Comparison of survival estimates obtained from three different methods of recapture in the same population of the great tit

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SUMMARY *Recaptures of marked birds can be used to estimate their survival. We suspect that the various methods of capture might not be equally suited for this purpose. In the long-term study of the great tit at our institute, recaptures were routinely made in three different ways: capture of parents feeding their young at the nest; capture of birds roosting in nest-boxes; mist-netting. We analyzed 20 years of captures from the study site at the Hoge Veluwe to obtain estimates of adult survival and capture rates from captures obtained by each method. The three sets of estimates differ and our analyses suggest that the best method was the capture of breeding birds, while mist-netting was the least suitable.*

1 Introduction

To estimate their survival, birds are usually captured by one of many possible methods of capture. Our aim is to investigate the possibility that methods of capture may produce survival estimates that differ in mean and/or precision. In the long-term study of the great tit (*Parus major*) at our institute, three different methods of capture have been used simultaneously for many years in the same population: capture of parents feeding their young at the nest; capture of birds roosting in nest-boxes; and mist-netting. We suspect that each of these methods may produce non-random samples, and that the samples are selective in different ways. In the breeding bird sample, parents of broods that fail to produce fledglings are underrepresented, and any non-breeder would be absent from the sample. In autumn and especially in cold winters, some individuals leave the study site to return next spring. These individuals are absent from the roosting and the mist-net samples (Drent, 1984). Because the more dominant birds roost in nest-boxes, they are overrepresented in the roosting samples (van Balen, 1980). We also suspect that the methods of capture differ in the extent to which the desired high and stable capture rate is attained.

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We estimated adult survival from three data sets, each created by selecting the captures made by only one of the three methods, as if this method of capture was the only one in use. We then compared the estimates obtained.

2 Study site, species and methods of capture

The Hoge Veluwe is a mixed forest with 380 nest-boxes on 165 ha. The great tit is a common, hole-nesting songbird in woodlands. Almost all pairs breed in the nest-boxes. Virtually all birds will attempt to breed at age 1 (Drent, 1984). The sex ratio is balanced. During the nestling season (May–June/July), parents were caught when they fed their young. Birds roosting in the nest-boxes were caught by hand, at night, once every 1 or 2 months from October to March. Mist-nets were used from June to March or April, at 6–10 stations (total length of mist-nets: 123 m). In principle, each station was used one day every week prior to August 1992; subsequently, each station was used once every month. For some years, mist-net sites were provided with food and/or a decoy bird.

3 Selection of the data

Only captures of adult birds were considered. In the mist-nets, 33% of the captures were of adults; 58% in the roosting inspections. Very few captures were excluded either because adult status was uncertain (0.07%) or sex was unknown (0.03%). Our analyses are limited to the birds caught between 1974 and 1993.

The duration of sampling by roosting inspection and mist-net extend over 6–10 months per year (see previous section). This long duration is likely to introduce heterogeneity in the samples, which should theoretically be instantaneous. To minimize this problem, we have restricted the captures over periods of maximum 3 months (as they are in the breeding data set). For the roosting and mist-netting data, periods were chosen in order to maximize sample sizes, proximity to the breeding season and to make it possible to separate juveniles from adults. For the roosting data, the period chosen was October–December. For the mist-net data, the same period was used for the years 1974–1983 and 1993; for the other years the period was November–January. Captures made in January were attributed to the previous calendar year.

We created three data sets: breeding, roosting and mist-net. Each data set contained all captures made by the given method in the 3-month period chosen (for analysis with SURGE, each of these data sets was further divided by sex). The proportion of individuals appearing in the three data sets was 52%, 29% and 19%, respectively. The overlap (proportion of individuals in common) between pairs of data sets was: 0.66 (breeding–roosting), 0.65 (mist-net–roosting), and 0.37 (mist-net–breeding). Sample sizes for all data sets can be found in Table 2. The total number of captures was 14 220 for 3407 individuals.

