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Abundance estimation from point counts when replication is spatially intensive but temporally limited: comparing binomial *N*-mixture and hierarchical distance sampling models

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We investigated the performance of hierarchical distance sampling (HDS) versus binomial *N*-mixture (binmix) models, both aiming at abundance (or, equivalently, density) estimation. We tested the accuracy of density estimates using simulated data and compared them to the estimates coming from a Red-breasted Flycatcher (*Ficedula parva*) point count survey in the Darżlubie Forest (N Poland). In both the simulations and the actual data, we mimicked varying plot size (i.e., radius length, and site area) and song loudness from quiet to loud by modifying detection functions. We found that the resolution at which distance detection data are collected (i.e., the number and width of distance classes) had essentially no effect on estimates and their precision in HDS, even when birds were only assigned into two, wide distance classes, such as "close" and "far". Both site size (radius length) and song loudness affected density estimates in HDS only slightly: a positive bias (by 5%–17%) occurred when sites were small and a lower precision occurred for quiet singers. In general, however, estimates from HDS were accurate. In contrast, under binmix, density was heavily overestimated at smaller sites, but apparently correct at large sites. The latter may stem from the counterbalancing effects of overestimation at close distances and underestimation at large distances that cancel each other out on average, both of which are a function of song loudness and arise always when the observer is stationary. When applied to point count results, binmix models must be used with care, as the song loudness in relation to site size seems to affect abundance estimates. We suggest that when density (or population size) estimation is of interest, and with a limited number of visits, a study using point counts would profit from applying HDS models by using additional information on detection distances, even at low resolution. This cost-effective option represents an attractive alternative to be considered vs. simpler counts during which just the number of birds is noted.

1. Introduction

Animal abundance is of primary importance in understanding ecological relationships and tracking changes in numbers, which is crucial for conservation (Williams *et al*. 2002, Kéry & Schaub 2012). Perhaps the most accurate method developed to measure avian density, the spot-mapping (Tomiałojć 1980, Bibby *et al*. 2000), particularly when coupled with individual marking and nest search, is too time-consuming to be applied to larger areas. Quick methods developed as cost-efficient alternatives, such as point counts, frequently miss some individuals due to their much smaller field effort while density can be estimated from replicated visits with the models accounting for imperfect detection (MacKenzie *et al*. 2006, Kéry & Royle 2016). Distance sampling methodology, which does not require temporal replication, represents another option for density estimation (Buckland *et al*. 2015).

However, some models which are able to correct for imperfect detection – the binomial *N*-mixture model (Royle 2004) in particular – when applied to point count data, have been shown to either overestimate density (Chandler *et al*. 2011, Hunt *et al*. 2012, O'Donnell *et al*. 2015) or the direction in the density bias was density-dependent (Warren *et al*. 2013). *N*-mixture models are also sensitive to even small violations of model assumptions or unmodeled heterogeneity in either abundance, detection or both (Barker *et al*. 2017, Link *et al*. 2018). On the other hand, multiple studies have demonstrated the accordance between *N*-mixture model estimates and the more robust capture-mark-recapture estimates (Costa *et al*. 2019) or the actual population size (Bötsch *et al*. 2020). Because hierarchical models are still a relatively new branch of ecology, further studies validating their performance in simulations and case studies are needed (Dénes *et al*. 2015). This is still important in the case of the commonly used binomial *N*-mixture model.

How accurately a given model estimates density can only be tested in simulations (Kéry & Royle 2016). Simulation results can then be compared to estimates from actual data. In this paper, we use both simulations and true data collected during a point count survey to compare density estimates of the hierarchical distance sampling model (hereafter HDS, Kéry & Royle 2016) and the binomial *N*-mixture model (hereafter binmix, Royle 2004). The basic difference between the respective field protocols is in how the data are collected: with the distance sampling approach, detection distances of individuals are recorded, while the simpler version of data used by binmix models ignores this information (just the sum of individuals is noted). Our primary interest was to find out whether radius length (i.e., site area) within the point counts field protocol affects density estimates under each model and whether this depends on the loudness of songs. Additionally, we also tested if the number and width of distance classes (distance sampling approach only) affect density estimates in both simulated and actual data.

2. Materials and methods

2.1. Abundance models

Distance sampling methodology is based on the fact that the probability of detection declines with distance, so individuals at greater distances are more frequently missed by the observer. The curvilinear detection function, whose parameters are estimated within distance sampling models, describes this relationship, and allows to estimate the effective detection radius and thus the effective area, and, in consequence, true density (or, equivalently, abundance) because the area effectively surveyed becomes the known quantity. With detection distances and repeated surveys in our field study of the Red-breasted Flycatcher (*Ficedula parva*, see section 3.3. below), our choices for density estimations were hierarchical distance sampling models (HDS, Kéry & Royle 2016) from the R *unmarked* package (Fiske & Chandler 2011).

Apart from abundance or density and detection function, HDS models estimate another parameter of interest, called availability (Chandler *et al*. 2011, Kéry & Royle 2016), which describes the proportion of individuals available for detection. An individual might not be available for detection if it does not sing, or temporarily leaves the site, if the site is only partly overlapping with its territory, thus density can be estimated as the product of abundance and availability. The most important assumptions for the distance sampling methodology are that the distribution of animals is independent of observation points (or other locations), distance is measured exactly, animals are detected at their initial location and that animals positioned at the observation point are detected with certainty (HDS models relax the last assumption, see Kéry & Royle 2016).

A simpler, binomial *N*-mixture (binmix) model has been developed to estimate abundance given imperfect detection (Royle 2004) and has become very popular in abundance studies. It requires spatio-temporal replication and assumes that the population is closed over the study period. HDS models also need temporal replication to make availability estimable (in contrast to conventional distance sampling where it is missing), and multiple detections are needed to estimate a detection function. In conventional settings, density can be reliably estimated even with a single visit to transects or points, as information on detection is extracted from detection distances. Binmix models only use the number of individuals (e.g., singing males) recorded at surveyed sites over consecutive visits.

Since numbers recorded on the same sites over consecutive visits are hardly ever the same, then, under the assumption of population closure, detection probability is (almost) always less than one. Therefore, the binmix model allows one to obtain "true" abundance (i.e., recorded plus missed individuals). Binmix assumptions require that the population is closed over the study period, individual detections are independent from one another and the same among individuals (unless heterogeneity is modeled) and that individuals are not counted multiple times (i.e., false positives are not present, Kéry & Royle 2016).

2.2. Simulation study

We performed simulations to explore how accurately HDS and binmix models estimate density. We used the *simHDSopen* function from the *AHMbook* library, which offers great flexibility in setting input parameters (Kéry & Royle 2016). We mimicked our study system while simulating data (178 sites with a 200 m radius, two primary sampling periods with two replicate surveys, but only the first used, data collected with detection distances) and parameters ($\lambda = 1.5$ individuals per site and $\varphi = 0.8$ producing a density of 1.2 individuals per site, or 0.96 / 10 ha, standard deviation of the halfnormal detection function, SD = 85 or variable – see below). HDS models with halfnormal detection functions (preferred in actual data analysis) were used in all simulations.

First, with 1,000 simulated datasets, we verified whether the number and width of distance classes had any effect on density estimates from HDS models. We grouped the detected number of males into distance classes of variable and equal (for simplicity) widths of 10, 20, 25, 40, 50 and 100 m, which reflects 20, 10, 8, 5, 4 and just two distance classes. We then fitted HDS models to these datasets to explore the effects of distance class width on the point estimates and their variance.

In the second simulation, we were interested whether, and, if so, how much site area (radius length) affects density estimates for species whose songs vary from quiet to very loud. We used the same input parameters except for the detection function SD, which we varied to mimic species across a range of song loudness and its detectability as a function of distance: from singing quietly, detectable only at close range, to very loud and detectable at large distances. To achieve this, we used six fixed values of the halfnormal detection function SD: 3.5, 4, 4.275, 4.5, 4.75 and 5 (on the log scale), which translates to effective detection radii of *c* 47, 77, 100, 120, 144 and 160 m. We simulated 1,000 datasets for each SD value.

