

Teasing out biological effects and sampling artifacts when using occupancy rate in monitoring programs

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ABSTRACT. Recent declines in biodiversity stress the need for rigorous and reliable multispecies monitoring programs. A potential weakness of monitoring programs is a reliance on raw counts and the assumption either of complete detection or of constant detection probability for each species, regardless of the sampling situation. Until recently, these assumptions have largely remained untested and, therefore, to help insure accuracy, bird-monitoring programs have depended on standardization of counts and counts of longer duration. We tested the effectiveness of these strategies for providing unbiased occupancy rates using a method designed to accommodate situations where species detection probabilities are less than one and heterogeneous. We tested the effect of potential sources of heterogeneity in detection probability (vegetation structure, wind velocity, cloud cover, date, and time) on occupancy rate estimates of 13 bird species in southern France. We compared adjusted and raw occupancy rates for two sampling durations (10 and 20 min). Differences between raw and adjusted occupancy rates were low even for the shorter count duration, suggesting that standardized long counts should produce reliable estimates of occupancy rates even in the absence of correction by an appropriate method. This enhances the value of past monitoring programs where long standardized counts were used, but with designs that do not allow corrected estimates. However, we found that detection probability was heterogeneous for most species and that vegetation structure was an important source of heterogeneity. The possible effects of habitat on detection probability should be of special concern for long-term monitoring programs conducted in landscapes where habitats vary across time or space.

SINOPSIS. Dejando fuera el efecto biológico de artefactos de muestreo cuando se utiliza la tasa de ocupación en programas de monitoreo

Las recientes tasas de reducción en biodiversidad realzan la necesidad de programas de monitoreo rigurosos y confiables diseñados para múltiples especies. Una debilidad potencial de estos programas de monitoreo es depender en conteos crudos y tener que asumir detecciones completas o probabilidades de detección constante para cada especie, para casi todo tipo de situación. Hasta hace muy poco, los supuestos mencionados, no habían sido puesto a pruebas, y por ende, para ayudar a determinar su exactitud, los programas de monitoreos de aves dependieron de la estandarización de conteos y conteos de larga duración. Pusimos a pruebas la efectividad de dichas estrategias para proveer tasas de ocupación sin sesgo, utilizando un método designado para acomodar la situación en donde la probabilidad de detectar una especie era menos de uno (1) y heterogénea. Probamos la efectividad de fuentes potenciales de heterogeneidad en la probabilidad de detección (estructura de la vegetación, velocidad del viento, cubierta de nubes, fecha y hora del día) en estimados de tasas de ocupación de 13 especies de aves en el sur de Francia. Comparamos las tasas de ocupación cruda con una ocupación ajustada para dos periodos de monitoreo (10 y 20 minutos). Las diferencias entre las tasas de ocupación cruda y ajustada fueron bajas aún para los periodos cortos de conteo, lo que sugiere que conteos largos estandarizados deben producir unos estimados confiables inclusive bajo la ausencia de corrección para un método apropiado. Esto incrementa el valor de programas pasados de monitoreo, en donde se utilizaron conteos largos estandarizados, pero con diseños que no permitieron la corrección de dichos estimados. Sin embargo, encontramos que la probabilidad de detección fue heterogénea para la mayoría de las especies y que la estructura de la vegetación es una fuente importante de heterogeneidad. El posible efecto del habitat, en la probabilidad de detección, debe ser de especial preocupación para proyectos de monitoreo a largo alcance, en escenarios en donde el hábitat varíe a través del espacio y tiempo.

Key words: bird detectability, count duration, detection probability, habitat, Mediterranean, sampling artifact, site occupancy

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Multispecies monitoring programs are increasingly used to assess the distribution of bird species and to understand factors that cause changes in communities. Such programs often use occurrence data gathered from point counts (Bailey *et al.* 2004, 2007). Occurrence data are of critical importance for conservation planning and their quality determines the validity of managers' decisions (MacKenzie and Royle 2005, Pellet and Schmidt 2005, MacKenzie *et al.* 2006). Recent large-scale declines in biodiversity stress the need for extensive and rigorous multispecies monitoring programs.

