forest (E Poland) have shown, however, that Collared Flycatcher numbers can change twofold from year to year (Walankiewicz *et al*. 1997). The other point is that most population estimates produced by ornithologists, who do not correct their results for imperfect detection, are probably too low. While it is difficult to guess the extent to which particular population sizes are underestimated (as observers are likely to differ in their detection abilities), this is in line with the earlier results of Walankiewicz *et al*. (1997). Those authors stated

that even very intensive surveys (10 visits performed in April–June) enable the detection of at most two–thirds of the males/pairs that are actually breeding. In addition, the Białowieża population was breeding in nest-boxes, which also increases detection probability, since the males then sing at lower heights, close to the low-mounted nest boxes and are nearer to the observer (Walankiewicz *et al*. 1997). Nonetheless, estimating the abundance of Collared Flycatchers remains a difficult task. Apart from all the factors affecting detection probability already mentioned, there is substantial variation in the amount of time individual males spend singing in their territories related to their mating success. In effect, some males sing for just one day after arrival and some for a few days, whereas others – probably mainly unmated ones – may occupy territories and sing continuously for a few weeks. As in many other passerines, Collared Flycatcher males become silent after pairing (Walankiewicz *et al*. 1997).

With this in mind, we conclude that it is much better in terms of effort to carry out a number of short visits and estimate detectability, than to apply time-consuming mapping techniques followed by attempts to guess how many breeding pairs were actually there on the basis of unavoidably arbitrary criteria. The flexibility of occupancy modelling provides the opportunity to study much more than the actual numbers of breeding pairs. It is then up to the researcher to apply an appropriate study design, so that useful data can be collected and more questions addressed than just the estimation of population size.

Our results indicate that for monitoring purposes and to detect the highest possible proportion of males present, multiple visits should be undertaken at study plots/sites. When single males are considered, the proportion of detected males does not reach 1 even after four surveys. Whether surveys are better undertaken in early or late May remains unclear, as we did not detect any significant differences between these two periods. The later period may be better because more males are then present at the breeding sites (a clear result also when naive estimates are considered), but given that some early-arrived males may already be paired, they are easily missed due to reduced singing activity. Furthermore, optimal survey periods may be different in other populations across Eu-

rope owing to spatially varying arrival dates (Cramp & Perrins 1993, Král *et al.* 2011) and may vary year on year in the same area in response, for example, to weather conditions (Walankiewicz & Czeszczewik 2009).

In summary, the most important aspect of any study aiming to estimate population size or just to track changes in numbers is to obtain as high a detection probability as possible: this is best achieved by undertaking multiple surveys. Another key point is to know the optimal periods for surveying the species: frequently these are both spatially and temporally variable. The benefits of taking imperfect detectability into account by means of multiple visits and modelling are hard to overrate, particularly in the case of "difficult" species. The possibility of obtaining results of known precision is important, especially when estimations of abundance are to be carried out over large areas, requiring considerable observer effort.

Sepelsiepon (*Ficedula albicollis*) havaitsemistodennköisyys toistetuissa laskennoissa: esimerkki Pohjois-Puolalaisesta isoloituneesta populaatiosta

Tutkimme tekijöitä, jotka vaikuttivat sepelsiepon havaitsemistodennäköisyyteen. Laji on metsässä elävä piilotteleva varpuslintu, jonka levinneisyys rajoittuu Keski- ja Itä-Eurooppaan. Laulavien koiraiden läsnäoloa kartoitettiin 78 kohteessa Las Warmińskin luonnonsuojelualueella Pohjois-Puolassa, perustuen neljän keväällä 2012 tehtyyn laskentaan (kaksi huhti–toukokuun vaihteessa, ja kaksi toukokuun loppupuoliskolla).

Aineistoon sovitettiin usean kauden asutusmalleja, jotka osoittivat, että havaitsemistodennäköisyys vaihteli huomattavasti habitaatin laadun mukaan. Todennäköisyys havaita laskentakerran yhteydessä ainakin yksi koiras oli samankaltainen eri malleissa: 0.383–0.419 kohteissa jossa on vain yksi koiras läsnä, 0.815–0.837 kahden koiraan kohteissa, 0.970–0.974 kolmen koiraan kohteissa, ja 0.999 kohteissa joissa on neljä koirasta läsnä. Laskennan vuorokaudenaika ei vaikuttanut havaitsemistodennäköisyyteen, mikä viittaa siihen, ettei lauluaktiivisuus olennaisesti vähentynyt päivän edetessä.

Arvioitu lokaali "sukupuuttotodennäköisyys" oli nolla. Tämä on tulkittavissa siten, että aikaisemmin keväällä asutettua reviiriä ei normaalisti hylätä – koiraat lauloivat aktiivisesti useita päiviä saapumisen jälkeen. Koska koiraat pariuduttuaan vähentävät lauluaktiivisuuttaan huomattavasti, kyseiset tulokset saattavat johtua matalasta pariutumismenestyksestä. Mikäli tämä pitää paikkansa, kolonisaation todennäköisyys, jonka arvio oli 1.0, selittyy parhaiten joidenkin koiraiden myöhäisellä saapumisella, pikemmin kuin jo saapuneiden koiraiden liikkumisella pesimäkauden sisällä.

Tämä tutkimus korostaa sitä, että asutusmallit ovat oiva työkalu useiden kovariaattien vaikutusten samanaikaiseen tarkasteluun, niin havaitsemistodennäköisyyden kuin muiden biologisesti kiinnostavien parametrien arvioimiseen.

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