Within each simulated dataset, we created subsets which would emerge if surveys were performed within progressively smaller radii (and smaller site areas). These subsets were obtained by (1) grouping distance detection data into ten 20 m wide distance zones and (2) successively left out one or more of the most distant zones. This created nine subsets within a single simulated dataset: the full dataset included all detections within a radius of 200 m (ten 20 m wide distance classes), the second one missed the most distant 20 m wide zone, thus had a radius reduced to 180 m (nine distance classes; all birds detected at 181–200 m excluded) and so on, up to just 40 m (with two 20 m wide distance classes and only including birds recorded within this distance). In all these subsets, detections were grouped into 20 m wide distance classes and both HDS and binmix models were fitted to each subset. For binmix, we used the same progressively smaller sites, but with no distance classes. The 40 m short radius (site area of 0.5 ha) might seem very small, but similar site sizes are used in some field studies on birds (e.g., Chandler *et al*. 2009). In total, 18 models (nine HDS models and nine binmix models) were fitted to each of the nine subsets within each of the 6,000 simulated datasets (1,000 per each song loudness). In this setting, the radius (and thus the site area) is progressively smaller, and so is the number of males detected.

2.3. Red-breasted Flycatcher data

Our study illustrates a not-so-uncommon situation, where the surveys are spatially rather intensive (178 observation points), but temporally limited (just two visits). The actual results come from our medium-scale survey of the Red-breasted Flycatcher, a forest interior passerine, performed in 2016 in one of the most important refugees for the species in Poland (Sikora *et al*. 2018).

2.3.1. Study area

The Darżlubie Forest (6,453 ha) is located in northern Poland (54°37'–54°42' N, 18°12'–18°22' E). Typical forest communities are deciduous stands with European (Common) Beech (*Fagus sylvatica*) – *Luzulo pilosae-Fagetum*, *Galio odorati-Fagetum* and *Fago-Quercetum* – along hornbeam subatlantic forest (*Stellario holostellae-Carpinetum betuli*). The tree species composition is currently shaped by forestry in most of the area, with the dominant tree species represented by Scots Pine (*Pinus sylvestris*, 41%), European Beech (29%) and Norway Spruce (*Picea abies*, 9%).

2.3.2. Study species

The breeding range of the Red-breasted Flycatcher includes central-eastern Europe and small, isolated areas in Asia (Flade 1997). The species has been apparently stable in Poland over the last two decades (Chylarecki *et al*. 2018), with a population estimated at 16,000–32,000 breeding pairs in 2013–2018 (Chodkiewicz *et al*. 2019), being more common in the northern and north-eastern parts of the country and – particularly – in the Carpathians (Wilk *et al*. 2016). The Red-breasted Flycatcher is a reliable indicator of forest bird biodiversity (Pakkala *et al*. 2014). It prefers the interior of deciduous forests with continuous tree crown coverage, providing deep shadow in the lower forest layers and avoids gaps (Fuller 2000), loose stands and forest edges (author's unpublished data).

2.3.3. Field surveys

We performed two 5-min long surveys at 178 observation points embedded in twenty 1 km2 (1 × 1 km) squares (see Fig. 1 in Sikora et al. 2018) on 9–12 May (survey 1) and 18–23 May 2016. ¾ of the observation points were allocated in "optimal" habitat, defined as either beech or mixed stands (with beech share of 50% or more) aged ≥ 70 years, while the remaining ones were allocated in "poor" habitat (i.e., predominantly conifer, or younger mixed stands). Within each square plot, observation points were located 200–400 m from each other. We performed observations between early morning and afternoon (04:30–16:30 CET), provided that the species was also actively singing during the mid-day and afternoon hours (Neubauer & Sikora 2016), in good weather conditions.

During observations at each point, we noted singing Red-breasted Flycatcher males within a radius of 200 m (12.6 ha covered). To avoid false positives (double counting), a male was treated as a different individual only when countersinging was recorded. After the 5-min observation ended, we approached the place from which a male sang to obtain its geographical coordinates with GARMIN GPSmap 60Cx, accurate to 3–5 m in most cases; in a few cases when birds moved or ceased singing, accuracy could be lower, up to ± 10 m. Exact detection distances were then calculated, producing continuous variable – detection distances in meters. This allowed a *post-hoc* grouping into distance classes of the desired width for the analysis of the data. We also estimated detection distances during observation in the field without the knowledge of exact distances (they

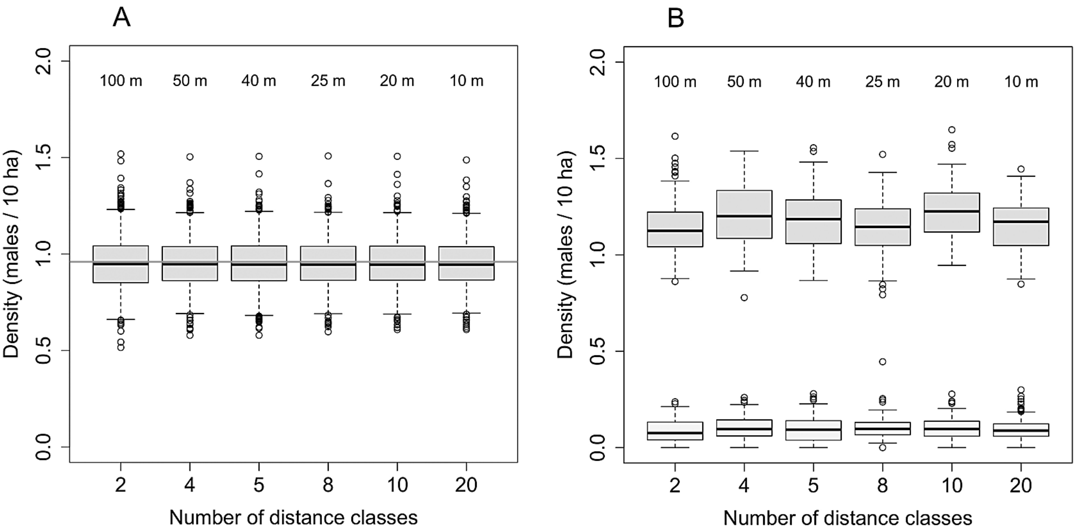


Fig. 1. (A) Simulation results: density estimates for variable number and width of distance classes under HDS models with the halfnormal detection function. Distance class widths given at the top. Grey horizontal line shows simulated density value (0.96 males / 10 ha). (B) Red-breasted Flycatcher density estimates for variable number and width of distance classes under HDS models. Horizontal lines inside the boxes denote medians, boxes represent 25%–75% percentiles, whiskers stand for ± 1.5 interquartile range, circles – outlying values. Top row – "optimal" habitat, bottom row – "poor habitat".

were measured afterwards) and classified each detected male into one of four pre-defined distance classes (0–50 m; 51–100 m, 101–150 m, 151–200 m).

2.4. Data analysis

We used models sufficiently complex to both answer our questions, and, at the same time, to keep the whole analysis simple. For HDS models we used data grouped into distance classes, separately for both surveys, while the number of males recorded at a site on surveys 1 and 2 (temporal replication) represents the site-level datum for a binmix model. Both model types, HDS and binmix had only habitat effect in the submodel for abundance and thus produced two estimates: for "optimal" and "poor" habitats. We also fitted HDS models with survey-dependent availability to address within-season changes in density, but since they had slightly worse support while being more complex, we preferred the simpler models (in addition, within-season change in abundance would not be possible to address with just two surveys and simple binmix models).

We kept detection probability in binmix models and both detection function SD and availability in HDS constant, which were plausible assumptions, given the short study time during the highest vocal activity of the species. We did not consider a simpler model with no habitat effect, since the mean abundance between habitats was so different that it would not make much sense. We fitted models using the *unmarked* package (Fiske & Chandler 2011) in R 3.6.1 (R Core Team 2019) using *gdistsamp* (HDS) and *pcount* (binmix) fitting functions. We set model outputs to be expressed in individuals per ha (optional in HDS and available by adding an offset of log(site area) to the submodel for abundance in binmix) which makes them directly comparable.

