



## COMMENTARY

# The estimation of size and change in composition of avian song repertoires

LÁSZLÓ ZS. GARAMSZEGI\*†, THIERRY BOULINIER‡, ANDERS P. MØLLER\*, JÁNOS TÖRÖK†, GÁBOR MICHL† & JAMES D. NICHOLSS§

\*Laboratoire d'Ecologie Evolutive Parasitaire CNRS UMR 7103, Université Pierre et Marie Curie

†Behavioral Ecology Group, Department of Systematic Zoology and Ecology, Eötvös Loránd University, Hungary

‡Laboratoire d'Ecologie, CNRS UMR 7625, Université Pierre et Marie Curie

§U.S. Geological Survey, Biological Resources Division, Patuxent Wildlife Research Center, U.S.A.

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Repertoire size has been used to quantify the complexity and variety of bird song, and the determination and comparison of repertoire size have been crucial to many behavioural studies investigating the role of songs in sexual selection and the ontogeny of singing behaviour (Catchpole & Slater 1995).

However, researchers aiming to work with repertoire size are often faced with challenging problems because (1) technological constraints, time and other limiting factors may mean few songs are available for analysis, and (2) the organization of vocalizations can vary between bird species (Shiovitz 1975; Krebs & Kroodsma 1980). For example, it is difficult to detect all repertoire components in a given record. Indeed, some songs or song elements can be sung less frequently than others and such components can be missed in species with large repertoires (Krebs & Kroodsma 1980). Hence, one cannot simply enumerate song elements to determine repertoire size, as this will yield a number with negative bias of unknown magnitude. Instead repertoire size must be estimated with methods that incorporate the possibility (likelihood) that some elements are 'missed' during sampling (Kroodsma 1982).

Repertoire size is traditionally estimated from sonagrams, and the usual estimation approach is based on plotting the number of new repertoire elements or components (such as notes, figures, syllables, motifs, etc.) in a recorded sample against the total number of elements or songs sampled. The more songs analysed, the fewer new elements are found (Wildenthal 1965; Catchpole & Slater

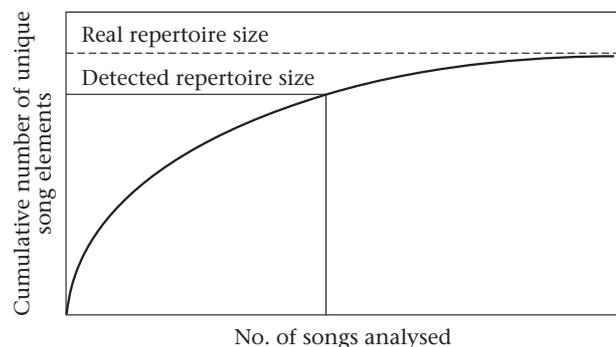


Figure 1. A hypothetical cumulative plot of song elements as an increasing number of songs are analysed to determine the repertoire size of a bird species with a large repertoire.

1995; Fig. 1). The asymptote of this function (i.e. the number of elements that would be found if a very large number of songs could be analysed) is then thought to represent the repertoire size. The difficulty is that the functional form of the relationship between elements detected and sample size must be known or estimated to estimate the asymptote. In practice, researchers just simply use the number of unique repertoire elements in a given number of songs as repertoire size.

A practical problem in studies of repertoire size and composition is that an individual is unlikely to sing all its song components in a single song or bout of singing, especially since some elements are sung less often than others (Molles & Vehrencamp 1999). If the probability that each repertoire component will be sung varies between individuals, song elements and conditions of recording (e.g. time during the season relative to

Correspondence: L. Zs. Garamszegi, Laboratoire d'Ecologie Evolutive Parasitaire CNRS UMR 7103, Université Pierre et Marie Curie, Bât. A, Case 237, 7ème étage, 7 quai St. Bernard, F-75252 Paris Cedex 5, France (email: laszlo.garamszegi@snv.jussieu.fr).