Monitoring programs often rely on raw occurrence counts and typically require two untested assumptions. First, each species is systematically detected when present at a location, that is, its detection probability is equal to one (Bailey *et al.* 2004, Kéry and Schmid 2004). Second, if the detection probability of a species is less than one, it is constant regardless of the sampling situation (Bailey *et al.* 2004, Kéry and Schmid 2004). Although these two assumptions remain largely untested, it is likely that most sampling methods do not allow perfect detection of a species when it is present (Thompson 2002, Royle and Nichols 2003) and detection probabilities may vary with the sampling situation (Bailey *et al.* 2004, Kéry and Schmid 2004, MacKenzie and Royle 2005). Uncorrected occupancy rate estimates could lead to sampling biases that confound potential biological effects and lead to inappropriate management decisions (Drapeau *et al.* 1999, Yoccoz *et al.* 2001, MacKenzie *et al.* 2002, MacKenzie and Royle 2005, MacKenzie *et al.* 2006).

The increased need for unbiased and reliable occupancy rate estimates encouraged the design of solutions to circumvent these shortcomings. A common intuitive, but partial, solution to deal with variation in detection probability caused by sampling variables independent from the sample location (e.g., time of the day, time of the season, and weather) was to standardize them (e.g., by restricting sampling to the early morning hours or to optimal weather conditions). This increases and homogenizes the probability of detection of a given species at a given location, but there is still some residual variability in sampling conditions that may bias occupancy rate estimates.

To deal with variables that depend on sample location characteristics, such as habitat, many investigators increased the duration of counts, with an increase in the potential number of de-

tections providing a more accurate characterization of populations (Drapeau *et al.* 1999). Using this approach, obtaining an unbiased occupancy probability for a given species requires the assumption that the species detection probability is similar for all sample locations where occupancy rate comparisons are made (Nichols *et al.* 2000). However, although many investigators assume that sampling variables have no influence on actual occupancy rate at a given location (Thompson 2002), little is known about the concomitant effect of the characteristics of the sample location on estimates of species detection probability and occupancy rate (Boulinier *et al.* 1998, Gu and Swihart 2004).

We tested the effectiveness of long count duration and of standardized sampling procedures in providing accurate occupancy rates even in the absence of correction. We took advantage of point-count surveys conducted in southern France and studied occupancy rates of 13 songbirds listed in the Bern Convention that ensures the conservation of European wildlife and natural habitats. Proper monitoring of these bird populations and their habitats should provide useful information on the dynamics of Mediterranean songbirds and improve management decisions (Sirami *et al.* 2007).

We used a standardized sampling design with sampling conducted at a series of locations in two types of habitats. Our objectives were to determine if (1) classic standardized songbird sampling procedures (restriction of sampling to early morning hours and avoiding steady rain and strong wind) are sufficient to homogenize detection probability of species, (2) habitat structure is a significant cause of heterogeneity in detection probability and, in particular, if species are more detectable in more vertically structured habitats (as suggested by Boulinier *et al.* 1998), and (3) corrected occupancy probabilities improve occupancy estimates, especially in longer counts.

METHODS

Principles and assumptions of site occupancy models. We used the MacKenzie *et al.* (2002) likelihood-based method to calculate corrected estimates of the proportion of sample locations occupied by a species when its detection probability is less than one. This method is based on an extension of the traditional

closed-population capture-recapture theory. Its estimation models assume that (1) sample locations are "closed" to changes in occupancy during the study, and (2) species are never detected by error at a sample location when actually absent. Species are analyzed separately, thus species-specific parameters can be estimated. Estimated parameters include ψ_i , the probability that a species is present at sample location i (occupancy probability), and p_{it} , the probability that a species is detected at sample location i at time t , given that it is present (detection probability). Both parameters may be expressed as the logit-link function of sample location-specific covariates (e.g., habitat) and in addition p_{it} may be expressed as the logit-link function of covariates of sampling occasion. This method also assumes no heterogeneity among sample locations in either ψ_i or p_{it} , except for those attributable to specified covariates. We used the PRESENCE software to fit the models described by MacKenzie et al. (2002) to our data.

Study area. Our study was conducted in southern France (ca. 43°47'N, 03°50'E). The study area covered 2800 ha located around Pic Saint Loup mountain and is part of a European network of protected areas (Sirami et al. 2007). The climate was Mediterranean, with moist cold winters (Debussche and Escarre 1983). Complex geology and topography together with a long history of human activity have resulted in a Mediterranean habitat mosaic composed of open habitats and woodlands (Preiss et al. 1997, Sirami et al. 2007). Open habitats are grasslands with shrubs, and the grassy layer is dominated by false brome (*Brachipodium retusum*), thinleaf false brome (*Brachipodium phoenicoides*), and erect brome (*Bromus erectus*). The shrub layer is dominated by cade juniper (*Juniperus oxycedrus*), aulaga (*Genista scorpius*), box tree (*Buxus sempervirens*), and rosemary (*Rosmarinus officinalis*). In the woodlands, holm oak (*Quercus ilex*) is the dominant tree species.

