

Predicting detection probabilities to estimate species' population sizes

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Abstract

1. Information on species' population sizes is essential for setting conservation priorities, but it is notoriously difficult to obtain and usually involves intense monitoring efforts. A core step towards estimating a species' population size is first estimating its detection probability. Here, we test the value of possible shortcuts in deriving species' detection probabilities and the implications of using these shortcuts for population size estimates.
2. Using a distance-sampled dataset for breeding birds in Denmark, we tested the ability of species' traits to predict their detection probabilities and contrasted the population size error from using trait-based estimates versus direct estimates of detection probabilities. We also assessed the sample size requirements for direct estimates of detection probabilities to surpass the performance of trait-based estimates.
3. Species' detection probabilities were highly predictable—across species and across years. Across species, detection probabilities were predicted by a combination of morphological traits and ecological niche metrics. Body size alone explained 40% of the variation among species. Phylogeny was unimportant once key traits were taken into account.
4. Error in population size estimates from using a trait-based probability rather than a direct estimate of detection probability was within the 95% confidence intervals of the population size estimates for most species. However, the error in population size was lower using a previous direct estimate of species detection probability (i.e. using data from the previous year) than using a trait-based estimate. Moreover, direct estimates outperformed trait-based estimates even when only a relatively small number (median of 40) of distance-sampled observations was available.
5. *Practical implication:* Our findings indicate that information on species' detection probability can be borrowed across species, using traits and across years. This raises the potential of mixed study designs that collect detection probability information in only some sampling units (sites, years and even species), reducing the

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demands for intensive monitoring and enhancing the scalability of approaches for estimating species' population sizes.

KEY WORDS

effective strip width, imperfect detection, population abundance, species' traits

1 | INTRODUCTION

Estimates of species' absolute abundances (i.e. total number of individuals within a defined area) are essential for many questions within ecology (e.g. energy fluxes), conservation (e.g. assessing extinction risk) and environmental management (e.g. assessing hunting quotas) (Callaghan et al., 2024; Waldock et al., 2022). Methods to estimate absolute abundance, however, typically involve intensive or complex sampling protocols (Dénes et al., 2015), meaning they are not frequently employed in large-scale monitoring. Instead, most monitoring schemes focus on collecting relative abundance data (Kissling et al., 2018), which can be used to derive abundance indices for assessing trends under assumptions of constant detection probabilities. Ignoring variation in detectability, however, can lead to incorrect inferences about spatio-temporal patterns (Bennett et al., 2024).

A range of methods is available to estimate species' absolute abundances. Some early methods, such as territory mapping, aimed to directly survey all individuals within an area (Budka & Kokociński, 2015). Newer and more popular methods for estimating absolute abundances instead recognise that only a subset of individuals are seen during a survey, but collect data in a way that allows detection probabilities to be estimated. For instance, distance-sampling methods or replicate surveys during the season are alternative ways to statistically estimate detection probabilities and use them to correct the observed abundance for imperfect detection (Dénes et al., 2015; Kéry, 2018). However, both of these approaches are more time-consuming than simple point or line transect counts, which make them less attractive for citizen scientists who undertake the majority of large-scale species monitoring (Chandler et al., 2017; Mandeville et al., 2023; Moussy et al., 2022). Simpler approaches for estimating detection probability could help make more effective use of the limited funds available for conservation action (Buxton et al., 2020). Several studies have already investigated possible shortcuts, primarily by calibration of available data on absolute abundances with data from other methods (Anadón et al., 2010; Brand et al., 2006; Callaghan et al., 2021; Stillman et al., 2023).

Species traits (or more generally species characteristics) are a potentially useful approach for predicting species detection probabilities and correcting for imperfect detection, reducing monitoring data demands. Traits are used in many predictive frameworks in ecology and are also now widely available in various databases. Detection probabilities can vary for a range of reasons. Especially

among citizen science programmes that recruit a diverse set of participants, observers may differ in their ability to detect species (Pocock et al., 2023; Schmidt et al., 2023). Detection rates may also depend on habitat or weather conditions during the survey (Morelli et al., 2022; Rigby & Johnson, 2019). However, we can expect that properties of species play a large role in determining their detection probabilities (Garrard et al., 2013; Morelli et al., 2022; Sólymos et al., 2018). An advantage of using species traits is that they can be used to predict species detectability when no direct data are available to estimate it (Garrard et al., 2013; Schlossberg et al., 2018). For instance, body size is probably positively related to detection probability—large-bodied species are more visible to the human eye than small-bodied species (Johnston et al., 2014). Ecological traits such as foraging behaviour may also explain variation; for instance, aerial feeders might be more visible than mid-canopy feeders. Habitat preference also might explain variation, with forest birds having lower mean detection probabilities than open habitat species (Johnston et al., 2014). Traits related to loudness and frequency of song will also be important, although these attributes are not routinely included in trait databases.

While previous studies have explored the predictive potential of species' detection probabilities (Garrard et al., 2013; Johnston et al., 2014; Sólymos et al., 2018), the implications of exploiting this to derive absolute abundance estimates remain unclear. If reasonable predictions of species' detection probabilities can be made using the available data (e.g. distance-sampled data or repeat surveys within a season), predicted values of detection probabilities could instead be used to account for imperfect detection and calculate species' absolute abundances. Alternatively, if predictions have a large error, any abundance estimates based on them might lead to poor decision-making in conservation. In this study, we tested this prediction by using a distance-sampling dataset collected over 4 years for breeding birds in Denmark. We estimated the detection probabilities of each species and explored trait-based associations with both the mean and spatial variation in them. Using the modelled relationships, we then tested whether we could predict a species' detection probability assuming only data for other species were available and contrasted the error in estimated total population size when using a predicted trait-based detection probability compared with direct estimates. Finally, we explored the sample size needed for a direct estimate of detection probability to be superior to a trait-based estimate. Overall, our findings help understand whether predictive models of detection probabilities represent opportunities for reduced monitoring effort in conservation science.