**Table 1.** Similarity between estimating community species richness and repertoire size of birds, as both are based on using the pattern of repeated sequences among series of sampling occasions

	Species richness estimation	Repertoire size estimation
Units		
Unit of interest	Species	Song element
Sampling ('capture') occasion or unit	Transect or point count	Song
Sampling period	Survey	Series of songs
Subject	Habitat/community	Bird species/individual
Data type	Presence/absence	Presence/absence
Detectability problem	Rare species	Rare elements/nonrandomness/aggregation
The observer's effect	Different ability to detect species	Different ability to recognize elements on a spectrogram
Spatial differences	Geographical variation of the same habitat in species richness and composition	Geographical variation in song repertoire size and composition, spatial heterogeneity
Temporal changes	Local species colonization, turnover and extinction probability	Temporal changes in repertoire size and composition (i.e. 'element' extinction, colonization and turnover)
Application	Community ecology, conservation, wildlife management	Behavioural ecology, ethology

reproduction of each individual), then comparisons of repertoire size and composition between individuals, or species, may be biased, because reported sizes will represent unknown, yet possibly different, fractions of true repertoire sizes. This is especially true if some characteristics of the males studied, such as their respective territory sizes, affect the probability of detecting some of the song elements of their repertoires. It is surprising that despite these obvious problems few attempts have been made to deal with variability in probability of detection of song components.

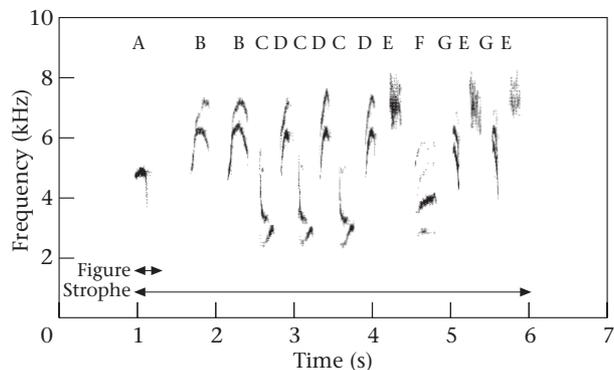
Here we suggest a new way to estimate repertoire size, controlling for differences in the occurrence of song elements. We propose methods for drawing inferences about song repertoires based on typical sampling methods. These methods explicitly incorporate variable element detection probabilities that are less than 1, and will thus be especially useful for comparative investigations. We propose here to regard the issue of estimating the number of song elements in the repertoire of an individual, or group of individuals, from data on detection of song elements in samples as analogous to the issue of estimating the number of species in a community, using the pattern of detection of each species among a series of sampling occasions (Table 1). Estimators of this type have themselves often been derived from 'capture-recapture' estimators of the abundance of animals in a 'closed' population, that is, a population sampled at several occasions over a period during which it is assumed not to have lost or gained individuals (Burnham & Overton 1979). A large body of literature now exists on the application of such models in the field of quantitative community ecology (Burnham & Overton 1979; Bunge & Fitzpatrick 1993; Colwell & Coddington 1994; Nichols & Conroy 1996; Boulinier et al. 1998; Nichols et al. 1998a; Cam et al., in press). It is noteworthy that a classical paper on the question of estimating species richness was concerned with estimating the word repertoire size of William Shakespeare (Efron & Thisted 1976). In this

paper we present simple estimation procedures that can be applied to important questions dealing with repertoire size and differences or changes in repertoire composition. We first describe how repertoire size can be estimated with a sampling design and estimator derived from population and community ecology. We illustrate the use of this estimator with song data from the collared flycatcher, *Ficedula albicollis*. We then describe how parameters associated with differences and changes in repertoire size and composition can also be estimated with recently proposed estimators for the dynamics of communities.

### Sampling Design and Repertoire Size Estimation

Studies aiming at determining bird repertoire size involve repeated recording of singing individuals and some standardized way of identifying song components or parts of the songs as different element or syllable types (Catchpole & Slater 1995). Quantifying differences between these units and defining categories of elements or song types can involve variously refined techniques, and we assume here that this can be done with sufficient reliability. Such reliability can be assessed from within- and between-observer analyses of repeatability (Falconer & Mackay 1996). What we are interested in here is how to estimate the size of a given repertoire when one can replicate the sampling of this repertoire through a series of song records. When such replicated sampling data are available, 'capture-recapture' methods can be applied to the pattern of detection/nondetection of the song elements among the sampling occasions to estimate total repertoire size and the probability of detecting song elements.

