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COMDYN: software to study the dynamics of animal communities using a capture–recapture approach

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COMDYN is a set of programs developed for estimation of parameters associated with community dynamics using count data from two locations or time periods. It is Internet-based, allowing remote users either to input their own data, or to use data from the North American Breeding Bird Survey for analysis. COMDYN allows probability of detection to vary among species and among locations and time periods. The basic estimator for species richness underlying all estimators is the jackknife estimator proposed by Burnham and Overton. Estimators are presented for quantities associated with temporal change in species richness, including rate of change in species richness over time, local extinction probability, local species turnover and number of local colonizing species. Estimators are also presented for quantities associated with spatial variation in species richness, including relative richness at two locations and proportion of species present in one location that are also present at a second location. Application of the estimators to species richness estimation has been previously described and justified. The potential applications of these programs are discussed.

In population studies, the need to use probabilistic models to estimate proportions of animals not detected at each sampling occasion is widely recognized. Capture–recapture approaches and software are readily available to population biologists.[1–4] Conversely, at the community level, most published studies use unadjusted counts of species, and do not deal explicitly with the fact that not all species are likely to be detected in the areas or time periods of interest. For instance, most studies on the effect of habitat fragmentation on bird communities compare the number of species detected in different study plots without taking into account potential differences in detectabilities of species among plots.[5,6] However, methods are available to estimate species richness accounting for such problems.[7–9] Failure to account for potential differences in species detectability may produce biased estimates and inappropriate hypothesis tests because:

- communities from different habitats or time periods may be associated with different detection probabilities; and
- the probability of detection is likely to vary strongly among species.

In order to monitor local changes in biodiversity and to investigate specific ecological hypotheses, such as the effect of habitat fragmentation on the dynamics of bird commu-

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nities, estimation procedures taking into account the fact that not all species are detected need to be used.[10–11]

Community attributes can be estimated using closed population models that are commonly used to estimate population abundance.[1,7] Individual species in the community ecology context correspond to individual animals in the population ecology context, hence detections of species in a sample correspond to captures of individual animals. Lists of species detected at different occasions close in time and/or in space may constitute samples of the same community.[12] The community under study is thus a 'population of species', and the total number of species is estimated using the pattern of detection/non-detection obtained over replicated sampling occasions.[7,12–14] The community can include all the species present in a given location at a given time period, or inference can be limited to a subset of species. In relation to the sampling scheme used, the defined community needs to contain species that have a non-null probability of being detected. Many different community sampling schemes permit the use of a capture–recapture approach to estimate species richness.[12–15] Using the robust design approach to estimation,[16] richness estimates for specific subsets of species can be combined to estimate quantities relevant to community dynamics.[14]

All of the available closed population models and corresponding estimators can be applied to community studies, allowing different assumptions about the pattern of detection probabilities (varying among individuals, varying over time and/or including a behavioural response[1]). The CAPTURE program can be used to select the appropriate model for a given data set and then to compute estimates of species richness[17] (see ref. 13 for an application to species richness estimation).

In applying closed population models to bird community data, Boulinier *et al.*[13] showed that model M_h, assuming heterogeneity in probability of detection among species, was by far the model most frequently selected by the CAPTURE model selection procedure. The jackknife estimator of M_h [7,18] has been shown to be robust,[1,19–21] and its use can thus logically be suggested in most community sampling situations.[13] A limiting form of the jackknife estimator permits the use of empirical species abundance distributions (number of individual observed for each species) in place of the pattern of detection/non-detection of species among different sampling occasions.[7]

Nichols *et al.*[14,22] proposed several estimators to study changes in animal communities over time and space. Estimators for quantities associated with temporal change in an animal community include rate of change in species richness over time, local extinction probability, local species turnover, number of local colonizing species, and time-specific probability of local recolonization.[14] Estimators associated with geographic variation include relative species richness of two areas, probabilities of species co-occurrence, and number of species in one area that are not present in the other area.[22]

The COMDYN program was developed to estimate the parameters associated with community dynamics using species presence/absence data from sampling within two locations or time periods. It also incorporates subprograms to estimate species richness using the classical jackknife approach.[7] COMDYN is an Internet-based program that uses a World Wide Web browser as the user interface and conducts the analysis on a SUN workstation at the Patuxent Wildlife Research Center in Laurel, MD, USA. The program has the capability of conducting analyses on user-supplied data sets, but also allows users directly to access and analyse information from the North American Breeding Bird Survey (BBS).[23] The BBS was begun in 1966, and consists of >3000 roadside survey routes located on secondary roads throughout the USA and southern Canada. Each route is 39.4 km long and is surveyed once each year in June. A competent observer conducts 50 3-min point-counts at 0.8-km intervals on the roadside, recording all birds heard and seen during the counts.