2 | MATERIALS AND METHODS

2.1 | Bird dataset

Distance-sampled data on bird abundances were collected from 2014 to 2017 by experienced volunteers in Denmark for an atlas project, Atlas III (<https://dofbasen.dk/atlas/>). In the Atlas III project, Denmark was divided into 5×5 km squares, and in a 1×1 km square preferably in the centre of each 5×5 km square (but not in water), the 1 km transect was carried out. In total, we had data for 1687 transects (see Figure 1a). As far as possible, each transect was a straight line through the grid, parallel to its edges (either north–south or east–west). Surveyors visited each transect twice—once between 1st of April and 12th of May and again between 13th of May and 22nd of June (separated by at least 2 weeks) to sample different parts of the breeding season and ensure late-arriving migrants were sufficiently sampled. There was also a winter survey but they are not considered here, so we focus on breeding population sizes including both residents and migratory species. Surveyors were asked to slowly walk their transects (c. 1 h), starting between 30 min after sunrise and 10 AM, and asked only to record birds detected ahead of them as they walked. While birds may be initially detected visually and/or aurally, distance was assessed visually. For each bird, or group of birds detected, the surveyors recorded their perpendicular distance from the line transect in three bands: 0–25, 25–50 and 50–100 m (Figure 1b), ensuring they note which band was first detected. For our study, observations recorded as flying overhead or greater than 100 m from the transect were discarded.

We initially subset the full dataset to species observed at least 50 times. We then excluded species for whom distance-sampling assumptions are unlikely to be met, including primarily aerial or aquatic species (based on the ‘primary lifestyle’ and ‘trophic niche’ data available in the Avonet database, see below), as well as the common cuckoo, *Cuculus canorus*, typically recorded at longer distances by sound. In the end, this meant we focused on data for 72 species (Table S1).

2.2 | Estimating detection probabilities

We fit a distance model to the distance-sampled data for each species to estimate their detection probability. This model assumed perfect detection for individuals on the line transect and a decay in detection probability with increasing distance from it. This distance decay was assumed to follow a half-normal distribution, after data exploration revealed that other distributions produced similar results. The detection probability is the fraction of individuals observed within the surveyed region, represented by the fraction of area under the detection curve. We fit two different distance models to each species separately. In the main models, we did not include any site-level covariates and only estimated a mean detection probability for each species (see ‘spatial variation’ where we relax this in the alternative models). We bootstrapped the data (e.g. resampling with replacement) and refitted the model 1000 times in order to generate 95% confidence intervals of the detection probabilities.

2.3 | Traits-based associations

We compiled a set of 65 morphological and ecological traits for each species from several databases (Storchová & Horák, 2018; Tobias et al., 2022; Wilman et al., 2014; see Table S2 for all traits). We also created an additional trait based on observations in Denmark of the flocking propensity of species on a four-point scale. We then analysed the relationships between these traits and species’ mean detection probabilities. For this, we compared two different modelling approaches—a multiple regression approach and a machine learning approach. To align with each of these approaches, we also defined two groups of traits, a smaller set of ‘core traits’ that were tested together in the multiple regression models and a larger broad set of traits that were tested in the boosted regression trees that were able to deal with greater dimensionality. For the core traits, we selected body mass, main habitat preference, diet, foraging strata (i.e. ground foraging) and flocking propensity.

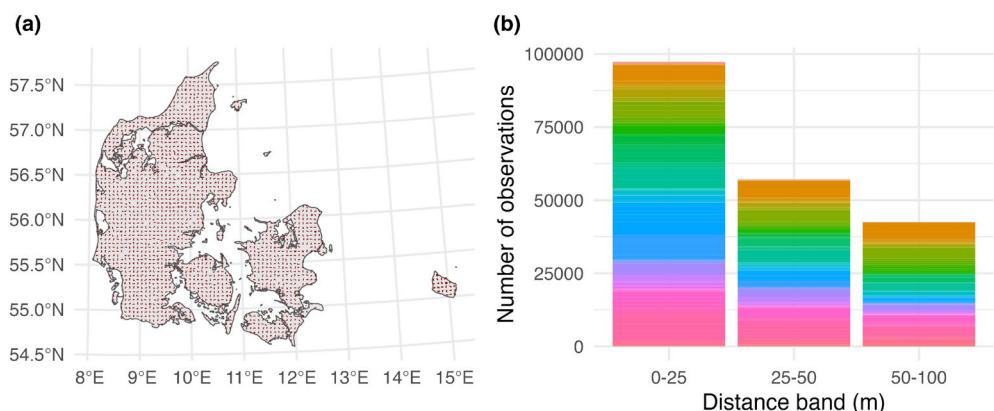


FIGURE 1 (a) Location of the 1 km line transects (shown by the red lines) within Denmark. (b) Number of observations within each distance band, with the colours reflecting different species—only shown to highlight the high number of species and the general decay in detections with increasing distance.

For the multiple regression approach, we used linear models with simple additive terms for all the trait predictors. We tested whether there was a phylogenetic signal of the residuals of the main model, using a consensus tree of 100 (Eriksen) samples from Jetz et al. (2012). For the machine learning approach, we used boosted regression trees with all 65 trait variables. We first performed a grid search over a set of tree parameters (number of trees, learning rate, tree complexity and step size) for fine-tuning on a test dataset (30% of original dataset). We then identified the parameter that led to the lowest root mean squared error and used those for the final model.

To test the capacity of the models to predict the mean detection probability of each species, we used a leave-one-out cross-validation approach in which we dropped each species from the model and predicted its detection probability based on a model (either the regression or boosted regression tree) fit to the remaining species. We refer to the estimates of species detection probability based on data for that species as 'direct estimates' and those based on the trait models as 'trait-based'. We assessed the difference between the direct estimates and the trait-based estimates by calculating the absolute difference between them for each species as well as the Pearson's and concordance correlation coefficients.

2.4 | Spatial variation

The above analysis focused on mean detection probability of species, but typically we can expect them to be modified by local environmental contexts. We explored whether species' traits could also predict spatial variation in the detection probabilities of species. We first fit a new set of distance models that included site-level covariates hypothesized to generate spatial variation in detection probabilities among transects. These covariates were the area of paths/roads and the area of forest within a 5-m buffer from the line transect, taken using land use data (Table S3). We focused on this narrow buffer to reflect the conditions immediately adjacent to the transect, which had most potentially to affect near and far-distance visibility. We extracted the coefficients for the effects of these covariates on each species' detection probability and explored whether habitat preference explained variation in them (i.e. whether habitat preference explained variation in the effects of paths/roads and forest on detection probabilities). Since this analysis found little support for either the effects of the covariates or the ability of traits to explain variation in their effects, we focused the remainder of the analysis on using the original mean detection probability estimates for each species.