Data analysis followed simulations: in the first analysis, we investigated the effect of the number and width of distance classes on density estimates. In the second, progressively smaller site areas were created, as in the simulation study. To get variance estimates, we resampled the same (actual) data with the nonparametric bootstrap technique and fitted HDS and binmix models to each resample. In both cases, the bootstrapping procedure was repeated 100 times and the resulting

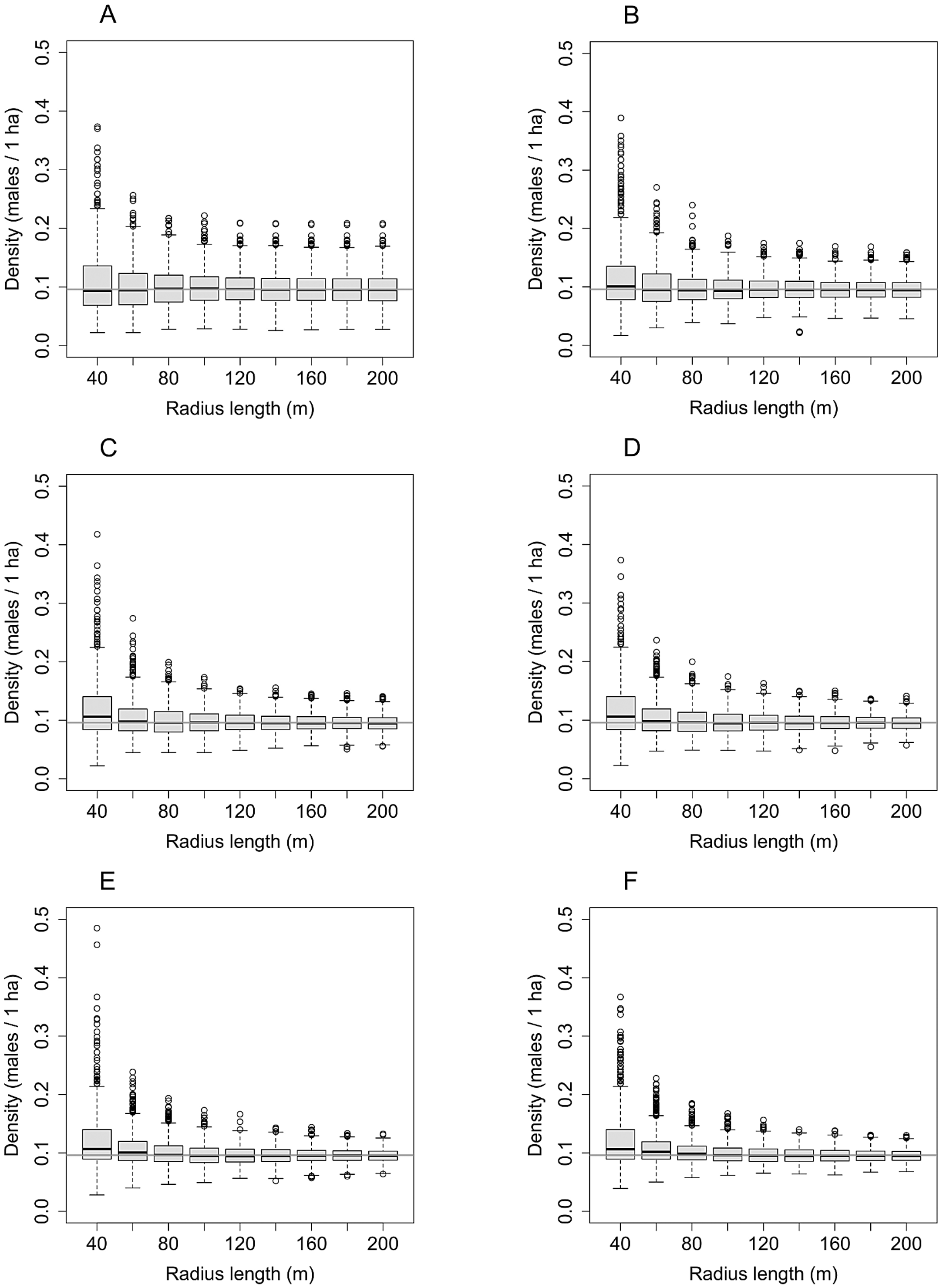


Fig. 2. Simulation results: density estimated by HDS models fitted to point count data for hypothetical species ranging from quiet (A) to very loud (F) song (see Methods) across increasing radii lengths (site areas). Estimated density and simulated value (0.096) are given per 1 ha. Remaining denotations as on Fig. 1.

distributions of parameters were then used to compute the desired statistics (means and their standard deviations, along with 95% confidence intervals). To each resample, we fitted models with all four detection functions available in the *unmarked gdistsamp* fitting function: half-normal, hazard, exponential and uniform.

3. Results

3.1 Simulation study

The number and width of distance classes had no effect on the density estimates: no matter how many distance classes were used, parameters were estimated properly (Fig. 1A). Similarly, HDS estimates of density proved to be rather accurate irrespective of the song loudness and radius length (site area) (Fig. 2A–2F). A slight tendency of density overestimation occurred as the radius and site area decreased, reaching up to 17% for loud singers and less for quiet singers (Table 1). There were also clear differences in the precision of density estimates in respect to song loudness: the louder the song, the more precise the estimates. An upward bias in estimates of the detection function SD was evident as site size decreased, reaching 5–17%.

Binmix overestimated density across all radii lengths, particularly strongly at small sites (Fig. 3A–3F), while keeping the same patterns in terms of precision as HDS estimates. This becomes evident when simulation results from both models are plotted together with the log scale for density (Fig. 4A–4F). In addition, under binmix, there seems to be an effect of song loudness on density estimates at the largest sites: density is actually underestimated for quiet singers (Fig. 4A), apparently correct for species with moderately loud songs (Fig. 4C and 4D) and clearly overestimated for species with very loud songs (Fig. 4F).

3.2 Analysis of Red-breasted Flycatcher data

3.2.1. Distribution of detection distances

The largest detection distance was about 200 m with just three out of 148 males recorded were detected at a distance close to 200 m: at 203, 199 and 197 m from the observer. The distribution of Red-breasted Flycatcher males detections peaked roughly in the middle of the maximum distance assumed in this study (200 m): between 50–150 m during Survey 1 (Fig. 5A) and 30–150 m during Survey 2 (Fig. 5B). There were significantly more detections in the 0–20 m distance class, the closest to the observer, during Survey 1 than during Survey 2 (Fig. 5C and 5D). The observer's assignment of detections into four predefined distance classes was moderately correct, with the proportion of correctly assigned detections ranging from 54% to 100%, depending on the distance class and survey (Fig. 6) – the average percentage of correct assignments across the two surveys and four distance zones was 75.8%.

3.2.2. Effects of the number and width of distance classes

There were no clear leaders among the four models fitted to each of the six datasets differing in the number of distance classes. The top-supported models gained AIC weights between 0.34 and 0.56. Models with the halfnormal detection function were slightly preferred over models with a hazard detection function (5 out of 6 cases), but differences in support were small (1 to 3 AIC units, Table 2). Models with exponential and uniform detection functions received much less support.

Density estimates under the top models appeared robust to varying number and width of distance classes (Fig. 1B). The SD of the detection function was estimated at values around 4.5, which translates to an effective detection radius of *c* 118 m (range 106–131 m, Table 3). In all the cases, availability estimates were close to 1 (mean 0.99, range 0.61–1.00) and did not affect the estimated density strongly (Table 3).

3.2.3. Effects of radius length (site area)

With decreasing radii lengths and site areas (radii range from the biggest 200 m to the smallest tested – 40 m, and site areas declining accordingly from 12.6 ha to 0.5 ha), estimates of density were stable to a radius of about 120 m under HDS models and increased with smaller radii (Fig. 7A). Binmix

Table 1. Results of 1,000 simulations of fitting HDS models to point survey data for hypothetical species ranging from quiet to very loud song for decreasing radii lengths (site areas). Parameters (with 95% intervals) are given on log (λ, abundance and p, detection function SD) and logit (φ, availability probability) scales.