The basic estimator[7] for species richness underlying all COMDYN estimators makes the assumption of heterogeneity in species detectability. Application of this estimator to species richness estimation is described and justified by Boulinier *et al.*[13] We used the procedure proposed by Burnham and Overton[7] to select the appropriate order jackknife and to compute the interpolated estimator. The estimators for community-dynamic parameters and their variances are presented by Nichols *et al.*[14,22]

OVERVIEW OF THE COMDYN PROGRAM

COMDYN is a set of programs available for use interactively on the World Wide Web site of the Patuxent Wildlife Research Center (http://www.mbr-pwrc.usgs.gov/comdyn.html), where it can be used:

- to compute estimates of species richness and community dynamics parameters from data input by the user; and
- directly to carry out analyses on North American bird communities using data from the North American Breeding Bird Survey (BBS).

The main set of subprograms of COMDYN focuses on computing estimates of parameters reflecting spatial and temporal changes in communities, based on the estimators described in Nichols *et al.*[14,22] The first three subprograms allow users to conduct analyses using BBS data to estimate and compare community attributes between any two survey routes and/or years. The fourth subprogram computes estimators from summary data that can be input by the user.

COMDYN1 computes species richness and parameters of community change (rate of increase in species richness, local extinction rate, species turnover, and number of locally colonizing species) for any two BBS routes/years using all species recorded on the BBS routes. COMDYN1 uses a bootstrap approach to compute standard errors and confidence intervals for the different estimates.[14,22]

COMDYN2 computes the same parameters describing community change between two BBS routes/years, but for two subsets of forest-breeding bird species; species categorized as 'area sensitive' or 'non-area sensitive' according to the study carried out by Robbins *et al.*[24] in the Middle Atlantic states of the USA.

COMDYN3 also computes the parameters describing community change between two BBS routes/years, but for groupings of species that can be defined by the user from the list of species names. Often, groups of species are of particular management interest (for example, grassland-breeding birds and neotropical migrant birds are of particular conservation interest in North America[23]), and COMDYN3 permits estimation for these groupings.

COMDYN4 accepts summary data input by the user and computes the parameters describing community change between two locations and/or time periods. This program requires the user to summarize detection pattern information from presence/absence data. Required summary statistics include the total number of species detected and the number of these detected exactly one, two, three, four and five times at both locations and/or time periods. Required summary statistics also include the total number of species detected at one location and/or time period that were also detected at the other location and/or time period (and reciprocally), as well as the number of species in these subsets (of species detected in the other location/period) detected exactly one, two, three, four and five times.

A second set of two subprograms computes species richness estimates from user input data from a single sample location or time period using the jackknife approach proposed by Burnham and Overton.[7,18] The SPECRICH program computes the limiting form of the jackknife,[7] which can be used in cases where there is no information on the number of detection/capture occasions but when the number of individuals detected for each species is available. The SPECRICH2 program computes the jackknife estimator of Burnham and Overton[7] when the number of detection/capture occasions for a given community is known.[7]

COMPUTING SPECIES RICHNESS ESTIMATES

Two types of estimators are used in the program to estimate species richness. Both estimators make the assumption of heterogeneity in species detectability (corresponding to model M_h).

SPECRICH

SPECRICH computes species richness using the limiting form of the jackknife estimator described by Burnham and Overton.[7] This method is based on sampling at a single time and location. It uses the number of species for which exactly one, two, three, ..., five individuals are seen, and the total number of species seen. The program first asks the user to input this information. A set of default values is

provided as an example of the kind of input data needed. If any of the input data cells are left blank, the program will treat them as '0' values. The program computes and outputs the interpolated jackknife estimate of species richness, its standard error, and a table with details dealing with the jackknife order selection procedure. In the table, the first column provides the order (K) of each computed jackknife estimator; the second and third columns provide the corresponding jackknife estimates and their standard errors; and the fourth and fifth columns report the test statistics and associated P values used to select the order of the jackknife estimate (see ref. 7, page 929).

