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Distribution-abundance relationship for passerines breeding in Tunisian oases: test of the sampling hypothesis

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Abstract The positive relationship between local abundance and distribution of species is a widely recognized pattern in community ecology. However, it has been suggested that this relationship can simply be an artefact of sampling because locally rare species are less detectable then locally abundant ones, and hence their distribution can easily be underestimated. Here, we use count data to investigate the relationship between distribution and abundance of passerines breeding in a sample of oases from southern Tunisia, and we provide a test of the sampling artefact hypothesis. In particular, we checked for a difference in detection probability between localized and widespread species, and we tested if increasing the sampling effort affects the significance of the relationship. A significant positive relationship between the average local abundance of passerine species and the proportion of occupied oases was found. The use of a capture-recapture approach allowed us to estimate and to compare the detection probabilities of localized and widespread species subsets. We found that localized species were locally less detectable than widespread species, which is consistent with the main assumption of the sampling artefact hypothesis. However, increasing the detection probability of species by conducting more counts did not affect the significance of the relationship, which did not give support to the sampling artefact hypothesis. Our work implies that sampling contributed to the distribution-abundance relationship we found, but that it is unlikely that such a relationship could entirely be explained by an artefact of sampling. It also underlines the insight that can be gained by using probabilistic approaches of estimating species number and detection probability when attempting to disentangle sampling from ecological effects in community ecology studies.

Keywords Bird detectability · Capture-recapture estimate · Community patterns · Sampling artefact · Sampling effort

Introduction

A positive relationship between local abundance of species and their distribution has been documented for a diversity of taxa, from a variety of habitats, and at different spatial scales (e.g. Hanski 1982; Bock and Ricklefs 1983; Brown 1984; Gaston and Lawton 1990; Lawton 1993; Gaston 1994, 1996; Warren and Gaston 1997; Thompson et al. 1998). Within a taxonomic assemblage, widely distributed species tend to be more abundant locally than narrowly restricted ones. Even though the distribution-abundance relationship is one of the most widely recognized patterns in community ecology (Hanski 1999), it lacks a widely recognized ecological explanation. Indeed, several non-exclusive ecological hypotheses have been suggested (see Gaston et al. 1997). Moreover, it has been proposed that a positive relationship between local abundance and distribution of species can simply be an artefact of sampling (Brown 1984; McArdle 1990; Wright 1991; Hanski et al. 1993; Gaston 1994). According to this sampling artefact hypothesis, the distribution of locally rare species is underestimated because one species can be easily overlooked when it has a low local abundance. As a consequence, a potentially strong but spurious positive relationship between abundance and distribution can result. This hypothesis also predicts that with a greater sampling effort this relationship will disappear (Brown 1984).

Given the possible insight that could be gained by investigating the distribution-abundance relationship to

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understand better ecological factors and processes accounting for community diversity (Gaston and Lawton 1988; Brown 1995) and for problems of conservation (Lawton 1996; Lawton et al. 1994), there is a need to develop methods and approaches allowing us to disentangle sampling from ecological effects.

Since the sampling hypothesis makes the assumption that localized species are locally less detectable than widespread species, the simplest way to test this is to check for a difference in the detectability of widespread and localized species. This requires an estimate of the mean detection probability of each subset of species. One possible way to achieve this is to use a capture-recapture approach that relies on the pattern of detection/non-detection of species in a series of count replicates (Burnham and Overton 1978, 1979). This approach assumes that it is rare to detect all species of a given assemblage and allows us to estimate the number and mean detection probability of species (Burnham and Overton 1978, 1979; Nichols and Conroy 1996; Boulinier et al. 1998). This capture-recapture type of approach is increasingly used in community ecology studies and has been applied for a variety of purposes. For instance, it has proved useful in disentangling sampling from ecological effects when dealing with the species-area relationship (Cam et al. 2002).

In this paper, we use the results of series of point-counts conducted in a large sample of oases from southern Tunisia to investigate the relationship between local abundance and distribution of breeding passerines in the oasis system, and to provide a test of the sampling artefact hypothesis. Our aim is more to explore an important hypothesis behind the distribution-abundance relationship reported in many studies, rather than to present an original relationship. We use a capture-recapture type of approach to estimate species detection probability, and we propose a test of the sampling artefact hypothesis. In particular, we ask the following questions:

1. Is there a positive relationship between local abundance and occupancy in the case of passerines breeding in southern Tunisian oases?
2. Are localized species less detectable than widespread species, as assumed by the sampling artefact hypothesis?
3. Does increasing the probability of species detection, by increasing the sampling effort, affect the significance of the abundance-occupancy relationship, as predicted by the sampling artefact hypothesis?

