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DOES TAPE-LURING OF MIGRATING EURASIAN REED-WARBLERS INCREASE NUMBER OF RECRUITS OR CAPTURE PROBABILITY?

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ABSTRACT.—Tape-luring often is used in studies of bird migration, and the technique can strongly augment the total number of birds captured. Additional captures from tape-luring could result from increasing the capture probability of birds already at the stopover site, or from attracting birds that normally would have overflown the stopover site. We conducted an experiment in which we captured night-migrating Eurasian Reed-Warblers (*Acrocephalus scirpaceus*) during 32 consecutive days, using tape-luring every fourth night, on average. Based on recruitment analysis (a class of Cormack-Jolly-Seber models), average capture probability was one to four times higher on days with tape-luring. The probability that a bird was a new arrival at the stopover site varied between 50% and 85% on days with tape-luring and was almost zero on control days without luring. Because tape-luring can influence where and when migrants choose to land, answers to biological questions about migration could be compromised by data from tape-lured birds. *Received 6 July 1998, accepted 15 March 1999.*

THE CAPTURE AND MARKING of individuals is an important tool for studying bird migration. For some studies, it is important to use a non-attracting capture method and to perform capture in a standardized way to be able to compare data among habitats, regions, or years (Karr 1981, Kaiser and Berthold 1994). The goal of other studies, however, is to catch large numbers of birds or to attract birds that otherwise would not have been caught. An efficient technique to attract night migrants is to lure them by playing their songs from a tape recorder at night and during the following morning (Herremans 1990a, b, c; Weller 1995). By tape-luring, capture totals can be increased manyfold, and migrants can even be attracted to unsuitable habitats (Herremans 1990c). If tape-luring is performed at stopover sites where the species of interest normally occurs, capture totals usually will be a mixture of three kinds of birds: (1) birds that would have landed without tape-luring, (2) birds that would have overflown the area, and (3) birds that already had been present for at least one day. Birds in these three groups might differ in aspects such as body mass, energy reserves, and subsequent stopover behavior.

It is generally assumed that the increased number of birds caught by tape-luring results from induced landfall (Herremans 1990c). But it is also possible that birds already present in an area are more likely to be caught because of increased activity or attraction to the source of the sound. Therefore, if the capture total on a day with tape-luring is higher than that on a day without it, the increase can be due to new arrivals and / or to higher capture probability of birds already present. Because it is impossible to distinguish between these effects by inspection of capture totals alone, we investigated the effect experimentally. In a reed bed, the most typical stopover habitat for the species concerned, we played the song of Eurasian Reed-Warblers (*Acrocephalus scirpaceus*) during some nights and the following mornings. We analyzed the capture-mark-recapture data with a recruitment analysis (Pradel 1996) that yielded separate estimates of capture probability and the probability that a bird had arrived during the preceding night. From these results, we derived recommendations for the use of tape-luring in the study of bird migration.

METHODS

Study site and data sampling.—The data were collected in a small (15.8 ha) nature reserve (Wauwilermoos; 47°10′N, 8°00′E) on the Swiss Plateau during the autumn migration period of the Eurasian Reed-Warbler. Roughly 50% of the Wauwilermoos is covered by reeds (*Phragmites australis*), and the area is surrounded by intensively farmed land. The nearest other suitable reed bed for Eurasian Reed-Warblers to stop is 4 km away. Trapping was carried out daily

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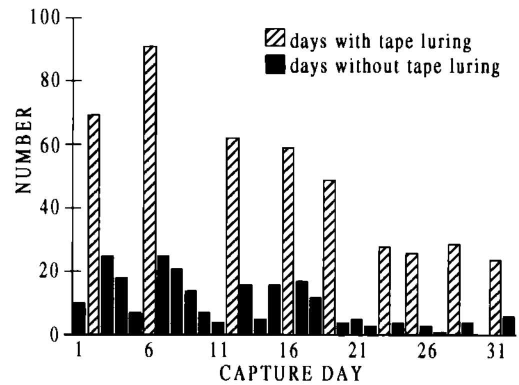

