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4 **Capitalizing on Opportunistic Data for Monitoring Species Relative**
5 **Abundances**

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Résumé

With the internet, a massive amount of information on species abundance can be collected under citizen science programs. However, these data are often difficult to use directly in statistical inference, as their collection is generally opportunistic, and the distribution of the sampling effort is often not known. In this paper, we develop a general statistical framework to combine such “opportunistic data” with data collected using schemes characterized by a known sampling effort. Under some structural assumptions regarding the sampling effort and detectability, our approach allows to estimate the relative abundance of several species in different sites. It can be implemented through a simple generalized linear model. We illustrate the framework with typical bird datasets from the Aquitaine region, south-western France. We show that, under some assumptions, our approach provides estimates that are more precise than the ones obtained from the dataset with a known sampling effort alone. When the opportunistic data are abundant, the gain in precision may be considerable, especially for the rare species. We also show that estimates can be obtained even for species recorded only in the opportunistic scheme. Opportunistic data combined with a relatively small amount of data collected with a known effort may thus provide access to accurate and precise estimates of quantitative changes in relative abundance over space and/or time.

Keywords : opportunistic data, species distribution map, sampling effort, detection probability

1 Introduction

How species abundance varies in space and time is a major issue both for basic (biogeography, macroecology) and applied (production of biodiversity state indicators) ecology. Professionals working on biodiversity thus spend considerable resources collecting data that are suitable for estimating this variation (Yoccoz et al., 2001). Most of the scientific literature recommends the implementation of both a statistically valid sampling design and a standardized protocol for collecting such data (e.g. see Williams et al., 2002, for a review). Many methods have been developed to estimate species abundance in a defined location, e.g., using mark-recapture methods (Seber, 1982) or distance sampling approaches (Buckland et al., 1993). However, these approaches require an intense sampling effort and are not always practical. Many authors have noted that most frequently, interest will not be in abundance itself, but either in the rate of population change, i.e., the ratio of abundance in the same location at two different time points, or in the relative abundance, i.e., the ratio of abundance at two separate locations (MacKenzie and Kendall, 2002).

Relative abundance is frequently monitored with the help of simpler schemes. For instance, a set of sites is randomly sampled in the area of interest, and counts of organisms are organized on these sites using a given protocol. At a given location, the resulting count can be used as an index of the true abundance. Indeed, assuming constant detectability over space and time, the average number of animals counted per sampled site is proportional to the true abundance of the species in the area. Log-linear models can be used to represent this average number of animals detected per site as a function of space and/or time (and, possibly, other factors such as the habitat; see for example van Strien and Pannekoek, 2001), and thereby, to infer population trends. Thus, such programs have been implemented in many countries to monitor the changes in the abundance of several groups of species, such as birds (e.g., for the French Breeding Bird Survey, see Julliard et al., 2004) or butterflies (e.g., for the European Butterfly Monitoring Scheme, see van Swaay et al., 2008). Estimates of relative abundance have also been commonly used for mapping the spatial distribution of several species (e.g., Gibbons et al., 2007).

In addition to such data characterized by a known sampling effort, a large amount of data can also be collected by non-standardized means, with no sampling design and no standardized protocol. In particular, the distribution of the observers and of their sampling effort is often unknown (Dickinson et al., 2010). These so-called “opportunistic data” have always existed, and with the recent development of citizen science programs, we observe a massive increase in the collection of these data on a growing number of species (e.g., Dickinson et al., 2010; Hochachka et al., 2012; Dickinson et al., 2012). Additionally, as the use of online databases facilitates the exchange and storage of data, such opportunistic data may now include millions of new observations per year that are collected in areas covering hundreds of thousands of square kilometres (e.g., the global biodiversity information facility, including more than 500 million records at the time of writing, see Yesson et al., 2007).

The temporal and spatial distributions of the observations in such data reflect unknown distributions of both observational efforts and biodiversity. Thus, a report of a high number of individuals of a given species at a given location compared to other locations could be because the focus species is abundant at this location or because numerous observers were present at this location. Using such opportunistic data to estimate changes in the space and time of species abundance is therefore complex, since any modeling approach should include a submodel of the observation process (Kéry et al., 2009; Hochachka et al., 2012) or an attempt to manipulate the data to remove the bias caused by unequal effort (see a discussion in Phillips et al., 2009).

As noted by MacKenzie et al. (2005), “In some situations, it may be appropriate to share or borrow information about population parameters for rare species from multiple data sources. The general concept is that by combining the data, where appropriate, more accurate estimates of the parameters may be obtained.” In this paper, we propose a general framework which enables to combine data with known observational effort (which we call “standardized” data) with “opportunistic” data with an unknown sampling effort. We focus on multi-species and multi-site data that correspond to the data typically collected in this context.

The purpose of this study is to estimate the relative abundance of the species at different sites (different locations and/or times). We base this estimation on two datasets recording the number of animals detected by observers for each species of a pool of species of interest and each spatial unit of a study area of interest : (i) one “standardized” dataset is collected under a program characterized by a known

86 sampling effort, possibly varying among spatial units, (ii) one “opportunistic” dataset is characterized by
 87 a completely unknown sampling effort. We take into account the variation across species of their detecta-
 88 bility, yet, as a first step, we assume that the observational bias towards some species are the same across
 89 the different sites. We show that, under this assumption, the information concerning both the distribu-
 90 tion of the observational effort and the biodiversity can be efficiently retrieved from “opportunistic” data
 91 by combining them with standardized data. Moreover, we prove that such a combination returns more
 92 accurate estimates than when using the standardized data alone. Our statistical framework allowing this
 93 win-win combination can open numerous avenues for application. We used data on French birds, which
 94 are typical of existing data, to illustrate the numerous qualities of this framework. Note however that the
 95 work presented in this paper is a first step, and that further work will be required to fully account for
 96 varying observational bias towards some habitat types across the different sites.

97 During the reviewing process of this paper, we became aware of an independent and simultaneous
 98 work by [Fithian et al. \(2014\)](#) which develops similar ideas for combining multi-species and multi-sites
 99 data with thinned Poisson models.

100 2 Statistical modeling

101 We want to estimate the relative abundance (relative number of individuals) of I species in J sites.
 102 The “sites” j can either refer to different spatial sites, to different times, or to different combinations of
 103 sites and times. We suppose that we have access to K datasets indexed by k which gather counts for
 104 each species i at each site j . We have in mind a case where some datasets have been collected with some
 105 standardized protocol, while some others are of opportunistic nature.

106 Let X_{ijk} be the count of individuals of the species i by the observers in the site j in the dataset k .
 107 In this paper, we propose to model the counts X_{ijk} by

$$X_{ijk} \sim \text{Poisson}(N_{ij}P_{ik}E_{jk}), \quad \text{for } i = 1, \dots, I, \quad j = 1, \dots, J \text{ and } k = 0, \dots, K - 1, \quad (1)$$

108 where N_{ij} is the number of individuals (animals, plants, etc) of a species i at site j , and P_{ik} , E_{jk} are two
 109 parameters accounting for the bias induced by the observational processes. The parameter P_{ik} reflects
 110 both the detectability of the species i (some species are more conspicuous than others, some are more
 111 easily trapped, etc.) and the detection/reporting rate of this species in the dataset k (the attention of the
 112 observers may systematically vary among species). The parameter E_{jk} reflects the impact of the varying
 113 observational effort (including number and duration of visits, number of traps, etc.) and the varying
 114 observational conditions met during the counting sessions. In the next two sections, we explain the origin
 115 of our modeling, the hypotheses under which it is valid (see also the discussion Section 5), and we describe
 116 precisely the meaning of the two dimensionless parameters P_{ik} and E_{jk} . We refer to the Appendix A for a
 117 discussion on the link with models based on thinned Poisson processes. Before moving to these modeling
 118 issues, we point out that estimation can be easily carried out in the model (1), since it can be recast into
 119 a linear generalized model, see Section 2.4.

120 2.1 Count modeling

121 The count X_{ijk} of individuals of the species i in the site j for the dataset k is assumed to gather
 122 the counts from all visits in the site j . We assume that an individual is only counted *once during a single*
 123 *visit*, yet it can be counted *several times* in any dataset due to the possible *multiple visits* to a site j for
 124 a dataset k . In particular, we may have X_{ijk} larger than the number N_{ij} of individuals of the species i
 125 in the site j . In the following, we neglect identification errors and false positives.

For an individual a_{ij} of the species i in the site j and a visit v_{jk} in the site j for the dataset k , we
 define the random variable $Z_{a_{ij}v_{jk}}$ which equals 1 if the individual a_{ij} has been *seen and recorded* during
 the visit v_{jk} , and 0 otherwise. Assuming that there is no multiple count of an individual during a single
 visit, the count X_{ijk} is then given by

$$X_{ijk} = \sum_{v_{jk} \in \mathcal{V}_{jk}} \sum_{a_{ij}=1}^{N_{ij}} Z_{a_{ij}v_{jk}},$$

126 where \mathcal{V}_{jk} is the set of all the visits v_{jk} in the site j for the dataset k . In the following, we denote by
 127 $p_{a_{ij}v_{jk}} = \mathbf{P}(Z_{a_{ij}v_{jk}} = 1)$ the probability for the individual a_{ij} to be seen and recorded during the visit
 128 v_{jk} .

129 If we assume that the random variables $\{Z_{a_{ij}v_{jk}} : a_{ij} = 1, \dots, N_{ij} \text{ and } v_{jk} \in \mathcal{V}_{jk}\}$ are independent
 130 and that

$$\sum_{v_{jk} \in \mathcal{V}_{jk}} \sum_{a_{ij}=1}^{N_{ij}} p_{a_{ij}v_{jk}}^2 \text{ is small compared to } \sum_{v_{jk} \in \mathcal{V}_{jk}} \sum_{a_{ij}=1}^{N_{ij}} p_{a_{ij}v_{jk}},$$

131 (which happens when $p_{a_{ij}v_{jk}}$ is small), then, according to Le Cam Inequality (Le Cam, 1960), the count
 132 X_{ijk} follows approximatively the Poisson distribution

$$X_{ijk} \sim \text{Poisson}\left(\sum_{v_{jk} \in \mathcal{V}_{jk}} \sum_{a_{ij}=1}^{N_{ij}} p_{a_{ij}v_{jk}}\right) = \text{Poisson}\left(N_{ij} \sum_{v_{jk} \in \mathcal{V}_{jk}} \bar{p}_{iv_{jk}}\right), \quad \text{with } \bar{p}_{iv_{jk}} = \frac{1}{N_{ij}} \sum_{a_{ij}=1}^{N_{ij}} p_{a_{ij}v_{jk}}. \quad (2)$$

133 The parameter $\bar{p}_{iv_{jk}}$ corresponds to the average probability to detect and report during the visit v_{jk} an
 134 individual of the species i which has been sampled at random in the site j . We observe that the mean of
 135 the Poisson distribution

$$N_{ij} \sum_{v_{jk} \in \mathcal{V}_{jk}} \bar{p}_{iv_{jk}} = N_{ij} O_{ijk}$$

136 is the product of a first term N_{ij} , which is the number of individuals of the species i present in the site
 137 j , by a second term O_{ijk} , which is a nuisance term due to the observational process. We underline that
 138 the term O_{ijk} can be larger than 1 when the number V_{jk} of visits in the site j for the dataset k is large,
 139 since an individual can be counted several times during the V_{jk} visits.