Materials and methods

Data collection

The study sites are 26 traditional oases in southern Tunisia, with areas ranging from 23 to 973 ha. These oases are semi-natural wood lots characterized by vegetation composed of three main layers: palm trees, fruit trees and herbaceous plants. Previous studies have suggested that several palearctic bird species have colonized the oasis system over the last century (Selmi 2000; Selmi et al. 2002). For these species, oases represent suitable isolated habitat patches within an inhospitable desert matrix, and it has been proposed that long-distance dispersal ability and metapopulation processes have played an important role in shaping oasis-dependent bird communities (Selmi et al. 2002; Selmi and Boulinier 2003).

Passerines breeding in the oasis sample were surveyed using the indices ponctuels d'abondance (IPA) method (Blondel et al. 1970; IBCC 1977). This survey method is specifically designed to account for differences among species in breeding phenology (Blondel et al. 1970; IBCC 1977), as is the case at the latitudes of southern Tunisia. Indeed, resident birds start breeding early (from mid-February onwards), while migratory species settle 2 months later. The IPA method consists of conducting two partial counts per point but at two different periods: (1) at the beginning of the breeding season to sample the early nesting resident species, and (2) after the migratory species have settled. Counts are carried out early in the morning and under optimal meteorological conditions, and during each count the observer records all birds heard or seen in the surroundings within an unlimited distance. The results of both partial counts are then pooled and an abundance index (IPA) is then obtained for each recorded species by retaining the highest count that the observer found during each partial count. Conventionally, one individual recorded (a bird simply seen or a call heard) is counted as 0.5, but a breeding pair (a pair of breeders, a singing male or a familial group) is counted as 1 (Blondel et al. 1970; IBCC 1977). Because it is a relative method, the IPA method cannot provide direct estimates of species abundance usable for interspecific comparisons. However, it was possible to convert the IPA values into density indices by using the results of preliminary work in which we combined the IPA method with the territory mapping method (Blondel 1969; IBCC 1969) on six study plots (13.8 ha, 13.6 ha, 12.2 ha, 10 ha, 18 ha and 20 ha) in different oases. This preliminary work was carried out during the breeding season of 1998 and permitted us to calculate for each species a coefficient of conversion of IPA values to density values expressed as "pairs of breeders per 10 ha". A full description of this approach and its advantages are given in Muller (1987). However, one problem is that this approach does not account for potential differences in detection probability among individuals, which may be critical.

Data used in this work were collected during the breeding season of 1999 by conducting five IPA counts at five different points within each of the 26 sampled oases. This provided us with: (1) five lists of records of species detection/non-detection per oasis, which allowed us to estimate the number and mean detection probability of species for each oasis; and (2) five IPA values per oasis for each recorded species, that we used to investigate the relationship between distribution of species and their average local abundances.

Data analyses

The five lists of records of species detection/non-detection obtained from each of the sampled oases by using a capture-recapture approach were used to estimate the number and mean detection probability of species. The estimates were computed using the jackknife estimator associated with the model M_h (Burnham and Overton 1978, 1979), which makes the assumption of a heterogeneous detection probability among species. Application of this estimator to point-count data for species richness and to estimate detection probability 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 match the total observed species number (detection probability may tend to equal 1) when no species is recorded in a low number of counts [$f_{(i)}$ tends to equal 0 for low i] and most species are detected during all counts [$f_{(n)}$, with

n as the total number of counts, tends to match the total number of observed species]. For each oasis, estimates were calculated for localized and widespread species considered separately, which provided us with their respective average detection probabilities in each of the sampled oases. We used the 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). Given the non-normality of our data, the difference between the detection probabilities of localized and widespread species subsets was then tested by means of the non-parametric Mann-Whitney U-test.

The relationship between occupancy (proportion of oases where the species was detected) and average local abundance ($\log_{10}$ transformed and calculated using only data from the oases where the species was found) was investigated by means of simple regression. In order to test whether sampling effort affects the form or the significance of the distribution-abundance relationship, as predicted by the sampling hypothesis, we used the following approach. In a first step, we investigated the relationship using only the results of the first IPA count for the estimation of species' local abundance and occupancy. Then we used the mean value of the first two IPA counts, the mean value of the first three IPA counts, the mean value of the four first IPA counts and finally the mean value of the five IPA counts. All statistical analyses and tests were performed using SAS software (SAS 1998).