Radius length / site area	HDS model parameters			Density (males/10 ha)
	λ	φ	p	
Log SD = 3.5, effective detection radius c 47 m				
200 m / 12.57 ha	–1.63 (–2.85; 0.76)	0.03 (–3.56; 7.24)	3.49 (3.28; 3.69)	0.94 (0.47; 1.69)
180 m / 10.18 ha	–1.42 (–2.80; 0.97)	–0.36 (–3.76; 7.28)	3.49 (3.28; 3.69)	0.94 (0.47; 1.69)
160 m / 8.04 ha	–1.16 (–2.75; 1.20)	–0.76 (–4.02; 7.25)	3.49 (3.28; 3.69)	0.94 (0.47; 1.68)
140 m / 6.16 ha	–0.90 (–2.69; 1.47)	–1.12 (–4.30; 7.21)	3.49 (3.28; 3.69)	0.95 (0.47; 1.70)
120 m / 4.52 ha	–0.59 (–2.63; 1.78)	–1.52 (–4.65; 7.13)	3.49 (3.28; 3.72)	0.95 (0.46; 1.71)
100 m / 3.14 ha	–0.22 (–2.38; 2.14)	–1.96 (–5.05; 6.37)	3.49 (3.27; 3.75)	0.96 (0.45; 1.72)
80 m / 2.01 ha	0.23 (–2.14; 2.59)	–2.50 (–5.60; 1.64)	3.49 (3.22; 3.94)	0.95 (0.42; 1.78)
60 m / 1.13 ha	2.01 (–1.77; 3.16)	–4.08 (–6.35; 0.26)	3.49 (3.09; 6.97)	0.96 (0.37; 1.86)
40 m / 0.50 ha	3.89 (–1.41; 3.95)	–6.07 (–7.11; –0.06)	3.60 (2.70; 7.48)	0.96 (0.34; 2.59)
Log SD = 4, effective detection radius c 77 m				
200 m / 12.57 ha	–2.08 (–2.61; 0.78)	1.46 (–3.23; 7.73)	4.01 (3.87; 4.13)	0.95 (0.65; 1.36)
180 m / 10.18 ha	–1.91 (–2.56; 1.00)	0.62 (–3.46; 7.67)	4.00 (3.87; 4.14)	0.96 (0.65; 1.37)
160 m / 8.04 ha	–1.68 (–2.45; 1.23)	0.07 (–3.74; 7.21)	4.00 (3.87; 4.16)	0.96 (0.63; 1.35)
140 m / 6.16 ha	–1.46 (–2.30; 1.50)	–0.40 (–4.00; 6.08)	4.00 (3.85; 4.20)	0.96 (0.62; 1.41)
120 m / 4.52 ha	–1.11 (–2.09; 1.80)	–0.90 (–4.35; 1.56)	4.01 (3.81; 4.26)	0.95 (0.60; 1.41)
100 m / 3.14 ha	–0.71 (–1.85; 2.17)	–1.46(–4.79; 0.45)	4.00 (3.75; 4.47)	0.96 (0.58; 1.46)
80 m / 2.01 ha	–0.14 (–1.51; 2.62)	–2.16 (–5.34; –0.12)	3.99 (3.65; 6.08)	0.96 (0.51; 1.56)
60 m / 1.13 ha	0.73 (–1.33; 3.18)	–3.08 (–5.95; –0.58)	4.03 (3.37; 7.85)	0.96 (0.52; 1.81)
40 m / 0.50 ha	3.90 (–1.18; 3.96)	–5.81 (–6.93; –0.50)	4.21 (2.81; 7.70)	1.01 (0.45; 2.59)
Log SD = 4.275, effective detection radius c 100 m				
200 m / 12.57 ha	–2.09 (–2.52; –0.07)	1.35 (–2.31; 7.82)	4.28 (4.16; 4.40)	0.95 (0.71; 1.24)
180 m / 10.18 ha	–1.91 (–2.43; 0.19)	0.58 (–2.61; 7.47)	4.28 (4.15; 4.41)	0.95 (0.70; 1.27)
160 m / 8.04 ha	–1.67 (–2.27; 1.04)	0.01 (–3.29; 3.53)	4.28 (4.13; 4.45)	0.95 (0.68; 1.30)
140 m / 6.16 ha	–1.40 (–2.07; 1.45)	–0.49 (–3.73; 1.37)	4.27 (4.10; 4.52)	0.95 (0.65; 1.32)
120 m / 4.52 ha	–1.09 (–1.84; 1.79)	–0.94 (–4.22; 0.61)	4.27 (4.03; 4.68)	0.95 (0.63; 1.37)
100 m / 3.14 ha	–0.68 (–1.63; 2.18)	–1.45 (–4.71; 0.03)	4.26 (3.95; 5.35)	0.96 (0.58; 1.43)
80 m / 2.01 ha	–0.22 (–1.38; 2.63)	–1.99 (–5.27; –0.30)	4.27 (3.79; 7.94)	0.96 (0.57; 1.55)
60 m / 1.13 ha	0.42 (–1.18; 3.19)	–2.72 (–5.84; –0.55)	4.29 (3.49; 7.93)	0.98 (0.57; 1.77)
40 m / 0.50 ha	3.90 (–1.18; 3.97)	–5.78 (–6.87; –0.58)	4.32 (2.90; 7.66)	1.06 (0.50; 2.48)
Log SD = 4.5, effective detection radius c 120 m				
200 m / 12.57 ha	–2.11 (–2.48; –1.28)	1.34 (–0.64; 7.54)	4.45 (4.33; 4.57)	0.96 (0.71; 1.23)
180 m / 10.18 ha	–1.90 (–2.35; –1.03)	0.57 (–1.15; 6.40)	4.44 (4.31; 4.62)	0.96 (0.71; 1.24)
160 m / 8.04 ha	–1.65 (–2.17; –0.59)	–0.01 (–1.69; 1.98)	4.44 (4.28; 4.66)	0.95 (0.70; 1.27)
140 m / 6.16 ha	–1.38 (–1.95; 0.02)	–0.49 (–2.45; 0.90)	4.45 (4.24; 4.78)	0.95 (0.67; 1.30)
120 m / 4.52 ha	–1.09 (–1.73; 1.27)	–0.94 (–3.61; 0.27)	4.44 (4.18; 5.16)	0.95 (0.63; 1.37)
100 m / 3.14 ha	–0.72 (–1.55; 2.15)	–1.48 (–4.56; –0.15)	4.44 (4.04; 7.99)	0.95 (0.60; 1.43)
80 m / 2.01 ha	–0.23 (–1.32; 2.62)	–1.97 (–5.19; –0.45)	4.43 (3.85; 8.16)	0.96 (0.61; 1.55)
60 m / 1.13 ha	0.42 (–1.15; 3.19)	–2.68 (–5.76; –0.69)	4.40 (3.49; 8.10)	0.99 (0.60; 1.82)
40 m / 0.50 ha	3.90 (–1.00; 3.97)	–5.78 (–6.87; –0.53)	5.21 (2.90; 7.72)	1.01 (0.50; 2.34)

Table 1, continued

Log SD = 4.75, effective detection radius c 144 m				
200 m / 12.57 ha	–2.13 (–2.41; –1.73)	1.36 (0.02; 7.58)	4.75 (4.61; 4.93)	0.95 (0.76; 1.18)
180 m / 10.18 ha	–1.91 (–2.26; –1.45)	0.59 (–0.52; 2.71)	4.75 (4.58; 5.00)	0.96 (0.74; 1.21)
160 m / 8.04 ha	–1.68 (–2.06; –1.05)	0.02 (–1.08; 1.36)	4.74 (4.54; 5.17)	0.95 (0.71; 1.24)
140 m / 6.16 ha	–1.41 (–1.86; –0.61)	–0.46 (–1.73; 0.67)	4.75 (4.46; 5.49)	0.95 (0.69; 1.26)
120 m / 4.52 ha	–1.08 (–1.65; 0.60)	–0.93 (–3.03; 0.17)	4.76 (4.34; 7.96)	0.95 (0.68; 1.31)
100 m / 3.14 ha	–0.71 (–1.42; 2.13)	–1.41 (–4.45; –0.28)	4.77 (4.20; 8.67)	0.95 (0.69; 1.39)
80 m / 2.01 ha	–0.27 (–1.23; 2.62)	–1.92 (–5.10; –0.62)	4.74 (3.96; 8.42)	0.97 (0.69; 1.51)
60 m / 1.13 ha	0.42 (–1.07; 3.19)	–2.62 (–5.74; –0.74)	4.69 (3.56; 8.10)	1.01 (0.67; 1.72)
40 m / 0.50 ha	3.90 (–1.09; 3.97)	–5.65 (–6.77; –0.72)	5.25 (2.90; 7.70)	1.07 (0.56; 2.38)
Log SD = 5, effective detection radius c 160 m				
200 m / 12.57 ha	–2.12 (–2.33; –1.87)	1.33 (0.36; 4.78)	5.01 (4.83; 5.31)	0.95 (0.76; 1.17)
180 m / 10.18 ha	–1.91 (–2.17; –1.58)	0.59 (–0.21; 1.72)	5.01 (4.76; 5.50)	0.95 (0.75; 1.19)
160 m / 8.04 ha	–1.68 (–1.98; –1.22)	0.04 (–0.82; 0.91)	5.01 (4.70; 5.88)	0.95 (0.73; 1.21)
140 m / 6.16 ha	–1.40 (–1.79; –0.70)	–0.46 (–1.49; 0.35)	5.00 (4.63; 7.94)	0.95 (0.72; 1.24)
120 m / 4.52 ha	–1.08 (–1.58; –0.05)	–0.93 (–2.28; –0.03)	5.03 (4.45; 8.52)	0.95 (0.72; 1.32)
100 m / 3.14 ha	–0.70 (–1.43; 2.04)	–1.41 (–4.39; –0.34)	5.03 (4.30; 8.94)	0.97 (0.72; 1.37)
80 m / 2.01 ha	–0.27 (–1.21; 2.62)	–1.89 (–5.08; –0.60)	4.96 (4.01; 8.50)	0.98 (0.71; 1.56)
60 m / 1.13 ha	0.38 (–1.15; 3.20)	–2.60 (–5.75; –0.66)	4.90 (3.59; 8.13)	1.02 (0.65; 1.79)
40 m / 0.50 ha	3.90 (–1.11; 3.97)	–5.70 (–6.72; –0.68)	5.16 (2.90; 7.70)	1.12 (0.56; 2.43)

models appeared to produce progressively higher density estimates across the whole range of increasing radii lengths (Fig. 7B), being apparently in agreement with HDS density estimates only for large site areas (a radius of 160 m or more). This becomes evident with estimates plotted together: density under HDS with a halfnormal detection function does not increase for a wider range of radii lengths and is also nearly two times lower than binmix for the smallest tested radius (site area) (Fig. 7C).

