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Does time of season influence bird species number determined from point-count data? A capture-recapture approach

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ABSTRACT. We investigated the effect of time of season on the accuracy of species number estimation from point-count data collected at 28 oases from southern Tunisia. Each oasis was visited at the beginning of the breeding season and two months later, which allowed us to conduct counts on five points per oasis per visit. For each oasis, we considered the observed species number as the total number of species recorded during each visit, and we used a capture-recapture approach to estimate species number from patterns of presence and absence of species over the five points. We found that birds were more detectable at the beginning of the breeding season than two months later, and the observed species number showed a significant decrease between the two periods. However, when a capture-recapture approach accounting for heterogeneity in species detectability was used, similar estimates were obtained from data collected during both periods. Nonetheless, the estimates obtained at the beginning of the breeding season were more precise than those obtained later. Overall, our results illustrate once more the need of taking into account time of season as an important source of bias when attempting to determine species richness from count data, and stress the need for using probabilistic approaches in such an investigation.

SINOPSIS. **¿Afecta el momento de la temporada el número de especies de aves determinado por datos de conteos de puntos? Un acercamiento basado en captura-recaptura**

Se investigó el efecto del momento de la temporada en la precisión del estimado de especies a través de conteos de puntos colectados en 28 oasis del sur de Túnez. Se visitó cada oasis al principio y al final de la época reproductiva y dos meses después, lo que nos permitió conducir cinco conteos de puntos por oasis por visita. Para cada oasis consideramos el número observado de especies como el número total de especies registrados en cada visita, y se utilizó el acercamiento de captura-recaptura para estimar el número de especie en base a los patrones de presencia y ausencia de especie a través de los cinco puntos. Hallamos que las aves fueron más detectables al principio de la época reproductiva que dos meses después, y el número observado de especies mostró una reducción significativa entre los dos períodos. Sin embargo, al utilizar un anális de captura-recaptura ejustado para la heterogeneidad en detectabilidad de especies, estimados similares se obtuvieron de datos colectados durante ambos períodos. Sin embargo, los estimados obtenidos al principio de la época reproductiva fueron más precisos que los obtenidos después. En general, nuestros resultados ilustran otra vez la necesidad de tomar en cuenta el momento de la temporada como una fuente importante de vicio al intentar determinar la riqueza de especies de datos de conteos, y refuerzan la necesidad de usar acercamientos probabilísticos en ese tipo de investigación.

Key words: bird communities, detection probability, population monitoring, species diversity, Tunisia

The point-count method is one of the most popular bird survey techniques. It has been increasingly used in a wide range of bird studies and for a variety of purposes, for instance for monitoring bird populations (e.g., Robbins et al. 1989; Ralph et al. 1995) and for investigating the relationships between habitat characteristics and various parameters of bird communities (e.g., Enoksson et al. 1995; Schiek et al. 1995; Riffel et al. 1996). However, it has been repeatedly demonstrated that point count results are subject to variation due to the effects of many factors such as count duration, time of day, and time of season (e.g., Ralph and Scott 1981; Drapeau et al. 1999; Bibby et al. 2000).

With regard to the effect of time of season, the ornithological literature often comments on variation in survey results during the breeding season. Most investigations have been, nevertheless, conducted at the level of individual species, and it is now commonly argued that the earlier the survey, the higher is the detection

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probability of a single species because vocalizations are more intense and frequent when territories are not yet established. The results of these investigations have been used to refine the use of point counts to increase the detection probability of individual species (Blondel et al. 1970; International Bird Census Committee 1977; Best 1981; Ralph 1981; Skirvin 1981; Wilson and Bart 1985; Gutz-willer 1993). However, little attention has been given to the effect of time of season on the detection probability at the level of the community or species assemblage and on its possible effect on the estimation of community parameters (but see Blondel et al. 1970; International Bird Census Committee 1977; Gutzwiller 1991; Drapeau et al. 1999). This issue is important because community level parameters are of particular interest for basic ecology and conservation issues. In this context, one could expect the time of season to affect our ability to determine the number of species in a bird assemblage from point-count data. In other words, the mean bird detection probability can be expected to decrease with the progress in the breeding season, and estimates of species richness derived from point-count data collected late in the breeding season may be biased and/or less precise than those obtained at the beginning of the breeding season.

