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Identifying sources of heterogeneity in capture probabilities: an example using the Great Tit *Parus major*

JUAN CARLOS SENAR[1*], MICHAEL J. CONROY [2], LUIS M. CARRASCAL[3], JORDI DOMÈNECH[1], INGRID MOZETICH[3] *and* FRANCESC URIBE[1] [1]*Museu de Zoologia, Ap. Correus 593, 08080 Barcelona, Spain,* [2]*US Geological Survey, Biological Resources Division, Georgia Cooperative Fish and Wildlife Research Unit, GA, USA and* [3]*Department of Ecology and Evolution, National Museum of Natural Science, José Gutiérrez Abascal 2, 28006 Madrid, Spain*

Heterogeneous capture probabilities are a common problem in many capture–recapture studies. Several methods of detecting the presence of such heterogeneity are currently available, and stratification of data has been suggested as the standard method to avoid its effects. However, few studies have tried to identify sources of heterogeneity, or whether there are interactions among sources. The aim of this paper is to suggest an analytical procedure to identify sources of capture heterogeneity. We use data on the sex and age of Great Tits captured in baited funnel traps, at two localities differing in average temperature. We additionally use 'recapture' data obtained by videotaping at a feeder (with no associated trap), where the tits ringed with different colours were recorded. This allowed us to test whether individuals in different classes (age, sex and condition) are not trapped because of trap shyness or because of a reduced use of the bait. We used logistic regression analysis of the capture probabilities to test for the effects of age, sex, condition, location and 'recapture' method. The results showed a higher recapture probability in the colder locality. Yearling birds (either males or females) had the highest recapture probabilities, followed by adult males, while adult females had the lowest recapture probabilities. There was no effect of the method of 'recapture' (trap or videotape), which suggests that adult females are less often captured in traps not because of trap-shyness but because of less dependence on supplementary food. The potential use of this methodological approach in other studies is discussed.

An important assumption of many capture–recapture studies is that all the animals in the population have equal capture probabilities, at least in the first sample.[1] However, several studies of birds have shown that all individuals in a population are not equally catchable (i.e. heterogeneity of capture probabilities).[1,2] Several methods are currently available to detect the presence of heterogeneity in capture probabilities.[1,3,4] Stratification of data has been suggested as a standard method to avoid its effects, provided that capture probabilities differ among identifiable subgroups of animals,[1] and for closed populations robust estimation procedures are available.[5] However, few studies have attempted to identify sources of heterogeneity and interactions among the sources. The aim of this paper is to suggest an analytical procedure

*Correspondence author.
E-mail: jcsenar@intercom.es

to identify some of the sources of heterogeneity in capture probabilities.

METHODS

We used data on sex, age and body condition of Great Tits *Parus major* captured in funnel traps baited with peanuts. Great Tits used in this study were trapped in the winter of 1994–95 at two localities: Sarria (Barcelona, northeast Spain), a typical mild weather Mediterranean area at sea level, and Ventorrillo (Madrid, central Spain) a mountainous (1500 m asl) cold continental area. The two localities also differed in the availability of natural food (four times more arthropods in Barcelona than in Madrid). In total, 36 Great Tits were captured in Barcelona, across six trapping occasions, during the first half of March 1995. In Madrid we captured a total of 31 birds, on nine trapping occasions during the first half of November 1994. On capture, each bird was given a numbered aluminium ring and a unique combination of three colour rings. For each bird we recorded sex and age,[6,7] body mass (to 0.1 g, with a digital balance), pectoral muscle thickness, measured with a portable Krautkramer ultrasound device,[8] and tarsus-length (to 0.1 mm with a digital caliper). Body mass and pectoral muscle depth were standardized for size[9,10] (i.e. tarsus), so that a short- and a long-term measure of body condition were obtained.

Capture histories were analysed with the program CAPTURE[3] to test for sources of variation in capture probabilities. Specifically, we were interested in whether capture probabilities varied only among individuals and sites (site-stratified model M_h), as opposed to a behavioural response to capture (models M_b, M_{bh}) or varying over time (models M_t, M_{th}, M_{tb}, M_{tbh}).[a] If these latter factors could be ruled out, analysis would be considerably simplified, as seen below.