SPECRICH2

SPECRICH2 computes species richness using the jackknife estimator described in Burnham and Overton[7] and implemented in the program CAPTURE.[17] This method uses summary information on species detected and not detected on a series of sampling occasions of the same community. The sampling occasions associated with a given community can be repeated samples from the same site, or a series of samples carried out at different sites situated within the area corresponding to the community under study.[12,13] To compute the estimator and its standard error, the program requires as input the f_i (i.e. the number of species detected at exactly $i = 1, ..., K$ sites/occasions, where K is the total number of sites/occasions; K must be at least 2). To compute a goodness-of-fit test of model M_h against the alternative of not model M_h,[1] the program requires the n_i, the numbers of species detected on site/occasion $i = 1, ..., K$. As for SPECRICH, a set of input values is provided by default, and the program produces one page of output. If some of the input data are inconsistent, the results page will contain asterisks (****) to warn the user. The output recalls the total number of species detected, the f_i and the n_i, and gives the estimate of species richness and its standard error. The χ^2 and P values of the goodness-of-fit test are also reported.

The estimator of species richness computed in SPECRICH2 is also the basic estimator used in the four subprograms of COMDYN computing the parameters describing community dynamics, and the COMDYN input and output files thus follow the same global format.

COMPUTING PARAMETERS DESCRIBING COMMUNITY DYNAMICS

Required data and possible computations

Most of the proposed estimators deal with changes in communities between two points in time[14] or space[22] and are based on Pollock's robust design.[16] In the current version of COMDYN, only data in the form of summary patterns of detection/non-detection of species in the two corresponding sets of sampling occasions may be used.

Before using COMDYN4 (the general program that allows user input of data), the user must summarize the data (either manually, or by using a program such as CAPTURE) in the form of a table basically including four parts:

- the f_i and n_i at the first location or time period;
- the f_i and n_i at the second location or time period for the subset of species detected in the first location or time period;
- the f_i and n_i at the second location or time period;
- the f_i and n_i at the first location or time period for the subset of species detected in the second location or time period.

In program COMDYN4, the program first requires the number of sampling sites/occasions for which data are available for sampling associated with the two communities (by default these are both set at 5; they may differ from one another). The program then creates the corresponding input file. The user has then to input the total numbers of species detected for each community (corresponding to 'Sample1' and 'Sample2'), the numbers of species detected in both communities (corresponding to 'Subset1' and 'Subset2'), and the different series of f_i and n_i. The program does not request exact f_i for $i > 5$ because only the first- to fifth-order jackknife estimators are computed (all detected species must nevertheless appear somewhere among the f_i). If $K < 5$ then only f_i to f_K will be requested. The order of the interpolated estimators selected are almost always < 3.[7,13] Number of species detected at each occasion, n_i ($i = 1, ..., K$), are needed to compute the goodness-of-fit tests. As for the other subprograms, it is possible to change the default number of iterations for the

bootstrap estimator and for the random number seed used in the bootstrap procedure.

The output provides information on species richness estimation for the two main samples and the two subsets (see the section on 'Computing species richness estimates'). Other parts of the output and their meanings are described below, and Fig. 1 shows the output obtained after running the input corresponding to the BBS survey route number 1 of Wisconsin between 1970 and 1990 when steps are analysed in groups of 10.

Programs COMDYN1–3 compute estimates of parameters describing changes in time or space

COMDYN4 – COMMUNITY DYNAMICS PROGRAM

iterations for bootstrap: 200 seed number: 54321

Sample 1:

Total species observed, R(1) = 66
Observed frequencies, f(i) = 17 19 9 10 11
Species richness, N(l) = 77, SE(N(1)) = 5.10760307
Observed species, n(i) = 34 35 38 34 36
M(h) GOF test: Chi-square = 0.812 df = 4 Prob = 0.9369

Sample 2:

Total species observed, R(2) = 80
Observed frequencies, f(i) = 23 15 9 12 21
Species richness, N(2) = 99, SE(N(2)) = 5.75499725
Observed species, n(i) = 41 46 52 48 46
M(h) GOF test: Chi-square = 4.451 df = 4 Prob = 0.3484

Test for unequal p's

Observed frequencies, f(i):
17. 19. 9. 10. 11.
23. 15. 9. 12. 21.
Expected values:
18.0821915 15.3698626 8.13698673 9.94520569 14.4657536
21.9178085 18.6301365 9.86301327 12.0547943 17.5342464
Total Chi-square: 3.36588985
Degrees of freedom: 4
Probability: 0.498560754