2.5 | Predicting species abundances

To explore the implications of different approaches for calculating detection probabilities, we also built models to estimate the total

population size of species across Denmark. We compiled a set of 32 land cover predictors (Table S3; European LUCAS 2015 dataset from Pflugmacher et al. (2018); and Danish Basemap03 2016 dataset from Levin (2019)), each at two spatial scales—a 'local-scale' 1000 m × 200 m over the intended coverage of each transect and a larger 'landscape-scale' 1000 m × 1000 m area to cover the broader landscape around each transect. These predictors were included in a machine learning model (extreme gradient boosting) to predict the observed relative species abundance (i.e. abundances with imperfect detection) on each transect (Chen et al., 2025). As additional predictors, we included latitude and longitude to account for any additional gradients unexplained by land cover, and day of year and time of day of survey to account for survey variation. For fine-tuning of each model, we conducted a grid search of the core hyperparameters (nrounds, eta, max_depth, colsample_bytree, min_child_weight). We then built a prediction data frame to use the fitted models to predict the species' relative abundances across the whole of Denmark. For this, we overlaid a regular grid across Denmark with the same area as the target area of the line transects (1000 m × 200 m). We calculated the same set of land cover covariates for each grid cell. For non-spatial predictors (day of year and time of day), we specified mean values (of the season of first or second visits as deemed most appropriate for each species by local partners). Local partners also identified which small islands should be removed from the prediction data frame for specific species. To avoid overestimating abundances at coastal grids, we multiplied the predicted abundances by the area of land. We then corrected the model predictions for each species to account for imperfect detection. We did this by dividing the predicted relative abundance value for each cell by either the direct estimates of detection probability (mean detection probability of the species from the distance models) or the trait-based estimates from the leave-one-out cross-validation models. We estimated the total population size as the sum of the corrected abundances across all grids across Denmark. We obtained 95% confidence intervals by independently bootstrapping both the detection probability estimates and the relative abundance estimates.

2.6 | Annual variation

We ran a series of additional analyses to explore the implications of only having distance-sampled data to calculate detection probabilities for some years and whether such data could be reused for other years. We refit the distance models and trait models (only using the multiple regression approach) for each year of data separately. We then recalculated the population size estimates for species but using different detection probability estimates. We contrasted the difference between using the direct estimates of detection probability available for a given year (i.e. assuming all species had distance-sampling data for that year) versus only having direct estimates available for the previous year or only having trait-based estimates using models of data from the previous year. Since we had 4 years of data, this gave us three possible comparisons (2014/15, 2015/16

and 2016/17). We assumed that the direct estimates in a given year were closest to the truth and refer to deviations from these estimates as error. This allowed us to ask whether missing detection probabilities would be better filled by previous direct estimates or trait-based estimates of detection probabilities.

2.7 | Effect of sample size

Finally, we explored the sample size needed to calculate robust direct estimates of species detection probabilities and for them to outperform trait-based estimates. We focused this analysis only on the most well-sampled species ($n=20$), with at least 1000 observations, so that we could produce the best estimates of their detection probabilities. For each species, we randomly subset any of the available distance-sampled observations for them to create sample sizes of between 10 and 1000 observations (and every increment of 10 in between, 100 replicates of each) and refit the distance model using each random subset. We then compared the detection probability estimates from these subsets with the direct estimate from the full datasets and the trait-based estimates from the leave-one-out cross-validation models. By this approach, we could determine the minimum sample size needed for the subset estimates to be closer to the direct estimate than the trait-based estimate.

2.8 | Software and libraries

Models were run in R version 4.4.0, using the following packages: Distance (Miller, Rexstad, et al., 2019) to estimate detection probabilities; Xgboost to model spatial variation in abundance (Chen et al., 2025) and dismo to predict trait associations using boosted regression trees (Hijmans et al., 2024).

3 | RESULTS

3.1 | Trait associations

Species' detection probabilities varied between 0.25 and 0.99 (median=0.54), with the minimum observed for the marsh tit, *Poecile palustris*, and the maximum for the Greylag goose, *Anser anser* (Figure S1). In multiple regression models, species' traits explained 60% of the variation in detection probabilities among species (Table S4). Body mass was strongly positively related to detection probability ($p\text{-value} < 0.001$; Figure 2a), explaining 41% of the variation alone. Ground foraging percentage was also positively related to detection probability; for instance, species spending more of their time foraging on the ground were more detectable ($p\text{-value} < 0.001$; Figure 2b). Detection probabilities depended on habitat (Figure 2c), with species associated with human-modified habitats having higher detection probabilities than forest species

($p\text{-value}=0.04$; Figure 2c). Diet also played a role, with carnivorous species having higher detection probabilities than herbivorous species ($p\text{-value}=0.001$; Figure 2e). Flocking propensity did not have a simple effect on detection probability (Figure 2d). After accounting for the effects of species traits, there was no phylogenetic signal in the residual variation in detection probabilities ($p\text{-value} > 0.9$).

The boosted regression trees, including a broader range of traits, also supported the importance of morphological traits: Tarsus length had a relative importance of 37% (Table S5). Four of the five traits with at least 5% relative influence were size-related (the other three, after tarsus length, were tail length, wing length and beak length). The remaining non-size-related trait with at least 5% relative influence was ground foraging percentage (13% relative influence). Exploration of the fitted functions indicated a threshold effect of size, with increasing detection probability seen at small sizes and plateauing detection probability at larger sizes (Figure S2).

We also explored whether traits could explain spatial variation in detection probabilities (Figure S3). The detection probability of few species was significantly affected by either path/road cover or forest cover. Five species were negatively affected by path/road cover and two species showed contrasting responses to forest cover. Species traits did not explain differences in the effect sizes among species (Figure S3), but there was a slight tendency ($p\text{-value}=0.11$) for more negative effects of path/road cover for species associated with human-modified habitats, that is, detection probability was smaller, or effective strip width of the transect was shorter, with greater path/road cover.