We must define a sampling occasion or unit in some unambiguous manner. One reasonable approach is to define strophes or songs on recordings (Fig. 2). This step is essential to standard analyses of song repertoire data. Unit definition presents a well-known problem, called



**Figure 2.** The spectrographic picture of a collared flycatcher song (strophe) as a sampling unit or occasion, which is usually built up by some figures as song elements.

the ‘unit problem’, and refers to the different terminologies applied in different species and differences in song element definitions (Krebs & Kroodsma 1980). In the following we assume that unit definition occurs in a proper way.

Each song element detected in any song or strophe would be characterized by a vector of  $K$  1’s and 0’s, where 1 indicates that the song element was detected on the record, and 0 that it was not, and  $K$  is the number of songs that were analysed, that is, the number of capture occasions (Bunge & Fitzpatrick 1993; Nichols & Conroy 1996; Boulinier et al. 1998). For example, if we sampled  $K=5$  songs of a given individual during a given period, then a possible detection history for a song element could be 01011. This history indicates a song element detected in the second, fourth and fifth, but not the first and third songs.

The identification of the replicate sampling units should be based on the types of inference that are desired. For example, if interest is focused on the repertoire size of an individual bird, then the relevant data are a series of song records for that individual. In some cases interest may focus not on an individual but on a group of individuals, for example of a particular population or species. In such cases, a song recorded from each of several individuals sampled from the group of interest would be an appropriate sampling occasion. Other questions can be envisioned, and sampling schemes can be tailored to address them.

Estimation of repertoire size from such data can be based on models developed originally for estimation of the size of closed animal populations (Otis et al. 1978; White et al. 1982). These models differ in their assumptions about sources of variation in detection probability. As noted in the Introduction, we expect heterogeneity in the detection probabilities associated with different elements of a repertoire, as certain elements are more commonly used than others. We thus expect models permitting heterogeneous detection probabilities to be especially useful. Model  $M_h$  of Otis et al. (1978) permits such heterogeneity of detection probabilities among elements but assumes that there is no other variation, for example, between the different songs or sampling units.

Because detection probability refers to the conditional probability of detecting an element in a sampling unit (song or strophe), given the presence of the element in the repertoire of interest, the sources of variation in detection probability will be likely to depend on the sampling scheme. For example, if songs of multiple individuals are analysed to estimate a repertoire at the level of a population, then we might expect not only heterogeneity, but also variation in detection probabilities of elements between individual birds (e.g. some birds may be more likely than others to use certain elements). In such cases, model  $M_{th}$  of Otis et al. (1978) may prove useful. If some song elements are ‘known’ by some individuals, but not others, then the closure assumption underlying models  $M_h$  and  $M_{th}$  does not hold. However, if detection probability is now redefined to include the probability that a sampled individual ‘knows’ the element, then the estimate of repertoire size now applies to the total repertoire of the group of individuals from which the sample of individuals was drawn (see Kendall 1999; Cam et al. 2002).

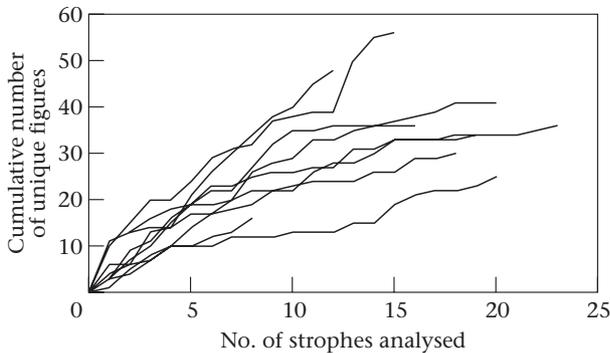
The availability of various models requires an objective approach to selecting models. Otis et al. (1978) recommended a model selection algorithm based on a discriminant function analysis of simulated data. The discriminant function is based on test statistics from between-model tests and goodness-of-fit tests. Estimates under the various models and associated standard errors, as well as various tests and model selection statistics, are computed by the program Capture (Otis et al. 1978; Rexstad & Burnham 1991). With this program, the investigator can select the most appropriate model for the data set considered and obtain estimates under this model.