4 Statistical methods for survival analyses

All the survival analyses were made with the Cormack–Jolly–Seber (CJS) model, according to the statistical framework reviewed in Lebreton *et al.* (1992). We used program SURGE 4.2 (Pradel & Lebreton, 1993). In summary, capture histories are modelled as outcomes of a probabilistic process involving survival and capture. Both survival and capture rates can differ between years and/or between classes of individuals (e.g. sex). The method of maximum likelihood provides estimates of survival and capture rates and their variances. Starting from a full rank model, reduced models can be constructed and tested by likelihood ratio tests (LRTs); this ANOVA-type approach enables the testing of factors potentially affecting survival and/or capture rate. To select the most parsimonious model which adequately describes the capture histories, we used the Akaike Information Criteria (AIC; see Lebreton *et al.*, 1992). Selection between models having close (difference < 2) AIC values was done on the basis of the LRTs. In none of the selected models was any significant (LRT, $P < 0.05$) factor excluded. The goodness-of-fit to the CJS model was tested by the method developed by Burnham *et al.* (1987; program RELEASE).

We have first analyzed each data set separately, the factors considered being time (year) and sex. Adult age was not included here because: its effect on adult survival is small; it complicates the analysis with an extra factor; the sample sizes would be reduced (to birds of known age) and would be insufficient for the larger number of parameters needed. In a second step, we have combined all data sets in a single analysis to test the effect of the recapture method.

5 Model selection

For each data set, we have first tested the fit to the CJS model (i.e. survival and capture are both time dependent; sexes were pooled here). Because of the high capture rate and sparsity of the data, only the component 3.SR of the tests (Burnham *et al.*, 1987) could be used (cf. Lebreton *et al.*, 1992). The fit to the CJS model was accepted ($P > 0.30$) for all data sets. Secondly, we obtained the most parsimonious models and tested which factors (year, sex) have an effect on survival or capture probability (Table 1).

The effect of sex on survival was never signficant (Table 1). On the other hand, the effect of time on survival was signficant in all data sets (Table 1). This was a major *a priori* expectation from our knowledge of the population biology of the great tit (e.g. van Noordwijk & van Balen, 1988). Note, however, that the effect of time is stronger in the breeding and roosting data sets; in the mist-net data set, the AIC value for the model without time dependence on survival is the lowest (although this model was rejected because another model had a very close (difference < 2) AIC value and the LRT was significant).

The capture rate is dependent on sex for the breeding and the roosting data (Table 1). For both methods, the behaviour of the birds readily explains that sexes have different probability of capture. Breeding birds are caught when they feed their young and sexes have a different pattern of feeding activity. Male great tits are notoriously more difficult to trap than females, and some of the females were already identified when incubating. In the case of roosting birds, males roost more than females early in the winter season (non-roosting birds spend the night in trees), while the trend is reversed later in the season (e.g. Drent, 1987).

The effect of time on capture rate is highly significant for the mist-net data; it is only marginally significant for the breeding data and the model without this factor has the lowest AIC (Table 1).

TABLE 1. Model selection

	Model				LRT test		Factor tested	
	Surv.	Capt.	np	DEV	(*P*)	AIC	Surv.	Capt.
Breeding								
1	t,s	t,s	74	6363.3		6511.3		
2–1	t	t,s	56	6380.9	0.48	6492.9	sex	
3–2	t	t	37	6430.7	0.0001	6504.7		sex
4–2	**t**	**s**	**20**	**6431.9**	**0.050**	**6471.9**		time
5–3	t		20	6474.6	0.0003	6514.6		sex
6–4		s	3	6629.7	<0.0001	6635.7	time	
Roosting								
1	t,s	t,s	74	3113.3		3261.3		
2–1	t	t,s	56	3134.6	0.26	3246.6	sex	
3–2	t	t	37	3148.3	0.80	3222.3		sex
4–2	**t**	**s**	**21**	**3178.2**	**0.15**	**3220.2**		time
5–3	t		20	3185.4	0.003	3225.4		sex
6–4		s	3	3316.9	<0.0001	3322.9	time	
Mist-net								
1	t,s	t,s	74	1448.9		1596.9		
2–1	t	t,s	56	1458.2	0.95	1570.2	sex	
3–2	**t**	**t**	**37**	**1473.8**	**0.69**	**1547.8**		sex
4–3	t		20	1516.6	0.0005	1556.6		time
5–3		t	20	1506.2	0.013	1546.2	time	
ALL								
1	t,m	(t,s)	80	11084		11244		
2–1	t	(t,s)	42	11154	0.001	11238	method of capture	