Bird surveys. Surveys consisted of a single visit to 199 locations. At each location, a 50-m-radius point-count was conducted and all birds seen or heard during a 20-min period were recorded. Each 20-min record was divided into four 5-min detection periods to provide presence-absence detection histories. Counts were conducted from 5 April to 26 June 2003 (by C. Sirami) in the absence of steady rain and strong wind (≤ 30 km/h) and restricted to the

4 h following sunrise (Bibby et al. 1992). To minimize disturbance caused by the observer's arrival, we waited 5 min before recording birds at each location. Because all species were territorial, we considered that detections of a species during the 5-min intervals were as independent as if detection occasions would have been conducted over different days.

We analyzed the effects of count duration for two count lengths (20 min and 10 min). For the latter, we used the first two 5-min periods of each count.

Sampling location variables and sampling conditions. Habitat requirements of birds are correlated with vegetation structure (MacArthur and MacArthur 1961, James and Wamer 1982). Survey locations were placed in two habitat categories, those with little vertical structure and those with complex vertical structure. Boulinier et al. (1998) suggested that this classification was relevant to test habitat influence on bird detection probability. Habitat structure was based on the vegetation structure in a 25-m radius around the point-count center. Visibility was impaired beyond this distance at most sites. For each location, we estimated the height at which the vegetation canopy had a cover exceeding 25% (principal canopy). We also estimated vegetation cover in the 2–4 m, 4–8 m, and 8–16 m layers. These layers were in geometrical progression based on the logarithmic functions found by Prodon and Lebreton (1981) to link bird species and vegetation structure variables. When the principal canopy was < 4 m and the sum of the three cover estimates $< 100\%$, we considered the habitat to have limited vertical vegetation structure. Otherwise, habitats were considered to have a marked vertical vegetation structure. This threshold was chosen based on Preiss et al.'s (1997) definition of habitat types in the study area. We used the two habitat categories as a categorical covariate *Habitat*.

At each location, wind velocity (*Wind*) was estimated with the help of a graduated scale (0, 10, 20, and 30 km/h) and cloud cover (*Cloud*) with the help a reference chart (Prodon and Lebreton 1981). Finally, the date (*Date*) and time (*Hour*) were also noted. All of these variables influence bird detection probabilities (Bibby et al. 1992). They were standardized and used as continuous covariates as required by MacKenzie et al.'s (2002) model.

Model definition and selection. To be consistent with MacKenzie et al. (2002), we modeled the occupancy probability (ψ) either as a function of *Habitat* or as a constant for all sample locations. We also modeled detection probability (p) as a function of *Wind*, *Cloud*, *Date*, *Hour*, or *Habitat*, as constant over sample locations or equal to 1. We tested the resulting 14 possible models. All models included intercepts for both ψ and p . We used the Akaike Information Criterion (AIC) to rank models. The best models do not necessarily represent all of the biological and environmental processes that influence ψ and p .

Parameter estimates. We computed Akaike weights to determine the strength of support for each model (Burnham and Anderson 1998). We performed model averaging (Burnham and Anderson 1998) to obtain occupancy probability, detection probability estimates, and the associated standard errors for the two sampling durations. We also report results of raw counts (observed ψ values) for the two sampling durations.

RESULTS

Model selection. Constant model ($\psi(.)$, $p(.)$) and variable dependent submodels were fitted to the data for all species. For all species, at least one model that ranked among the best equivalent models ($\Delta\text{AIC} < 2$) included the *Habitat* covariate in the ψ estimate for both sampling durations (Table 1), that is, habitat structure consistently explained a significant fraction of the variation in species distribution.

Most models that constrained p to equal 1 did not perform well compared to models that took into account heterogeneity and detection probabilities < 1 . Models including constant detection probability over sample locations ($p(.)$) were not ranked among the best models for eight of the 13 species using 20-min counts and for seven species using 10-min counts (Table 1). Moreover, when models that included constant detection probability over sample locations ($p(.)$) were ranked among best models, they were equal in terms of explanatory power ($\Delta\text{AIC} < 2$) to models that described heterogeneous p (Table 1). Most species exhibited heterogeneous detection probabilities among sample locations.

Our results confirmed that time of day could affect p , with six species having probabilities affected by the variable *Hour* in the 20-min counts and seven in the 10-min counts (Table 1). Sources of heterogeneity in detection probability varied among species.