3.2 | Predicting detection probabilities

Both the linear regression and boosted regression tree modelling approaches worked relatively well to predict species' detection probabilities (Figure 3). Based on the multiple regression models, the correlation between the observed estimates (produced using data for each species) and trait-based estimates (predicted for each species based on a model of the traits of other species) was relatively strong (Pearson's rho=0.69; Lin's rho=0.67; Figure 3a). There was some indication of bias (bias correlation factor [Cb]=0.97), reflecting the propensity to slightly overestimate detection probabilities for hard-to-detect species and underestimate detection probabilities for easy-to-detect species (Figure 3a). The predicted value of the estimated half strip width of the species deviated, on average, from the observed values by 9.56 m (interquartile range=3.82–13.75 m). Using body mass alone to predict each species' detection probability performed slightly less well (Pearson's rho=0.61; Lin's rho=0.55; mean deviation=10.97 m; Figure 3c), with slightly more bias (Cb=0.9). The boosted regression trees did not perform better than the multiple regression model, whether all traits were used (Pearson's rho=0.64; Lin's rho=0.57; Cb=0.9; Figure 3b) or the subset of the top predictors was used (Pearson's rho=0.67; Lin's rho=0.62; Cb=0.93; Figure 3d).

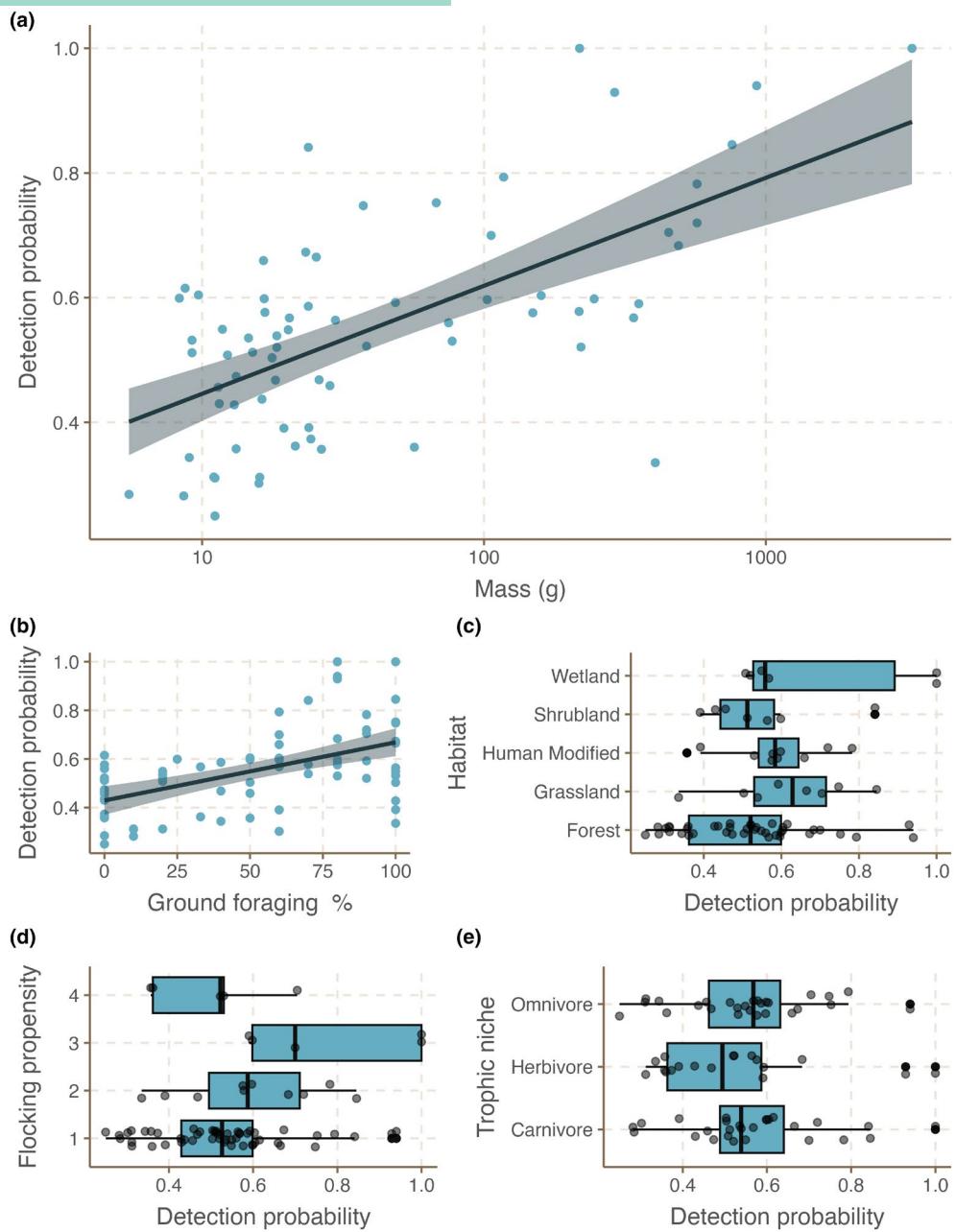


FIGURE 2 Relationships between species traits and their detection probabilities estimated by distance sampling. (a) Body mass (in g, logarithmic scale); (b) ground foraging percentage; (c) main habitat; (d) flocking propensity (from 1 = always seen alone to 4 = always seen in groups); (e) trophic niche. (a) and (b) show simple regression lines; other panels show boxplots; all show separate species as points.

3.3 | Implications for population size estimates

We compared the implications of using the direct estimate of detection probability, using distance-sampled data for each species, versus using the trait-based estimate, for calculating species' population sizes. The population size estimates using each approach were highly correlated when using either the multiple regression model ($r=0.97$; **Figure 4a**) or the boosted regression tree ($r=0.97$; **Figure S4**), but this primarily reflects the greater difference among species in their population sizes than in their detection probabilities.