In the first column, the first digit gives the number of the model, the second digit indicates against which other model the test was made. In the second and third columns, the model structure is given: first, the factor(s) included to model survival, then the factor(s) for capture rate. The factors are abbreviated as follows: s for sex, t for time (years), m for method of capture. The selected models are in bold. For the last two models, probability of capture is modelled for each method as in the selected models described above. Surv. = survival rate; Capt. = recapture rate; np = number of parameters; DEV = deviance; LRT = likelihood ratio test; AIC = Alcaike Information Criterion.

6 Comparisons of the estimates

Survival estimates for each method of capture are compared in Table 2 and Fig. 1. These estimates differ significantly, as shown by an analysis where method of capture is introduced as a group in SURGE (Table 1; similar tests of methods of capture in 2×2 comparisons were also significant).

The variances of the survival estimates were compared among methods of capture in two ways. First, we simply computed the average STD of the point estimates. Second, the variance of the mean survival estimate was obtained from a model where survival is constant. It was not possible to obtain the variances of the mean survival estimate from the variance–covariance matrices because, in the mist-net data, this matrix was incomplete. In both comparisons, the STD is lowest for the breeding data, slightly higher for the roosting data, while the STD of the mist-net data is twice that from the breeding data.

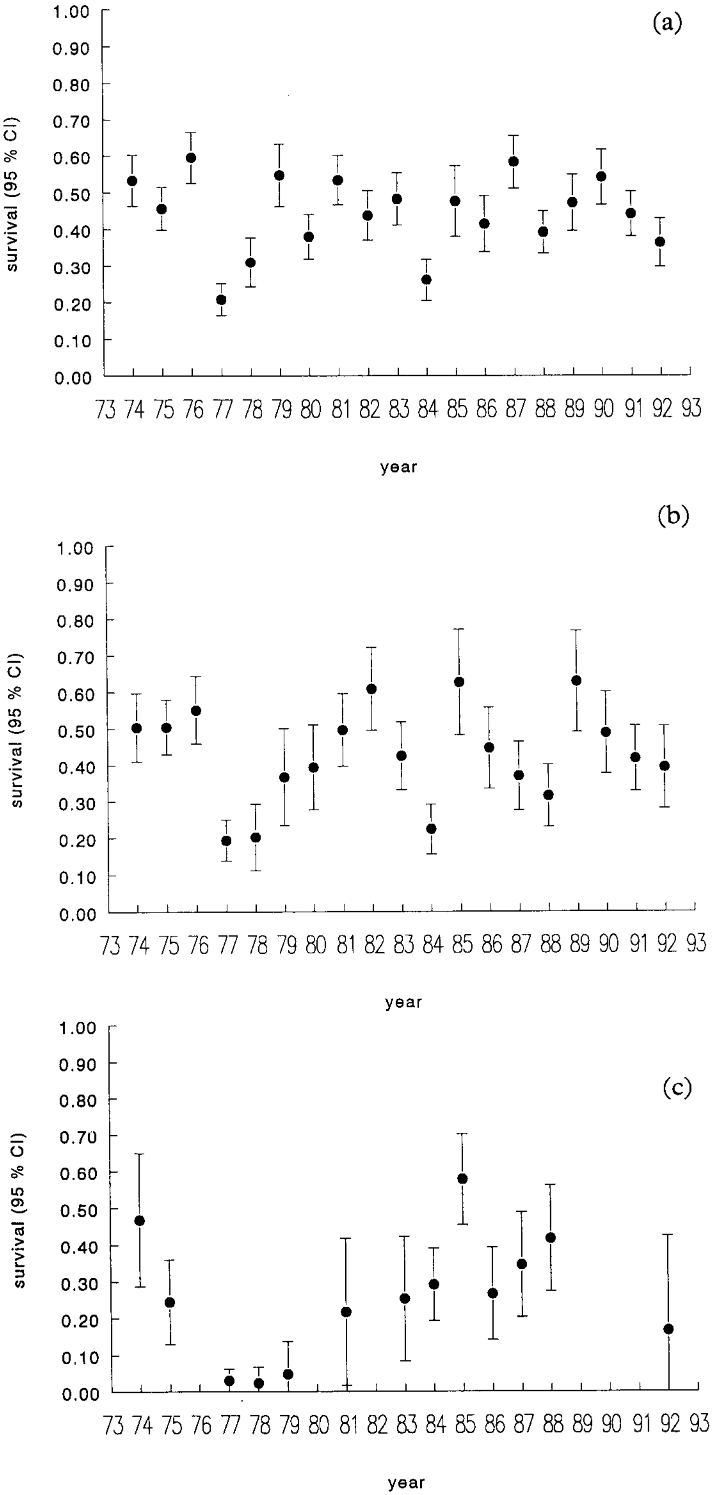

FIG. 1. Survival estimates of adult great tits with 95% confidence interval obtained from the (a) breeding, (b) roosting and (c) mist-net data sets, plotted against the years.

TABLE 2. Description of samples and estimates of survival and capture rate

Method of capture	No. captures (No. ind.)	Average point estimates of survival and STD	STD of average survival rate	Capture rate (STD)
Breeding (May–July)	6312 (2877)	0.43 0.035	0.008	females: 0.94 (0.01) males: 0.80 (0.02)
Roosting (Oct–Dec)	4265 (1525)	0.39 0.049	0.011	females: 0.82 (0.04) males: 0.90 (0.02)
Mist-net (Oct–Dec or Nov–Jan)	3643 (1279)	0.26 0.068	0.018	mean: 0.45 (0.12)

For the mist-net data set, point estimates could only be obtained for 13 of the 19 periods; the same 13 periods were selected to compute the statistics for the breeding and roosting data sets.

7 Conclusions