In this situation, simple methods can be used to relate the proportion of times an individual animal is captured to individual attributes and sites. Given the short trapping period, we considered that the population was closed to additions and deletions. Model selection criteria used within CAPTURE are based on goodness-of-fit tests and tests between models.[1]

In addition to capture–recapture data, we used resighting data obtained by videotaping at a feeder (with no associated trap), where the different colour-ringed tits were recorded. This allowed us to test whether individuals in different classes (age, sex and condition) were not trapped because of differential trap shyness, or because of a reduced use of the bait. These data were not analysed with CAPTURE, but were used in the logistic regression approach (see later). The videotape observations were treated as separate occasions interspersed among capture occasions.

If model M_h is appropriate,[5] then the analysis is based only on the frequency of captures, i.e. the number of animals caught once, twice, etc. We used logistic regression analysis to model the response of the number of captures for each animal, as a proportion of the total number of capture occasions, to test for the effects of age (yearling versus adult), sex, mass, muscle condition, location (mild versus cold weather) and 'recapture' method (true capture versus videotape recording). We used the proportion of days on which an individual bird was captured as the response variable, instead of the typical binary response variable normally used in logistic regression analyses. We therefore performed analyses with binomial errors and a logit link function. We constructed all six possible variable models using the above factors and evaluated them using AIC.[11] Based on these results we then added interaction terms and evaluated these by AIC.

RESULTS

Barcelona capture–recapture data, analysed with CAPTURE, showed significant heterogeneity in capture probabilities (Table 1). No behavioural or time-specific variation in trapping probabilities was detected. The same result was obtained with the Madrid data (Table 1). For both localities, the model selection criteria strongly suggested the heterogeneity model (Table 2). Using the jackknife estimator we estimated a population size of 64 (se = ±10.9) Great Tits for Barcelona, and 42 (se = ±6.6) for Madrid. Average recapture probabilities on individual trapping occasions were 0.20 for Barcelona birds, and 0.28 for Madrid.

We evaluated 68 logistic regression models of capture probability including the factors age, sex, mass, muscle thickness, locality and obser-

Table 1. Model selection results from the analyses of Great Tit capture–recapture data (program CAPTURE) based on trapping, according to locality (Barcelona versus Madrid). Models 'not M_h' and 'not M_b' refer to the alternative hypotheses that data do not fit these models, compared with the null hypothesis of fit. χ^2 values are for likelihood-ratio tests between models.

Models tested	χ^2	*df*	P
Barcelona			
M_0 vs. M_h	9.12	2	0.01
M_0 vs. M_b	1.89	1	0.17
M_0 vs. M_t	5.46	5	0.36
M_h vs. not M_h	5.21	5	0.39
M_b vs. not M_b	9.43	8	0.31
M_h vs. M_{bh}	3.81	7	0.80
Madrid			
M_0 vs. M_h	54.51	3	<0.001
M_0 vs. M_b	0.03	1	0.87
M_0 vs. M_t	4.50	8	0.81
M_h vs. not M_h	5.55	8	0.70
M_b vs. not M_b	7.61	11	0.75
M_h vs. M_{bh}	6.91	8	0.54

vation method, and several interaction terms (see Table 3). Based on AIC, the best model included locality, age, sex and the interaction between sex and age (Table 3); all other models had AIC values more than four times that for the best model, which exceeds the two to three times minimal difference considered to represent substantial improvement in model performance (D.R. Anderson, pers. comm.). Great Tits showed a higher recapture probability in Madrid. Yearling birds (either males or females) had higher recapture probabilities, followed by adult males and, lowest, adult females (Fig. 1). There was no effect either of body mass, or recapture method (trap or videotape).

Table 2. Model selection criteria for trapping data for both localities as displayed by program CAPTURE. Values are obtained from a special application of multivariate discriminant function analysis. The populations are the eight models and the measurements are the significance levels from the seven tests. The objective of the discriminant analysis is to weight and linearly combine the significance levels of the seven tests in some fashion so that the models are forced to be as statistically distinct as possible. The 'best' model, which should be selected, is the one with the maximum value from the discriminant function (in this case M_h). See Otis *et al.*[5]

Model	*Barcelona*	*Madrid*
M_0	0.90	0.89
M_h	1.00	1.00
M_b	0.50	0.27
M_{bh}	0.67	0.45
M_t	0.00	0.00
M_{th}	0.55	0.33
M_{tb}	0.42	0.31
M_{tbh}	0.79	0.57

Table 3. Ranking, by AIC, of the best 10 models out of 68 fitted for testing effects of individual animal attributes, location, and method (capture or video) on capture frequency of Great Tit.