Here, we test this prediction by using results of point counts conducted at Tunisian oases at the beginning of the breeding season and again two months later. We used a capture-recapture approach (Burnham and Overton 1978, 1979; Nichols and Conroy 1996) to estimate species number from patterns of detection and non-detection of species in each oasis during each sampling period and to calculate the corresponding mean detection probability. We investigated variation in observed and estimated species numbers, and we compared bird detection probability between the two sampling periods. Finally, we used the results to explore the effect of time of season on bird detectability and on the accuracy of species richness estimates.

STUDY AREAS AND METHODS

Study sites were 28 isolated oases in southern Tunisia. In these oases, resident bird species start breeding from mid-February onwards (Selmi 2000), and bird detection probability is very high because of the simple vegetation structure and the low number of species (Selmi et al. 2001; Selmi and Boulinier 2003). During the breeding season of 1999, each oasis was visited twice, with approximately a two-month interval between visits. Each series of visits was spread over approximately one month: from 24 February to 27 March for the first series of visits and from 28 April to 3 June for the second. In each oasis, five points were retained and mapped for conducting counts during both visits. Points were carefully selected to be surrounded by a vegetation representative of the oasis habitat, including the three different layers characterizing the oasis habitat (palm trees, fruit trees, and herbaceous vegetation), and to be located at least 250 m from one another and from the oasis edge. Points situated in the same oasis were visited during the same morning and in a predetermined sequence. Counts started 30 min after sunrise and were spaced by 10-min intervals. In order to maximize the chance of detecting birds, we followed Blondel et al. (1970) and conducted counts of 20 min, which are among the longest counts used by ornithologists (see Blondel et al. 1970; International Bird Census Committee 1977). Moreover, counts were conducted only under optimal meteorological conditions, and during each count the observer recorded all birds heard or seen in the surroundings at unlimited distances (Blondel et al. 1970, 1981). All counts were conducted by the same observer (S. Selmi) in order to avoid a possible observer effect on survey results.

Data were summarized in five lists of records of species presence/absence for each sampled oasis at each visit. These lists were used to obtain the observed and the estimated species numbers for each oasis at each visit. The observed species number (R) is a cumulative parameter and corresponds to the total number of recorded species. The estimated species number ($\hat{N}$) was estimated on the basis of patterns of detection/non-detection of species in the five points, using a capture-recapture approach (Burnham and Overton 1978, 1979). The estimates were computed using the jackknife estimator associated with model M_h (Burnham and Overton 1978, 1979), which makes the assumption of heterogeneous detection probability among species. Application of this estimator to point-count data for species richness and detection probability estimation is described and justified by Boulinier et al. (1998). The basic parameters used by the jackknife estimator to estimate the average species number (and average detection probability) of a "closed" community from counts carried out on a series of sites/occasions are the observed frequencies of detections ($f_{(i)}$), i.e., the number of species detected at exactly *i* sites/occasions (Burnham and Overton 1979). Using the jackknife procedure, the estimated species number may tend to the observed species number (detection probability may tend to 1) when no species is recorded in a low number of counts ($f_{(i)}$ tend to 0 for low *i*) and most species are detected during all counts ($f_{(n)}$ tend to R, with *n* the total number of counts). We used computer program COMDYN (Hines et al. 1999), which implements a procedure of selecting an interpolated estimator from the series of jackknife estimators of different orders (see Burnham and Overton 1978, 1979) and provides the corresponding estimates. It also provides a χ^2 test of goodness-of-fit of the M_h model to data (Hines et al. 1999).