Based on the simple mathematical relationship, there is a negative relationship between error in the detection probability estimate and error in the estimated population size (**Figure 4b**). In other words, overestimating species detection probability leads to underestimating the population size, by expecting that fewer individuals were missed during the survey. On average, a 1% error in the estimated detection probability led to a 17% error in the population size estimates (**Figure 4c**). Overall, the error in the population size estimate by using a trait-based estimate of detection probability versus the direct estimate was 13% (median; interquartile range=7%–26%) based on the linear regression models, which was slightly smaller than that based on the

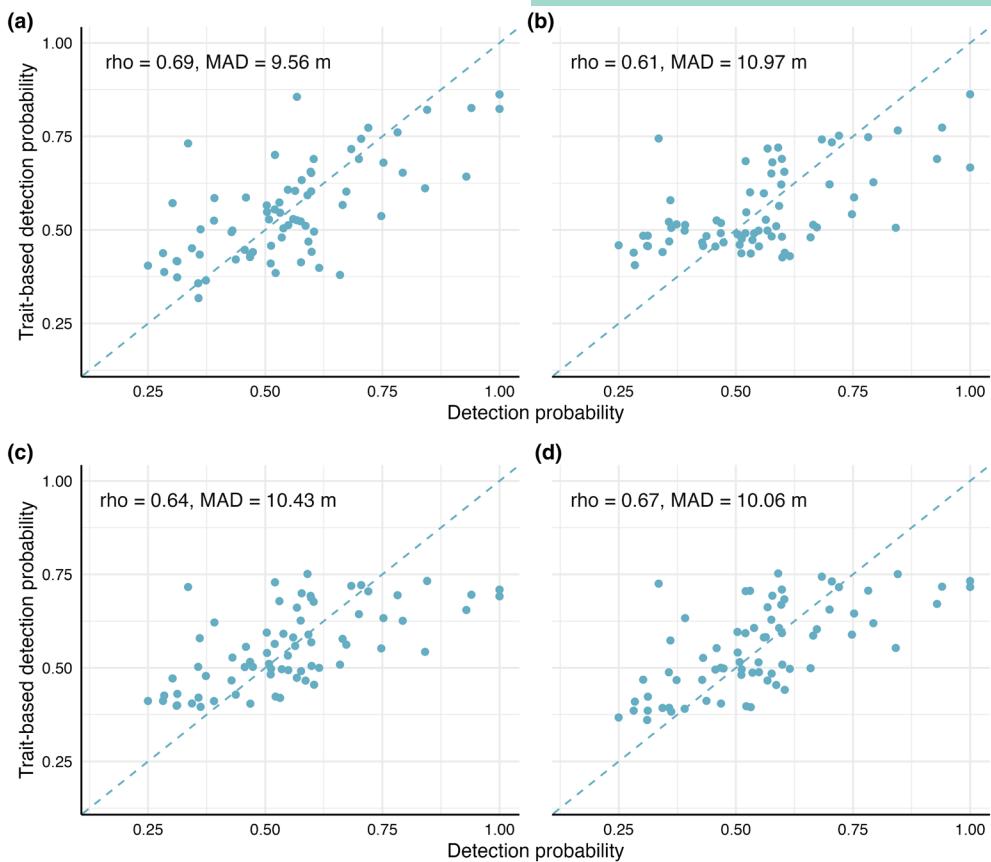


FIGURE 3 Relationships between detection probability based on direct data (x-axis) and the predicted detection probability based on traits (y-axis) under different modelling approaches. (a) Multiple regression model using the significant core traits (body mass, ground foraging, habitat and trophic level); (b) simple regression model including only body mass as the predictor; (c) boosted regression tree using all traits; (d) boosted regression tree using the top set of predictors. Trait-based detection probability shows the predictions from a model that excluded each respective species. The dashed straight line is the line of equality. On each panel is shown Pearson's correlation coefficient (ρ) and the mean absolute deviation (MAD) of the estimated half strip width in metres.

boosted regression tree (median=17%, interquartile range=8%–27%), consistent with its slightly better predictive performance (Figure 3). Importantly, most estimates (82% of species with the linear regression model; 75% with the boosted regression tree) using the trait-based detection probability were still within the range of the 95% confidence interval of the estimated population size. Species with the smallest error, for whom the approach worked best, included *Passer domesticus*, *Columba livia*, *Coloeus monedula*, *Turdus pilaris*, *Curruca curruca* and *Pyrrhula pyrrhula*; all with less than 1m difference between the direct and trait-based estimate of effective strip width.

3.4 | Past estimates versus trait-based estimates

Species detection probabilities were highly correlated across years, ranging from correlation values of 0.76 to 0.87 (Figure 5a; Figure S5). Consistent with this, the trait regression models revealed broadly similar effects of the trait variables across the years (Table S4). Body mass and ground foraging percentage had consistent positive effects in all years, while the effects of habitat and trophic level were similar, although not consistently significant across years (Table S4).

When comparing the direct estimate of detection probability of each year with either the direct estimate from the previous year or with the trait-based estimate (Figure 5b), the past direct estimate tended to be closer than the trait-based estimate, assessed by the smaller mean absolute difference (2014–2015: 0.075 vs. 0.093; 2015–2016: 0.066 vs. 0.097; 2016–2017: 0.060 vs. 0.099); the greater concordance correlation coefficient (2014–2015: 0.80 vs. 0.66; 2015–2016: 0.85 vs. 0.70; 2016–2017: 0.84 vs. 0.68) and a simple Wilcoxon paired test (2014–2015: $p=0.06$; 2015–2016: $p<0.01$; 2016–2017: $p<0.01$).

Consistent with this general pattern, the previous year estimates resulted in lower population size error than using the trait-based estimates (2014–2015: 10% vs. 12%; 2015–2015: 9% vs. 14%; 2016–2017: 6% vs. 14%; Figure 5c). On average across all years, the error with the previous year estimate was 8% (interquartile range=4%–18%) compared to 13% (interquartile range=8%–25%) with the trait-based estimate. Exceptions were *Buteo buteo*, *Corvus corone*, *Hippolais icterina* and *Periparus ater*, for whom the use of the trait-based estimate, rather than the previous estimate, resulted in population size estimates that were consistently closer to those calculated with the direct estimate of detection probability.