In previous work, we have found the heterogeneity model,  $M_{th}$ , to be especially useful for the estimation of species richness (e.g. Boulinier et al. 1998), and we suspect that this model will prove useful in estimating song repertoire sizes as well. There are many estimators currently available for this general model, and in our previous work we have primarily used the jackknife estimator of Burnham & Overton (1978, 1979). This estimator is known to be fairly robust to potential departures from model assumptions and has performed well in various simulations (e.g. Burnham & Overton 1979; Baltanas 1992; Zelmer & Esch 1999) and empirical (Palmer 1990) studies.

The general form of the jackknife estimator for repertoire size ( $\hat{N}_k$ ), is

$$\hat{N}_k = R + \sum_{h=1}^{k-1} \alpha_{hk} f_h$$

where  $R$  is the observed repertoire size,  $f_h$  is the frequencies or numbers of song elements detected in exactly  $h=1, 2, \dots, K$  songs or other sampling units,  $\alpha_{hk}$  is a constant (see Burnham & Overton 1978, 1979) generated by the jackknife procedure of order  $k$  ( $\alpha_{hk}=0$  for  $h>k$ ) and  $K$  is the total number of songs analysed. Available computer programs select and compute the estimate by using a procedure to interpolate between jackknives of different orders. Although the reader is referred to



**Figure 3.** A cumulative plot of figures of collared flycatcher song recordings from nine males.

Burnham & Overton (1978) for the derivation of the jackknife estimators, we note that they do correspond to intuition in a general way. If all song elements are detected many times (e.g. in nearly all sampled songs) the estimated repertoire size will be similar to the number of elements actually observed. However, if many elements are observed only in one or two songs, it is likely that there are others that were not observed at all, and the estimated repertoire will be substantially larger than the number of elements observed.

To illustrate the use of the jackknife estimation procedure for repertoire size we provide an example analysis with song data from the collared flycatcher. In this example we used the software Comdyn (Hines et al. 1999; <http://www.mbr-pwrc.usgs.gov/comdyn.html>) to compute the jackknife estimator of Burnham & Overton (1979). The standard errors of the estimates computed by the software are obtained by using a bootstrap approach (Hines et al. 1999; see Nichols et al. 1998a for a description of the variance estimation procedure).

The song composition of the collared flycatcher is very simple (Gelter 1987; Lundberg & Alatalo 1992). It consists of simple calls and variable strophes (song) that include different figures (song elements; Fig. 2). In theory, strophes are sampling units or occasions, and using series of song records we intended to estimate the number of figures that represents repertoire size.

Owing to differences in singing activity between individuals, the available number of strophes per recording varied between birds ( $\bar{X} \pm \text{SE} = 16.44 \pm 1.42$ ,  $N=9$ ). In the following analyses we used 8–23 strophes as sampling units per individual. The average number of unique elements per individual, which represents a traditional estimate of repertoire size, was  $31.44 \pm 2.75$ . Figure 3 gives the cumulative repertoire size against the cumulative number of song strophes analysed for each male.

We computed the jackknife estimates of number of elements from the element detection history data (Table 2) and obtained a mean  $\pm$  SE of  $\hat{N} = 40.67 \pm 4.14$  per individual, with the average detection probability of  $0.73 \pm 0.04$ , which is strong evidence that we did not detect all elements; thus differences in detection probabilities should be taken into account when estimating repertoire size. The goodness-of-fit tests for model  $M_h$  had  $P_s > 0.05$  for all but one bird.

## Temporal Changes and Individual Differences

Estimates of temporal change in repertoire size within an individual or within groups of individuals (rate of increase in repertoire size, rate of extinction and rate of turnover of song elements in the repertoire) can be computed with methods analogous to those used in studying community dynamics (Nichols et al. 1998a).