FIG. 1. Daily capture totals for initial captures of Eurasian Reed-Warblers.

between 18 August and 22 September 1996 from early morning until midday, except on four days when capture was impossible because of bad weather. These four days were excluded from all analyses. We played the tape during nine nights and the following mornings. The intervals between two tape-luring nights varied from one to five nights (Fig. 1). Tape-luring always started about one hour after sunset and ended at noon on the next day. The tape contained the songs of Eurasian Reed-Warbler, Sedge Warbler (*Acrocephalus schoenobaenus*), and Bluethroat (*Luscinia svecica*) and was played continuously and as loud as possible during the entire night from two 20-W loudspeakers. The volume was reduced to normal room level from dawn until noon. Birds were caught in 147 m of mist nets that were arranged in a cross with the tape recorder placed at the midpoint. All captured birds were banded, measured, and released about 100 m from the nets immediately thereafter. Recaptures were handled in the same manner.

Data analysis.—From capture-mark-recapture data we can estimate the capture probability for each capture event and the seniority probability between two successive capture events (Pradel 1996). The seniority probability (γ_i) is the probability that an animal that is present just before capture event i was also present just after capture event $i - 1$. The capture probability (p_i) is the probability that an animal that is present at the capture locality at capture event i is captured during that event. Such an analysis is equivalent to a capture-mark-recapture analysis (Lebreton et al. 1992) but is run backwards in time (Pradel 1996). In this case, the natural counterpart of survival probability is the probability of being in the population before time i. The probability that a bird has entered the population during the last time interval is calculated as $1 - \gamma$ and is called recruitment probability.

First, we assessed the goodness-of-fit for the Cormack-Jolly-Seber model with program RELEASE (Burnham et al. 1987). The goodness-of-fit test for the data reversed in time was significant ($\chi^2 = 124.08$, df $= 91$, $P = 0.012$), indicating that this model did not fit the data. The reason for the lack of fit could be that the model structure was not appropriate for these data, or that the data were overdispersed (Anderson et al. 1994). Next, we examined the value of $\hat{c}$, the ratio of χ^2 to its degrees of freedom from the global model. If the model structure is appropriate, then $\hat{c}$ should be equal to 1. In our study, $\hat{c}$ was close to 1 (1.364) and compatible with overdispersed count data (Burnham et al. 1987). One way of finding out whether structural failures are in the model is to look at the $\hat{c}_i$ for the four subcomponents of the goodness-of-fit test (Pradel et al. 1997). In the presence of overdispersion, all subcomponents should be affected equally. All of the corresponding $\hat{c}_i$ of the subcomponents (1.476, 1.697, 1.434, 0.967) were sufficiently close to 1 (Burnham et al. 1987) and were not very different from each other. A careful inspection of the single tests within the four subcomponents of the goodness-of-fit test did not indicate any significant heterogeneity among animals. Therefore, we concluded that the observed lack of fit did not result from structural problems of the starting model, but rather was the result of overdispersion. Sample size (664) compared with the number of estimated parameters in the global model (61) was quite small and might have caused an additional bias in the model-selection procedure. Consequently, we based model selection on a derivation of the Akaike Information Criterion ($QAIC_c$) that corrected for biases due to overdispersion and small sample size (Anderson et al. 1994, Burnham and Anderson 1998). This statistic is calculated as:

$$QAIC_c = \frac{-2\log(L(\hat{\theta}))}{\hat{c}} + 2K + \frac{2K(K+1)}{n-K-1}, \quad (1)$$

where $-2\log(L(\hat{\theta}))$ is the maximized log-likelihood value, K is the number of estimated parameters, and n is the total sample size. The model with the lowest $QAIC_c$ was considered to be the best one. Furthermore, we calculated the difference (Δ_i) between the current and the best model, and the Akaike weights (w_i) for identifying how much support a particular model has compared with another model (Burnham and Anderson 1998).