Model rank	*Variables included*	AIC
1	Sex Age Location Sex×Age	1402.31
2	Sex Age Location	1406.82
3	Sex Age Location Sex×Location	1408.06
4	Sex Age WBC Location	1408.59
5	Sex Age Location Age×Location	1408.60
6	Sex Age MBC Location	1408.72
7	Sex Age WBC Location Method	1410.34
8	Sex Age MBC Location Method	1410.44
9	Age Location	1410.53
10	Sex Age WBC MBC Location	1410.58

Sex, male or female; Age, juvenile or adult; WBC, mass body condition; MBC, muscle body condition; Location, Barcelona or Madrid; Method, capture or video.

DISCUSSION

There are many kinds of trapping device available.[12–14] Several of them rely on bait, since this attracts a large number of animals to the trap. However, it is generally known that the use of bait may lead to several types of trap response.[1,2,15] Distinguishing differential trap response between different classes from true heterogeneity (e.g. differential use of bait) is more difficult. However, the lack of an effect of recapture method (trap or videotape) on capture probabilities suggests certain animals are captured less frequently not because of differential trap response, but because of a reduced use of supplementary food. Thus, yearling Great Tits were found to use feeders more heavily than adults. Adult females were least dependent on food supplementation. The

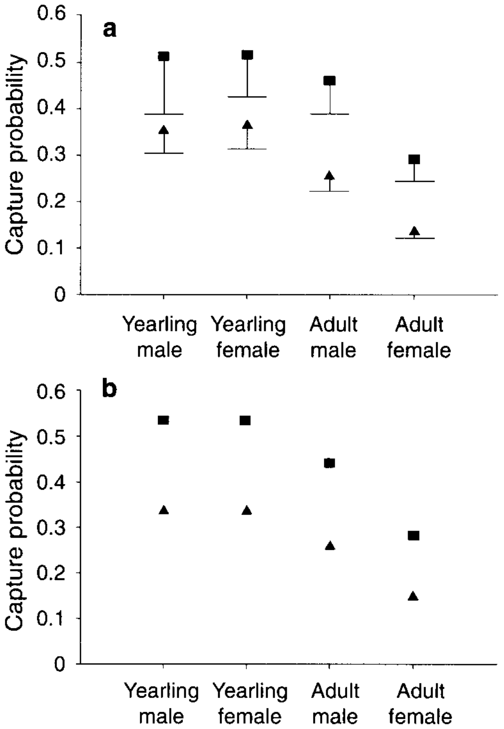

Figure 1. Variation in capture probabilities according to locality, sex and age. (a) Observed values and standard errors; (b) predicted values. ▲, Barcelona; ■, Madrid.

Madrid trap site had higher recapture probabilities, presumably because of lower availability of natural food, lower temperatures or both. The difference between the two sites may be confounded with the time of the year, since Madrid birds were trapped in November and Barcelona ones in March. However, since inter-locality differences in food availability and temperature was much higher than that between periods within a locality (pers. obs.), we think that the confounding effect is minimal. Additionally, any confounding effect of this kind would not change our main conclusion that capture probabilities are not fixed within each sex or age class, but may vary among individuals and between different samples.

These results are not surprising, but a review of the literature shows that the direction of the differences in capture probability varies among species and even localities.[16] For instance, Black-capped Chickadees *Parus atricapillus* do not show sex or age differences in the use of feeders, and ambient temperature has no apparent effect.[17] In Britain, female Great Tits use supplementary food more than males,[18] whereas in The Netherlands it is adults which mostly take advantage of this additional energy supply.[19] Thus it is important to consider both the possibility that a given trapping method results in heterogeneity of capture probabilities (and thus biases in estimates), as well as to identify the likely sources of heterogeneity, as these may differ among species, study sites and populations. Trapping heterogeneity (or 'bias') is not necessarily a problem, provided it is taken into account in study design and analyses.[20] Our approach is simple, it was powerful enough to detect interactions in this study and it may be valuable to other capture–recapture studies.