140 2.2 Main modeling assumption

141 The main hypothesis of our modeling (1) is that the observational parameter O_{ijk} can be decom-
 142 posed as

$$O_{ijk} = P_{ik} E_{jk}. \quad (3)$$

143 Let us give three examples where such a decomposition holds.

144 **Example 1. (single habitat type)** Assume that the ratios $\bar{p}_{iv_{jk}}/\bar{p}_{i'v_{jk}}$ depend only on the species i
 145 and i' and on the dataset k , so that $\bar{p}_{iv_{jk}}/\bar{p}_{i'v_{jk}} = \bar{p}_{iv'_{j'k}}/\bar{p}_{i'v'_{j'k}}$ for all i, i', j, j', v_{jk} , and $v'_{j'k}$. This means
 146 that the detection/reporting probability $\bar{p}_{iv_{jk}}$ of an individual of the species i during the visit v_{jk} can be
 147 decomposed as

$$\bar{p}_{iv_{jk}} = P_{ik} q_{v_{jk}}, \quad (4)$$

148 with P_{ik} the mean detection/reporting probability of the species i during a visit for the dataset k and $q_{v_{jk}}$
 149 depending only on the visit v_{jk} (not on the species i). The parameter $q_{v_{jk}}$ represents the influence of the
 150 observational conditions during the visit v_{jk} on the detection/reporting probability. The parameter $q_{v_{jk}}$
 151 is then a very complex function of the observational duration, the visibility conditions (weather condi-
 152 tions during the visit, vegetation met, etc.) and many other variables that affect the detection/reporting
 153 probability (number of traps, length of line transects, etc.). When the decomposition (4) holds, we have
 154 the decomposition (3) with $E_{jk} = \sum_{v_{jk} \in \mathcal{V}_{jk}} q_{v_{jk}}$.

155 The decomposition (4) enforces that the detection/reporting probability $\bar{p}_{iv_{jk}}$ does not depend on
 156 interactions between the species i and the visit v_{jk} . This property is quite restrictive and it is not likely
 157 to be met when several habitat types are present within a site j . Actually, if two visits v_{jk} and $v'_{j'k}$ take
 158 place in two different habitat types h_{jk} and $h'_{j'k}$ then the ratios $\bar{p}_{iv_{jk}}/\bar{p}_{i'v_{jk}}$ and $\bar{p}_{iv'_{j'k}}/\bar{p}_{i'v'_{j'k}}$ are not
 159 likely to be equal for all i and i' since some species may be specialized to the habitat type h_{jk} and some
 160 others to the habitat type $h'_{j'k}$. We can weaken the assumption (4) by allowing interactions $\epsilon_{iv_{jk}}$ between
 161 the species i and the visit v_{jk} as long as they cancel on average on each site j

$$\bar{p}_{iv_{jk}} = P_{ik} q_{v_{jk}} + \epsilon_{iv_{jk}}, \quad \text{with } \sum_{v_{jk} \in \mathcal{V}_{jk}} \epsilon_{iv_{jk}} \simeq 0. \quad (5)$$

162 When (5) holds, we again have the decomposition (3) with $E_{jk} = \sum_{v_{jk} \in \mathcal{V}_{jk}} q_{v_{jk}}$. Such interactions $\epsilon_{iv_{jk}}$
 163 can take into account heterogeneous observer attention bias toward the species i , but it does not allow
 164 for some systematic bias induced by heterogeneous habitat types. Actually, assume that the site j has
 165 two habitats h and h' and the site j' has only the habitat h' . Then if the species i (respectively i') is
 166 specialized to habitat type h (respectively h') we will have either $\sum_{v_{j'k}} \epsilon_{iv_{j'k}} < 0$ or $\sum_{v_{jk}} \epsilon_{i'v_{jk}} < 0$. So
 167 (5) cannot hold. The next two examples focus on the impact of heterogeneous habitat types.

168 **Example 2. (known habitat types)** Assume that for each count, we know in which habitat type it
 169 has occurred. Let us introduce the parameter $\tilde{k} = (h, k)$ where h represents the habitat type h and k
 170 the dataset. For each dataset k , we can then pool together the counts occurring in the same site j and
 171 habitat type h . Let us denote by $X_{ij(h,k)}$ the counts of the species i in the site j , the habitat type h
 172 for the dataset k . We assume in the following that each visit occurs in a single habitat type : If not, we
 173 can artificially split a single visit in H different habitat types into H different visits, each occurring in a
 174 single habitat type.

175 Our main modeling assumption in this example is that the ratios $\bar{p}_{iv_{j(h,k)}}/\bar{p}_{i'v_{j(h,k)}}$ depend only on
 176 the species i and i' , the dataset k and the habitat type h . This means that for each i, i', j, j' and $\tilde{k} = (h, k)$
 177 we have $\bar{p}_{iv_{j\tilde{k}}}/\bar{p}_{i'v_{j\tilde{k}}} = \bar{p}_{iv_{j'\tilde{k}}}/\bar{p}_{i'v_{j'\tilde{k}}}$ for all visits $v_{j\tilde{k}}, v_{j'\tilde{k}}$ in the same dataset and the same habitat type.
 178 In this case, the probability $\bar{p}_{iv_{j(h,k)}}$ can be decomposed as

$$\bar{p}_{iv_{j(h,k)}} = P_{i(h,k)} q_{v_{j(h,k)}}, \quad (6)$$

179 with $P_{i(h,k)}$ the mean detection/reporting probability of a typical individual of the species i during a visit
 180 in the habitat type h for the dataset k and $q_{v_{j(h,k)}}$ not depending on i . We then have for $\tilde{k} = (h, k)$

$$O_{ij\tilde{k}} = P_{i\tilde{k}} E_{j\tilde{k}}, \quad \text{with } E_{j\tilde{k}} = \sum_{v_{j\tilde{k}} \in \mathcal{V}_{j\tilde{k}}} q_{v_{j\tilde{k}}} \text{ and } P_{i\tilde{k}} = P_{i(h,k)} \text{ defined by (6).}$$

181 As above, we can allow some non-systematic heterogeneity by merely assuming that $\bar{p}_{iv_{j(h,k)}} = P_{i(h,k)} q_{v_{j(h,k)}} +$
 182 $\epsilon_{iv_{j(h,k)}}$ with $\sum_{v_{j(h,k)} \in \mathcal{V}_{j(h,k)}} \epsilon_{iv_{j(h,k)}} \simeq 0$.

183 **Example 3. (homogeneous habitat type proportions)** We assume again that each visit v_{jk} occurs
 184 in a single habitat type $h(v_{jk})$ (by artificially splitting non-homogeneous visits). Yet, we assume that this
 185 habitat type is not reported in the dataset. As in the second example, we also assume that the ratios
 186 $\bar{p}_{iv_{jk}}/\bar{p}_{i'v_{jk}}$ depend only on the species i and i' , the dataset k and the habitat type $h(v_{jk})$. Hence, the
 187 probability $\bar{p}_{iv_{jk}}$ can be decomposed as

$$\bar{p}_{iv_{jk}} = P_{ih(v_{jk})k} q_{v_{jk}}, \quad (7)$$

188 with P_{ihk} the mean detection/reporting probability of a typical individual of the species i during a visit
 189 in the habitat type h for the dataset k and $q_{v_{jk}}$ not depending on i . Writing $\mathcal{V}_{jk}(h)$ for the set of the
 190 visits v_{jk} in the habitat type h we have

$$O_{ijk} = \sum_{h=1}^H \sum_{v_{jk} \in \mathcal{V}_{jk}(h)} \bar{p}_{iv_{jk}} = \sum_{h=1}^H P_{ihk} E_{jhk}, \quad \text{with } E_{jhk} = \sum_{v_{jk} \in \mathcal{V}_{jk}(h)} q_{v_{jk}}.$$

191 The parameters E_{jhk} are likely to depend on h since there can be some observational bias towards some
 192 habitat types. If we assume that the observational bias is the same for each site j , which means that
 193 $E_{jhk}/E_{j'hk}$ does not depend on h , we have the decomposition

$$E_{jhk} = E_{jk} Q_{hk}, \quad (8)$$

194 where Q_{hk} reflects the observational bias towards the habitat type h in the dataset k . When the decom-
 195 positions (7) and (8) hold, we have

$$O_{ijk} = \sum_{h=1}^H P_{ihk} Q_{hk} E_{jk} = P_{ik} E_{jk}, \quad \text{with } P_{ik} = \sum_{h=1}^H P_{ihk} Q_{hk},$$

196 so O_{ijk} fulfills the decomposition (3). Again, as in the two first examples, we can weaken (7) by merely
 197 assuming that

$$\bar{p}_{iv_{jk}} = P_{ih(v_{jk})k} q_{v_{jk}} + \epsilon_{iv_{jk}}, \quad \text{with } \sum_{v_{jk} \in \mathcal{V}_{jk}} \epsilon_{iv_{jk}} \simeq 0.$$

198 Let us explore when the decompositions (7) and (8) are likely to hold. We first observe that the decompo-
 199 sition (7) will be met as long as we include in the definition of the "habitat type" $h(v_{jk})$ all the exogenous
 200 variables which induces an interaction between the species i and the visit v_{jk} . The decomposition (8) is
 201 much more stringent. It requires that, for each dataset k , the observational bias towards some habitat
 202 types is the same across the different site j . It may not hold when the proportions on habitat types differ
 203 among the different sites. For example, if an habitat h is missing in a site j , then $E_{jhk} = 0$, so (8) cannot
 204 hold if $E_{j'hk} \neq 0$ for another site j' . An example where this property is more likely to be met is when
 205 the "sites" j correspond to the same spatial unit observed at different years j . In such a case, we can
 206 expect that the observational bias towards some habitat types remains stable years after years. When the
 207 observational bias towards some habitat types is not constant across the site, the decomposition (3) is
 208 not met in general. This case requires a substantial additional modeling that will be developed elsewhere.