For six of 13 species, detection probabilities were significantly affected by *Habitat* for both 20-min and 10-min counts (Table 1). Our results identified *Habitat* as one of the main sources of heterogeneity in p .

Detection probability estimates. For the 20-min counts, detection probability estimates varied among species from 0.28 for Short-toed Treecreepers (*Certhia brachydactyla*) to 0.97 for Nightingales (*Luscinia megarhynchos*) and, for the 10-min counts, from 0.20 to 0.98 for the same two species (Table 1). Depending on species, vertical vegetation structure had widely different effects on detection probability estimates, enhancing it for Blackcaps (*Sylvia atricapilla*), European Robins (*Erithacus rubecula*), Great Tits (*Parus major*), and Firecrests (*Regulus ignicapillus*) and diminishing it for Melodious Warblers (*Hippolais polyglotta*), Sardinian Warblers (*S. melanocephala*), European Blackbirds (*Turdus merula*), and Subalpine Warblers (*S. cantillans*; Fig. 1).

Occupancy probability estimates. Observed occupancy probabilities for the 13 species varied from 0.10 to 0.70 (Fig. 2). Maximum difference between estimated ψ value and observed ψ value reached 0.02 for Blue Tits (*Parus caeruleus*) when using 20-min sampling periods and 0.07 for European Blackbirds when using 10-min counts. For each of the 13 species, ψ estimates were more accurate for 20-min sampling periods than for 10-min sampling periods. $\text{SE}(\text{estimate})/\text{estimate}$ varied from 4% to 22% for ψ estimates based on 20-min sampling periods and from 5% to 36% for estimates based on 10-min sampling periods. Observed occupancy rates were close to the corrected values, especially for the 20-min counts, with the two values very similar for 10 of 13 species.

DISCUSSION

Most multispecies monitoring surveys that investigate species occupancy rates based on presence-absence data have relied on the assumption of constant proportionality between the actual number of sample locations where

Table 1. Model selection, detection probability estimates and standard error for the 13 species ($N = 199$ sample locations). For each species, the best equivalent models are in bold ($\Delta AIC < 2$). Estimated p result from model averaging performed using the best equivalent models. (A) 20-min sampling periods. (B) 10-min sampling periods.

A	Chaffinch ¹	Nightingale	Blackcap	European Blackbird	Subalpine Warbler	Sardinian Warbler	Firecrest	European Robin	Blue Tit	Melodious Warbler	Great Tit	Short-toed Treecreeper	Chirl Bunting ²
ΔAIC	308.6	366.0	176.1	15.8	219.0	34.0	39.4	181.2	6.8	78.9	12.1	24.5	19.7
$\psi(\cdot)$ and $p = 1$	19.3	7.6	25.8	9.3	23.7	5.9	9.3	26.5	8.7	23.2	2.2	9.2	7.3
$\psi(\cdot)p(\cdot)$	20.9	9.3	9.3	11.0	25.5	7.5	9.1	12.8	8.5	5.5	0.7	7.1	9.1
$\psi(\cdot)p(\text{habitat})$	10.5	8.9	26.7	5.7	21.7	7.3	8.5	19.8	8.9	25.2	2.1	10.3	9.0
$\psi(\cdot)p(\text{date})$	18.8	3.9	26.9	5.5	25.1	5.8	10.4	25.3	5.5	22.4	1.5	1.9	9.0
$\psi(\cdot)p(\text{hour})$	0.0	5.7	27.3	10.0	15.7	6.6	11.2	27.9	9.8	24.8	0.0	10.5	9.1
$\psi(\cdot)p(\text{cloud})$	18.8	0.0	27.7	8.9	25.4	7.6	11.1	28.0	7.5	19.8	1.5	11.1	7.6
$\psi(\cdot)p(\text{wind})$	310.5	366.5	166.5	11.3	203.3	28.1	30.8	168.3	2.4	61.5	13.2	22.9	14.6
$\psi(\text{habitat})p(\cdot)$	17.6	8.1	16.2	0.0	12.3	0.0	0.7	13.5	3.2	1.6	3.3	7.6	0.0
$\psi(\text{habitat})p(\text{habitat})$	22.9	9.8	0.0	6.8	9.7	1.7	0.9	0.0	4.7	0.0	2.0	5.8	4.0
$\psi(\text{habitat})p(\text{date})$	12.5	9.4	17.1	1.4	6.0	1.4	0.0	6.8	3.3	7.9	3.2	8.7	3.9
$\psi(\text{habitat})p(\text{hour})$	20.8	4.4	17.2	1.1	9.4	0.0	1.7	12.3	0.0	5.0	2.6	0.0	3.9
$\psi(\text{habitat})p(\text{cloud})$	1.9	6.2	17.7	5.5	0.0	0.7	2.6	14.9	4.3	7.4	1.0	8.8	4.0
$\psi(\text{habitat})p(\text{wind})$	20.8	0.5	18.1	4.7	9.7	1.7	2.4	15.0	2.0	2.4	2.6	9.5	2.5
Detection probability	0.79	0.97	0.70	0.57	0.91	0.69	0.68	0.74	0.34	0.78	0.58	0.29	0.72
Estimated p	0.03	0.12	0.04	0.03	0.08	0.05	0.04	0.05	0.05	0.04	0.04	0.07	0.02