Subset 1:

Subset of species observed in Sample 2 that were also observed in Sample 1. Total species observed, m2(R1) = 57
Observed frequencies, f(i) = 9 10 6 11 21
Species richness estimate, M2(R1) = 61, SE(M2(R1)) = 3.71264982
Observed species, n(i) = 33 38 45 40 40
M(h) GOF test: Chi-square = 8.500 df= 4 Prob = 0.0749

Subset 2:

Subset of species observed in Sample 1 that were also observed in Sample 2. Total species observed, m1(R2) = 57
Observed frequencies, f(i) = 10 17 9 10 11
Species richness estimate, M1(R2) = 62, SE(M1(R2)) = 3.90882826
Observed species, n(i) = 31 34 36 31 34
M(h) GOF test: Chi-square = 1.593 df= 4 Prob = 0.8100

continued

Figure 1. Output of COMDYN4. The output corresponds to the input corresponding to changes in the total bird community sampled on Wisconsin BBS survey route number 001 between 1970 and 1990 (see COMDYN1).

Figure 1 *continued*

Parameter estimates

				95% confidence interval	
parameter	data estimate	bootstrap average	standard error	lower	upper
N(1)	77.22	78.00	6.11	67.83	88.97
N(2)	99.92	102.81	11.56	85.37	130.62
M2(R1)	61.57	61.86	4.11	54.24	70.23
M1(R2)	62.52	63.53	5.47	53.60	74.47
PHI	0.9329	0.9278	0.0636	0.7864	1.0000
GAMMA	0.7815	0.7918	0.0785	0.6439	0.9673
LAMBDA	1.2940	1.3257	0.1808	1.0396	1.8058
altLAMBDA	1.2121	1.2197	0.0765	1.0714	1.3770
B	27.88	30.63	12.77	11.55	61.32
p(l)	0.8548	0.8509	0.0617	0.7360	0.9722
p(2)	0.8007	0.7872	0.0821	0.6098	0.9299

Definitions:

R(l): Number of species observed in Sample 1
R(2): Number of species observed in Sample 2
f(i): Observed frequencies – number of species observed at exactly i sites/occasions
n(i): Observed species – number of species observed at the ith site/occasion
N(1): Estimated number of species present in Sample 1
N(2): Number of species present in Sample 2
M2(Rl): Estimated number of species present in Sample 2 which were observed in Sample 1
M1(R2): Estimated number of species present in Sample 1 which were observed in Sample 2
PHI: Estimated complement of extinction probability – proportion of Sample 1 species still present in Sample 2
GAMMA: Estimated complement of species turnover – proportion of Sample 2 species present in Sample 1
LAMBDA: Estimated rate of change of species richness estimated as N(2)/N(l)
altLAMBDA: Estimated rate of change of species richness estimated using alternate method, R(2)/R(l)
B: Estimated local colonizing species – number of species not present in Sample 1, but present in Sample 2
p(l): Estimated species detection probability in Sample 1
p(2): Estimated species detection probability in Sample 2
95% confidence interval computed by ordering bootstrap replicate estimates and using the values ranked at 2.5% and 97.5%
top of printout
Back to input screen

using data from the BBS.[23] Data are summarized for each route in five lists of species detected on each group of ten point counts. In Boulinier *et al.*[13] and Nichols *et al.*,[14,22] the sampling scheme used to estimate community parameters associated with a given BBS survey route in a given year considers the five summaries of ten stops as five sampling replicates of that community. It is also proposed to analyse stops individually. The availability of this data set associated with COMDYN should allow researchers to carry out bird community studies at the landscape scale (the locations of all routes are clearly identified). Information on yearly abundance of species and population trends have been already made available on the Internet, and potential users may want to look at the BBS World Wide Web home page for a detailed description of the data and their general availability (http://www.mbr-pwrc.usgs.gov/bbs/bbs.html).

Test for equal detection probabilities

All the COMDYN programs perform a test of equal detection probabilities between the two

sampling sessions ('Test for unequal *ps*'). The test is a contingency χ^2 test comparing the f_i of the two sessions.[14] The expected f_i under the null hypothesis of equal detection probabilities, the χ^2 value, the degrees of freedom and the associated *P* value are provided. Small values of *P* (e.g. $P < 0.05$) provide evidence of a difference in the detection probabilities between the two sessions. This test may be used to decide among alternative estimators of the rate of increase in species richness (see below and refs 14–22). For the case presented in Fig. 1, there is no evidence of a difference between the species detection probabilities in 1970 and 1990 ($\chi^2 = 3.37$; $df = 4$; $P = 0.50$).