209 **Interpretation.** Let us interpret more precisely the parameters P_{ik} and E_{jk} in the decomposition (3).
 210 Writing V_{jk} for the number of visits in the site j for the dataset k , we first observe that

$$\frac{1}{J} \sum_{j=1}^J \frac{1}{V_{jk}} \sum_{v_{jk} \in \mathcal{V}_{jk}} \bar{p}_{iv_{jk}} = \frac{1}{J} \sum_{j=1}^J \frac{O_{ijk}}{V_{jk}} = \frac{1}{J} \sum_{j=1}^J P_{ik} \frac{E_{jk}}{V_{jk}} = P_{ik} \bar{E}_k, \quad \text{with } \bar{E}_k = J^{-1} \sum_{j=1}^J E_{jk}/V_{jk}.$$

211 We can always replace (P_{ik}, E_{jk}) in the decomposition (3) by $(P'_{ik}, E'_{jk}) = (P_{ik} \bar{E}_k, E_{jk}/\bar{E}_k)$. Applying
 212 this renormalization step and dropping the prime (for notational simplicity), we obtain

$$P_{ik} = \frac{1}{J} \sum_{j=1}^J \frac{1}{V_{jk}} \sum_{v_{jk} \in \mathcal{V}_{jk}} \bar{p}_{iv_{jk}}, \quad (9)$$

213 which means that P_{ik} is the mean detection/reporting probability of a typical individual of the species i
 214 during a typical visit for the dataset k .

215 As explained in the three above examples, the parameter E_{jk} in (3) is a complex function of the
 216 conditions met during the visits in the site j for the dataset k , including the observational effort. This
 217 parameter E_{jk} can be (much) larger than 1 when the number V_{jk} of visits in the site j for the dataset
 218 k is very large. We point out that we can have E_{jk} very large even if O_{ijk} is smaller than 1, when
 219 the probability P_{ik} of detection/reporting of a typical individual of the species i is very small. In the
 220 remaining of the paper, we call *observational intensity* at the site j in the dataset k the parameter E_{jk} .

221 2.3 Identifiability issues

222 In the following, we deal with two datasets. A first dataset labeled by $k = 0$, in which we suppose
 223 that the observational intensities E_{j0} are known up to a constant. Henceforth, we will call this dataset
 224 the *standardized dataset*. We also consider a second dataset labeled by $k = 1$, characterized by unknown
 225 observational intensities E_{j1} . We will refer to this dataset as the *opportunistic dataset*.

226 2.3.1 A single opportunistic dataset is not enough

227 We consider first the case where we have a single dataset, i.e. $K = 1$. For notational simplicity,
 228 we drop the index k in this paragraph. Our observations X_{ij} then follows a Poisson distribution with
 229 intensity λ_{ij} , where $\lambda_{ij} = N_{ij} P_i E_j$. We cannot recover the $IJ + I + J$ parameters N_{ij} , P_i , and E_j from
 230 the IJ intensities λ_{ij} . Yet, if we are only interested by the relative abundances $N_{ij}/N_{ij'}$ with respect to
 231 a reference site, say $j' = 1$, can we recover the $I(J - 1)$ ratios $\{N_{ij}/N_{i1} : j = 2, \dots, J, i = 1, \dots, I\}$ from
 232 the IJ parameters λ_{ij} ?

233 Let us write $\lambda_{ij} = \tilde{N}_{ij} \tilde{P}_i \tilde{E}_j$ with $\tilde{N}_{ij} = N_{ij} P_i E_1$, $\tilde{P}_i = 1$ and $\tilde{E}_j = E_j/E_1$. The parameters \tilde{N}_{ij}
 234 differ from the N_{ij} by a multiplicative constant $P_i E_1$ depending only on the species i . Therefore, we have
 235 $N_{ij}/N_{ij'} = \tilde{N}_{ij}/\tilde{N}_{ij'}$, which means that the parameters \tilde{N}_{ij} give access to the relative abundances N_{ij}/N_{i1}
 236 of the species i . When the dataset has been collected with a known sampling design, the observational
 237 intensity in a given site E_j is known up to an unknown constant, so that the ratios $E_j/E_{j'}$ are known
 238 and we can recover the \tilde{N}_{ij} (and hence the relative abundances) from λ_{ij} since the \tilde{P}_i and \tilde{E}_j are known.
 239 The situation is different with opportunistic datasets characterized by unknown ratios $E_j/E_{j'}$. In this

240 case, the \tilde{E}_j are also unknown, so we cannot recover the \tilde{N}_{ij} from the parameters λ_{ij} . Hence, we do not
 241 have access to the relative abundance N_{ij}/N_{i1} . As explained in the next paragraph, we need to combine
 242 different datasets.

243 2.3.2 Combining an opportunistic dataset with a standardized one

244 Let us now investigate the identifiability issues when we combine a standardized dataset (labeled
 245 by $k = 0$) with an opportunistic one (labeled by $k = 1$). In this case, we have $2IJ$ parameters $\lambda_{ijk} =$
 246 $N_{ij}P_{ik}E_{jk}$ for $IJ+2(I+J)$ parameters N_{ij} , P_{ik} and E_{jk} . For $IJ > 2(I+J)$, which typically holds for large
 247 J and $I \geq 3$, we have more parameters λ_{ijk} than parameters N_{ij} , P_{ik} and E_{jk} . Nevertheless, as explained
 248 in the Appendix B, the model is not identifiable without $J+I+1$ additional identifiability conditions. As in
 249 Section 2.3.1, we introduce some renormalisation \tilde{N}_{ij} , \tilde{E}_{jk} of \tilde{P}_{ik} of N_{ij} , E_{jk} and P_{ik} , which enables us to
 250 easily express these identifiability conditions while preserving the identity $\tilde{N}_{ij}\tilde{E}_{jk}\tilde{P}_{ik} = \lambda_{ijk} = N_{ij}E_{jk}P_{ik}$.

251 In the following, we assume that the ratios $\{E_{jk}/E_{j'k} : j \neq j'\}$ are known for the dataset $k = 0$
 252 (standardized dataset), but not for the dataset $k = 1$ (opportunistic one). As above, we define $\tilde{E}_{j0} =$
 253 E_{j0}/E_{10} (which is known) and $\tilde{P}_{i1} = 1$ for all i . We could have set $\tilde{P}_{i0} = 1$ instead of $\tilde{P}_{i1} = 1$, but the
 254 latter choice is more suited for handling species i monitored in the dataset $k = 1$ but not in the dataset
 255 $k = 0$, as we will show later. We must still set one more constraint. We choose $\tilde{P}_{10} = 1$ for convenience.
 256 These $I + J + 1$ constraints combined with the identity $\tilde{N}_{ij}\tilde{E}_{jk}\tilde{P}_{ik} = \lambda_{ijk} = N_{ij}E_{jk}P_{ik}$ lead to the change
 257 of variables :

$$\begin{aligned}\tilde{N}_{ij} &= N_{ij}P_{i1}E_{10}\frac{P_{10}}{P_{11}}, \\ \tilde{E}_{jk} &= \frac{E_{jk}}{E_{10}} \times \frac{P_{1k}}{P_{10}} \\ \tilde{P}_{ik} &= \frac{P_{ik}}{P_{i1}} \times \frac{P_{11}}{P_{1k}}.\end{aligned}\tag{10}$$

258 In terms of these new variables, we have the simple statistical model $X_{ijk} \sim \text{Poisson}(\tilde{N}_{ij}\tilde{E}_{jk}\tilde{P}_{ik})$ with
 259 $\tilde{E}_{j0} = E_{j0}/E_{10}$ for all j , $\tilde{P}_{i1} = 1$ for all i and $\tilde{P}_{10} = 1$. These $J + I + 1$ quantities are known, and the
 260 resulting statistical model is identifiable.

261 Let us interpret these new quantities. The parameter \tilde{N}_{ij} is proportional to the abundance N_{ij} by
 262 an unknown factor $P_{i1}E_{10}P_{10}/P_{11}$ depending only on the species i . As in Section 2.3.1, these parameters
 263 give access to the relative abundance $N_{ij}/N_{i1} = \tilde{N}_{ij}/\tilde{N}_{i1}$ of each species i in each site j . The parameters
 264 \tilde{E}_{j1} are equal, up to a constant, to the observational intensity E_{j1} ; therefore, they provide the relative
 265 observational intensities E_{j1}/E_{11} for each site j in the dataset 1. Finally, \tilde{P}_{i0} is proportional to the ratio
 266 P_{i0}/P_{i1} by an unknown factor P_{11}/P_{10} , so we can compare the ratios P_{i0}/P_{i1} across the different species.
 267 The ratio P_{i0}/P_{i1} reflects the systematic difference of attention toward some species among the observers
 268 of the two schemes.

269 In addition, we emphasize that we can consider the case where some species i are not monitored in
 270 the dataset 0 but are recorded in the dataset 1. This case can be handled by merely adding the constraints
 271 $\tilde{P}_{i0} = P_{i0} = 0$ for the concerned species i .

272 2.4 Estimation via a Generalized Linear Model

273 We can estimate the parameters \tilde{N}_{ij} , \tilde{E}_{jk} and \tilde{P}_{ik} by the maximum likelihood estimators $(\hat{N}_{ij}, \hat{E}_{jk}, \hat{P}_{ik})$
 274 with the constraints $\hat{E}_{j0} = \tilde{E}_{j0}$ for all j , $\hat{P}_{i1} = 1$ for all i and $\hat{P}_{10} = 1$. This estimation can be carried out
 275 with the help of a generalized linear model. Indeed, with the notations $n_{ij} = \log(\tilde{N}_{ij})$, $e_{jk} = \log(\tilde{E}_{jk})$ and
 276 $p_{ik} = \log(\tilde{P}_{ik})$, Model (1) can be recast as a classical generalized linear model from the Poisson family
 277 with a log link :

$$X_{ijk} \sim \text{Poisson}(\lambda_{ijk}), \quad \text{with } \log(\lambda_{ijk}) = n_{ij} + e_{jk} + p_{ik}.\tag{11}$$

278 Indeed, we only have to define $e_{j0} = \log \tilde{E}_{j0}$ as a known offset in the model, $p_{i1} = 0$ for all i , and fit the
 279 resulting model with any statistical package (see Supplementary materials).

3 Theoretical gain of combining two datasets

It is important to investigate whether the estimates of the relative abundance obtained by combining the dataset 1 with unknown observational intensity ratios $E_{j1}/E_{j'1}$ to the dataset 0 with known observational intensity ratio $E_{j0}/E_{j'0}$ improves upon the estimates obtained with the single dataset 0. In this section, we investigate this issue analytically. An improvement is expected simply by looking at the balance between the number of observations and the number of free parameters. With the dataset 0, we have IJ observations, and we want to estimate IJ free parameters; whereas with the two datasets 0 and 1, we have $2IJ$ observations for $IJ + J + I - 1$ free parameters. The balance between the number of observations and the number of free parameters is better in the second case. Below, we quantify the theoretical improvement more precisely by comparing the variance of the maximum-likelihood estimators in the two cases. Then, we show that dataset combination also allows to estimate relative abundance for species i not monitored in the dataset 0.