First, we fitted the Cormack-Jolly-Seber model (γ_t, p_t) and then used the estimates to reduce the number of parameters until we found the most-parsimonious models (Table 1). Estimation of the parameters based on the logit-link function and calculation of test statistics were done with program SURGE (Pradel and Lebreton 1991).

Exclusion from the data set of four capture occasions without trapping activity might change the estimates of the seniority probabilities for the interval just preceding each excluded day. To test for such an effect, we fitted the model (γ_t, p_t) to the total data set

TABLE 1. Models used to estimate seniority (γ) and capture (p) probabilities for Eurasian Reed-Warblers. Shown are model notation (Lebreton et al. 1992), model explanations, and results of fitting different models. K is the number of estimated parameters, $QAIC_c$ is the small-sample bias and quasi-likelihood-corrected Akaike Information Criterion, Δ_i is $QAIC_{ci} - QAIC_{cmin}$, and w_i is Akaike weight. $QAIC_c$ is based on an estimated overdispersion factor of $\hat{c} = 1.364$; l = luring and n = non-luring days.

Model	Seniority modeling	Recapture modeling	K	$QAIC_c$	Δ_i	w_i
1 γ_t, p_t	Time-dependent	Time-dependent	61	1,045.0	89.5	0.000
2 $\gamma_{T*[l,n]}$, p_t	Linear time trend with different slopes and intercepts for luring and non-luring days	Time-dependent	34[a]	991.5	36.0	0.000
3 $\gamma_{T+[l,n]}$, p_t	Linear time trend with equal slopes and different intercepts for luring and non-luring days	Time-dependent	34	991.5	36.0	0.000
4 $\gamma_{[l,n]}$, p_t	Constant over time, different for luring and non-luring days	Time-dependent	33	993.7	38.2	0.000
5 γ_T, p_t	Linear time trend	Time-dependent	33	1,038.4	82.9	0.000
6 $\gamma_{T+[l,n]}$, $p_{T^2*[l,n]+T*[l,n]}$	As model 3	Quadratic time trend with different slopes and intercepts for luring and non-luring days	9	957.4	1.9	0.124
7 $\gamma_{T+[l,n]}$, $p_{T^2+T*[l,n]}$	As model 3	As model 6, but without interaction between the quadratic time trend and treatment	8	955.5	0.0	0.322
8 $\gamma_{T+[l,n]}$, $p_{T^2+T+[l,n]}$	As model 3	Quadratic time trend with equal slopes and different intercepts for luring and non-luring days	7	956.2	0.7	0.227
9 $\gamma_{T+[l,n]}$, $p_{T+[l,n]}$	As model 3	Linear time trend with equal slopes and different intercepts for luring and non-luring days	6	955.6	0.1	0.306
10 $\gamma_{T+[l,n]}$, $p_{[l,n]}$	As model 3	Constant over time, different for luring and non-luring days	5	962.6	7.1	0.009
11 $\gamma_{T+[l,n]}$, p_T	As model 3	Linear time trend	5	962.0	6.5	0.012

[a] Model 2 had the same number of estimable parameters as model 3, and the estimates were identical. Seniority probabilities for days without tape luring were close to zero, which could explain the estimation failure of the slope × treatment interaction.

and forced the capture probabilities for the days without trapping activity to be zero. The maximized log-likelihood value was exactly the same as that for the data set reduced by the four days, and the estimates for the seniority probabilities were not affected. The four days without trapping activity were always between two nights when we did not use tape-luring. Because the seniority probabilities were estimated to be 1 for all nights on which we did not use tape-luring (see below), exclusion of the four days without trapping activity was justified without correcting the estimates.

RESULTS

During days with tape-luring, we caught 3 to 13 times as many Eurasian Reed-Warblers as during days without tape-luring (Fig. 1). The number of trapped Eurasian Reed-Warblers decreased during the season in both treatment groups. In total we captured 664 individuals; 493 were captured only once, 123 were captured twice, 32 were captured three times, 13 were captured four times, and 3 were captured five times.