Survival estimates obtained from each method of capture differ in magnitude and variance. The difference in magnitude between the breeding and the other two data sets can be attributed to the difference in sampling time. This timing effect could be the only source of the differences between the breeding and roosting data. On the other hand, there is a large difference between the roosting and the mist-net samples, which have been taken in the same period of the year. At least for this pair of data sets, other sources of variation must exist, probably the fact that each method samples different groups of birds (see introduction). Transients are likely to be overrepresented in mist-net data but removing their potential effect by deleting first captures had little effect on the results (not shown).

The breeding data provide survival estimates with the lowest variance, probably because capture rate is high, relatively constant, and therefore sample sizes are the largest. The roosting data set produces a slightly higher variance and this increase could be explained by the lower sample size. In the mist-net data the variance is the largest (and for some periods, no estimates could be obtained), although the size of the mist-net sample is comparable to the roosting sample. This large variance could be attributed to the low and variable capture rate. However, the effort of capture was relatively large (average effort per annual sampling period: 104 days*station). This effort was variable but we could not find any correlation between the probability of capture and effort of capture (nor with winter severity, winter food or decoy use). Mist-netting is a dominant method in bird studies, particularly of passerines, and is often used to draw conclusions pertaining to the breeding population. In our study, however, the breeding population clearly behaves differently from the population sampled by mist-netting. The major factor of interest in population studies is the fluctuation in adult survival through time. While the breeding and roosting data give clear indication of these fluctuations, the mist-net data do not; for the latter, one might even be led to the conclusion that survival is time independent (see AIC values, Table 1). Peach and Baillie (in press) have compared estimates of abundance obtained by standardized mist-netting (constant effort sites) and by territory counts. For the 21 species examined, only the great and blue tits showed significant differences between the two sets of estimates. This confirms that mist-netting may produce results diverging from those obtained by another proven method but suggests that this problem might be limited to tit species.

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