3.1 Variance reduction

For mathematical simplicity, we assume in the following that the ratios P_{i0}/P_{i1} are known for all i . In terms of the normalized variables, this means that the \tilde{P}_{i0} are known.

When we work with the single dataset 0, we can estimate \tilde{N}_{ij} with the maximum likelihood estimator $\hat{N}_{ij}^0 = X_{ij0}/(\tilde{E}_{j0}\tilde{P}_{i0})$. Let us investigate how the maximum likelihood estimator \hat{N}_{ij} associated with the model $X_{ijk} \sim \text{Poisson}(\tilde{N}_{ij}\tilde{E}_{jk}\tilde{P}_{ik})$ improves upon \hat{N}_{ij}^0 . We consider the case where the (unknown) observational intensities E_{j1} in the dataset 1 is much larger than the observational intensities E_{j0} in the dataset 0. Hence, we consider the asymptotic setting where E_{j1} goes to infinity. In the Appendix B, we show that the limit variance of \hat{N}_{ij} when $E_{j1} \rightarrow \infty$ is given by

$$\text{var}(\hat{N}_{ij}) \xrightarrow{E_{j1} \rightarrow \infty} \text{var}(\hat{N}_{ij}^0) \times \frac{P_{i0}N_{ij}}{\sum_l P_{l0}N_{lj}}. \quad (12)$$

In particular, the variance of the estimate is reduced by a factor

$$\frac{\text{var}(\hat{N}_{ij})}{\text{var}(\hat{N}_{ij}^0)} \xrightarrow{E_{j1} \rightarrow \infty} \frac{P_{i0}N_{ij}}{\sum_l P_{l0}N_{lj}},$$

when working with the two datasets instead of the sole dataset 0. This factor can be very small for rare species (N_{ij} small), hardly detectable species (P_{i0} small), or when the number I of monitored species is large.

Let us explain the origin of this variance reduction in the simple case where the ratios P_{i0}/P_{i1} are the same for all the species i (which formally corresponds to $\tilde{P}_{i0} = 1$ for all i). In this case, we have a closed-form formula for \hat{N}_{ij} (see Formula (21) in the Appendix B)

$$\hat{N}_{ij} = \frac{X_{ij0} + X_{ij1}}{\sum_l (X_{ij0} + X_{lj1})} \times \frac{\sum_l X_{lj0}}{\tilde{E}_{j0}},$$

which reveals the contribution of each dataset to the estimation of the (normalized) relative abundance. Actually, the estimator \hat{N}_{ij} is the product of two terms, where the first term mainly depends on the opportunistic dataset 1 when the observational intensities E_{j1} are large, whereas the second term only depends on the dataset 0

$$\hat{N}_{ij} \xrightarrow{E_{j1} \rightarrow \infty} \frac{X_{ij1}}{\sum_l X_{lj1}} \times \frac{\sum_l X_{lj0}}{\tilde{E}_{j0}}.$$

Let us interpret these two terms. The first ratio on the right-hand side provides an estimation of the proportion $\tilde{N}_{ij}/\sum_l \tilde{N}_{lj}$ of individuals in a site j that belong to a species i . This proportion is estimated by the ratio of the number X_{ij1} of individuals of the species i observed at site j in the opportunistic dataset to the total number $\sum_l X_{lj1}$ of individuals observed at site j in the same data. When the observational intensities E_{j1} in the opportunistic dataset 1 is large, the ratio $X_{ij1}/\sum_l X_{lj1}$ provides a very accurate

317 estimation of the abundance proportion $\tilde{N}_{ij}/\sum_l \tilde{N}_{lj}$, and we have (see Formula (22) in the Appendix B)
 318

$$\hat{N}_{ij} \stackrel{E_{j1} \rightarrow \infty}{\approx} \frac{\tilde{N}_{ij}}{\sum_l \tilde{N}_{lj}} \times \frac{\sum_l X_{lj0}}{\tilde{E}_{j0}}. \quad (13)$$

319 The second term in the right-hand side of (13) provides an estimation of the total (normalized) relative
 320 abundance $\sum_l \tilde{N}_{lj}$ at the site j . This total (normalized) abundance is estimated from the dataset 0 by
 321 dividing the total number $\sum_l X_{lj0}$ of individuals counted at the site j in the dataset 0 by the (norma-
 322 lized) observational intensity \tilde{E}_{j0} . Let us now explain the reduction of variance observed in (12). The
 323 formula (13) shows that we estimate \tilde{N}_{ij} by first estimating the total (normalized) relative abundance
 324 $\sum_l \tilde{N}_{lj}$ with the dataset 0 and then renormalize this estimation with the ratio $\tilde{N}_{ij}/\sum_l \tilde{N}_{lj}$ which has
 325 been accurately estimated with the dataset 1. The reduction of variance observed in (12) then results
 326 from the use of the whole counts $\sum_l X_{lj0}$ at site j in the dataset 0 for estimating \tilde{N}_{ij} instead of the sole
 327 counts X_{ij0} of the species i at site j .

3.2 Species not monitored in the scheme characterized by a known sampling ob- 328 servational intensity 329

330 As already mentioned, combining the two datasets also allows to estimate \tilde{N}_{ij} for some species i
 331 that are not monitored in the dataset 0, but are monitored in the opportunistic dataset 1. This situation
 332 formally corresponds to the case where $P_{i0} = 0$. For $E_{j1} \rightarrow \infty$, the limit variance of the estimator \hat{N}_{ij} is
 333 (see Formula (25) in the Appendix B)

$$\text{var}(\hat{N}_{ij}) \stackrel{E_{j1} \rightarrow \infty}{\approx} \frac{\tilde{N}_{ij}^2}{\sum_l \tilde{P}_{l0} \tilde{N}_{lj} \tilde{E}_{j0}}.$$

334 Because the species i is not monitored in dataset 0, the (normalized) relative abundance \tilde{N}_{ij} cannot
 335 be estimated with the sole dataset 0. Thus, there is an obvious improvement to be made by using our
 336 estimation scheme that combines the two datasets. To reveal the power of our approach, let us compare
 337 the variance $\text{var}(\hat{N}_{ij})$ of our relative abundance estimator with the variance of the imaginary estimator
 338 $\hat{N}_{ij}^{0,\text{imaginary}}$ based on an imaginary dataset 0 where the species i would have been monitored with some
 339 (imaginary) detection/reporting probability $P_{i0}^{\text{imaginary}}$. The variance of the maximum likelihood estimator
 340 $\hat{N}_{ij}^{0,\text{imaginary}}$ of \tilde{N}_{ij} with this imaginary dataset 0 would be $\tilde{N}_{ij}/(\tilde{E}_{j0} \tilde{P}_{i0}^{\text{imaginary}})$ so that

$$\text{var}(\hat{N}_{ij}) \stackrel{E_{j1} \rightarrow \infty}{\approx} \text{var}(\hat{N}_{ij}^{0,\text{imaginary}}) \times \frac{P_{i0}^{\text{imaginary}} N_{ij}}{\sum_l P_{l0} N_{lj}}.$$

341 In particular, the estimation provided by \hat{N}_{ij} can significantly outperform the imaginary estimation we
 342 would have obtained with the sole imaginary dataset 0 (where the species i would have been monitored).
 343 Moreover, if we compare the estimator \hat{N}_{ij} with the imaginary estimator $\hat{N}_{ij}^{\text{imaginary}}$ based on both the
 344 imaginary dataset $k = 0$ and the dataset $k = 1$, we observe that the ratio of their variance

$$\frac{\text{var}(\hat{N}_{ij})}{\text{var}(\hat{N}_{ij}^{\text{imaginary}})} = \frac{P_{i0}^{\text{imaginary}} N_{ij} + \sum_l P_{l0} N_{lj}}{\sum_l P_{l0} N_{lj}}$$

345 remains close to one when $P_{i0}^{\text{imaginary}} N_{ij} \ll \sum_l P_{l0} N_{lj}$. This means that with our estimation scheme,
 346 there is not much difference between the estimation based on a dataset collected with known observa-
 347 tional intensities where a species i is rare and the estimation based on a dataset collected with known
 348 observational intensities where a species i is not monitored. In other words, there is no instability on
 349 the estimation of the relative abundance of a species when it is not present in the dataset collected with
 350 known observational intensities.

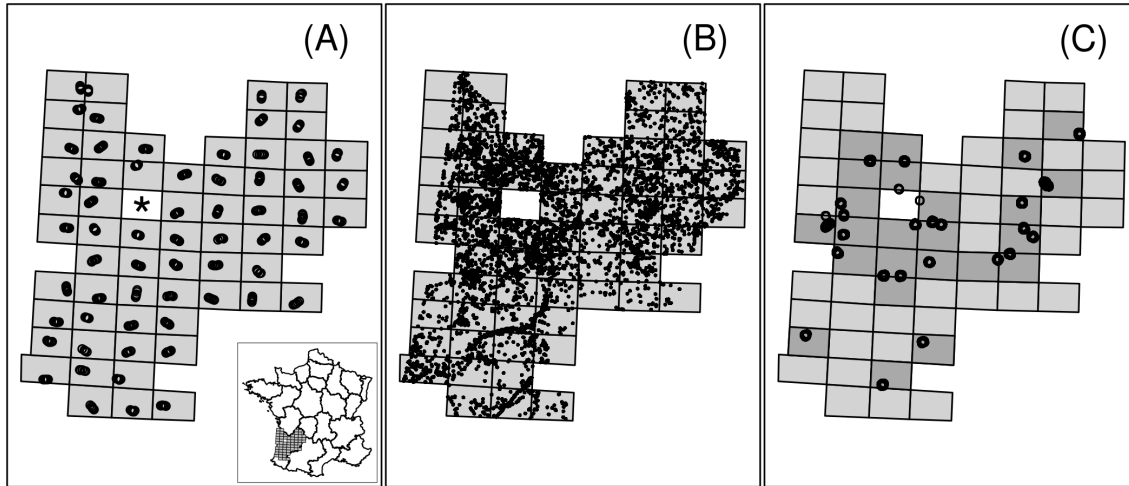


FIGURE 1 – The datasets used to illustrate our statistical framework. The location of the Aquitaine region in France is displayed in the insert. (A) distribution of the ACT listening points in the region; (B) distribution of the LPO records (opportunistic dataset) in the region; (C) distribution of the STOC listening points in the region. The grey quadrat cells are used as the “sites” in our analysis (they measure $\approx 30 \times 20$ km). Note that the quadrat cell containing the Bordeaux metropolitan area (indicated by an asterisk in (A)) has been removed from the dataset.