4. Discussion

Two main conclusions emerge from our analyses. Simulation results showed that the number and width of distance classes has no effect on the density estimates in HDS models and the same was observed in the analysis of actual data. It may seem surprising, but very little precision is lost with increasing distance class widths (see Kéry & Royle 2016, pages 415–416). With respect to site area (radius length), in simulation, HDS density estimates seem to be robust except for decreased precision as the site area declines and small overestimations when the site area is very small. Density estimates also seem to be affected by song loudness (and thus detectability as a function of distance – the louder the song, the larger the effective detection distance): simulated species with a loud song produce more precise results than the species singing quietly.

In the case of our actual data on Red-breasted Flycatchers, more-than-expected detections at close distances during survey 1 could be responsible for higher density estimates in the smaller site areas under HDS models. It is unclear why there were so many detections close to the observers, but birds could respond positively to the observer's presence and approach him to be detected closer than their initial locations. We note that these detections occurred in the closest 20 m-wide distance class (Fig. 5A and 5C), so these birds couldn't be miss-assigned at larger distances which are more prone to error – i.e., between 0–50 and 51–100 m distance classes. The degree of overestimation of density in Red-breasted Flycatcher data increased with radius decline, i.e., the smaller the radius, the higher overestimation, but this was only clear for

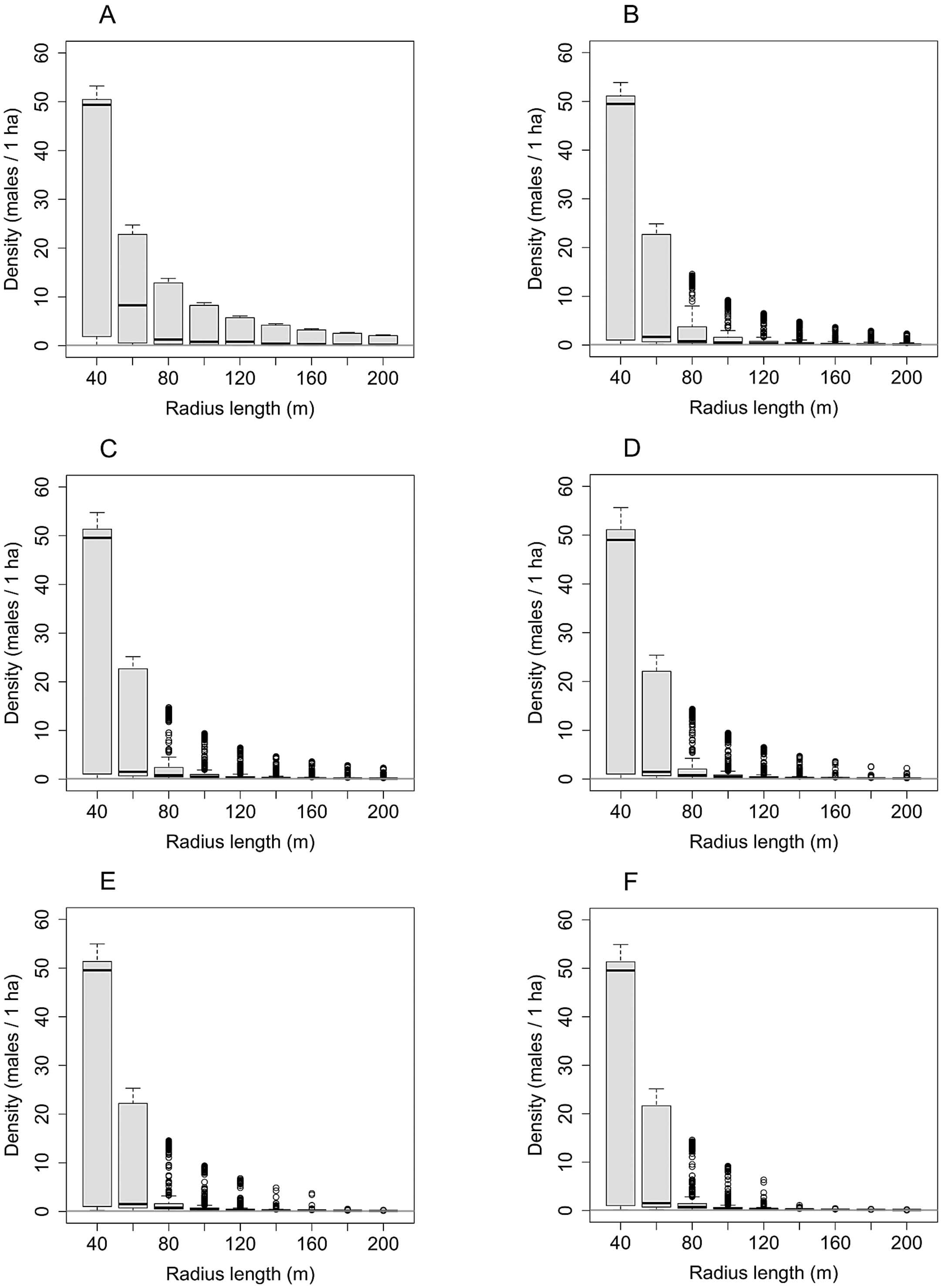


Fig. 3. Simulation results: density estimated by binmix models fitted to point count data for hypothetical species ranging from quiet (A) to very loud (F) song (see Methods) across increasing radii lengths (site areas). Remaining denotations as on Fig. 2.