In order to assess the potential change in observed species number (R), estimated species number ($\hat{N}$), and mean estimated detection probability ($\hat{P}$) between the two sampling periods, we used Wilcoxon signed-rank tests for matched pairs. The use of this nonparametric procedure was justified by the lack of normality in our data. Analyses were carried out with the SAS statistical package (SAS Institute 1998).

RESULTS

The sampled bird communities included low numbers of species. Only 13 resident breeding bird species were recorded in the entire oasis sample (Table 1). Using the raw data (Table 2), we found a significant difference in the number of records between the two visits for four of the 13 species (Table 3), suggesting that the detectability of these species was higher at the beginning of the breeding season than two months later. The observed number of species (R) per oasis varied from six to eight during the first visit and from five to eight during the second visit (Table 4). In seven oases (25% of sampled oases), there was a change in the observed species number between the two visits (Table 4). One to two species from those recorded during the first visit were missed during the second visit, under the hypothesis of closed communities (Tables 2, 4). Overall, a significant difference in observed species number between the two visits was found (Wilcoxon test, $N = 7$, $S = 14$, $P = 0.0156$), suggesting that the observed species number did not seem to provide an accurate measure of species number, and that it could be negatively biased when using data collected late in the breeding season.

Table 1. List of early-nesting resident bird species recorded at southern Tunisian oases.

Common name	Scientific name
Barbary Partridge	*Alectoris barbara*
Palm Dove	*Streptopelia senegalensis*
Hoopoe	*Upupa epops*
Crested Lark	*Galerida cristata*
Blackbird	*Turdus merula*
Fan-tailed Warbler	*Cisticola juncidis*
Fulvous Babbler	*Turdoides fulvus*
Blue Tit	*Parus caeruleus*
Great Grey Shrike	*Lanius excubitor*
House Sparrow	*Passer domesticus*
Chaffinch	*Fringilla coelebs*
Serin	*Serinus serinus*
House Bunting	*Emberiza striolata*

With regard to species richness estimation, the M_h model provided a good model for species richness estimation (χ^2 goodness-of-fit test; $P > 0.05$ in all oases). Using this model, we found that the estimated species number ($\hat{N}$) per oasis varied from six to eight during the first visit, and from five to 9.6 during the second visit (Table 4). However, there was no difference between the two visits in estimated species number (Wilcoxon test, $N = 19$, $S = -14$, $P = 0.5779$). This suggests that the capture-recapture approach allowed us to obtain similar estimates from both types of data. Thus, when a capture-recapture approach was used, the species number estimated from data collected late in the breeding season was not biased compared to that estimated from data collected much earlier. Nevertheless, there was a significant difference in the standard errors associated with the estimates (Wilcoxon test, $N = 14$, $S = -52.5$, $P = 0.0001$), showing that the estimates obtained by using data from the first visit were more precise than those obtained from data collected at the second visit.

Table 2. Number of records of each of the 13 species recorded during the two visits (V1 and V2) at each of the 28 sampled oases.