Results

Twelve breeding passerine species were recorded in the oasis sample (Table 1). Five species (*Cercotrichas galactotes, Hippolais pallida, Passer domesticus, Serinus serinus*, *Emberiza striolata*) occurred in almost all sampled oases, while seven species (*Turdus merula, Cisticola juncidis, Sylvia hortensis, Muscicapa striata, Parus caeruleus, Lanius senator, Fringilla coelebs*) were more localized (Table 1, Fig. 1). The count results also show that increasing the sampling effort by conducting more counts per oasis allowed us to detect some species previously overlooked in some oases (Table 1, Fig. 1). For example, when only the results of the first IPA count were considered, six species were overlooked in some oases where they occurred: four localized species (*Turdus merula, Sylvia hortensis, Parus caeruleus, Lanius senator*) and two widespread species (*Cercotrichas galactotes, Emberiza striolata*). Thus, a low sampling effort led to an underestimation of the occupancy of some species, especially the occupancy of the more localized and locally rare species (Table 1, Fig. 1).

With regard to the estimate of the probability of species detection made from the lists of records of species detection/non-detection, we found that the M_h model provided a good fit to the data (χ^2 goodness of fit-test; P >0.05 in all oases). Using this model, we found that the average probability of detecting species per individual IPA count was very high (0.958±0.006). This high detection probability could be explained by the good fieldwork conditions within the oases, especially the high visibility due to the relatively simple vegetation. The use of the M_h model for widespread and localized species subsets considered separately showed that the average probability of detection of all species per individual IPA count was high for both species subsets: 0.982±0.005 for widespread species and 0.906±0.013 for localized species.

With regard to the relationship between average local abundance and occupancy, a strong positive relationship was found when only one IPA count (the first IPA count) was used for the estimation of species' occupancy and local abundance (Table 2, Fig. 1). According to the sampling artefact hypothesis, this relationship may be obvious because localized species may be less detectable than the more widely distributed ones. This assumption is supported by the result of the comparison of the detection probability of both species subsets. Indeed, even though the average detection probability of both species subsets was high (see above), localized species were significantly

Table 1 Number of occupied oases (n) and average local abundance (expressed as number of breeding pairs per 10 ha and calculated using only data from the oases where the species was recorded) of the 12 recorded passerine species in the oasis sample. Total number of sampled oases is 26. Species' occupancy and local abundance are obtained using only the first indice ponctuel d'abondance (IPA) count (*A*), the first two IPA counts (*B*), the first three IPA counts (*C*), the first four IPA counts (*D*) and all five IPA counts (*E*)

Species	A		B		C		D		E	
	n	Abundance	n	Abundance	n	Abundance	n	Abundance	n	Abundance
Cercotrichas galactotes	25	7.722	26	7.462	26	7.642	26	7.725	26	7.62
Turdus merula	19	1.847	21	1.703	21	1.643	21	1.659	21	1.616
Cisticola juncidis	11	2.818	11	2.909	11	2.789	11	2.886	11	2.945
Hippolais pallida	26	17.042	26	17.042	26	16.921	26	16.901	26	16.703
Sylvia hortensis	19	7.147	19	7.442	20	7.56	20	7.857	20	8.092
Muscicapa striata	9	3	9	2.583	9	2.667	9	2.833	9	3.133
Parus caeruleus	7	2.957	10	2.295	10	2.64	10	2.52	10	2.79
Lanius senator	4	1.012	6	0.75	6	0.65	7	0.578	7	0.707
Passer domesticus	26	25.183	26	24.871	26	24.438	26	24.43	26	23.449
Fringilla coelebs	20	5.962	20	5.906	20	6.03	20	6.109	20	6.259
Serinus serinus	25	7.88	25	7.98	25	7.933	25	7.79	25	7.8
Emberiza striolata	25	3.2	26	3.096	26	3.045	26	3.038	26	3.092