### Rate of change in repertoire size

The rate of change in the number of song elements between two consecutive periods of sampling (e.g. series of occasions before and after a treatment, or at two different ages or years) is simply estimated as the number of song elements estimated ( $\hat{N}$ ) to be present during the second sampling period ( $j$ ) divided by the number of song elements estimated to be present during the first sampling period ( $i$ ):

$$\hat{\lambda}_{ij} = \frac{\hat{N}_j}{\hat{N}_i}$$

An alternative estimation can be applied in a special situation when average song element detection probabilities are found or assumed to be equal ( $p_i = p_j$ ) for the two periods of recording:

$$\hat{\lambda}_{ij} = \frac{R_j}{R_i}$$

where  $R_i$  and  $R_j$  are the number of song elements observed during sampling in periods  $i$  and  $j$ , respectively. The assumption of equal detection probabilities can be tested with the raw frequency data,  $f_{hn}$ , with a  $2 \times K$  contingency table  $\chi^2$  test with the null hypothesis that the proportions of song elements found in  $h=1, 2, \dots, K$  secondary samples are similar for the two primary records,  $i$  and  $j$ . Note that rate of change in song element richness does not permit insight about song composition changes, and that additional estimators for extinction, turnover and addition of song elements are needed to provide such inferences.

### Extinction probability and turnover rate

The extinction probability between two sampling periods ( $i$  and  $j > i$ ) can be viewed as the expected proportion of song elements lost from the song repertoire between the two sampling periods, that is, the probability that a song element present in record  $i$  is not present in a later record  $j$ :

$$1 - \hat{\phi}_{ij} = 1 - \frac{\hat{M}_j^{R_i}}{R_i}$$

where  $R_i$  represents the number of song elements observed in record  $i$ , and  $\hat{M}_j^{R_i}$  is the estimated number of these elements that are still present in record  $j$ . Thus  $\hat{\phi}_{ij}$ , which is the complement of extinction probability, denotes the probability that a song element present at time  $i$  is still present at time  $j$ .

**Table 2.** Jackknife repertoire size estimation of a collared flycatcher male by using figure presence/absence data from  $K=11$  strophes (columns)

	Strophes										
	str1	str2	str3	str4	str5	str6	str7	str8	str9	str10	str11
Figures											
A	1	1	0	0	1	1	1	0	0	0	1
B	1	1	1	1	1	1	0	1	0	0	1
C	1	0	0	0	0	0	1	0	0	0	1
D	1	0	0	0	0	0	0	0	0	0	0
E	1	0	0	1	0	0	1	0	1	1	1
F	1	1	0	0	0	0	0	0	0	0	1
G	1	0	0	0	0	0	0	0	0	0	1
H	1	0	1	1	1	1	0	1	0	0	1
I	0	1	0	0	0	0	0	0	0	0	0
J	0	1	0	0	0	0	0	0	0	0	0
K	0	1	0	0	0	0	1	0	0	0	0
L	0	1	0	0	0	1	0	0	0	0	0
M	0	1	0	0	0	0	1	0	0	0	0
N	0	1	0	1	0	0	1	0	0	0	0
O	0	1	0	0	0	0	0	0	0	0	0
P	0	0	1	0	0	0	1	0	1	1	0
Q	0	0	1	0	0	0	1	0	1	1	0
R	0	0	1	0	0	0	1	0	1	1	0
S	0	0	1	0	1	1	0	1	0	0	0
T	0	0	1	0	1	0	0	0	0	0	0
U	0	0	1	0	0	0	0	0	0	0	0
V	0	0	1	1	1	0	1	0	0	0	0
W	0	0	0	1	1	0	1	0	0	0	0
X	0	0	0	1	0	0	1	0	0	0	0
Y	0	0	0	1	0	0	0	0	0	0	0
Z	0	0	0	1	0	0	0	0	0	0	0
A'	0	0	0	1	0	0	1	0	1	0	0
B'	0	0	0	0	0	0	1	0	0	0	0
C'	0	0	0	0	0	0	0	0	1	0	0
D'	0	0	0	0	0	0	0	0	1	1	0
E'	0	0	0	0	0	0	0	0	0	1	0
Jackknife input											
$K$	11										
$n_h$	8	10	9	10	7	5	14	3	7	6	7
$f_h$	10	7	5	5	0	2	1	1	0	0	0
Jackknife output											
$R$	31										
$\hat{N}$	37.77±4.40										
$\hat{p}$	0.821										
Goodness of fit	$\chi^2_{10}=15.753, P=0.107$										