	A. barbara		*S. senegalensis*		*U. epops*		*G. cristata*		*T. merula*		*C. juncidis*		*T. fulvus*		*P. caeruleus*		*L. excubitor*		*P. domesticus*		*F. coelebs*		*S. serinus*		*E. striolata*	
Oasis	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2
1	0	0	5	5	5	2	0	0	4	1	4	5	0	0	0	0	0	0	5	5	5	5	5	5	4	2
2	0	0	5	5	5	3	0	0	4	2	5	1	0	0	0	0	0	0	5	5	5	5	5	4	5	3
3	0	0	5	5	4	2	0	0	3	0	5	5	0	0	0	0	0	0	5	5	5	5	5	5	5	3
4	0	0	5	5	5	4	0	0	4	3	5	5	0	0	0	0	0	0	5	5	4	3	5	5	5	5
5	0	0	5	5	5	5	0	0	5	2	5	4	0	0	0	0	0	0	5	5	3	4	5	4	5	5
6	0	0	5	5	4	1	0	0	4	2	0	0	0	0	0	0	0	0	5	5	5	5	5	3	5	4
7	0	0	5	5	5	2	0	0	0	0	5	5	0	0	0	0	0	0	5	5	5	5	5	2	4	0
8	0	0	5	5	5	5	0	0	5	5	0	0	0	0	0	0	0	0	5	5	5	5	5	5	4	1
9	0	0	5	5	5	2	0	0	5	5	4	5	0	0	0	0	0	0	5	5	5	5	5	5	2	2
10	0	0	5	5	4	3	0	0	5	5	0	0	0	0	0	0	0	0	5	5	5	5	5	5	5	2
11	0	0	5	5	4	5	0	0	5	4	0	0	0	0	0	0	0	0	5	5	5	5	5	5	5	2
12	0	0	5	5	5	5	0	0	2	0	0	0	0	0	0	0	0	0	5	5	5	4	5	2	5	5
13	0	0	5	5	5	2	0	0	5	3	5	5	0	0	0	0	0	0	5	5	5	5	5	5	2	1
14	0	0	5	5	4	1	0	0	3	0	5	3	0	0	0	0	0	0	5	5	5	5	5	5	4	0
15	0	0	5	5	2	1	0	0	2	1	4	5	0	0	0	0	0	0	5	5	5	5	5	3	3	0
16	0	0	5	5	5	2	0	0	2	2	0	0	0	0	2	2	0	0	5	5	5	5	5	5	5	4
17	0	0	5	5	3	1	0	0	4	1	0	0	0	0	3	3	0	0	5	5	5	5	5	5	5	3
18	0	0	5	5	4	2	0	0	4	2	0	0	0	0	3	4	0	0	5	5	5	5	4	5	5	5
19	0	0	5	5	4	1	0	0	4	1	0	0	0	0	3	3	0	0	5	5	5	5	5	5	4	2
20	0	0	5	5	5	1	0	0	5	4	0	0	0	0	4	4	0	0	5	5	4	5	5	4	5	2
21	0	0	5	5	4	1	0	0	4	2	0	0	0	0	0	0	0	0	5	5	0	0	5	5	5	1
22	0	0	5	5	3	2	0	0	5	4	0	0	0	0	5	5	0	0	5	5	0	0	5	1	5	5
23	0	0	5	5	3	3	0	0	0	0	0	0	0	0	3	3	0	0	5	5	0	0	5	4	5	5
24	0	0	5	5	3	1	0	0	0	0	0	0	0	0	5	5	0	0	5	5	0	0	4	2	5	5
25	0	0	5	5	4	1	0	0	0	0	0	0	0	0	3	1	0	0	5	5	0	0	5	2	5	5
26	0	0	5	5	4	0	0	0	0	0	5	5	0	0	5	5	0	0	5	5	0	0	0	0	5	5
27	0	0	5	5	4	0	5	5	0	0	5	5	5	5	0	0	5	5	4	3	0	0	0	0	0	0
28	4	1	5	5	4	4	5	5	0	0	0	0	5	4	0	0	5	4	3	4	0	0	0	0	0	0

Table 3. Results of Wilcoxon rank sum tests for the difference between the two visits in the number of counts during which each species was recorded (total number of counts per oasis, 5). For each species, the sample size (*N*) is the number of oases where the difference between the two visits was non-zero.

Species	*N*	S	*P*
Alectoris barbara	1	0.5	1.000
Streptopelia senegalensis	0	—	—
Upupa epops	23	135	0.0001
Galerida cristata	0	—	—
Turdus merula	17	76.5	0.0001
Cisticola juncidis	6	3	0.6563
Turdoides fulvus	1	0.5	1.000
Parus caeruleus	6	5.5	0.3438
Lanius excubitor	0	—	—
Passer domesticus	2	0	1.0000
Fringilla coelebs	4	0	1.0000
Serinus serinus	12	36	0.0029
Emberiza striolata	16	68	0.0001

This difference in precision of the estimates is likely related to the decrease in mean detection probability between the two visits. Indeed, even though the mean detection probability was high during both visits at all oases, it differed between the two visits (Table 4). For instance, considering only data from oases where the observed species number was unchanged (R1 = R2) and for which the same species assemblages were detected during both visits, we found that the detection probability was significantly higher at the beginning of the breeding season than two months later (Wilcoxon test, $N = 12$, $S = 39$, $P = 0.0005$).