Continued.

Table 1. Continued.

B	European Subalpine										Girl Bunting		
	Chaffinch	Nightingale	Blackcap	Blackbird	Warbler	Sardinian Warbler	Firecrest	Robin	Blue Tit	Melodious Warbler		Great Tit	Short-toed Treecreeper
ΔAIC													
$\psi(\cdot)$ and $p = 1$	138.5	176.8	88.7	8.2	99.2	14.1	28.3	95.2	9.5	48.8	6.2	19.1	11.4
$\psi(\cdot)p(\cdot)$	3.3	2.7	21.6	4.5	8.9	2.6	5.2	22.2	7.4	22.6	1.2	11.4	6.4
$\psi(\cdot)p(\text{habitat})$	5.1	4.7	8.3	6.5	9.1	3.3	4.4	10.6	2.9	0	2.7	10.7	6.8
$\psi(\cdot)p(\text{date})$	3.2	4.7	23.6	4.2	7.8	4.6	7	19.4	9.3	24.5	0.3	10.9	5.3
$\psi(\cdot)p(\text{hour})$	4.6	2	22.8	2.9	9.3	2.1	7	23.9	1.6	24.5	1.7	2.3	8.4
$\psi(\cdot)p(\text{cloud})$	0	4.5	22	5.9	7.7	2	6.6	24.2	9.3	22.8	2.3	11.1	7.9
$\psi(\cdot)p(\text{wind})$	5.3	0	20.6	6.2	10.5	4.3	7	24	7.3	23.8	2.1	13.2	8.1
$\psi(\text{habitat})$ and $p = 1$	140.5	178.8	75.2	5.1	91.4	12.1	23	82	7.1	31.3	6	17.3	6.3
$\psi(\text{habitat})p(\cdot)$	4.7	3.2	8.1	1.4	1.1	0.6	0	9	4.9	5.2	1.1	9.6	1.3
$\psi(\text{habitat})p(\text{habitat})$	6.4	5.2	0	1.6	1.9	2.3	0.9	0	4.1	2	2.9	10.2	3.3
$\psi(\text{habitat})p(\text{date})$	4.6	5.2	10	1.3	0	2.6	1.8	6.3	6.9	7.1	0	9.1	0
$\psi(\text{habitat})p(\text{hour})$	6	2.5	9.1	0	1.5	0.2	1.8	10.7	0	7.1	1.5	0	3.3
$\psi(\text{habitat})p(\text{cloud})$	1.4	4.9	8.3	2.7	0	0	1.3	11	6.9	5.4	1.9	8.9	2.9
$\psi(\text{habitat})p(\text{wind})$	6.7	0.5	6.2	3	2.7	2.3	1.8	10.8	4.9	6.7	2	11.4	3.1
Detection probability													
Estimated p	0.84	0.98	0.72	0.60	0.93	0.77	0.78	0.78	0.28	0.97	0.50	0.20	0.91
SE(p)	0.06	0.27	0.08	0.07	0.12	0.07	0.08	0.10	0.08	0.22	0.08	0.09	0.08

¹ *Fringilla coelebs*.

² *Emberiza citrinus*.