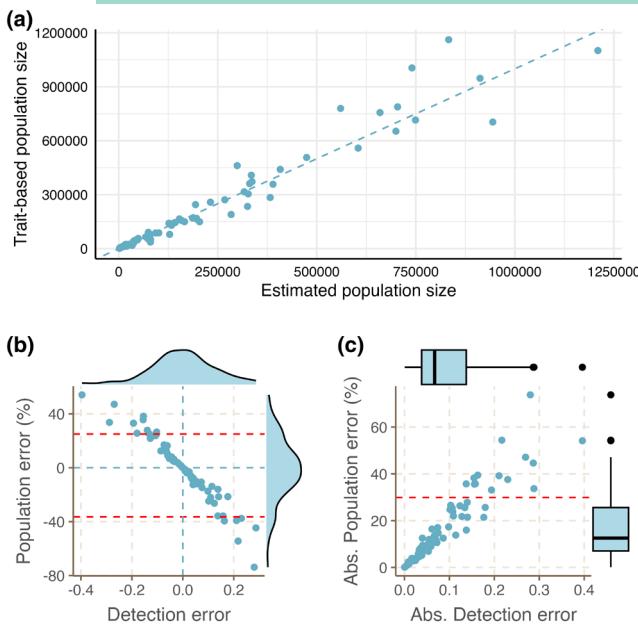


FIGURE 4 Implications of using trait-based estimates of species' detection probabilities for deriving estimates of population sizes. (a) Correlation between the population size estimates based on direct estimates of detection probabilities (x-axis) and the trait-based estimates of detection probabilities (y-axis). (b, c) Detection error is the difference between the direct estimate of detection probability, using data for that species and the trait-based estimate, predicted from a model of data for other species. (b) shows raw error values; (c) shows absolute values. Red-dashed lines show the 95% confidence intervals of the population size estimates based on bootstrapping of the direct estimates. All trait-based predictions are from the multiple regression model; see the Supporting Information for those from the boosted regression tree results (Figure S4). Table S6 contains all the population estimates.

3.5 | Effect of sample size

The above analysis assumed that the direct (mean or 'best') estimates of species detection probability were always closest to the true estimates. However, with decreasing sample size (i.e. number of detections of a species), the direct estimate of a species' detection probability had a greater standard error ($p < 0.001$) and hence may not be closest to the truth. We assessed the minimum sample size needed for a direct estimate from a small sample size to be closer than the trait-based estimate to the direct estimate from the full dataset. This analysis indicated that, on average, with only 40 distance-sampled observations, a direct estimate would be better than a trait-based estimate (interquartile range = 10–83 across the 20 most sampled species; Figure 6).

4 | DISCUSSION

By exploring alternatives to traditional approaches of estimating population sizes, we provide insights into whether predicted or trait-based estimates of detection probabilities can be used to fill

information gaps in ecology and conservation. Our study builds on previous work that highlights the predictive value of species' traits (Garrard et al., 2013; Johnston et al., 2014; Sólymos et al., 2018), but assessed the implications of using trait-based detection probabilities for species' population size estimates. Despite the high predictive value of species' traits, we found consistently greater information within direct estimates of detection probabilities, even when derived from a small sample size or from data collected in a different year. Our findings highlight the importance of attempts to directly estimate and account for imperfect detection in species monitoring by using methods such as distance sampling but support the use of trait-based approaches when that is not feasible.

Species traits influence detection probabilities through diverse mechanisms. Morphological traits such as body size directly link with species' visibility, which has been highlighted in previous studies (Johnston et al., 2014; Sólymos et al., 2018). Other traits or characteristics, such as diet and trophic level, are likely important because they covary with behaviours that affect detectability (Morelli et al., 2022). We found that ground foraging propensity was positively associated with detection probability, which may partly reflect a greater difficulty to detect and identify individuals moving in the tree canopy than on the ground. For similar reasons, species' habitat preference plays a role in detection since it provides information on the environmental context of an observation during a survey; for instance, open habitat species are more detectable than forest species. The role of these and other traits, however, will critically depend on the survey method. For instance, body size may also play a different role when detecting birds acoustically: Larger birds have lower singing rates (Bennett & Harvey, 1987; Ryan & Brenowitz, 1985), but lower frequency and louder songs (Cardoso, 2010; Storchová & Horák, 2018). Indeed, we expect that accounting for acoustic traits of species may further improve the predictability of detection probabilities. A physics-based model of acoustic signal detection showed the importance of external factors such as habitat attenuation and ambient sound levels that vary across the diel cycle (Haupert et al., 2023). Hence, the use of the trait-based methods will need to consider the specific set of traits that directly or indirectly affect detection by a specific survey method.

Trait associations, and consistency in species' detection probabilities across years, support the transferability of detection probability estimates across species or years. Overall, we found greater support for using any available direct estimates, even from previous years or small samples, over trait-based estimates. First, the direct estimates from a previous year were more correlated with and deviated less from those of a given year than the trait-based estimates. This indicates that year-to-year variation in detection probabilities is smaller than the difference between direct and trait-based estimation methods. Second, due to slight bias in the modelled trait relationships, the trait-based models tended to underestimate the detection probabilities of easy-to-detect species, with high detection probabilities, and overestimate the detection probabilities of hard-to-detect species, with low detection probabilities. Finally, a relatively small sample size was needed for a direct estimate to be usually better than the trait-based estimate. These patterns support