Variation in capture probabilities between sites because of climatic differences, and within sites because of individual attributes (sex and age), reaffirms the importance of proper incorporation of capture probabilities into estimation of demographic parameters, in lieu of *ad hoc* estimation.[1] Knowledge of the sources of this variation can be useful in study design, for example in utilizing Pollock's robust design[1] incorporating both open and closed capture–recapture models. Knowledge that individual and site-specific factors may influence capture probabilities also makes it important to record these factors, and where possible to incorporate them as covariates to reduce the variability of estimates of the parameters of primary interest, such as abundance[21] or survival rates.[22]

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ENDNOTE

a. The different models in CAPTURE differ in the manner in which capture probability is modelled. M_0 assumes that every animal in the population has the same probability of capture for each sampling period. M_h allows heterogeneity but no trap response, and assumes that each animal has its own unique capture probability which remains constant over all the sampling times. M_b allows trap response but no heterogeneity or temporal variation. M_t assumes that capture probabilities vary only with time, but does not allow heterogeneity or trap response and assumes that every animal in the population has the same probability of capture at each sampling period. The other models are combinations of previous one-factor models: for instance, M_{bh} allows for both heterogeneity and trap response and assumes that capture probabilities remain constant over all sampling times.[1,3]

REFERENCES

1. Pollock, K.H., Nichols, J.D., Brownie, C. & Hines, J.E. (1990) Statistical inference for capture–recapture experiments. *Wildl. Monogr.*, **107**, 1–97.
2. Nichols, J.D., Noon, B.R., Stokes, S.L. & Hines, J.E. (1981) Remarks on the use of mark–recapture methodology in estimating avian population size. In *Estimating Numbers of Terrestial Birds* (eds C.J. Ralph & J.M. Scott), pp. 121–136. Studies in Avian Biology no. 6, Cooper Ornithological Society, Lawrence, KS.
3. White, G.C., Anderson, D.R., Burnham, K.P. & Otis, D.L. (1982) *Capture–Recapture and Removal Methods for Sampling Closed Populations*. Los Alamos National Laboratory, LA 8787-NERP, Los Alamos, NM.
4. Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. & Pollock, K.H. (1987) *Design and Analysis Methods for Fish Survival Experiments Based on Release-Recapture*. American Fisheries Society, Monograph 5, Bethesda, MD.
5. Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978) Statistical inference from capture data on closed animal populations. *Wildl. Monogr.*, **62**, 1–135.
6. Svensson, L. (1992) *Identification Guide to European Passerines*. L. Svensson, Stockholm.
7. Jenni, L. & Winkler, R. (1994) *Moult and Ageing of European Passerines*. Academic Press, London.
8. Newton, S.F. (1993) Body condition of a small passerine bird: ultrasonic assessment and significance in overwinter survival. *J. Zool. Lond. (A)*, **229**, 561–580.
9. Senar, J.C., Lleonart, J. & Metcalfe, N.B. (1994) Wing-shape variation between resident and transient wintering Siskins *Carduelis spinus*. *J. Avian Biol.*, **25**, 50–54.
10. Pilastro, A., Bertorelle, G. & Marin, G. (1995) Winter fattening strategies of two passerine species: environmental and social influences. *J. Avian Biol.*, **26**, 25–32.
11. Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle, In *International Symposium on Information Theory* (eds B.N. Petran & F. Csaki), pp. 267–281. Akademiai Kiadi, Budapest.
12. Bateman, J.A. (1979) *Trapping. A Practical Guide*. David & Charles, London.
13. Davis, P.G. (1981) *Trapping Methods for Bird Ringers*. BTO, Tring.
14. McClure, H.E. (1984) *Bird Banding*. Boxwood Press, Pacific Grove.
15. Pollock, K.H. (1981) Capture–recapture models: a review of current methods, assumptions, and experimental design. In *Estimating Numbers of Terrestial Birds* (eds C.J. Ralph & J.M. Scott), pp. 426–435. Studies in Avian Biology no. 6, Cooper Onithological Society, Lawrence, KS.
16. Boutin, S. (1990) Food supplementation experiments with terrestial vertebrates: patterns, problems, and the future. *Can. J. Zool.*, **68**, 203–220.
17. Brittingham, M.C. & Temple, S.A. (1992) Use of winter bird feeders by Black-capped Chickadees. *J. Wildl. Manage.*, **56**, 103–110.
18. Gosler, A.G. (1993) *The Great Tit*. Hamlyn, London.
19. Balen, J.H.V. (1980) Population fluctuations of the great tit and feeding conditions in winter. *Ardea*, **68**, 143–164.
20. Weatherhead, P.J. & Greenwood, H. (1981) Age and condition bias of decoy-trapped birds. *J. Field Ornithol.*, **52**, 10–15.
21. Huggins, R.M. (1989) On the statistical analysis of capture experiments. *Biometrika*, **76**, 133–140.
22. Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modeling survival and testing biological hypothesis using marked animals: a unified approach with case studies. *Ecol. Monogr.*, **62**, 67–118.