For each figure, a detection history can be created (rows) and these are used to obtain the frequencies of figures detected in exactly  $h=1, 2 \dots 11$  strophes ( $f_h$ ), and the observed number of figures observed in each strophe ( $n_h$ ). These summary statistics are used by the program to calculate the jackknife estimator of the individual repertoire size ( $\hat{N} \pm SE$ ), which controls for differences in figure detection probabilities ( $\hat{p}$ : average detection probability). The goodness-of-fit test indicates how the estimation model fits the data.  $R$  is the total number of figures detected in the 11 song records, that is the traditional repertoire size estimation neglecting differences in figure detection probability.

The rate of turnover between two sampling periods is defined as the proportion of song elements that are new (in the sense of not having been present in the first sampling period) among those present during the second sampling period:

$$1 - \hat{\phi}_{ji} = 1 - \frac{\hat{M}_i^{R_j}}{R_j}$$

where  $j > i$ ,  $\hat{M}_i^{R_j}$  is the estimated number of song elements observed in record  $j$  that were also present in record  $i$ , and

$R_j$  is the number of song elements observed in record  $j$ .  $\hat{\phi}_{ji}$  can be viewed as the expected proportion of song elements at time  $j$  that are 'old' and is defined as the estimated complement of song element turnover (proportion of song elements observed in record  $j$  that were also present in record  $i$ ).

The extinction probability and turnover rate parameters achieve their maximum values at 1 (when all song elements present in record  $i$  are not present in record  $j$ ) and their minimum value at 0 (when all song elements present in record  $i$  appear in record  $j$ ).  $M_i^{R_j}$  and  $M_j^{R_i}$  can be

estimated in two ways (see Nichols et al. 1998a for details). Briefly, the first approach uses song element occurrence data for the members of  $R_i$  or  $R_j$  that were also observed in record  $j$  or  $i$ . The other method is based on average detection probability estimation for record  $j$  or  $i$ , followed by an application of these estimates to the number of song elements in record  $j$  or  $i$  that were also observed in record  $i$  or  $j$ . The first approach requires fewer assumptions and should have smaller bias and larger variance than the second approach (Nichols et al. 1998a).

#### Number of new song elements

We can define  $B_{ij}$  to represent the number of new song elements that are not present at time  $i$ , but that appear in the repertoire later and are present at subsequent time  $j$ . This can be estimated by simply subtracting the estimated number of song elements in period  $j$  that are 'old' (are survivors from period  $i$ ) from the estimated repertoire size of record  $j$ :

$$\hat{B} = \hat{N}_j - \hat{\phi}_{ij} \hat{N}_i$$

The above estimators have been presented to deal with temporal changes in repertoire size, either within individual birds or within populations or other groups of interest. In addition to questions about temporal change, these estimators can be used to estimate relative differences between individuals or groups of individuals. In that case, this can be viewed as analogous to redefining community-dynamic parameters to deal with spatial variation in species richness and community composition (Nichols et al. 1998b).

It is possible to apply the software Comdyn to compute the estimators of rate of increase in species richness, local extinction and turnover, as described by Nichols et al. (1998a). In Comdyn, the estimators of change in repertoire size and composition are based on the use of the jackknife estimator (i.e. they make the assumption that there is heterogeneity in the probability of detecting song elements). Estimates of the difference in repertoire between individuals or groups (relative repertoire size, proportional overlap of song elements, etc.) can also be computed following Nichols et al. (1998b) using Comdyn. If certain data sets (e.g. songs of individuals within different groups) require models other than  $M_n$  (e.g.  $M_{th}$ ), the estimators described above can still be used, but they cannot be computed by the current version of Comdyn.