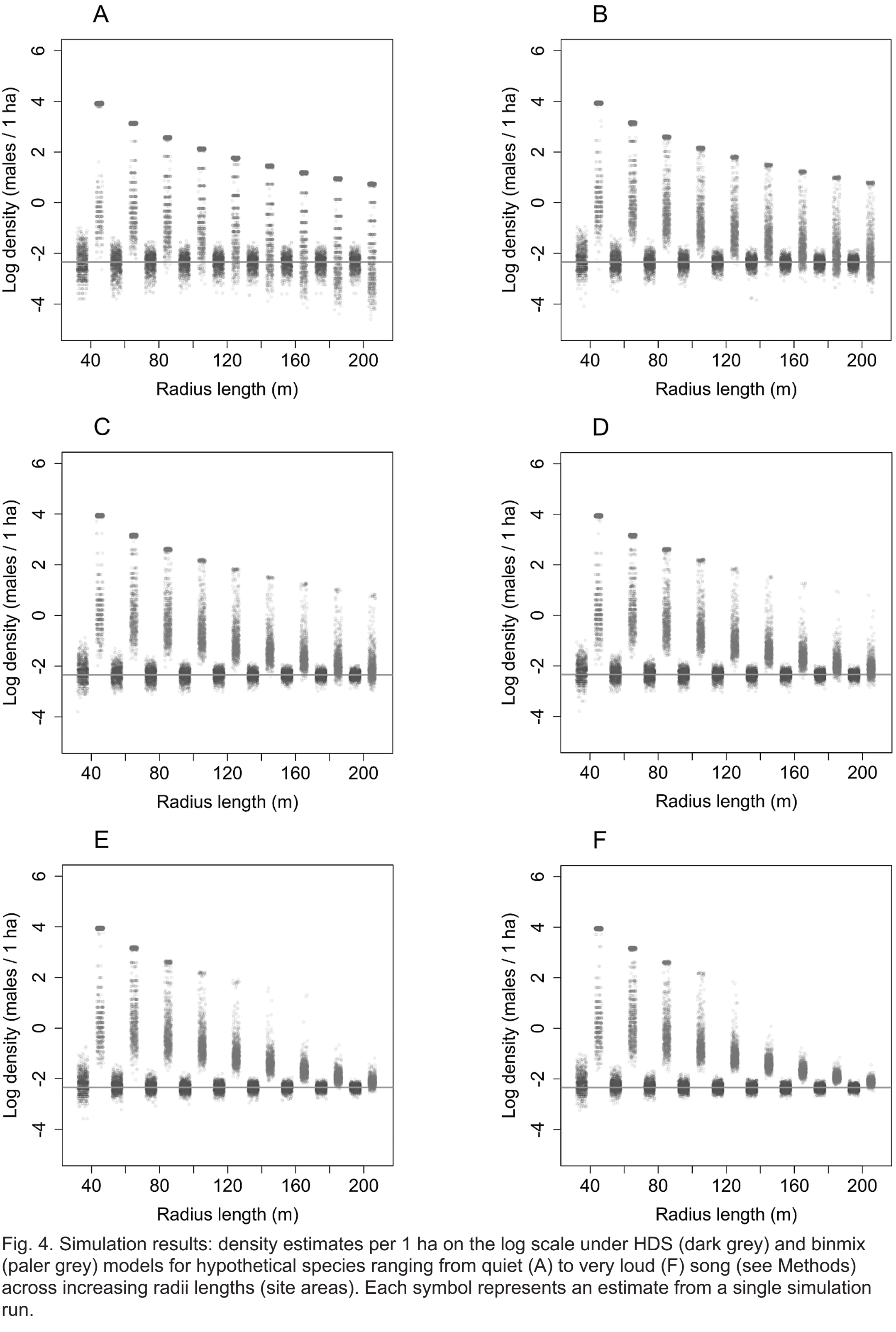


Fig. 4. Simulation results: density estimates per 1 ha on the log scale under HDS (dark grey) and binmix (paler grey) models for hypothetical species ranging from quiet (A) to very loud (F) song (see Methods) across increasing radii lengths (site areas). Each symbol represents an estimate from a single simulation run.

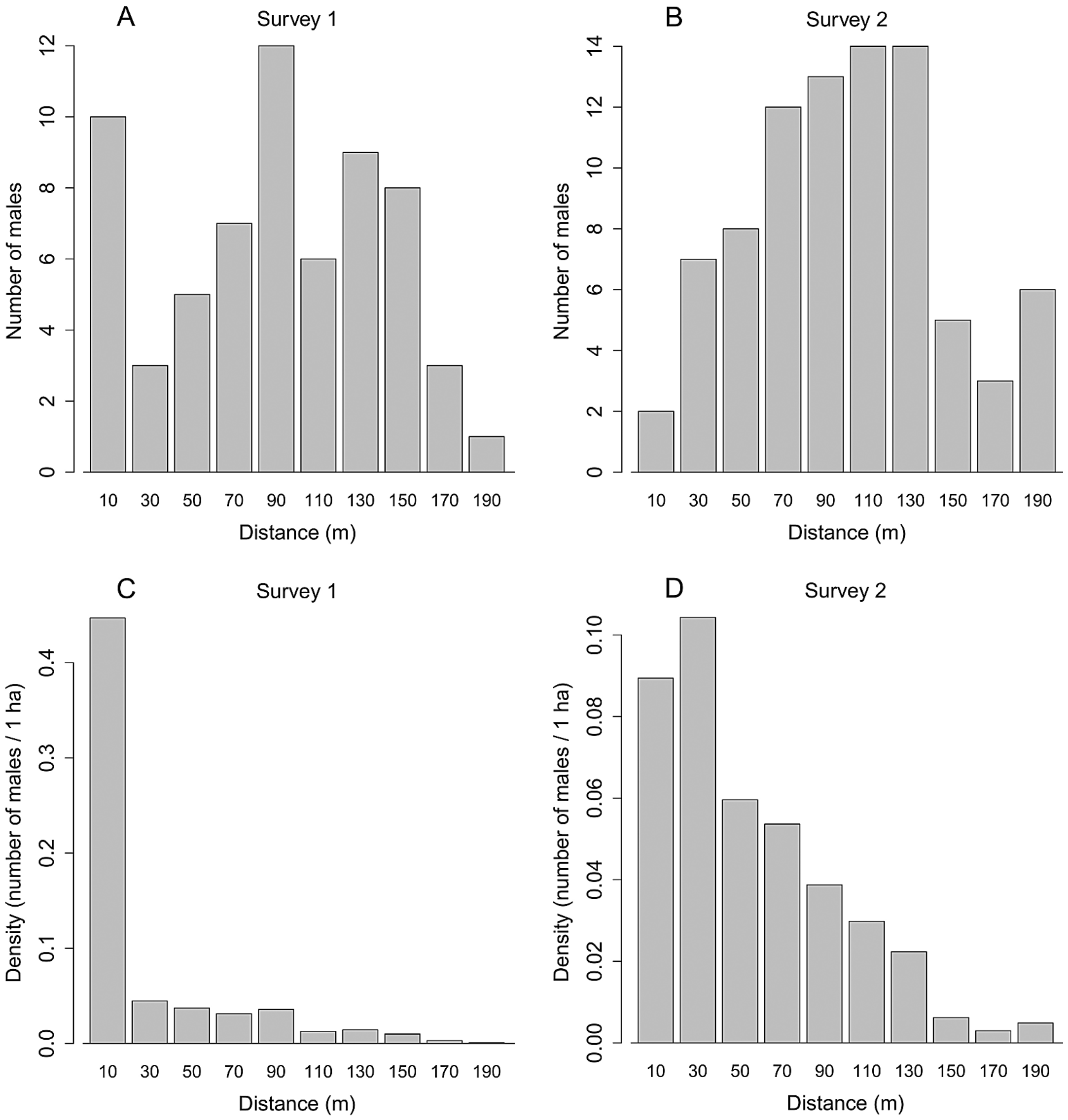


Fig. 5. Numbers (A and B) and density / 1 ha (C and D) of Red-breasted Flycatcher males pooled into ten 20 m wide distance zones during surveys 1 (A and C, 9–12 May) and 2 (B and D, 18–23 May) at (the same) 178 sites, Darżlubie Forest, N Poland, May 2016. Labels on X axes are centres of the 20 m wide distance classes at progressively bigger distances from the observer.

radii smaller than the effective detection distance (*c* 118 m in our case) and could result from more-than-expected number of birds close to the observer (the smaller site, the stronger effect). Therefore, with the data arising from point counts, the violations of model assumptions can affect density estimates, and this can be particularly important when very small sites (i.e., with short radii) are surveyed. Density estimates seem robust to such deviations, as long as the radius length is large (probably larger than the effective detection radius). It would be instructive to perform a simulation study exploring how more-than-expected detections close to the observer affect density estimates.

In our study, the effective detection radius is rather large (Table 3), because Red-breasted Flycatchers sing loudly and because beech forests (a

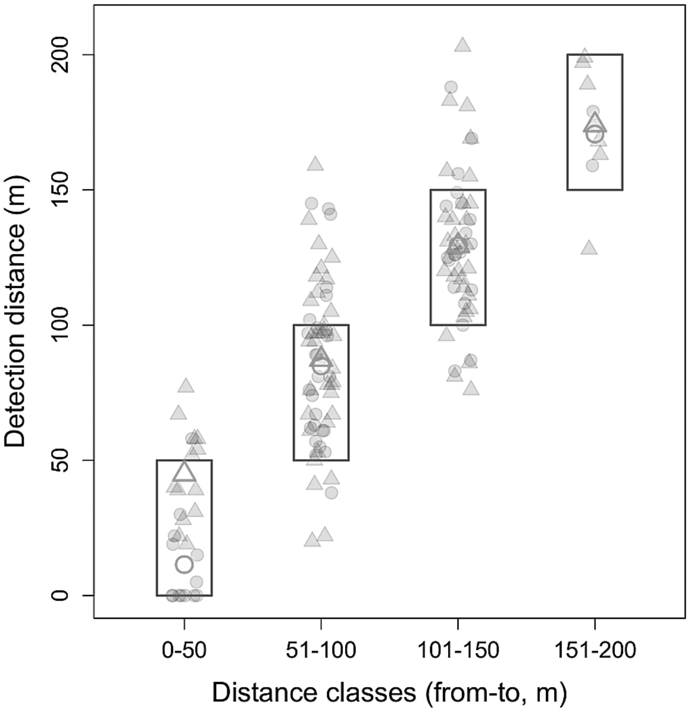


Fig. 6. Observer's assignment of singing males detections into distance classes (boxes) and actual detection distances (symbols). Circles – Survey 1, triangles – Survey 2. Each symbol represents a single detection. Means for each distance class and the two surveys shown with larger, empty symbols, boxes show the "correct", predefined four distance classes. Symbols are jittered slightly along the X axis to reduce overlap.