4 Illustration

4.1 Datasets

In this section, we investigate on some datasets the predictive power of our modeling approach. We estimated the relative abundance of 34 bird species in the non-urban habitat of 63 sites in the Aquitaine region (South West of France). We fitted our model with an opportunistic dataset and a dataset collected with known observational intensity. We then assessed the predictive power of our approach with the help of an independent dataset collected with known observational intensity in the same area, hereafter referred as “validation dataset”. We therefore illustrate the ability of our approach to provide better predictions of species relative abundance than other approaches based on either of the two datasets alone.

We first describe the opportunistic dataset. We used the recent online database developed by the Ligue de Protection des Oiseaux (LPO, Bird Life representative in France, largest French bird watcher NGO, with regional delegations). This online system was launched successively by the different regional LPO groups, and we acquired data from one of the first groups to start, Aquitaine, South-Western France, with data collection starting in 2007 (www.fauneaquitaine.org). Any citizen who can identify bird species can register on this website and record any bird observation s/he wishes, noting the species, date, and location (to the nearest 500 m). Hundreds of observers thus record hundreds of thousands observations. We typically ignore why these observations were made, e.g., the motivation of the observer, the reason for choosing to report these observations over others, whether they report all the species they have seen at a given place and time, the underlying observational intensity, etc. We selected all such opportunistic records between April and mid-June 2008–2011. For each record, we considered the number of animals detected by the observer. Data were pooled over years, because we will focus here only on spatial variation in relative abundance. Over 115 000 species records detected in a non-urban habitat were considered in this study (see Fig. 1B).

We then describe the dataset collected with known observational intensity, used for the fit of the model. We used the data from the ACT monitoring plan jointly carried out by the French National Game and Wildlife Agency (ONCFS, Office National de la Chasse et de la Faune Sauvage), the national hunter association (FNC, Fédération Nationale des Chasseurs) and the French departmental hunters associations (FDC, Fédérations Départementales des Chasseurs). The main objective of the ACT survey was to monitor the breeding populations of several migratory bird species in France (Boutin et al., 2003); ACT stands for *Alaudidae*, *Columbidae*, *Turdidae*, which were the main bird clades of interest for this

381 monitoring, though this program also monitors several *Corvidae* species (see table 1 for the list of species
382 of interest for our study). Thus, only a fraction of the species recorded by the LPO program was also
383 studied by the ACT survey. The Aquitaine region was discretized into 64 quadrat cells, and in each cell,
384 a 4km long route was randomly sampled in the non-urban habitat of the cell (see Fig. 1(A)). Each route
385 included 5 points separated by exactly 1 km. Each route was traveled twice between April and mid-June,
386 and every point was visited for exactly 10 minutes within 4 hours after sunrise in appropriate weather
387 conditions. Every bird heard or seen was recorded, and for each point and each species, the maximum
388 count among the two visits was retained. The observers were professionals from the technical staff of
389 either the ONCFS or the hunters associations. Note that due to organization constraints, some listening
390 points in a site were not necessarily counted every year. Between 2008 and 2011, over 9 500 birds were
391 counted.

392 Finally, we describe the validation dataset, used to assess the predictive power of our model.
393 We used the data from the STOC program (*Suivi temporel des oiseaux communs*), a French breeding
394 bird survey carried out by the French museum of natural history (MNHN, Museum National d’Histoire
395 Naturelle) for the same region and the same years. The STOC survey (Jignet et al., 2012) is based on
396 a stratified random sampling, with each volunteer observer being assigned a 2×2 km square randomly
397 chosen within 10 km of his house. The observer then homogeneously distributed 10 points within the
398 square. Each point was visited twice between April and mid-June (before and after May 8th, with at
399 least 4 weeks between visits) for exactly 5 minutes within 4 hours after sunrise in appropriate weather
400 conditions (no rain or strong winds). Every bird heard or seen was recorded, and for each point and each
401 species, the maximum count among the two visits was retained. These counts were then summed for a
402 given square, year and species. Between 2008 and 2011, 251 listening points belonging to 29 such squares
403 have been surveyed in non-urban habitat (to allow the comparison with the other datasets, we removed
404 the listening points located in urban habitat), most of them for several years, and over 15241 birds were
405 detected by the observers.

406 Our aim was to test our model ability to provide a better prediction of the spatial variation in
407 species relative abundance than any model based on either of the two datasets alone. The “sites” of our
408 model were the 63 quadrat cells defined for the ACT survey; we removed the quadrat cell containing the
409 metropolitan area of Bordeaux (a large town with a population of > 1 million inhabitants), where the
410 sampling process in the opportunistic dataset could not be supposed to be the same as in the other areas
411 (see Fig. 1(A)). We focused on $I = 34$ bird species (see Table 1). Note that the smaller number of species
412 monitored in the ACT survey allowed to demonstrate the ability of our approach to estimate the relative
413 abundance of species monitored only in opportunistic dataset. For both the ACT survey and the STOC
414 survey, the observational intensity in the site j was measured as the number of points-years sampled
415 in the quadrat cell j during the period 2008–2011. We used the validation STOC dataset to assess the
416 predictive power of our modeling approach. Only 24 sites contained at least one STOC listening point
417 (Fig. 1(C)), so that this assessment was restricted to these sites.

418 4.2 Comparison of the predictive power

419 Let X_{ijk} be the number of animals of the species i detected in the site j in the dataset k . Let $k = a$
420 denote the dataset with known observational intensity collected by the ACT survey; let $k = \ell$ denote the
421 opportunistic dataset collected by the LPO; finally, let $k = s$ denote the validation dataset collected by
422 the STOC survey. We compared different statistical approaches to estimate the relative abundances of
423 the species in the sites.

424 Let \widehat{N}_{ij}^m be the relative abundance estimated for the species i in the site j with the statistical
425 approach m . We estimated the relative abundance of each species i in each site j with the following
426 approaches :

$$\widehat{N}_{ij}^a = X_{ija} / \pi_j^a \quad (14)$$

$$\widehat{N}_{ij}^s = X_{ijs} / \pi_j^s \quad (15)$$

$$\widehat{N}_{ij}^{\ell 1} = X_{ij\ell} / S_j \quad (16)$$

$$\widehat{N}_{ij}^{\ell 2} = X_{ij\ell} / \sum_i X_{ij}^{\ell} \quad (17)$$

TABLE 1 – List of the 34 bird species under study. The 13 species monitored only by the ACT survey are indicated by an asterisk. All species were surveyed by the STOC and the LPO program.

Latin name	species
<i>Aegithalos caudatus</i>	Long-Tailed Tit
<i>Alauda arvensis</i> *	Eurasian Skylark
<i>Alectoris rufa</i> *	Red-Legged Partridge
<i>Carduelis carduelis</i>	European Goldfinch
<i>Carduelis chloris</i>	European Greenfinch
<i>Certhia brachydactyla</i>	Short-Toed Treecreeper
<i>Columba palumbus</i> *	Common Wood Pigeon
<i>Coturnix coturnix</i> *	Common Quail
<i>Cuculus canorus</i>	Common Cuckoo
<i>Dendrocopos major</i>	Great Spotted Woodpecker
<i>Erithacus rubecula</i>	European Robin
<i>Fringilla coelebs</i>	Common Chaffinch
<i>Garrulus glandarius</i> *	Eurasian Jay
<i>Hippolais polyglotta</i>	Melodious Warbler
<i>Lullula arborea</i> *	Woodlark
<i>Luscinia megarhynchos</i>	Common Nightingale
<i>Milvus migrans</i>	Black Kite
<i>Cyanistes caeruleus</i>	Eurasian Blue Tit
<i>Parus major</i>	Great Tit
<i>Passer domesticus</i>	House Sparrow
<i>Phasianus colchicus</i> *	Common Pheasant
<i>Phoenicurus ochruros</i>	Black Redstart
<i>Phylloscopus collybita</i>	Common Chiffchaff
<i>Pica pica</i> *	Eurasian Magpie
<i>Pica viridis</i>	Eurasian Green Woodpecker
<i>Sitta europaea</i>	Eurasian Nuthatch
<i>Streptopelia decaocto</i> *	Eurasian Collared Dove
<i>Streptopelia turtur</i> *	European Turtle Dove
<i>Sylvia atricapilla</i>	Eurasian Blackcap
<i>Troglodytes troglodytes</i>	Eurasian Wren
<i>Turdus merula</i> *	common Blackbird
<i>Turdus philomelos</i> *	Song Thrush
<i>Turdus viscivorus</i> *	Mistle Thrush
<i>Upupa epops</i>	Eurasian Hoopoe

427 where π_j^k denotes the number of listening points of the site j sampled in the dataset k , and S_j denotes
 428 the area of the site j (determined by intersecting each ACT quadrat with the Aquitaine region). For the
 429 LPO dataset $k = \ell$, we had to account for the site-specific unknown intensity. We estimated this intensity
 430 with two proxies that are commonly used in such cases. First, we assumed that observational intensity
 431 was spatially uniform so that it varied only with quadrat cell area S_j (the resulting approach is labeled
 432 $\ell 1$). Another proxy considered that the observational intensity within a site was proportional to the total
 433 number of records across the sites (pooled over all species; the resulting approach is labeled $\ell 2$).

434 Finally, we fitted the model described in the previous sections, using the ACT dataset a as the
 435 dataset collected with known observational intensity ($k = 0$), and the LPO dataset ℓ as the opportu-
 436 nistic dataset ($k = 1$). Note that we supposed a quasi-Poisson distribution, to account for moderate
 437 overdispersion in our dataset. Thus, we could estimate the value of $\widehat{N}_{ij}^{\ell+a}$ with our approach.

438 The relative abundance is the absolute abundance multiplied by an unknown constant, and this
 439 constant may vary among approaches. Therefore, to allow the comparison between the various approaches,
 440 we standardized the relative abundance estimates in the following way :

$$\widetilde{N}_{ij}^m = \frac{\widehat{N}_{ij}^m}{\sum_j \widehat{N}_{ij}^m}$$

441 We want to investigate whether the estimates obtained by our model are closer or not to the true
 442 densities than any of the estimates that could be obtained from the individual datasets. We used the
 443 value \widetilde{N}_{ij}^s estimated with the validation STOC dataset as the value of reference. We assessed the predictive
 444 power of each approach m by calculating, for each species, the Pearson correlation coefficient between
 445 the standardized relative abundance \widetilde{N}_{ij}^m estimated with the method m and the standardized relative
 446 abundance \widetilde{N}_{ij}^s estimated with the validation dataset. We summarized this power by calculating the
 447 median and interquartile range (IQR) of these coefficients over the different species of interest. Although
 448 the relative abundance estimates were calculated on the complete dataset, these results were presented
 449 by separating the species monitored in the ACT survey, and the species not monitored in this survey.
 450 This allowed to evaluate the ability of our approach to estimate the relative abundance of species not
 451 monitored in the standardized dataset.