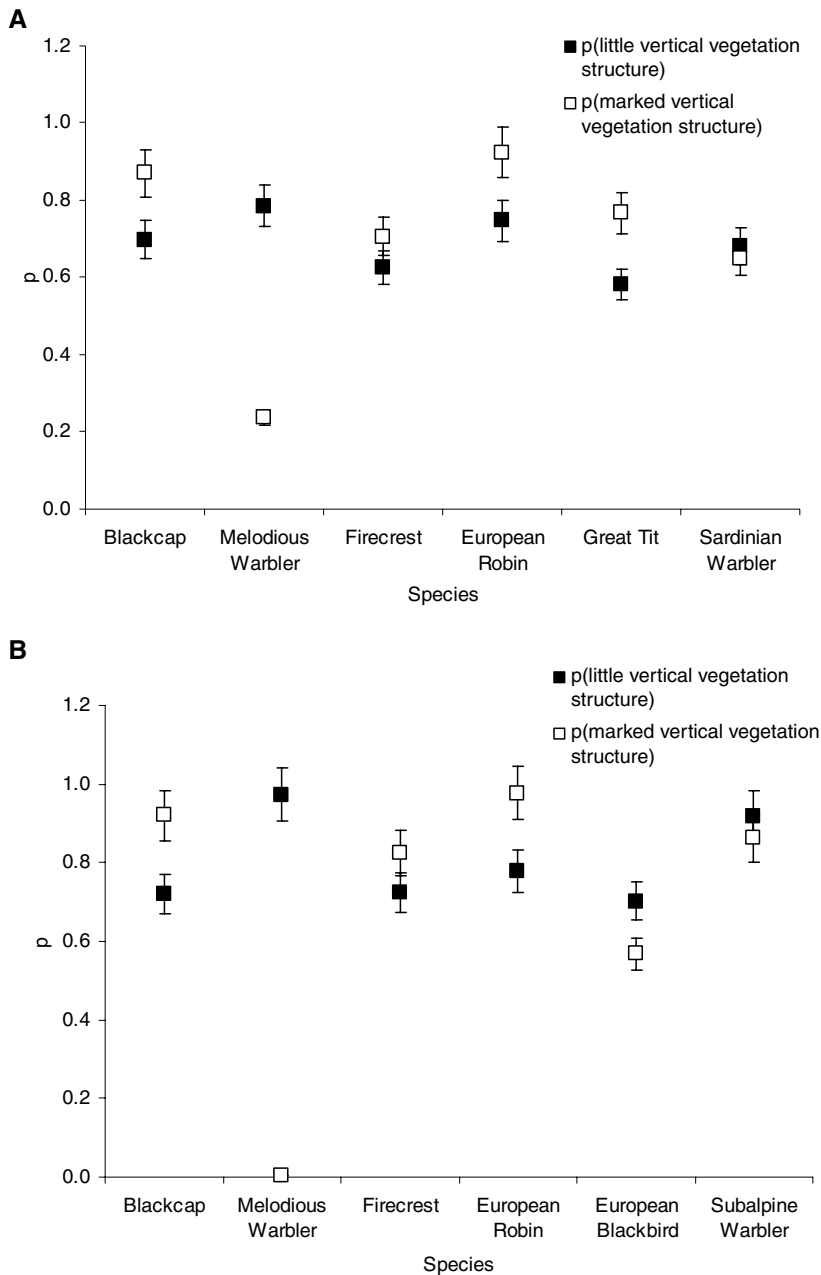


Fig. 1. Estimated (\pm SE) detection probability relative to vertical vegetation structure for species where p depends on habitat. Estimates are computed using $[\psi(\text{habitat})p(\text{habitat})]$ model when ΔAIC of this model is < 2 . (A) 20-min sampling periods. (B) 10-min sampling periods.

the species was present and the number of sample locations where the species was detected. The validity of this assumption of proportionality has been questioned for decades (Burnham

1981, Boulinier et al. 1998, Thompson 2002). Capture-mark-recapture methods have been developed to provide less biased estimates in population biology. Nevertheless, they are seldom