With regard to oases 3, 7, 12, 26 and 27, the observed species number was lower during the second visit than during the first visit (R2 < R1). But during each of both visits almost all species that were recorded on at least a single point were actually recorded on all points, and thus only a few species were recorded on a low number of points. That is why when using the jackknife estimator, the estimated species number was equal to the observed species number for both visits ($\hat{N}1$ = R1 and $\hat{N}2$ = R2). This led to an estimated detection probability equal to 1 for both visits ($\hat{P}1 = \hat{P}2 = 1$), despite the decrease in the observed and estimated species numbers between both visits. These results are due to the structure of our data and to the properties of the jackknife estimator. Using the jackknife, the calculation of $\hat{P}$ for both visits does not take into account the rate of change in R and $\hat{N}$. Each of both probabilities represents the mean detection probability of the species with a non-zero probability of being detected ("detectable" species). The jackknife es-

Table 4. Changes in observed (R) and estimated ($\hat{N}$) species number and in detection probability ($\hat{P}$) between the two visits. The values of detection probability estimates of 1 with SE of 0 are due to the properties of the estimation procedure and to the structure of our data (see text).

Oasis	R1	R2	$\hat{N}1$ (± SE)	$\hat{N}2$ (± SE)	$\hat{P}1$ (± SE)	$\hat{P}2$ (± SE)
1	8	8	8.00 ± 0.00	8.80 ± 0.72	1 ± 0.00	0.9091 ± 0.0714
2	8	8	8.00 ± 0.00	8.80 ± 1.06	1 ± 0.00	0.9091 ± 0.0867
3	8	7	8.00 ± 0.00	7.00 ± 0.00	1 ± 0.00	1 ± 0.0000
4	7	7	7.00 ± 0.00	7.80 ± 1.00	1 ± 0.00	0.8974 ± 0.0904
5	8	8	8.00 ± 0.00	8.00 ± 0.00	1 ± 0.00	1 ± 0.0000
6	8	8	8.00 ± 0.00	8.00 ± 0.00	1 ± 0.00	1 ± 0.0000
7	7	6	7.00 ± 0.00	6.00 ± 0.00	1 ± 0.00	1 ± 0.0000
8	7	7	7.00 ± 0.00	7.80 ± 1.45	1 ± 0.00	0.8974 ± 0.1141
9	8	8	8.00 ± 0.00	8.00 ± 0.00	1 ± 0.00	1 ± 0.0000
10	7	7	7.00 ± 0.00	7.00 ± 0.00	1 ± 0.00	1 ± 0.0000
11	7	7	7.00 ± 0.00	7.00 ± 0.00	1 ± 0.00	1 ± 0.0000
12	7	6	7.00 ± 0.00	6.00 ± 0.00	1 ± 0.00	1 ± 0.0000
13	8	8	8.00 ± 0.00	8.80 ± 1.00	1 ± 0.00	0.9091 ± 0.0850
14	8	6	8.00 ± 0.00	6.80 ± 1.39	1 ± 0.00	0.8824 ± 0.1206
15	8	7	8.00 ± 0.00	8.60 ± 3.26	1 ± 0.00	0.8140 ± 0.1967
16	8	8	8.00 ± 0.00	8.00 ± 0.00	1 ± 0.00	1 ± 0.0000
17	8	8	8.00 ± 0.00	8.00 ± 0.00	1 ± 0.00	1 ± 0.0000
18	8	8	8.00 ± 0.00	8.00 ± 0.00	1 ± 0.00	1 ± 0.0000

timates $\hat{N}$ and $\hat{P}$ from the observed frequencies of detection of species for each sample. The low total number of species in each oasis, with most species highly detectable but a few becoming nondetectable later in the season, thus contributes to these results.