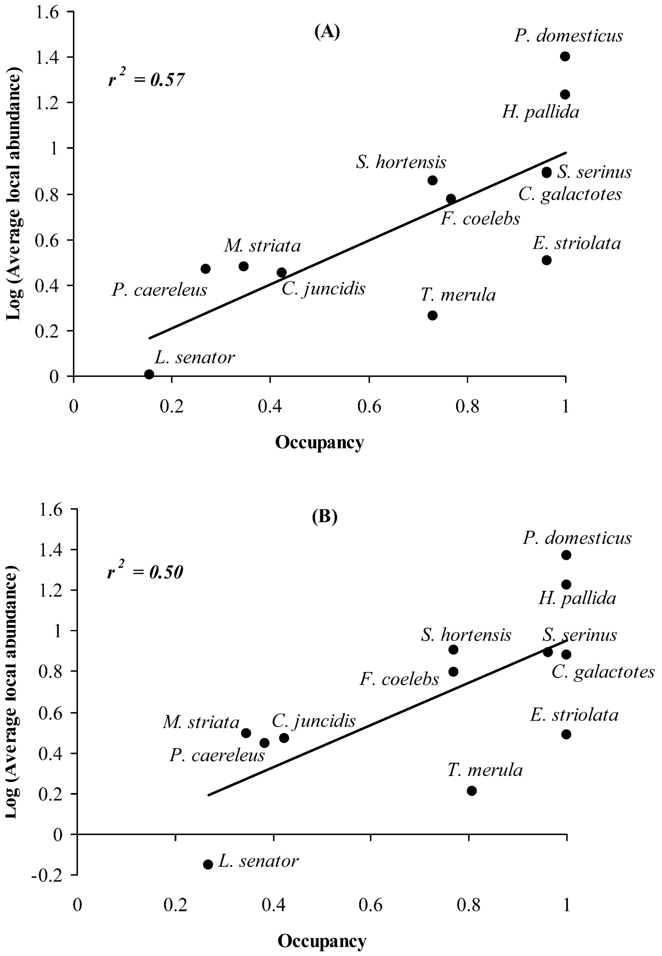

Fig. 1A, B Plot of average local abundance ($\log_{10}$-transformed and calculated using only data from the oases where the species was recorded) on occupancy (proportion of oases where the species was recorded) of the 12 recorded passerine species. Species' occupancy and local abundance were obtained using **A** the first IPA count and **B** all five IPA counts. *C. galactotes Cercotrichas galactotes, H. pallida Hippolais pallida, P. domesticus Passer domesticus, S. serinus Serinus serinus, E. striolata Emberiza striolata, T. merula Turdus merula, C. juncidis Cisticola juncidis, S. hortensis Sylvia hortensis, M. striata Muscicapa striata, P. caeruleus Parus caeruleus, L. senator Lanius senator, F. coelebs Fringilla coelebs*

less detectable than widespread species (Mann-Whitney U-test: $Z=-5.200$, $P<0.001$). However, our results suggest that increasing the sampling effort did not affect the significance of the relationship (Table 2), which did not give support to the sampling artefact hypothesis. For instance, when local abundance and occupancy were estimated using the results of the five IPA counts, the probability of detection of detected species (per 5 IPA counts as a single sampling occasion) was equal to 1 for both localized and widespread species subsets. However, a weaker but significant relationship between the average local abundance and occupancy was found (Table 2, Fig. 1).

Discussion

Our results suggest that even though sampling likely contributed to the positive distribution-abundance relationship found for passerines breeding in southern Tunisian oases, this relationship could not be entirely attributed to an artefact of sampling. Localized species were found to be locally less detectable then widespread species, as assumed by the sampling hypothesis. However, the positive abundance-occupancy relationship was still significant even when the chance of detecting birds was increased by increasing the effort of sampling, which did not give support to the sampling artefact hypothesis as the only explanation for the observed relationship. Widely distributed species (*Cercotrichas galactotes, H. pallida, Passer domesticus, Serinus serinus*, *E. striolata*) were globally more abundant locally than the more localized ones (*T. merula, Cisticola juncidis, Sylvia hortensis, M. striata, Parus caeruleus, L. senator, F. coelebs*).