The models considered for the selection procedure are shown in Table 1. The parameter estimates of the Cormack-Jolly-Seber model (model 1) showed that the probability of being in the population previously was lower, and the capture probability was higher, on days with tape-luring than on days without tape-luring (Fig. 2). For tape-luring days, the seniority probabilities increased during the season and might have been a linear function of time (with different slopes and intercepts for luring vs. non-luring days). Therefore, we used the initial parameter structure ($T * [l, n]$) and compared it with the simpler alternative of two different constant seniority probabilities. Capture probabilities decreased during the first part of the study period and stayed fairly constant thereafter, particularly for days without tape-luring. Consequently, capture probabilities were first described by a quadratic parameter structure ($T^2 * [l, n] + T * [l, n]$) with different slopes and intercepts for luring and non-luring days. Simpler alternatives considered structures without the quadratic term, with equal slopes and different intercepts, with linear time trends, and with constant but different capture probabilities for tape-luring and non-luring days.

Model 7 with increasing linear time trends for the seniority probability and decreasing

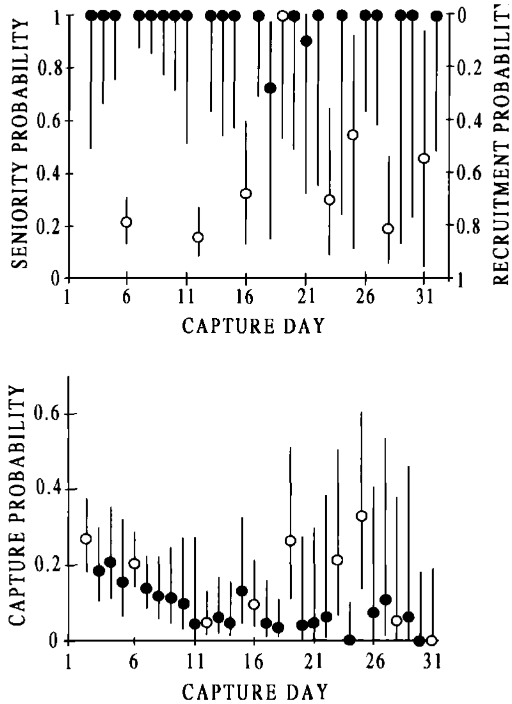

FIG. 2. Estimated seniority (γ), recruitment ($1 - \gamma$), and capture (p) probabilities for Eurasian Reed-Warblers under model (γ_t, p_t). Closed symbols indicate days without tape-luring, and open symbols indicate days with tape-luring. Vertical lines indicate 95% profile-likelihood confidence intervals. These intervals do not incorporate a component for model-selection uncertainty and therefore are too narrow. Capture probability cannot be estimated for the first capture day. Recruitment probability i refers to the period from day $i - 1$ to day i.

trends for capture probability (Fig. 3) had the lowest $QAIC_c$. However, this model differed only slightly from the simpler model (model 9; $\Delta_9 = 0.1$) and had only slightly better support ($w_9/w_7 = 1.052$) given the data. The estimated recruitment probabilities from the two models were almost identical, but the estimated capture probabilities differed slightly (Fig. 4). Confidence intervals from model 7 were larger because this model had a higher number of parameters. However, the main conclusions from the two models were identical.