DISCUSSION

Our results suggest that the detection probability of early-nesting resident bird species at southern Tunisian oases was very high at the beginning of the breeding season as well as two months later. This high detection probability might be related to good conditions for field works within oases and also to the duration of the point counts conducted. However, despite this high detection probability and as predicted, we found that advancement of the breeding season was associated with a decrease in the detectability of resident bird species, resulting in a decrease in our ability to correctly estimate species richness from point-count data. Our results point out three main conclusions.

First, resident bird species were more detectable at the beginning of the breeding season than two months later, and hence the accuracy of bird surveys using the point-count method in the oasis habitat was higher at the beginning of the breeding season than at the middle of the breeding season. We point out that such a result was obtained in a relatively simple system where bird detectability is very high because of the high visibility within oases, the low number of species, and the high abundance of local populations. The use of counts of 20 min may also have contributed to such a result. Therefore, we expect greater differences in the estimates and in the precision associated with the estimates between different sampling periods in systems where bird richness is higher and detection probability is lower than in oasis habitat (e.g., in temperate or tropical forests) or when using shorter counts.

Second, based on the raw data, there was a drop in the observed species number between the two visits, as some species were missed at some oases during the second visit. These species were unlikely to become locally extinct over the period of the study. For instance, in a related work we used mist nets for bird capture, which revealed the existence of these species at the oases where they had not been recorded by point counts. Thus, one should conduct counts early in the breeding season if one wants to use the observed species number as a measure of species richness of breeding bird communities.

Third, using a capture-recapture approach, we obtained similar estimates from both types of data. However, due to the decrease in mean detection probability with the advancement of the breeding season, estimates obtained from data collected at the beginning of the breeding season were more precise than those from later. So, even when a capture-recapture approach is used to estimate species number from count data, one should conduct counts at the beginning of the breeding season if the aim is to optimize the precision of the estimates.

Our results stress once more the need for considering seasonal variation in detection probability when investigating the dynamics of bird communities and their responses to environmental changes. This may be of particular significance in communities composed of species with different breeding phenologies, for example, when resident birds start breeding much earlier than migratory ones, as was the case at southern Tunisian oases. In such cases, using the number of bird species recorded from count data collected after the arrival of migratory species as a measure of species richness of the entire community is likely to give particularly biased results. Early-nesting resident birds will be less detectable than migratory ones. A point-count method specifically designed to reduce such a bias is available, the IPA method (Blondel et al. 1970, 1981). This method consists of doing two counts at the same point but at two different times of the breeding season, the beginning of the breeding season for resident species and after the settlement of migratory species. The cumulative list of species recorded during both visits is retained for each point and used to measure species richness of the community based on the total number of recorded species in each locality.

However, it has been argued that patterns of changes in detections through time of season vary among species (Skirvin 1981). For instance, the number of broods per season and the mating system (monogamous or polygamous) have been shown to affect song phenology, which may lead to different patterns of seasonal variation in detection probabilities among different species (Wilson and Bart

1985). Therefore, even at the beginning of the breeding season, the species-specific differences in detectability should also be considered when the objective is to determine the species richness of a community.

These considerations and the results of our study emphasize that factors affecting bird detectability are so complex that it may be rare to detect all species and to obtain a reasonable measure of species richness by relying simply on the total number of recorded species. There is a need to use probabilistic estimators that take into account heterogeneity in detection probability among species and thus allow the estimation of species number regardless of the source of any heterogeneity. The high flexibility of the capture-recapture approach (Nichols and Conroy 1996; Nichols et al. 1998a,b; Nichols et al. 2000) makes it particularly useful for such investigations. For example, the IPA method (Blondel et al. 1970, 1981) can be used with a capture-recapture framework to account for time of season and to obtain more accurate estimates of bird community parameters. This may be relatively expensive in terms of manpower and time, but it should increase the reliability of inferences about bird community parameters. Comparable methods can be implemented to infer abundance estimates of different bird species from point-count data (Farnsworth et al. 2002).

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