The positive relationship between local abundance and occupancy documented in this study constitutes an example of a well-known pattern. Nevertheless, it is interesting that such a relationship was found in a largely unexplored area and situated at the margin of the geographic range of the considered species. Indeed, investigations of the distribution-abundance relationship have exclusively been concerned with data from northern temperate zones, and there is a need for examples from unexplored regions and habitats (Gaston 1996). The passerine species studied are also among the most generalist palearctic bird species (Cramp and Simmons 1977–1994). Therefore, it is unlikely that the positive distribution-abundance relationship we found is a consequence of differences in species ecological specialization level, as predicted by the niche breadth hypothesis (Brown 1984). Furthermore, given the importance of dispersal and metapopulation processes in shaping local oasis bird communities (Selmi et al. 2002, Selmi and Boulinier 2003), it is possible that the distribution-

Table 2 Results of the regression of average local abundance ($\log_{10}$-transformed and calculated using only data from the oases where the species was recorded) on occupancy (proportion of oases where the species was recorded) of the 12 recorded passerine species. Species' occupancy and local abundance are obtained using A, B, C, D and E. For abbreviations, see Table 1

	A	B	C	D	E
Slope estimate (±SE)	0.97±0.26	1.08±0.31	1.10±0.32	1.12±0.33	1.04±0.33
r^2	0.57	0.55	0.54	0.53	0.50
F-value	13.56**	12.30**	12.01**	11.22**	9.89*

$^*P<0.05$, $^{**}P<0.01$

abundance relationship we found is the expression of dynamic processes, as suggested by the metapopulation hypothesis (Hanski 1991, 1999; Nee et al. 1991). However, further investigations of regional dynamics and the dispersal of species among oases are needed to verify the role of metapopulation processes in shaping patterns of occupancy and local abundance.

Among the hypotheses proposed to explain the positive interspecific distribution-abundance relationship (see Gaston et al. 1997), the sampling artefact hypothesis is surely not the more biologically informative one. Furthermore, it is unlikely that all species occur everywhere, as implied by the sampling hypothesis. However, it has been suggested that sampling most likely makes a contribution to the distribution-abundance relationships found in most studies, but the bias introduced by sampling may vary with the considered taxa (Hanski et al. 1993; Hanski 1999). For instance, it has been argued that sampling may play a minor role for well-known and easily observed taxa (Brown 1984; Gaston et al. 1996). The bias introduced by sampling may also vary according to the habitat system considered, in that sampling may play a minor role in habitats where species detectability is high, such as the oasis system. However, despite the high detection probabilities for birds within oases, we found that the main assumption of the sampling artefact hypothesis was supported: localized bird species were less detectable than widespread ones. This suggests that sampling effects are more likely to occur in systems where bird richness is higher and bird detection probability is potentially lower than those characterising the oasis habitat (e.g. in temperate or tropical forests). This also stresses the need for using appropriate sampling methods and designs when attempting to disentangle sampling from ecological effects in community patterns.

As in the case of tests of the core-satellite hypothesis (see Novotny and Drozd 2001), species detectability is very rarely explicitly considered when investigating the effect of sampling on the form and significance of the relationship between distribution and abundance. The most well-known test of the sampling artefact hypothesis was based on the models developed by Wright (1991) and reformulated by Hanski et al. (1993). This test makes two fundamental assumptions. First, locally rare species are less detectable than are locally abundant species. Second, the distribution of local abundance is a negative binomial because nearly all species show an aggregated spatial distribution at all spatial scales (see also Hartley 1998; Gaston et al. 1998). The test consists of checking whether the number of sites at which a species is found is a monotonically increasing function of its average abundance (calculated across all sites) and a decreasing function of the coefficient of variation of local abundance (see also Gaston et al. 1997).

The idea that the difference in the probability of detection among species at a given locality is entirely explained by the difference in their local abundance, as assumed by both the model and its test, seems simplistic. As McArdle (1990) demonstrated, it is clear that the probability of detection of a given species increases with its abundance, but this does not automatically mean that more abundant species at a given site are more detectable than are less abundant ones, as is assumed by the test. Indeed, the detectability of a species is also strongly affected by the environmental conditions, as well as by its behaviour, such as the level of aggregation of individuals and/or its degree of conspicuousness. For instance, field observers know that one locally rare but very conspicuous species may more easily and frequently be detected than one more abundant but less conspicuous one. Even though this artefact has been investigated in some early studies (e.g. Bock 1987), it has not been given much importance in studies attempting to test the sampling model (e.g. Hanski et al. 1993).

In short, factors that can lead to a sampling artefact, and consequently to an underestimate of the distribution of some species (be they locally rare or abundant), are very complex. The probabilistic method of estimating species number of local communities and species detection probability based on a capture-recapture approach (Burnham and Overton 1978, 1979; Nichols and Conroy 1996; Boulinier et al. 1998) and used in our work allowed us to test the sampling model regardless of the source of among-species differences in detectability. This method is not concerned with why are some species less detectable than others, but it gives the answer to the most important question that the sampling hypothesis raises: are some species locally less detectable than others?

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