Temporal variations of communities

The various parameter estimates are given in the first column of the output table. The bootstrap standard errors and 95% confidence intervals of each estimate are also provided. They are computed following the method described in Nichols *et al.*[14] The bootstrap average of each estimate is also reported. The first four lines of the table deal with the species richness estimates of the two sessions and corresponding subsets (see above).

Rate of increase in species richness

The parameter *LAMBDA* is an estimate of the rate of increase of species richness of the community between the two points in time.[14] It is the ratio of the estimated number of species present at time 2 to the estimated number of species present at time 1. In the event that the detection probabilities are not different between the two time periods, *altLAMBDA* (the ratio of the actual number of species detected at time 2 to the number of species detected at time 1) may be used as to estimate the rate of increase in species richness.[14]

Local extinction probability

The parameter *PHI* is an estimate of the proportion of species still present at time 2 among those that were present at time 1. It is computed as the number of species detected at time 1 that are estimated to be present at time 2, divided by the number of species detected at time 1. 1 – *PHI* is thus an estimate of the local extinction probability of species between time 1 and time 2.

Species turnover

The parameter *GAMMA* is an estimate of the proportion of species present at time 2 that were also present at time 1. It is computed as the estimated number of species detected at time 2 that are present at time 1, divided by the number of species detected at time 2. 1 – *GAMMA* is thus an estimate of the species turnover, defined here as the proportion of species present at time 2 that are 'new' in the sense that they were not present in the community at time 1.[14]

Number of locally colonizing species

The quantity *B* is an estimate of the number of species present in the community at time 2 that were not present at time 1. *B* is computed as the number of species estimated to be present at time 2 minus the product of the number of species estimated to be present at time 1 and *PHI*. It is analogous to the recruitment parameter in population models.[14]

A general interpretation of the output presented in Fig. 1 is thus that the rate of increase in species richness of the local community between 1970 and 1990 is greater than 1. As detectabilities were not different between the two years ($P = 0.50$), the alternative estimate of the rate of increase in species richness can be used (1.21, with a standard error of 0.08). This estimate is based on the actual number of species detected at the two dates and is more precise than the one based on the ratio of the two estimates of species richness (as shown by the comparison of the 95% confidence intervals of the two estimates). Between 1970 and 1990 the rate of local extinction (1 – *PHI* = 0.07) was not different from 0 (95% CI for *PHI* includes 1.00), but the local species turnover was significant. Among the species estimated to be present in 1990, the proportion estimated to be locally new (not present in 1970) is 0.22 (95% CI for *GAMMA* does not include 1.00). The estimated number of locally colonizing species in the time interval was 28 (95% CI, 12–61).

Spatial variation of communities

When the two sampling sessions correspond to different communities in space, the parameters described above are still of interest.[22] In the spatial context, *LAMBDA* becomes an estimate of the relative species richness of area 2 relative to area 1.[22] Parameters *PHI* and *GAMMA* reflect

the probabilities of species co-occurrence depending on the order of the change considered[22] (e.g. PHI estimates the probability that a species occurring in community 1 also occurred in community 2). *B* estimates the number of species in area 2 that are not present in area 1.[22]

CONCLUSION

The COMDYN program is available interactively on the Internet and permits computations of parameters useful in the study of animal communities. Most of these estimators have been proposed recently,[14,22] and their availability permits the development of analyses that concern community change, but that do not require restrictive assumptions about species being detected with probability 1. They could also be applied to plant communities, where the probability of detecting individuals and species is also not necessarily 1.[25] Preliminary results of simulation studies of the performance of these estimators on known communities suggest that they perform well. Such investigations may nevertheless lead to further refinements and revisions of COMDYN. In addition, it may be that other estimators than those based on M_h are needed in some sampling situations,[13] and these could be incorporated into the software. Nevertheless, the current framework represents a reasonable approach for the estimation of parameters describing community change, and we hope that it will be useful for studying changes of biodiversity in time and space.[10,14,22]