suitable habitat, where most males were found in the Darżlubie Forest) has rather sparse undergrowth, which could increase distances at which a singing bird can still be detected. The songs of most European forest birds are sufficiently loud for this distance to be somewhere around 100 m, but there are also species that sing quietly (e.g., Goldcrest *Regulus regulus* and Firecrest *R. ignicapilla* or Siskin *Spinus spinus*) and cannot be heard further than some 60–70 m (personal observations). Such information is scarce in the literature, thus one cannot assume it *a priori*, but data allowing for estimation of effective detection radius with distance sampling methodology can be collected within a small-scale pilot study. A safe, general solution would be to make site areas – circular areas surveyed – sufficiently large (for example, a standard of 100, 150 or 200 m radius would work fine for most species) since effective area is likely to be (much) smaller than the site area. In general, however, simulation studies showed that the radius length and site area had little effect on density estimates in HDS except for slightly lower precision for small site areas.

Not surprisingly, binmix models produced higher abundance estimates than HDS models and the degree of overestimation was particularly high for small site areas. When this model is adopted to point count data collected in continuous habitats (like forests) and when the site area is small, the main issue is that one does not know the effective area to which estimates of abundance refer, since territories of recorded individuals cover greater areas than the one assumed within a predefined radius (Kéry & Royle 2016). Therefore, despite estimates still being "per site" numbers, the area effectively surveyed is unknown and larger than the site area, so density calculated using site area is too

Table 2. HDS models fitted to Red-breasted Flycatcher data collected at a point transect in Darżlubie Forest, N Poland, 2016. AIC values are given and the top-supported model is given in bold. AIC ω is Akaike model weight. Model parameters: λ – abundance, φ – availability, *p* – detection. Effects: habitat – abundance habitat-dependent (optimal vs poor), survey – availability survey-dependent (survey 1 vs survey 2), a dot denotes a parameter unaffected by any covariate. Detection functions: hn – halfnormal, hz – hazard, exp – exponential, unif – uniform.

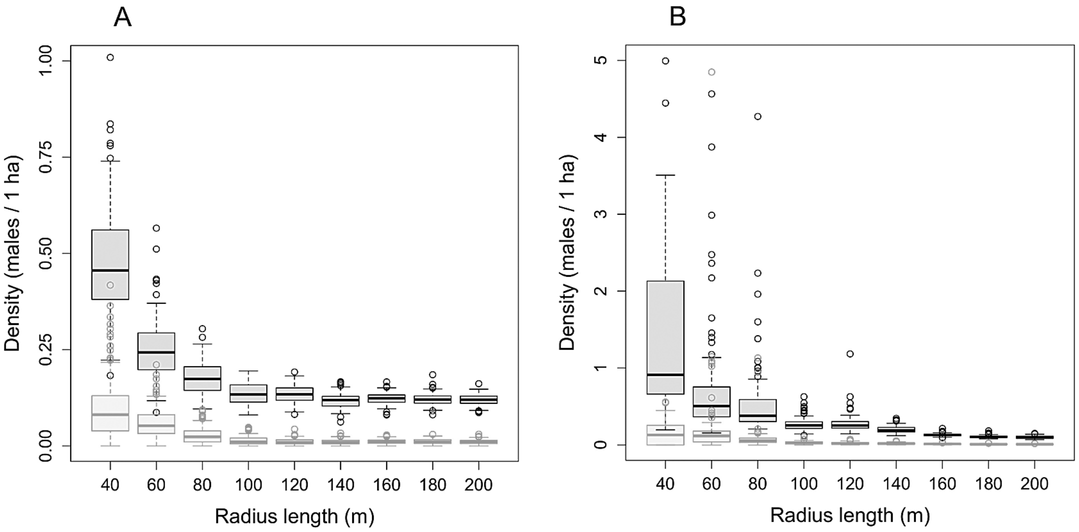
Model	Effects; detection function	Number of zones					
		2	4	5	8	10	20
		Zone width					
		100 m	50 m	40 m	25 m	20 m	10 m
1	$\{\lambda_{habitat}, \varphi., p.\}$; hn	**682.745**	862.744	**936.696**	**1084.022**	**1153.188**	**1364.458**
2	$\{\lambda_{habitat}, \varphi., p.\}$; hz	683.611	**862.304**	940.004	1085.401	1155.723	1366.800
3	$\{\lambda_{habitat}, \varphi., p.\}$; exp	688.444	876.215	947.080	1095.075	1162.962	1374.066
4	$\{\lambda_{habitat}, \varphi., p.\}$; unif	730.840	940.215	1012.370	1163.308	1234.758	1447.231
5	$\{\lambda_{habitat}, \varphi_{survey}, p.\}$; hn	684.256	864.281	938.207	1085.827	1155.001	1366.275
6	$\{\lambda_{habitat}, \varphi_{survey}, p.\}$; hz	684.351	862.977	940.646	1086.552	1156.922	1367.876
7	$\{\lambda_{habitat}, \varphi_{survey}, p.\}$; exp	690.183	877.859	948.725	1096.914	1164.817	1375.918
8	$\{\lambda_{habitat}, \varphi_{survey}, p.\}$; unif	731.568	941.318	1012.998	1164.315	1235.765	1448.238
Top model AIC ω		0.390	0.346	0.556	0.457	0.543	0.528

Table 3. Parameter estimates of the top-supported HDS models for variable number of distance classes and their widths. Means and (bootstrapped) 95% confidence intervals are given. “hn” and “hz” stand for the detection function (halfnormal and hazard, respectively), λ – abundance (estimates given for the two habitats, log scale), φ – availability probability (logit scale), p – SD of the detection function (log scale), effective detection radius – effective detection radius distance (in m). Density estimates given per 10 ha. For the simulation with four 50 m wide zones the log of the scale (dispersion) parameter of the hazard detection function has a mean of 1.62 (95% CI: 1.11; 2.07).

Number of zones / zone width	Top model	Parameter estimates				Effective detection radius	Density	
		Abundance, λ		Availability, φ	Detection, *p*			
		Habitat: optimal	Habitat: poor				Habitat: optimal	Habitat: poor
2 / 100 m	$\{\lambda_{habitat}, \varphi., p.\}$; hn	–2.16 (–2.39; –1.92)	–5.21 (–12.40; –3.83)	7.29 (1.53; 9.64)	4.49 (4.35; 4.61)	119.3 (106.0; 130.8)	1.15 (0.89; 1.47)	0.09 (0.00; 0.21)
4 / 50 m	$\{\lambda_{habitat}, \varphi., p.\}$; hz	–2.26 (–2.55; –1.92)	–5.50 (–13.07; –3.88)	4.19 (0.46; 9.61)	4.75 (4.56; 4.90)	117.6 (106.9; 126.4)	0.92 (0.67; 1.22)	0.08 (0.00; 0.19)
5 / 40 m	$\{\lambda_{habitat}, \varphi., p.\}$; hn	–2.12 (–2.34; –1.87)	–5.24 (–12.81; –3.69)	7.06 (1.56; 9.36)	4.46 (4.34; 4.57)	118.0 (106.8; 128.8)	1.19 (0.96; 1.47)	0.10 (0.00; 0.25)
8 / 25 m	$\{\lambda_{habitat}, \varphi., p.\}$; hn	–2.16 (–2.46; –1.94)	–4.77 (–5.88; –3.72)	7.48 (2.30; 9.62)	4.47 (4.37; 4.56)	119.2 (109.3; 127.1)	1.14 (0.85; 1.42)	0.10 (0.01; 0.24)
10 / 20 m	$\{\lambda_{habitat}, \varphi., p.\}$; hn	–2.10 (–2.30; –1.88)	–5.15 (–11.99;–3.75)	7.75 (4.07; 9.50)	4.45 (4.35; 4.56)	116.7 (107.9; 127.3)	1.23 (1.00; 1.51)	0.10 (0.00; 0.24)
20 / 10 m	$\{\lambda_{habitat}, \varphi., p.\}$; hn	–2.15 (–2.40; –1.96)	–5.18 (–12.91; –3.71)	7.48 (1.72; 9.62)	4.47 (4.38; 4.56)	119.0 (110.0; 127.7)	1.16 (0.91; 1.40)	0.09 (0.00; 0.24)

high. Enlarging the size of a site, by using a bigger radius, does not help either, since some individuals at larger distances are missed if the observer is stationary at a site because detection declines with distance, which in turn can lead to underestimation. The apparent agreement of estimates with the simulated density value could be produced this way.