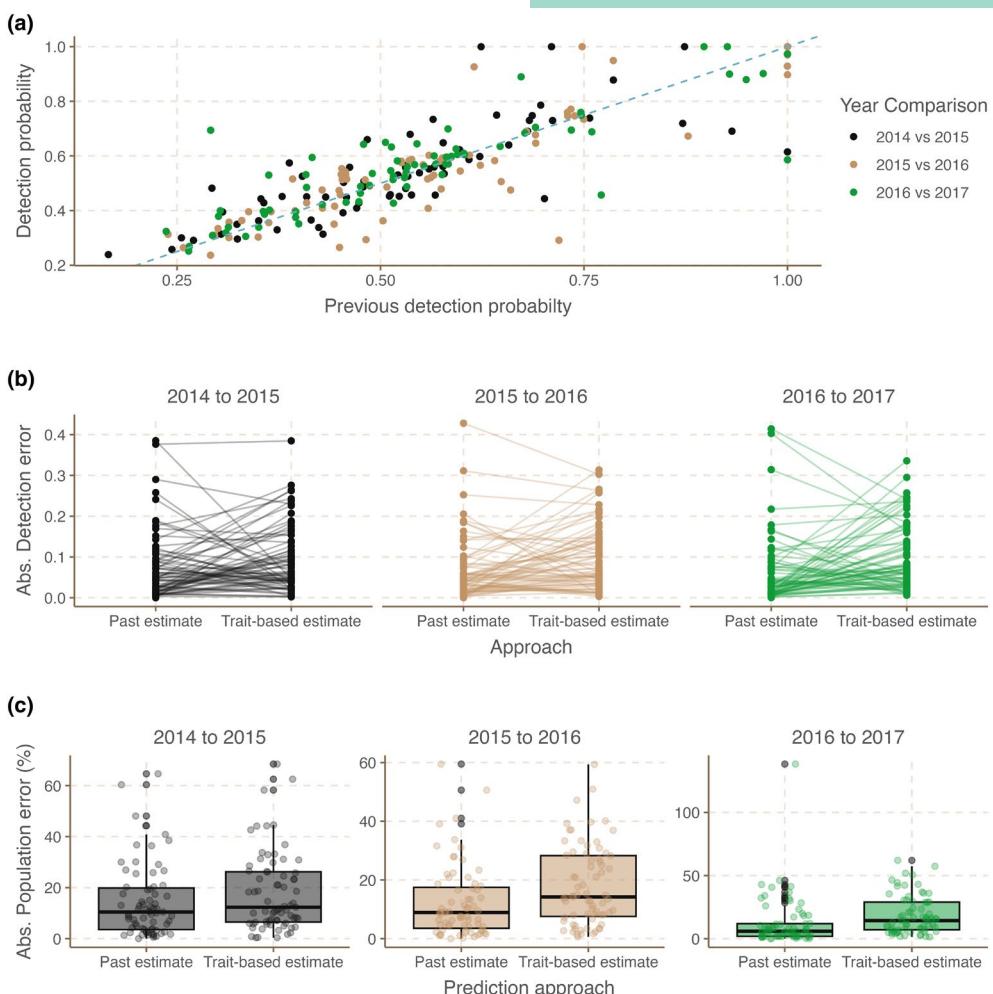


FIGURE 5 Predictability of detection probability across years. (a) The associations in the direct estimates of detection probability between each pairwise consecutive years. (b) Absolute difference in the error of detection probability when using past estimates (direct estimate from previous year) and trait-based estimate (based on model of data from previous year). (c) Absolute difference in the error of the population sizes estimates (direct estimate from previous year) and trait-based estimate (based on model of data from previous year).

the value of collecting some data on detection probabilities for species, as far as possible while a trait-based approach could be used to fill gaps for species that lack any data or are represented by a small number of observations.

Together, our findings suggest options for reducing the amount of survey effort needed to estimate detection probabilities. Other studies have also investigated ways to relax the constraints of specific models that account for imperfect detection, including time-for-space substitution (Costa et al., 2019; Neubauer et al., 2022). 'Partners in Flight' estimate US bird species' population sizes using species-species detection adjustments based on available literature, data and expert knowledge (Stanton et al., 2019). We offer an alternative approach involving a mixed monitoring design that reduces the total amount of monitoring effort needed. Since we find that detection probabilities are—to some extent predictable—Independent data on detection probabilities are not necessarily needed across all sites and years. Instead, some sites or years could be targeted with the survey protocols necessary to estimate detection probabilities, such as distance sampling or repeat surveys, while simpler protocols

for relative abundance data only could be used in other sites and years. In our case study of Danish breeding birds, the use of a trait-based detection probability would lead to a c. 13% difference in population size estimates while the use of a past estimate is c. 8%. This could still represent a large degree of error, especially in absolute terms, but this was still within the confidence intervals of the original population size estimates in our study. However, the specific application should dictate whether this amount of error is acceptable.

There are still enormous gaps in monitoring (Moussy et al., 2022), especially in estimates of species' population sizes. In the face of ongoing limited funds (Buxton et al., 2020; Nichols & Williams, 2006), monitoring efforts could be made more efficient and scalable by employing mixed survey protocols with the aim of formal statistical integration (Ardiantiono et al., 2025). Designed heterogeneity could take advantage of developments in the field of integrated models (Dorazio, 2014; Isaac et al., 2020; Miller, Pacifici, et al., 2019) and adaptive monitoring that plans future data collection based on existing data (Henrys et al., 2024). Integrated distribution models are increasingly used to combine different types of data, usually