452 We also investigated the stability of our statistical approach when the standardized dataset is small.
 453 We therefore assessed this stability by replacing our big standardized ACT dataset a by a much smaller
 454 dataset a' . We subsampled the dataset a : for each site, we randomly sampled only one listening point in
 455 every site, and we considered the bird counts of only one randomly sampled year for every point. Thus, we
 456 artificially divided the observational intensity by 18 in average in this dataset : the complete ACT dataset
 457 a stored the bird counts carried out in 1107 listening points-years, whereas the reduced dataset a' stored
 458 the bird counts carried out in only 63 listening-points-years (one in every site). We also estimated the
 459 standardized relative abundance $\widetilde{N}_{ij}^{a'} = X_{ij}^{a'} / \sum_j X_{ij}^{a'}$ with this reduced dataset. Finally, we estimated the
 460 relative abundance $\widetilde{N}_{ij}^{\ell+a'}$ by combining this reduced standardized dataset with the opportunistic dataset
 461 according to our model. We also assessed the predictive power of these two approaches by comparing the
 462 estimates with the reference values obtained with the STOC dataset.

463 The online supplementary material contains the data and the code for the R software ([R Core
 464 Team, 2013](#)) that will allow the reader to reproduce our calculations.

465 4.3 Results

466 We fitted our model on the LPO and ACT datasets. There was only a small amount of overdis-
 467 persion in our data (the coefficient of overdispersion was equal to 1.22); the examination of the residuals
 468 did not reveal any problematic pattern and the quality of the fit was satisfying. We observe in table 2
 469 that the predictive power was larger for our statistical approach than for all other approaches, whether
 470 based on the dataset a or ℓ alone.

471 The predictive power of our statistical approach did not decrease much when model was fit on
 472 the smaller standardized dataset a' , despite the fact that the observational intensity in this dataset was
 473 divided by about 20. In particular, the predictive power of our approach with a reduced dataset remained
 474 larger than the predictive power of the other approaches. We observe a strong positive correlation bet-

TABLE 2 – Predictive capabilities of the various possible approaches to estimate the relative abundance of 34 bird species in 63 sites in the Aquitaine region. For each possible estimation approach m , we present the median (calculated over the species) of the Pearson’s correlation coefficient between the relative abundance \tilde{N}_{ij}^m estimated by the approach m and the relative abundance \tilde{N}_{ij}^s estimated by the “reference” STOC approach. In parentheses, we present the interquartile range of this coefficient. These quantities are calculated for the set of species only monitored in the ACT survey and for the set of species not monitored in this survey.

Ratio	Species only in ACT	Species not monitored in ACT
$\tilde{N}_{ij}^{a+\ell}$	0.55 (0.38 – 0.68)	0.35 (0.19 – 0.47)
$\tilde{N}_{ij}^{a'+\ell}$	0.54 (0.25 – 0.61)	0.28 (0.08 – 0.40)
\tilde{N}_{ij}^a	0.27 (0.13 – 0.49)	—
$\tilde{N}_{ij}^{a'}$	0.06 (-0.07 – 0.23)	—
$\tilde{N}_{ij}^{\ell 1}$	0.29 (0.24 – 0.55)	0.11 (0.06 – 0.22)
$\tilde{N}_{ij}^{\ell 2}$	0.44 (0.35 – 0.51)	0.38 (0.13 – 0.46)

475 ween the estimates $\tilde{N}_{ij}^{\ell+a}$ obtained with the full standardized dataset and the estimates $\tilde{N}_{ij}^{\ell+a'}$ obtained
476 with the reduced standardized dataset (median Pearson’s $R = 0.84$, IQR = 0.81 – 0.90). This illustrates
477 clearly the gain of precision obtained by combining the small standardized dataset with a large amount of
478 opportunistic data, which we demonstrated in section 3.1. The very fine-grained distribution of observa-
479 tions contained in the opportunistic dataset can more efficiently predict site-specific variation in relative
480 abundance than can the standardized dataset.

481 We investigated the ability of our method to estimate the relative abundance of species not moni-
482 tored in the ACT survey. Note that the between-site variance of the log relative abundance estimated
483 with our method $\tilde{N}_{ij}^{a+\ell}$ was larger in average for the species monitored in the ACT survey (median = 2.41,
484 IQR = 1.1 – 104) than for the species not monitored in this survey (median = 1.15, IQR = 1.04 – 1.34),
485 which resulted in smaller Pearson’s coefficient for the latter species (Tab. 2). Our approach performed
486 better than the approaches based on the dataset a or $\ell 1$ alone. The predictive power of our approach and
487 the approach $\ell 2$ were similar. Actually, the log observational intensity estimated in a site by our approach
488 for the LPO dataset was strongly correlated with the logarithm of the total number of birds detected in
489 this site (Pearson’s $R = 0.85$), which supports to some extent the common practice of biologists to use
490 the total number of birds detected in a place as a measure of the observational intensity.

491 5 Discussion

492 5.1 Overview

493 We propose a general approach to estimate relative abundances of multiple species on multiple
494 ”sites” (corresponding to different times and/or locations) by combining one or several datasets collected
495 according to some standardized protocol with one or several datasets of opportunistic nature. The esti-
496 mation is performed with the generalized linear model (11). This modeling relies on several assumptions,
497 including : (i) the datasets have the same spatiotemporal extent, (ii) the individuals of the monitored
498 species do not cluster into large groups, (iii) either the habitat types are known or the observational bias
499 towards some habitat types are the same across the different sites. In particular, the third hypothesis is
500 quite restrictive and handling cases where it is not met requires significant additional modeling.

501 We have demonstrated both theoretically (under the assumption that the model is well-specified)
502 and numerically on some datasets, that combining opportunistic data with standardized surveys produces
503 more reliable estimates of the relative abundances than either dataset alone. In particular, we observe
504 an improvement in our example Section 4 even if the above hypothesis (iii) is probably violated. We
505 have also shown that combining opportunistic data with standardized data allows for estimating relative
506 abundance for species which are not monitored in the standardized dataset.

507 Our approach for combining opportunistic data with survey data is quite general : It requires to be

508 extended in order to overcome the current limitations (see the discussion in the next section) and to be
509 adapted to the specifics of each case study. Yet, we highlight two already promising applications of our
510 framework. First, we emphasize that our framework can be readily used to estimate temporal changes. In
511 such cases, the "sites" j correspond to different times j and E_{j1} represent the parameters describing the
512 unknown observational intensity at time j for the opportunistic dataset. For temporal variation, biased
513 attention for some habitats in the opportunistic dataset will meet the hypothesis (iii) as long as this
514 biased attention is constant over time. As explained in Section 2.2, such biases will be entirely captured
515 in the estimation of the P_{ik} . For example, the accuracy of bird population trends for France will be
516 considerably improved by the addition of opportunistic data to the current Breeding Bird Surveys.

517 Another very interesting feature of our framework is its ability to estimate the relative abundance
518 of very rare species, even if these species are not monitored with a scheme with known sampling effort.
519 This has important practical implications. For example, Guisan et al. (2006) noted "in a sample of
520 550 plots surveyed in a random-stratified way based on the elevation, slope, and aspect of the plot
521 during two consecutive summers in the Swiss Alps (704.2 km²), not one occurrence of the rare and
522 endangered plant species *Eryngium alpinum* L. was recorded. This was despite the species being easily
523 detectable if present and independent records of the species existing in the area within similar vegetation
524 types." Our framework would be very useful in this context. In particular, if a citizen science program
525 collects opportunistic data on this species along with some other more common species, then the relative
526 abundance of the rare species can be estimated by combining these opportunistic data with standardized
527 surveys monitoring the same common species.

528 5.2 Limitations and extensions

529 We derived from our analysis Section 2.1 a model based on the Poisson distribution. In practice, we
530 may observe some overdispersion in the data. Causes of overdispersion include clustering of individuals,
531 spatial auto-correlation, identification errors, etc. It is then wise to account for overdispersion in the
532 modeling (see Section 4).

533 The main assumption in our modeling (1) is that the observational bias O_{ijk} can be decomposed
534 into $O_{ijk} = P_{ik}E_{jk}$. As explained in Section 2.2, this mainly amounts to assume that the habitat types
535 are known or the observational bias towards some habitat types are the same across the different sites.
536 This assumption will not be met in many cases and we can expect a significant improvement by taking
537 habitat types heterogeneity into account. This issue requires a significant additional modeling and it will
538 be developed elsewhere.

539 In our estimation framework, we did not take into account any variable affecting the distribution of
540 the relative abundance in the different sites. However, it is well-known that there might be a spatial (if the
541 "sites" are spatial units) or temporal (if the "sites" are time units) autocorrelation in the densities. For
542 example, it is frequent that if the abundance of a given species is high in a given spatial unit, it will also
543 be high in neighboring units. Moreover, spatial units with a similar environmental composition will often
544 be characterized by similar abundances. Explicitly accounting for these patterns in the estimation process
545 could lead to an increased accuracy of the estimation (by reducing the effective number of parameters).
546 This could be done by modeling the relative abundances \tilde{N}_{ij} as a function of environmental variables,
547 or as a function of spatial effects (e.g. using conditional autoregression effects in a hierarchical model,
548 see Banerjee et al., 2004). Alternatively, it is possible to maximize a regularized log-likelihood, i.e. to
549 maximize for example :

$$\log \mathcal{L} - \sum_{i=1}^I \sum_{j=1}^J \sum_{m=1}^J \nu \pi_{jm} (\tilde{N}_{ij} - \tilde{N}_{im})^2$$

550 where \mathcal{L} is the likelihood of the model, π_{jm} is a measure of "environmental and spatial proximities"
551 between the unit j and the unit m , and ν is a positive parameter that determines the strength of the
552 penalty. The proximities could be of any sort (e.g. taking the value 1 if the two spatial units are neighbours,
553 and 0 otherwise ; inverse Euclidean distances between the units in the space defined by the environmental
554 variables, etc.). This kind of regularization would reduce the number of effective parameters in the model
555 and thereby increase the accuracy of the estimation (for example, see Malbasa and Vucetic, 2011).