In summary, the probability that a bird was in the population the day before a capture event differed between treatments and increased during the season (Figs. 3 and 4). During luring days, most of the captured birds had

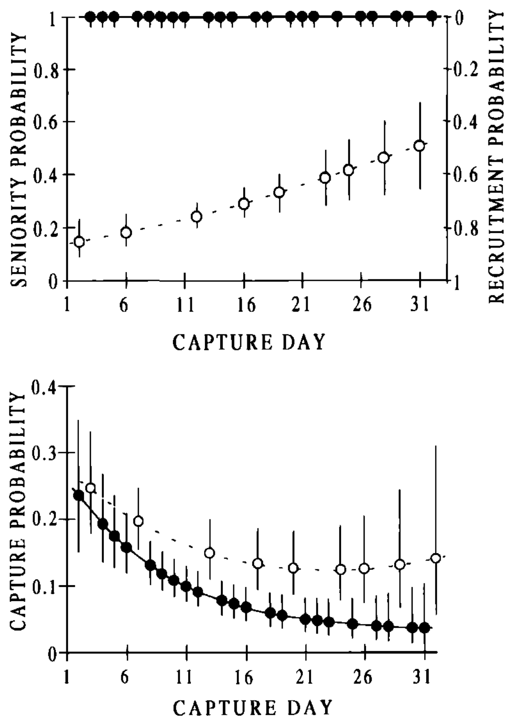

FIG. 3. Estimated seniority (γ), recruitment (1 − γ), and capture (p) probabilities for Eurasian Reed-Warblers under model 7 (see Table 1). Symbols are the same as in Figure 2.

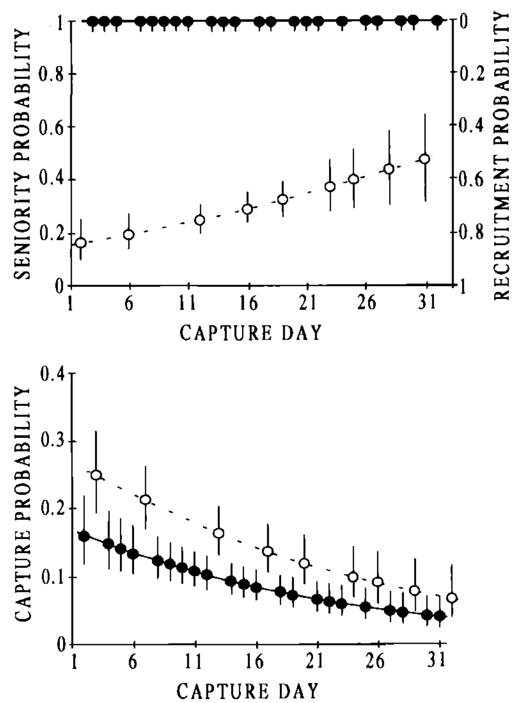

FIG. 4. Estimated seniority (γ), recruitment (1 − γ), and capture (p) probabilities for Eurasian Reed-Warblers under model 9 (see Table 1). Symbols are the same as in Figure 2.

not been present in the study area the day before and therefore were attracted by tape-luring while flying over the area at night. With tape-luring, an estimated 83 to 85% of the Eurasian Reed-Warblers captured were new arrivals at the beginning of the study, decreasing to 50 to 53% by the end. Compared with days without tape-luring, capture probabilities during tape-luring were 1.05 times higher at the beginning and 3.9 times higher at the end of the study period under model 7 (Fig. 3), and 1.6 times higher under model 9 (Fig. 4).

DISCUSSION

Our experiment revealed two explanations for increased numbers of captures with tape-luring: (1) capture probability of birds already present was increased, and (2) a considerable number of new birds was attracted to the site. The nearest suitable stopover place for Eurasian Reed-Warblers in the vicinity of the study site was beyond the range at which songs played from the tape could be heard. Therefore, the new birds must have been migrating over the area at night and then induced to land. Eurasian Reed-Warblers migrate exclusively at night in Switzerland, but birds entered our mist nets only from early dawn and afterward. Therefore, induced landfall most likely happened during the night, and the attracted birds were captured the following day. Capture probabilities were 1.05 to 3.9 times higher with than without tape-luring. Because capture totals on luring days were 3 to 13 times higher compared with the preceding and following non-luring days, induced landfall probably was a more important factor than increased capture probability in the high capture totals on luring days (Fig. 1).