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REFERENCES

1. Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978) Statistical inference from capture data on closed animal populations. *Wildl. Monog.* **62**, 1–135.
2. Pollock, K.H., Nichols, J.D., Brownie C. & Hines, J.E. (1990) Statistical inference for capture–recapture experiments. *Wildl. Monog.* **107**, 1–97.
3. Nichols, J.D. (1992) Capture–recapture models: using marked animals to study population dynamics. *BioScience*, **42**, 94–102.
4. Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.*, **62**, 67–118.
5. Greenberg, R., Bichier, P., Agon, A.C. & Reitsma, R. (1997) Bird populations in shade and sun coffee plantations in Central Guatemala. *Conserv. Biol.*, **11**, 448–459.
6. Wilson, C.J., Reid, R.S., Stanton, N.L. & Perry, B.D. (1997) Effects of land-use and Tsetse fly control on bird species richness in Southwestern Ethiopia. *Conserv. Biol.*, **11**, 435–447.
7. Burnham, K.P. & Overton, W.S. (1979) Robust estimation of population size when capture probabilities vary among animals. *Ecology*, **60**, 927–936.
8. Bunge, J. & Fitzpartrick, M. (1993) Estimating the number of species: a review. *J. Am. Stat. Assoc.*, **88**, 364–373.
9. Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. R. Soc. Lond. B*, **345**, 101–118.
10. Rosenzweig, M.L. (1996) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
11. Gaston, K.J. (1996) Species richness: measure and measurement, In *Biodiverstity. A Biology of Numbers and Differences* (ed. K.J. Gaston) pp. 77–113. Blackwell Science, Oxford.
12. Nichols, J.D. & Conroy, M.J. (1996) Estimation of species richness, In *Measuring and Monitoring Biological Diversity. Standard Methods for Mammals.* (eds D.E. Wilson, F.R. Cole, J.D. Nichols, R. Rudran & M. Foster) pp. 226–234. Smithsonian Institution Press, Washington, DC.
13. Boulinier, T. Nichols, J.D., Sauer, J.R., Hines, J.E. & Pollock, K.H. (1998) Estimating species richness: the importance of heterogeneity in species detectability. *Ecology*, **79**, 1018–1028.
14. Nichols, J.D., Boulinier, T., Hines, J.E., Pollock, K.H. & Sauer, J.R. (in press) Estimating rates of local species extinction, colonisation and turnover in animal communities. *Ecological Applications.*
15. Dawson, D.K., Sauer, J.R., Wood, P.A., Berlanga, M., Wilson, M.H. & Robbins, C.S. (1995) Estimating bird species richness from capture and count data. *J. Appl. Stat.*, **22**, 1063–1068.
16. Pollock, K.H. (1982) A capture–recapture sampling design robust to unequal catchability. *J. Wildl. Manage.*, **46**, 752–757.
17. Rexstad, E. & Burnham, K. (1991) *User's Guide for Interactive Program CAPTURE. Abundance Estimation of Closed Animal Populations.* Colorado State University , Fort Collins, Colorado, USA.
18. Burnham, K.P. & Overton, W.S. (1978) Estimation

of the size of a closed population when capture probabilities vary among animals. *Biometrika*, **65**, 625–633.
19. Pollock, K.H. & Otto, M.C. (1983) Robust estimation of population size in closed animal population from capture–recapture experiments. *Biometrics*, **39**, 1035–1049.
20. Lee, S.-M. & Chao, A. (1994) Estimating population size via sample coverage for closed capture–recapture models. *Biometrics*, **50**, 88–97.
21. Norris, J.L. III & Pollock, K.H. (1996) Nonparametric MLE under two closed capture-recpature models with heterogeneity. *Biometrics*, **52**, 639–649.
22. Nichols, J.D., Boulinier, T., Hines, J.E., Pollock, K.H. & Sauer, J.R. (in press) Inference methods for spatial variation in species richness and community composition when not all species are detected. *Conserv. Biol.*
23. Peterjohn, B.G. & Sauer, J.R. (1993) North American breeding bird survey annual summary 1990–1991. *Bird Populations*, **1**, 1–15.
24. Robbins, C.S., Dawson, D.K. & Dowell, B.A. (1989) Habitat area requirements of breeding forest birds of the middle Atlantic states. *Wildl. Monogr.*, **103**, 1–34.
25. Alexander, H.M., Slade, N.A. & Kettle, W.D. (1997) Application of mark-recapture models to estimation of the population size of plants. *Ecology*, **78**, 1230–1237.