## DISCUSSION

It is sometimes difficult to estimate the repertoire size of a given bird reliably (Kroodsma 1982), for example not all song elements appear in every song. Capture–recapture models were developed specifically for dealing with variable and unknown detection probabilities and are thus ideally suited for drawing inferences about repertoire size from samples of songs. They have the additional advantage of associated measures of uncertainty (sampling variances) by which results can be judged. The idea of

using capture–recapture techniques from population biology to assess repertoire size was suggested by Catchpole & Slater (1995), and we agree that this approach is reasonable. Here we have described some methods that we believe may be useful for providing inferences about repertoire size and composition.

A few attempts have been made to deal with detection probabilities when drawing inferences about song repertoires. For example, Bertram (1970) defined the '99% repertoire', the minimum number of song elements that could account for 99% of the songs sampled. Half-hour repertoire size was introduced in a study on the song sparrow, *Zonotrichia melodia* (Hiebert et al. 1989), as it could 'represent an ecologically more relevant measure of repertoire size perceived by the listeners'. To assess the repertoire size of the brown thrasher, *Toxostoma rufum*, Kroodsma & Parker (1977) counted the repetition rate of song types by using every 100th song. These procedures may be useful in some specific cases, however, they require very intense recording.

Although we believe that our new methods should be preferable to ad hoc approaches for dealing with detection probabilities, we view them as a first step in the development of a set of methods appropriate for drawing inferences about repertoire size. There are many problems and methodological questions that should be addressed. Regarding methodology, we note that many estimators now exist for estimating abundance (repertoire size) from models with heterogeneous detection probabilities (e.g. Burnham & Overton 1978, 1979; Chao et al. 1992; Mingoti & Meeden 1992; Bunge & Fitzpatrick 1993; Lee & Chao 1994; Norris & Pollock 1996; Pledger 2000). In particular, we believe that the finite mixture models of Norris & Pollock (1996) and Pledger (2000) hold great promise. The advantage of these models is that they are dealt with using standard likelihood methods, permitting maximum likelihood estimation and likelihood-based testing (e.g. likelihood ratio tests) and selection (e.g. Akaike's Information Criterion, Akaike 1973; Burnham & Anderson 1998) methods. We believe that the utility of these finite mixture models for investigating song repertoires should be investigated.

Song element data present special problems that require additional investigation. For example, capture–recapture methods such as those we present assume that the appearance of an element in a particular sampling unit (e.g. song) is independent of the appearance of any other element in that unit. This assumption will not be met in cases of correlated song elements in which one element typically follows another in song, so that songs do not represent random sequences of elements (e.g. Kroodsma 1982). A first point to note is that we suspect that such lack of independence will not influence the point estimates of repertoire size and related parameters of change. Conversely, we expect the variance estimates derived under this assumption to be too small (see similar reasoning in Pollock & Raveling 1982).

In behavioural ecology, besides repertoire size, the determination of temporal and spatial changes and group differences in a secondary sexual character, such as bird song, or a comparison of its expression among different

individuals, can be an important aim (see [Catchpole & Slater 1995](#)). Many experimental situations can be imagined where the scientist intends to follow the effects of a manipulation on song features, to examine seasonal or geographical changes in song composition, to estimate the rate of change in song as an individual ages or following introduction of an immigrant individual into a new group or population, to compare the song of different males with different attributes, or to determine the effect of a playback song.

Our knowledge of the evolution of bird song is confounded by many problems concerning the investigation of the singing behaviour of birds ([MacDougall-Shackleton 1997](#)). The sampling problem, namely how to estimate the repertoire size of different bird species ([Krebs & Kroodsma 1980](#)), is important in comparative studies. Several authors have called for standardization (e.g. [Shiovitz 1975](#); [Thompson et al. 1994](#)), but nomenclature, mode of data collection and methods of analysis still vary ([MacDougall-Shackleton 1997](#)). Although our recommended approach still does not solve the unit problem, arising from species-specific unit definitions, we hope that the use of the species richness estimator on song data will help researchers to conduct comparative studies among species using data from descriptive studies based on the same probabilistic approach to estimate repertoire sizes.

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