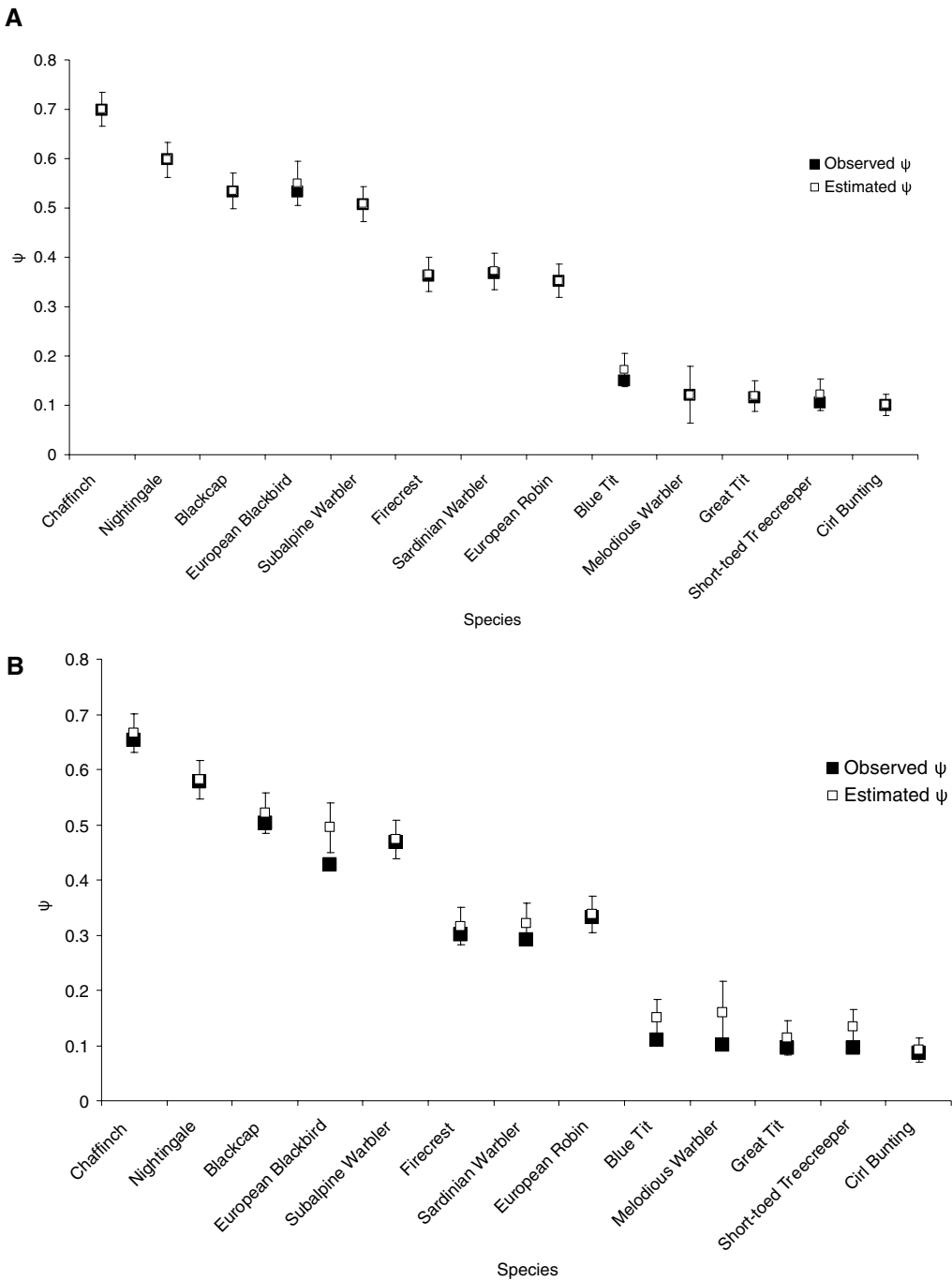


Fig. 2. Estimated (\pm SE) and observed species occupancy probabilities. Estimates are computed using model averaging for species-specific models with the lowest AIC values (Δ AIC < 2). (A) 20-min sampling periods. (B) 10-min sampling periods.

used for multispecies monitoring programs because they are more expensive and less practical than presence-absence data. We took advantage of the availability of a method based on presence-absence data and that has been shown to provide a realistic alternative to more costly methods (MacKenzie et al. 2002, MacKenzie et al. 2006) to test this assumption in a Mediterranean bird community.

Our results show that when standardized bird census point counts are used, expected and observed occupancy rates are very similar, especially for 20-min long counts. Substantial differences were observed only for Short-toed Treecreepers (ψ underestimated by 19%), a species that is not very conspicuous, and Blue Tits (ψ underestimated by 14%). Although our results confirmed that raw values of occupancy rate obtained from long counts (20 min) provided better estimates than those from shorter counts (10 min), the corrections did not affect occupancy rates. Such similarity in the corrected and uncorrected estimates could be an artifact attributable to a weak parameterization of the tested models caused either by a low number of sampling occasions per site or by a lack of independence in successive subsamples, especially for the time-variable covariates. Such weaknesses could affect the accuracy and precision of ψ estimate (MacKenzie et al. 2006). Our sampling design followed the recommendation of Mackenzie and Royle (2005). In particular, our four sampling opportunities exceeded the minimum of three suggested by MacKenzie et al. (2002) for detection probability > 0.5 . Our relatively long sampling periods (4×5 min) relative to the frequency of singing by songbirds during the breeding season, the 5-min wait before the onset of counting, and the high detection probabilities for most species are, therefore, more likely to explain the good estimates of occupancy rate obtained in the absence of correction for detection probability than faulty model parameterization. Thus, the usual and trivial solution of conducting long counts to increase the number of detection opportunities together with rigorous standardization of sampling procedures provide good occupancy rate estimates in situations where correction by an appropriate method is not feasible.