556 Our statistical approach relies on the assumption that the measurement errors (identification errors,
557 false positive) were negligible. This is a common assumption in this type of study, although recent studies

558 seem to indicate that (i) even a small number of false positives can lead to biases in estimates (Royle
559 and Link, 2006), and (ii) even highly trained professionals may be subject to such errors (e.g. McClintock
560 et al., 2010). As a solution to this problem, Miller et al. (2011) proposed to combine data collected
561 using different approaches characterized by different probabilities of identification errors (e.g. hear counts
562 vs. visual counts). This approach has not yet been thoroughly tested though, especially in the context
563 of (relative) abundance estimation. Taking into account measurement errors in our framework, e.g. by
564 integrating the approach of Miller et al. (2011), still requires further study.

565 The detectability of a given species is not necessarily constant across sites j in the standardized
566 dataset, as documented in the literature (Link and Sauer, 1997; MacKenzie and Kendall, 2002). This
567 unaccounted variation of detection probability will result into an unaccounted variation of the observa-
568 tional intensity. Because the knowledge of this intensity plays a crucial role in the fit of the model, such
569 errors may bias the estimates if this variation of detection probability is structured according to some
570 exogenous variables (e.g. habitat types). Many statistical frameworks based on a particular sampling
571 design have been suggested to estimate detectability, such as using mixture models based on repeated
572 counts (Royle, 2004). Further work is required to adapt such methods to our proposed framework.

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662 A Link with thinned-Poisson processes

663 In Section 2.1, we described a first modeling of the count data X_{ijk} leading to our model (1). In
664 this appendix, we explain how the model (1) can also be motivated by another point of view relying
665 on the inhomogeneous point process (IPP, see Cressie, 1993). Indeed, IPPs have recently been shown to
666 be a central approach to model species distribution in ecology. Aarts et al. (2012) have shown the close
667 connections existing between IPPs and resource selection functions, a commonly used approach to model
668 habitat selection by the wildlife (Boyce and McDonald, 1999). Moreover, IPPs have also been shown to
669 generalize other statistical approaches commonly used to model species distribution, such as the MaxEnt
670 approach (Renner and Warton, 2013) or the classical logistic regression (Fithian and Hastie, 2013). We
671 compare the IPP with our approach in this section.

672 The framework of IPPs suppose that the individuals of the species i are distributed on a domain
673 \mathcal{D} according to a Poisson point process with intensity $\lambda_i(s)$. If we assume that the individual at location
674 s is detected and recorded in the dataset k with probability $b_{ik}(s)$, then the individuals of the species i
675 recorded in the dataset k are distributed according to a Poisson point process with intensity $\lambda_i(s)b_{ik}(s)$.
676 The multiplication of $\lambda_i(s)$ with $b_{ik}(s)$ results in a “thinning” of the IPP ; for this reason, the resulting
677 point process is sometimes called thinned-Poisson process (e.g. Fithian et al., 2014). Note that in the
678 context of IPPs, each individual is supposed to be counted at most once in each dataset (undercounting).
679 On the contrary, in Section 2.1, we allowed multiple counts of a single individual during the multiple visits
680 in a site, which makes our development more sensible for studies characterized by a strong observational
681 intensity (which is generally the case of citizen science data).

682 However, even with this difference, our model (1) can be motivated in the context of IPPs. We can
683 adopt different points of view for estimating relative abundances with this modeling based on IPPs. A
684 first point of view is to introduce a model for the abundance intensities $\lambda_i(s)$ and the probabilities $b_{ik}(s)$
685 and then estimate these quantities accordingly. Such a point of view has been successfully developed in
686 a simultaneous and independent work by Fithian et al. (2014) : They model the abundances intensities
687 by $\lambda_i(s) = e^{\alpha_i + \beta_i^T x(s)}$ with $x(s)$ some observed environmental variables, the probabilities by $b_{i1}(s) =$
688 $e^{\gamma_i + \delta_i^T z(s)}$ with $z(s)$ some other observed environmental variable and $b_{i0}(s) = 1$ at locations where survey
689 data are available and $b_{i0}(s) = 0$, else. The abundance intensities are then estimated by $\hat{\lambda}_i(s) = e^{\hat{\alpha}_i + \hat{\beta}_i^T x(s)}$,
690 with $\hat{\alpha}_i$ and $\hat{\beta}_i$ some penalized maximum likelihood estimators of α_i and β_i .

691 An alternative point of view, which corresponds to the point of view developed in this paper, is
692 not to try to infer the intensities $\lambda_i(s)$ for each s , but instead, to work at the scale of a whole site $S_j \subset \mathcal{D}$
693 and infer the mean abundance $\Lambda_{ij} = \int_{S_j} \lambda_i(s) ds$ of the species i on S_j . An important feature is that
694 we do not model the abundance intensities $\lambda_i(s)$ and the probabilities $b_{ik}(s)$ in terms of some observed

695 environmental variables, but rather simply assume some structural properties on these functions. In
 696 particular, the mean abundance Λ_{ij} in the site j is not assumed to be completely driven by some observed
 697 environmental variables.

698 Let us explain how the model (1) can arise in such a context. Let us denote by $d_{ij}(s) = \lambda_i(s)/\Lambda_{ij}$
 699 the probability density distribution describing the probability for a given individual of the species i in
 700 the site j to be located in $s \in S_j$. The number X_{ijk} of individuals of the species i counted in the site j
 701 in the dataset k is then distributed according to

$$X_{ijk} \sim \text{Poisson}(\Lambda_{ij}O_{ijk}) \quad \text{with} \quad O_{ijk} = \int_{S_j} d_{ij}(s)b_{ik}(s) ds.$$

702 Let us describe some scenarii, where the observational bias O_{ijk} can be decomposed as $O_{ijk} = P_{ik}E_{jk}$,
 703 leading to the model (1).

704 In the three examples below, we will assume that the detection/reporting probability $b_{ik}(s)$ can
 705 be decomposed in

$$b_{ik}(s) = p_{ik}\phi_k(s) \tag{18}$$

706 with $\phi_k(s)$ not depending on i . This means that the detection/reporting bias $b_{ik}(s)/b_{1k}(s) = p_{ik}/p_{1k}$
 707 towards the species i in the dataset k is independent of the location s (in other words the functions
 708 $b_{1k}(s), \dots, b_{Ik}(s)$ are proportional one to the others). When this property is met we have the decompo-
 709 sition

$$O_{ijk} = p_{ik} \int_{S_j} d_{ij}(s)\phi_k(s) ds.$$

710 The decomposition does not give a decomposition $O_{ijk} = P_{ik}E_{jk}$ in general. Yet, such a decomposition
 711 arises in the three scenarii described below (which are the counterparts of the three examples described
 712 in Section 2.2).

713 **Example 1 : sites with homogeneous habitat type.** Assume that the species intensity ratios
 714 $\lambda_i(s)/\lambda_{i'}(s)$ depend on the species i, i' and the site j , but not on the location $s \in S_j$. Such a property is li-
 715 kely to be met if the site j has an homogeneous habitat type. In this case, we have $\lambda_i(s)/\lambda_{i'}(s) = \Lambda_{ij}/\Lambda_{i'j}$
 716 and hence $\lambda_i(s) = \Lambda_{ij}g(s)$ for all i and $s \in S_j$. Then, we have

$$O_{ijk} = P_{ik}E_{jk} \quad \text{with} \quad P_{ik} = p_{ik} \quad \text{and} \quad E_{jk} = \int_{S_j} g(s)\phi_k(s) ds.$$

717 **Example 2 : observations with known habitat type.** In this example, we assume that for each
 718 observation we know in which habitat type $h(s)$ it has occurred (in particular, it will be the case if we
 719 know the location s of each observation). Exactly as in the Example 2 in Section 2.2, we define \tilde{k} as
 720 the couple $\tilde{k} = (h, k)$. Assume that the density distribution $d_{ij}(s)$ depends on the species i only through
 721 the habitat $h(s)$ of s : For any i, i' and $s, s' \in S_j$ such that $h(s) = h(s')$ we have $d_{ij}(s)/d_{i'j}(s) =$
 722 $d_{ij}(s')/d_{i'j}(s')$. In this case, we have a decomposition $d_{ij}(s) = \alpha_{ih(s)}g(s)$ for all $s \in S_j$. Let us denote by
 723 $S_{jh} = \{s \in S_j : h(s) = h\}$ the portion of the site S_j with habitat type h . For any i, j and $\tilde{k} = (h, k)$, the
 724 counts $X_{ij(h,k)}$ of individuals of the species i in the habitat h in the site j for the dataset k is distributed
 725 according to

$$X_{ij(h,k)} \sim \text{Poisson}(\Lambda_{ij}P_{i(h,k)}E_{j(h,k)}) \quad \text{with} \quad P_{i(h,k)} = \alpha_{ih}p_{i(h,k)} \quad \text{and} \quad E_{j(h,k)} = \int_{S_{jh}} g(s)\phi_{(h,k)}(s) ds.$$

726 We then have the decomposition $O_{ij\tilde{k}} = P_{i\tilde{k}}E_{j\tilde{k}}$ with $\tilde{k} = (h, k)$. We emphasize that in this case the
 727 probability $p_{i(h,k)}$ appearing in the decomposition (18) is allowed to depend on the habitat type h (the
 728 bias towards some species may differ depending on the habitat type).

729 **Example 3 : homogeneous distribution of habitat types.** We do not assume anymore that the
 730 habitat type $h(s)$ for each observation is known. We assume again that we have the decomposition
 731 $d_{ij}(s) = \alpha_{ih(s)}g(s)$ for all $s \in S_j$, hence

$$O_{ijk} = p_{ik} \sum_h \alpha_{ih} \int_{S_{jh}} g(s)\phi_k(s) ds.$$

732 If we assume in addition that

$$\int_{S_{jh}} g(s)\phi_k(s) ds = Q_{hk} \int_{S_j} g(s)\phi_k(s) ds, \quad (19)$$

733 then

$$O_{ijk} = P_{ik}E_{jk} \quad \text{with} \quad P_{ik} = p_{ik} \sum_h \alpha_{ih}Q_{hk} \quad \text{and} \quad E_{jk} = \int_{S_j} g(s)\phi_k(s) ds.$$

734 Let us investigate when the decomposition (19) can be met. Assume first that $\phi_k(s) = \beta_{kh(s)}\gamma_k(s)$ where
735 $\gamma_k(s)$ reflects local fluctuations independent of the habitat type. The function $g(s)\gamma_k(s)$ then represents
736 small scale fluctuations and we can expect to have

$$\int_S g(s)\gamma_k(s) ds \approx q_k|S|,$$

737 for S large enough. It would be the case for example if $g(s)\gamma_k(s)$ was the outcome of a stationary process.
738 We then have

$$\frac{\int_{S_{jh}} g(s)\phi_k(s) ds}{\int_{S_j} g(s)\phi_k(s) ds} \approx \frac{\beta_{hk}q_k|S_{jh}|}{\sum_h \beta_{hk}q_k|S_{jh}|}.$$

739 When the ratios $|S_{jh}|/|S_j|$ do not depend on j , the above ratio depends on h and k only, so (19) holds.
740 This case corresponds to sites S_j all having a similar distribution of habitat types. This property will be
741 met if the sites S_j correspond to the same location at different times j .