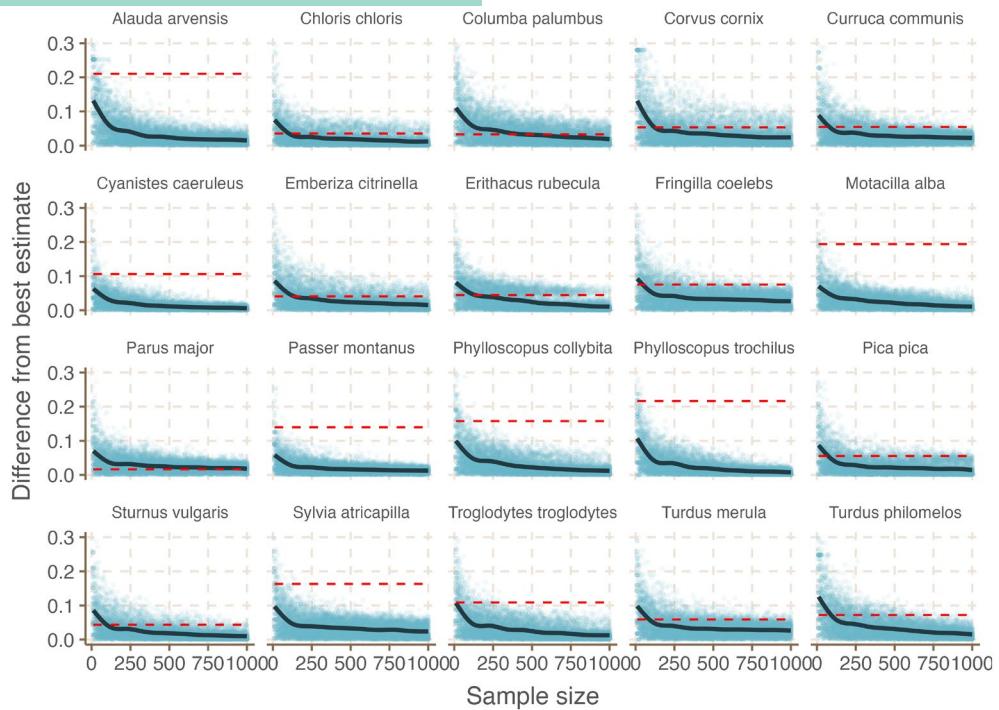


FIGURE 6 Effect of sample size on the relative value of sample-based direct estimates versus trait-based estimates of species' detection probabilities. Sample size is the number of distance-sampled observations for each species that were randomly sampled from the full dataset. Points show the absolute difference between the estimated detection probability from the sample and the best estimates from the full dataset; black line is a gam curve fit to these points to highlight the general relationship. The red lines show the absolute deviations of the trait-based estimates from the direct estimates from the full dataset. Where the red line crosses the black line, the trait-based estimate becomes better (i.e. closer to the best estimate from the full sample) than the sample-based estimate.

of different structures such as abundance and occurrence data (Hertzog et al., 2021) or presence-absence and presence-only data (Fletcher et al., 2019). We suggest that similar approaches could be used to integrate simple monitoring data with data from more complex protocols to derive estimates of species' population sizes. Some models have already combined distance-sampling data with data from another monitoring method (Bowler et al., 2019; Farr et al., 2021; Kéry et al., 2024; Nabias et al., 2025), which increases sample size, reduces sampling biases and expands spatio-temporal coverage, collectively increasing precision and accuracy of parameter estimates. Simultaneous modelling of the ecological and observational processes using these hierarchical models also offers a natural solution to propagate uncertainty of detectability into population size estimates (Bravington et al., 2021; Miller et al., 2013). In planning a heterogeneous study design, it will remain important to verify data quality and ensure sufficient statistical power to detect trends of interest using simulations or power analysis (Guillera-Arroita & Lahoz-Monfort, 2012). Specific design choices will also vary between atlas projects that focus on a single-time frame, often aiming to sample as many sites as possible, versus studies of long-term change that focus on repeat measurements at the same sites.

Traits could also be integrated in hierarchical modelling frameworks to leverage information on detection probabilities across species, taking advantage of the growing array of databases on species' traits (Tobias et al., 2022). Multi-species models offer ways to borrow

information across species within the same modelling framework (Riecke et al., 2021; Tobler et al., 2019), which have also been extended to multi-species integrated models (Zipkin et al., 2023). At least in our case study, our results suggest that trait-based estimates alone are best used for first proxies of detection probabilities for species that lack any monitoring data. Alternatively, when data are sparse, trait-based estimates could be used as informative priors in a Bayesian framework.

We focused on predicting and using mean detection probabilities, but detection probabilities will often vary in space and time for a given species. Such spatio-temporal variation is important to consider since it could bias assessment in how species respond to environmental gradients and conservation interventions (Bennett et al., 2024). In our case study, we did not find strong effects of environmental covariates on detection probabilities, but we were limited by the availability of relevant data that might affect detectability at local scales (e.g. on the presence of hedges bordering the transects). Future work could, however, seek to extend our approach to predict not only mean detection probabilities but also the variation of them using models that predict detection probabilities at local scales by including interaction terms between environmental variables and traits. On the assumption that most of the spatio-temporal variation in detection probabilities is driven by local variation in habitat, we expect this is more important for habitat generalists that are found in a variety of habitats, generating spatial variation in detection probabilities. By contrast, mean detection probability may be

sufficient to consider for habitat specialists that are detected in a limited range of habitat types and have lower spatial variation in their detection probabilities.

Quantifying population abundances will remain an important component of conservation and biodiversity research (Callaghan et al., 2024), and understanding if, and when, inferences can be broadened should be an important area of work. We provide a step in this direction, finding that detection probabilities are partly predictable. Integrating species traits into estimates of population sizes is viable but should not replace targeted species monitoring that allows direct estimates of species' detection probabilities. Future work could explore approaches to optimise the amounts of different data types across species, sites and years, minimising the amount of survey effort and complexity of survey protocol while maximising the precision of population size estimates. Although we focused on birds, we speculate that our approach could be extended to other taxa, including mammals, amphibians and insects. Further tests of the ability to transfer detection probability estimates from one context to another would help understand the limits to the value of information sharing across large spatial and temporal scales. We argue that there is great potential for building planned data integration into the design of monitoring schemes to fill the large knowledge gaps that remain in species' population sizes.

AUTHOR CONTRIBUTIONS

Diana E. Bowler conceived the idea and designed methodology; Daniel P. Eskildsen and Thomas Vikström were involved in the bird data collection and contributed expertise on the species, ecology and monitoring methods; Diana E. Bowler, Brittany M. Mason and Corey T. Callaghan analysed the data; Diana E. Bowler led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Statistical code and data products (detection probabilities, population size estimates) are available in Zenodo: <https://doi.org/10.5281/zenodo.1787939> (Bowler, 2025). The agreements are not

in place to make the bird data publicly available, but they can be requested from DOF-BirdLife (dof@dof.dk).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Summary of raw data for each species included in the analysis.

Table S2. Traits taken from each respective bird traits database.

Table S3. Land use predictors and data product code merging.

Table S4. Linear model result of the trait associations for each year.

Table S5. Table of variable relative influence based on Boosted Regression Tree.

Table S6. Population size and detection probability estimates for each species.

Figure S1. Estimated detection probabilities for each species using distance-sampled data.

Figure S2. Relationships for the top variables predicting detection probability in the boosted regression tree.

Figure S3. Effect of environmental covariates, and modifying effects of habitat preference, on species detection probabilities.

Figure S4. Implications of using trait-based estimates of species' detection probabilities for deriving estimates of population sizes using boosted regression trees.

Figure S5. Correlation of species detection probabilities across years.

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