Two independent problems, which bias results in opposite directions, cancel each other out: to-



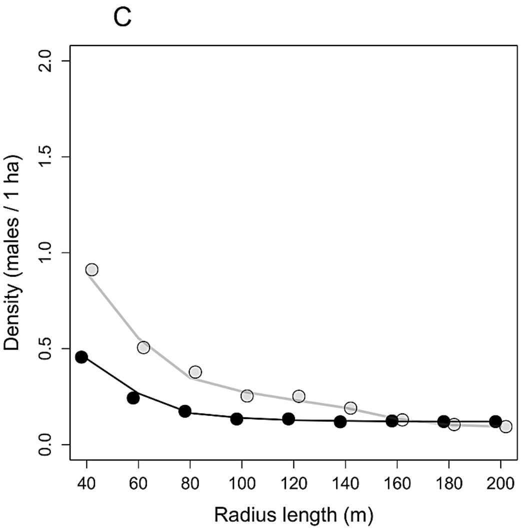


Fig. 7. Red-breasted Flycatcher density estimates in relation to site area under HDS and binmix models: A – HDS with the halfnormal detection function, B – binmix (note different scales on A and B). Density estimates were obtained with the nonparametric bootstrap method (see Methods for more details). Horizontal lines inside the boxes denote median, boxes represent the 25%–75% percentiles, whiskers stand for ± 1.5 interquartile range, circles – outlying values. Black – "optimal" habitat, pale grey – "poor habitat". C shows a summary of density estimates for "optimal" habitat (black and grey boxes on A and B; "poor" habitat not illustrated) on a common scale: black – HDS with halfnormal detection function, grey – binmix model. Only medians from A and B are shown on C for clarity, trend visualised with the loess function.

wards overestimation that occurs when sites are small and underestimation which occurs far away from the observer when sites are large. How strongly this is visible on small versus large size sites depends on song loudness. In consequence, the apparent agreement occurs when sites surveyed are of some given size relative to song loudness (and therefore species-specific), leading to a more or less "correct" density, while in fact this stems from the two counterbalancing effects, each biasing estimates. There is a suggestion of this effect in our simulation study in the case of quiet singers: density seems to be underestimated at the largest sites (radius of 200 m, Fig. 4A), overestimated at small sites and apparently correct estimates occur at sites of intermediate size. No such effect is present for loud singers at the largest sites (Fig. 4F), perhaps because little underestimation occurs due to loud songs and high detectability far from the observer. In line with this, the density of species singing moderately loudly at the largest sites is apparently approximately correct (Fig. 4C and 4D). Clearly, more simulation-based studies are needed here.

Overestimation due to temporary emigration (geographical openness) at small sites can be solved with an associated availability parameter, but this requires data collected under the robust design protocol (Chandler *et al*. 2011). Overestimation is not so much an issue when study plots are larger areas and hold more territories (Bötsch *et al*. 2020) or when sampled sites are isolated habitat patches or islands so that the local population occupies an object (Costa *et al*. 2019) or a restricted area which is exactly the plot size (e.g., like in shorebirds, Lyons *et al*. 2012). Some other solutions to the "area issue" have been proposed (Kéry & Royle 2016: pages 279–282).

While originally applied to bird point count data (Royle 2004), certain limitations of binmix models became evident relatively recently (Joseph *et al*. 2009). These models have been shown to be sensitive to violations of their assumptions (see Kéry & Royle 2016, pages 248–250, including Table 6.2 for a discussion on this issue). Link *et al*. (2018) point out that multiple counting of the same individuals (so-called false positives), openness of the population over the study course, or unmodelled heterogeneity in detection probability, bias the abundance estimates heavily. Along with this, our study shows that care is needed when binmix is to be adopted for estimating density from point count data, as is frequently done.

Exact (to within a few meters) detection distances obtained directly in the field allowed us to perform this study, but it is not necessary to possess exact values in order to succeed with distance sampling models – usually observers assign detections into distance classes, which is far easier to apply in the field. Exact detection distances are hard to obtain (but easy to simulate), although rangefinders can be used in open and semiopen habitats. Dense, forest habitats actually exclude the possibility of using rangefinders for bird detections since most detections are vocalisation-based. Also, correct assignment of detections into distance classes requires some experience.

In addition, it can vary with song species-specific characteristics as well as with topography, weather and other variables, so that a pilot, training study could improve assignments greatly. In our study, the observer's assignment into distance classes was moderately correct, showing that even with experience (both observers performing surveys have 30+ years of experience with forest birds), some assignment errors do occur. We believe that with experience and training, assignment errors should occur relatively rarely and be small enough to have little effect on parameter estimates. Density estimates will always benefit from collecting detection distances, even at few – two, in the extreme case – wide distance classes.

In summary, if density is of interest, and the temporal replication within the study is limited (as in our case), assigning detected birds into wide distance classes represents the recommended option in dense, forest habitats. If no distance data are collected, other approaches are possible, notably the robust design approach, but they require more intensive temporal replication to make the availability parameter estimable. Binmix models in their simplest version, despite the simplicity of the data to be collected, have to be applied to the results of point count surveys with care, primarily because detections are distance-dependent and the surveyed area remains unknown. Despite the high sensitivity of these models to violations of assumptions, these models can still be highly reliable and useful tools in estimating abundance in other situations.

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Pistelaskennan populaatioestimaatit kun seurannassa olevan alueen pinta-ala on laaja mutta toistoja vähän: mallien vertailu

Tutkimme kahden populaatiotiheyksiä mallintavan menetelmän – HDS ja binmix – eroja populaatiokokojen/tiheyksien arvioimiseen. Testasimme tiheysestimaattien tarkkuutta käyttämällä simuloitua aineistoa, ja todellisessa pikkusiepon pistelaskenta-aineistossa Puolasta. Sekä simuloinneissa että empiirisessä aineistoissa mallinnettiin vaihtelevia pinta-aloja ja vaihtelevaa laulun voimakkuutta.

Havaitsimme että lintujen etäisyyteen laskentapisteestä käytetyillä luokilla tai näiden koolla ei ollut vaikutusta tiheysestimaatteihin tai niiden tarkkuuteen HDS-menetelmässä, edes tilanteessa,

jossa etäisyys laskentapisteestä oli luokiteltu vain kahteen luokkaan (lähellä vs kaukana). Myös tutkittavan alueen koko (halkaisijan pituus) ja laulun voimakkuus vaikutti HDS-menetelmän tiheysestimaatteihin vain vähän: tiheys yliarvoitiin 5–17 % kun alueen koko oli pienempi ja lajeilla, joiden laulu on hiljaisempi. Yleisesti ottaen HDS-menetelmän antamat estimaatit olivat tarkkoja. Sen sijaan binmix-mallinnus yliarvioi tiheyden pienillä alueilla, mutta estimaatit olivat tarkkoja isommille alueille. Tarkat estimaatit isoilla alueilla voi johtua siitä, että malli yliarvioi tiheydet kun havaittavat linnut ovat lähellä laskijaa, ja aliarvioi tiheydet, kun havaittavat linnut ovat kaukana laskijasta, jolloin keskimääräisesti arviot ovat tarkkoja.

Kun binmix-malleja sovelletaan pistelaskenta-aineistoon, täytyy täten huomioida kunkin lajin laulun voimakkuus suhteessa alueen pinta-alaan, koska nämä näyttävät vaikuttavan tiheysestimaatteihin. Täten suosittelemme, että kun tiheysestimaatteja arvioidaan pistelaskennalla, ja saatavilla on vain vähän toistoja, kerättäisiin aineistoa myös havaittavien lajien etäisyydestä (edes karkealla resoluutiolla), jolloin voidaan hyödyntää HDS-malleja. Tässä menetelmässä hyöty suhteessa kustannuksiin on suuri, ja täten se tarjoaa hyvän vaihtoehdon yksinkertaisiin pistelaskentoihin joissa vain lintujen lukumäärä tilastoidaan.

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