742 B Mathematical proofs

743 B.1 Identifiability conditions

744 With the notations $n_{ij} = \log(N_{ij})$, $e_{jk} = \log(E_{jk})$ and $p_{ik} = \log(P_{ik})$, the model (1) described in
745 our paper can be recast as a classical generalized linear model

$$X_{ijk} \sim \text{Poisson}(\lambda_{ijk}), \quad \text{with} \quad \log(\lambda_{ijk}) = n_{ij} + e_{jk} + p_{ik}.$$

746 The kernel of the design matrix associated with this linear regression has a dimension equal to $I + J + 1$.
747 Therefore, we need $I + J + 1$ constraints to ensure the identifiability of the model.

748 B.2 Properties of the estimators

749 The negative log-likelihood of the parameters $(\tilde{N}_{ij}, \tilde{E}_{jk}, \tilde{P}_{ik})$ is

$$\mathcal{L} = \sum_{i \in I} \sum_{j \in J} \sum_{k \in \{0,1\}} \left(\tilde{N}_{ij} \tilde{E}_{jk} \tilde{P}_{ik} - X_{ijk} \log(\tilde{N}_{ij} \tilde{E}_{jk} \tilde{P}_{ik}) + \log(X_{ijk}!) \right)$$

750 where the parameters $\{\tilde{E}_{j0}, j \in J\}$ and $\{\tilde{P}_{i0}, i \in I\}$ are known, $\tilde{P}_{10} = 1$ and $\tilde{P}_{i1} = 1$ for all $i \in I$.

751 To keep the mathematical analysis of the maximum likelihood estimators comprehensible, we focus
752 below on the case where the \tilde{P}_{i0} are known. The maximum likelihood estimators of \tilde{N}_{ij} and \tilde{E}_{j1} are then
753 the solutions of

$$\hat{N}_{ij} = \frac{X_{ij0} + X_{ij1}}{\tilde{P}_{i0} \tilde{E}_{j0} + \hat{E}_{j1}} \quad \text{and} \quad \hat{E}_{j1} = \frac{X_{\#j1}}{\hat{N}_{\#j}}, \quad (20)$$

754 where $X_{\#jk} = \sum_i X_{ijk}$ and $\hat{N}_{\#j} = \sum_i \hat{N}_{ij}$.

755 We first treat the simplest case where the \tilde{P}_{i0} are all equal.

756 **B.2.1 Case of constant ratios** P_{i0}/P_{i1}

757 We consider in this paragraph the case where $\tilde{P}_{i0} = \tilde{P}_{10}$ for all $i \in I$. This corresponds to the case
 758 where for all the species i , the detection/reporting probability ratios P_{i0}/P_{i1} are the same and equal to
 759 P_{10}/P_{11} . We derive from (20)

$$\hat{N}_{\#j} = \frac{X_{\#j0} + X_{\#j1}}{\tilde{E}_{j0} + \tilde{E}_{j1}}$$

760 and inserting this expression in the formula for \hat{E}_{j1} we obtain $\hat{E}_{j1} = \tilde{E}_{j0}X_{\#j1}/X_{\#j0}$. As a consequence,
 761 we obtain the closed-form expression for \hat{N}_{ij}

$$\hat{N}_{ij} = \frac{X_{ij0} + X_{ij1}}{X_{\#j0} + X_{\#j1}} \times \frac{X_{\#j0}}{\tilde{E}_{j0}}. \quad (21)$$

762 According to the strong law of large numbers for Poisson processes, we have

$$\hat{N}_{ij} \xrightarrow{E_{j1} \rightarrow \infty} \frac{\tilde{N}_{ij}}{\tilde{N}_{\#j}} \times \frac{X_{\#j0}}{\tilde{E}_{j0}} \quad (22)$$

763 and

$$\text{var}(\hat{N}_{ij}) \xrightarrow{E_{j1} \rightarrow \infty} \left(\frac{\tilde{N}_{ij}}{\tilde{N}_{\#j}} \right)^2 \times \frac{\tilde{N}_{\#j}}{\tilde{E}_{j0}} = \frac{\tilde{N}_{ij}}{\tilde{E}_{j0}} \times \frac{N_{ij}P_{i0}}{\sum_l N_{lj}P_{l0}}.$$

764 If we estimate \tilde{N}_{ij} with the sole ‘‘known-effort’’ data X_{ij0} , the maximum likelihood estimator is given by
 765 $\hat{N}_{ij}^0 = X_{ij0}/\tilde{E}_{j0}$ and its variance equals $\text{var}(\hat{N}_{ij}^0) = \tilde{N}_{ij}/\tilde{E}_{j0}$. We can then compare the variance of \hat{N}_{ij}
 766 and \hat{N}_{ij}^0

$$\text{var}(\hat{N}_{ij}) \xrightarrow{E_{j1} \rightarrow \infty} \text{var}(\hat{N}_{ij}^0) \times \frac{N_{ij}P_{i0}}{\sum_l N_{lj}P_{l0}}. \quad (23)$$

767 **B.2.2 Case of arbitrary ratios** P_{i0}/P_{i1}

768 We no longer assume that the \tilde{P}_{i0} are all equal. In this case, we have no closed-form formula for
 769 \hat{N}_{ij} but we can compute a first-order expansion of \hat{N}_{ij} in terms of the inverse of $X_{\#j1}$.

770 The first step is to check that $\hat{N}_{\#j}$ is upper-bounded independently of the X_{ij1} . When $P_{i0} > 0$ for
 771 all i (which means that the same species are monitored in the datasets 0 and 1), we have from (20)

$$\hat{N}_{ij} \leq \frac{X_{ij0} + X_{ij1}}{\min_i(\tilde{P}_{i0}\tilde{E}_{i0}) + X_{\#j1}/\hat{N}_{\#j}}.$$

772 Summing these inequalities we obtain the upper-bound

$$\hat{N}_{\#j} \leq X_{\#j0} / \min_i(\tilde{P}_{i0}\tilde{E}_{j0})$$

773 which does not depend on X_{ij1} . The case where $P_{i0} = 0$ for some i can be treated similarly : splitting
 774 apart the indices in $I_0 = \{i \in I : P_{i0} = 0\}$ and those out of I_0 , we get from (20)

$$\hat{N}_{\#j} \leq \frac{\sum_{i \in I_0} (X_{ij0} + X_{ij1})}{X_{\#j1}/\hat{N}_{\#j}} + \frac{\sum_{i \notin I_0} (X_{ij0} + X_{ij1})}{\min_{i \notin I_0}(\tilde{P}_{i0}\tilde{E}_{i0}) + X_{\#j1}/\hat{N}_{\#j}}.$$

775 This inequality is equivalent to

$$\hat{N}_{\#j} \left(1 - \frac{\sum_{i \in I_0} (X_{ij0} + X_{ij1})}{X_{\#j1}} \right) \leq X_{\#j0} / \min_{i \notin I_0}(\tilde{P}_{i0}\tilde{E}_{j0}).$$

776 In the asymptotic $E_{j1} \rightarrow \infty$ we obtain the asymptotic upper-bound

$$\hat{N}_{\#j} \leq \frac{X_{\#j0}}{\min_{i \notin I_0}(\tilde{P}_{i0}\tilde{E}_{j0})} \times \frac{\sum_{i \in I} \tilde{N}_{ij}}{\sum_{i \in I \setminus I_0} \tilde{N}_{ij}}.$$

777 Now that we have checked that $\widehat{N}_{\#j}$ is (asymptotically) upper-bounded independently of the X_{ij1} ,
 778 we can write a first-order expansion of the formula (20)

$$\widehat{N}_{ij} = \frac{(X_{ij0} + X_{ij1})\widehat{N}_{\#j}}{X_{\#j1}} - \frac{(X_{ij0} + X_{ij1})\widehat{N}_{\#j}^2 \widetilde{P}_{i0} \widetilde{E}_{j0}}{X_{\#j1}^2} + O\left(\frac{X_{ij1}}{X_{\#j1}^3}\right). \quad (24)$$

779 Summing these expansions over $i \in I$ and simplifying the expression gives

$$\widehat{N}_{\#j} = \frac{X_{\#j0} X_{\#j1}}{\widetilde{E}_{j0} \sum_l \widetilde{P}_{l0} (X_{lj0} + X_{lj1})} \left(1 + O\left(\frac{1}{X_{\#j1}}\right)\right).$$

780 Plugging this formula in (24) gives

$$\begin{aligned} \widehat{N}_{ij} &= \frac{X_{ij0} + X_{ij1}}{\sum_l \widetilde{P}_{l0} (X_{lj0} + X_{lj1})} \times \frac{X_{\#j0}}{\widetilde{E}_{j0}} \times \left(1 + O\left(\frac{1}{X_{\#j1}}\right)\right) \\ &\xrightarrow{E_{j1} \rightarrow \infty} \frac{\widetilde{N}_{ij}}{\sum_l \widetilde{P}_{l0} \widetilde{N}_{lj}} \times \frac{X_{\#j0}}{\widetilde{E}_{j0}}, \end{aligned}$$

781 where the last limit follows again from the law of large numbers for Poisson processes. Computing the
 782 asymptotic variance when $E_{j1} \rightarrow \infty$, we find after simplification

$$\text{var}(\widehat{N}_{ij}) \xrightarrow{E_{j1} \rightarrow \infty} \frac{\widetilde{N}_{ij}^2}{\sum_l \widetilde{P}_{l0} \widetilde{N}_{lj} \widetilde{E}_{j0}} = \frac{\widetilde{N}_{ij}}{\widetilde{P}_{i0} \widetilde{E}_{j0}} \times \frac{P_{i0} N_{ij}}{\sum_l P_{l0} N_{lj}}. \quad (25)$$

783 As in the previous case, we can compare this variance to the variance of the maximum likelihood
 784 estimator $\widehat{N}_{ij}^0 = X_{ij0}/(\widetilde{P}_{i0} \widetilde{E}_{j0})$ obtained by estimating \widetilde{N}_{ij} with the sole values X_{ij0} . The variance of \widehat{N}_{ij}^0
 785 being $\text{var}(\widehat{N}_{ij}^0) = \widetilde{N}_{ij}/(\widetilde{P}_{i0} \widetilde{E}_{j0})$, we obtain the reduction of variance

$$\text{var}(\widehat{N}_{ij}) \xrightarrow{E_{j1} \rightarrow \infty} \text{var}(\widehat{N}_{ij}^0) \times \frac{P_{i0} N_{ij}}{\sum_l P_{l0} N_{lj}}. \quad (26)$$