The estimated seniority probability on days without luring was 1 in all cases (Figs. 3 and 4), i.e. the proportion of new arrivals was estimated to be zero. Because at least a small number of birds must have arrived during some nights without luring, the value of zero must be an underestimate. The fact that most of the estimates of recruitment probability for days without tape-luring also were zero for the full model (Fig. 2) indicates that the failure of the estimate was not due to a flaw in the model structure but to an unusual distribution of the data. The analysis probably failed to estimate this small value correctly because the number of new arrivals on days with luring was very high compared with days without luring. A recruitment analysis of Eurasian Reed-Warbler data at Bolle di Magadino (Switzerland) during the same period, where no tape-luring was performed, gave an estimate of 15% (95% CI 10 to 20%) new arrivals per day under the model (γ, p). This value might be reasonable for the Wauwilermoos during non-luring periods as well.

Four studies have shown that capture totals of Skylarks (*Alauda arvensis*; Jenni 1978, Herremans 1984) and Blackcaps (*Sylvia atricapilla*; Herremans 1990b, 1991) are male biased when tape-luring is performed. This indicates that in some species, males are attracted more strongly by the songs of conspecifics during autumn migration than are females. In habitats that are regularly used for stopovers by the species concerned, this might have occurred because of a difference in capture probability or landfall probability between the sexes. Weller (1995) documented that capture totals of Blackcaps in a "suitable" habitat were higher than in an "unsuitable" habitat, although tape-luring was performed in both habitats. However, even without tape-luring, capture probabilities can vary among habitats (Jenni et al. 1996). Recruitment analysis is necessary to determine if induction of landfall is less efficient in unsuitable habitats.

Our study documents that broadcasting songs at night induces landfall of migrating Eurasian Reed-Warblers into favorable habitats. In earlier tape-luring experiments, Herremans (1990a) caught birds in habitats where they normally did not occur and where they must have been induced to land by the songs of conspecifics. By tape-luring, the natural decision of the birds about where and/or when to land is altered such that capture totals are changed substantially. Tape-luring is very likely to introduce additional biases in the data, e.g. regarding sex ratios, apparent habitat use (as recorded by the place of capture), energy stores, and subsequent stopover behavior. For studies that rely on data from long-term standardized captures, tape-luring will profoundly alter capture totals, which will make time-series incomparable and compromise analyses of recovery information of banded birds.

Tape-luring to increase capture totals could be detrimental to the welfare of the birds if densities of birds lured by tapes are unnaturally high, or if grounded birds are likely to face increased competition that might affect fat deposition and the success of migration. The problem would be especially acute if birds are attracted to unsuitable habitats that are located long distances from suitable habitat patches (Harper 1994).

Under certain circumstances, however, tape-luring is a useful technique for answering specific questions about bird migration. The main advantages are that (1) capture totals of the species played from the tape recorder and of species visiting similar habitats (Herremans 1990c) are greatly increased, and (2) captures include many birds (>50% in this study) that had performed a migratory flight the night before. Hence, tape-luring may be the best technique to attract very rare species or that part of the population that normally flies over an area without stopping. For instance, the Aquatic Warbler (*Acrocephalus paludicola*) was classified as a straggler in Belgium before tape-luring revealed that it migrated through the area on a regular basis (Herremans 1990c). Tape-luring may help to determine timing of migration, molt status, energy reserves, and physiological parameters of birds that actually were migrating the night before. However, some species respond better than others to tape-luring, and the method appears to be the least successful close to the nonbreeding grounds and during spring migration (Herremans 1990c, 1993; Weller 1995).

Unless it is known which birds are actually induced to land, answering biological questions about bird migration could be compromised by data derived from tape-lured birds. It could be that tape-luring attracts all birds that fly over an area, or that it attracts only a subset (e.g. those flying at lower altitudes, near their intended destination, or with few energy reserves). Clearly, more information about the utility of tape-luring is needed, and data that are derived from this technique should be used with caution.

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