Our results also show that heterogeneity of detection probability may be the rule for many bird species in our Mediterranean community. Models that included detection probability that

took into account the effects of covariates were better than models that assumed constant detection probability for most species. However, we also found substantial differences between 20-min and 10-min counts in best equivalent models for species such as Blue Tits, Melodious Warblers, Great Tits, or Short-toed Treecreepers, suggesting some instability in parameter estimates. Existence of colinearity between some covariates might influence parameter estimates. At the very least, these results highlight the need to evaluate the risk of bias caused by heterogeneity of detection probability across time and space, and point to the need to take it into account. To deal with the problem of varying detection probabilities, most monitoring programs attempt to standardize sampling conditions to maximize and homogenize species detection probability (Thompson 2002). Our results show that classical standardization of bird studies does not completely control for variation caused by weather, time of day, or season (see also Drapeau et al. 1999). Moreover, standardization does not allow consideration of variables that depend on the features of sample locations (like habitat) in the estimation of detection probability. MacKenzie et al.'s (2002) method deals simultaneously with these problems by taking into account heterogeneity in detection probability among sample locations caused by the specified covariates. However, it must be emphasized that using this method requires that potential sources of heterogeneity in detection probability must be defined *a priori* to make corrections of observed data study specific. Because most wide-scale monitoring programs involve multiple observers, a major source of heterogeneity will also result from observer effect and protocols should be designed in ways that correct for it (MacKenzie and Royle 2005).

We found that detection probability depended on habitat structure for some bird species. In a study of small mammals, Gu and Swihart (2004) also found that detectability was related to the habitat characteristic of the site. The imperfect detection of a species has important consequences for habitat models (MacKenzie and Royle 2005). In studies of species-habitat relationships, sampling effects on naïve estimates (resulting from raw counts) of occupancy rate caused by habitat can be more confounding than biases caused by covariates that are independent from the characteristics of

the sample location. Observed changes in naïve estimates of occupancy rate that are *a priori* explained by habitat structure could partly result from changes in species detection probability linked to changes in habitat structure. Models based on habitat structure with no consideration for detection probability could yield erroneous predictions of a species' response to habitat change (Gu and Swihart 2004, MacKenzie and Royle 2005). As a result, studies of species-habitat relationships should not only include detection probability in the models, but should also account for the dependence of detection probability on habitat structure with a proper sampling design. Understanding the relationship between detection probability and spatial and temporal changes in habitat structure becomes even more critical for long-term studies where changes in communities due to changes in land use are being assessed (Yoccoz et al. 2001). The increased use of presence-absence data when making decisions about habitat conservation and management, especially for diachronic studies, emphasizes the need for proper evaluation of the performance of habitat-based occupancy models (Gu and Swihart 2004).

The importance of habitat as a determinant of detection probability could be explained by the effects of habitat structure on bird behavior and observer perception. In our study, Blackcaps, European Robins, Great Tits, and Firecrests had higher detection probabilities in habitats with highly structured vegetation, a result consistent with Boulinier et al.'s (1998) hypothesis that species detection probabilities were greater in dense landscapes than open ones because the risk of predation is reduced by dense cover and, consequently, birds are more conspicuous. These species are typically associated with forest habitat and, to estimate the real difference of their occupancy rates between forest and other habitats, differences in detection probability between these habitats must be taken into account. Not doing so may lead to an overestimation of occupancy in forest habitat and underestimation in other habitats. Similarly, species associated with scrublands (Melodious Warbler, Sardinian Warbler, and Subalpine Warbler) had higher detection probabilities in locations with less vegetation structure, perhaps because these species might be observed more easily in these habitats than in forested habitats where detection relies on songs or calls. If this difference is not taken

into account, occupancy in scrublands may be overestimated and occupancy in other habitats underestimated.

We found that correction with MacKenzie et al.'s (2002) method may not always be essential to obtain good estimates of occupancy rate, especially when counts are long and detection probabilities high. However, classical standardization of bird surveys may not always be sufficient to homogenize detection probabilities, and detection probabilities of birds often depend on site-specific variables (e.g., habitat). Variation in detection probability may confound potential biological effects on occupancy rate and lead to inappropriate management decisions. To conclude, for multispecies monitoring programs, we recommend conducting long counts and evaluating the risk of bias using MacKenzie et al.'s (2002) method for at least a representative sample of the study sites.

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