

THE EFFECTS OF PERMANENT LOCAL EMIGRATION AND ENCOUNTER TECHNIQUE ON STOPOVER DURATION ESTIMATES AS REVEALED BY TELEMETRY AND MARK-RECAPTURE

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Abstract. Studies of stopover durations of migrating birds using mark-recapture and resighting techniques are usually restricted to only a part of a stopover site. Therefore, estimates of stopover duration may be negatively biased if birds leave the trapping area permanently, but remain within the stopover site (permanent local emigration). We tested this possible effect by comparing stopover durations of Orphean Warblers (*Sylvia hortensis*) estimated from recapture and resighting data obtained from a trapping area covering only a part of a stopover site with durations estimated from relocation data of radio-marked individuals sampled over the entire stopover site. To test a possible effect of the different reencounter techniques on stopover duration estimates we compared estimates of stopover duration derived from the recapture and resighting data with those derived from the relocation data restricted to the same trapping area. Stopover duration estimated from relocation data obtained from the entire stopover site was twice as long as stopover duration estimated from recapture and resighting data. While similar estimates of stopover duration were obtained from relocation data when data from only the restricted trapping area were used, the proportion of transients was different between the two data sets. The different estimates of stopover duration were most likely not due to permanent local emigration, but rather to violations of essential model assumptions, such as equal catchability or that the probability of staying for another day is independent of the time a bird has already spent at the stopover site.

Key words: *Cormack-Jolly-Seber models, encounter technique, migration, permanent local emigration, stopover duration, Sylvia hortensis, telemetry.*

Efectos de la Emigración Local Permanente y de las Técnicas de Encuentro sobre las Estimaciones de Duración de las Paradas Reveladas por Telemetría y Marcado-Recaptura

Resumen. Los estudios sobre la duración de las paradas de las aves migratorias que emplean técnicas de marcado-recaptura y observaciones repetidas están usualmente restringidos a una parte del sitio de parada. Por lo tanto, las estimaciones de la duración de la parada pueden estar sesgadas negativamente si las aves abandonan el área donde son capturadas de modo permanente, pero permanecen dentro del sitio de parada (emigración local permanente). Evaluamos este posible efecto comparando las duraciones de las paradas de *Sylvia hortensis* estimadas a partir de datos de recaptura y de observaciones repetidas obtenidos de un área de captura que cubría sólo una parte del sitio de parada, con la duración estimada a partir de datos de relocalización de individuos marcados con radios muestreados en todo el sitio de parada. Para evaluar un posible efecto de las diferentes técnicas de re-encuentro sobre las estimaciones de la duración de la parada, comparamos las estimaciones de duración de la parada derivadas de los datos de recaptura y de observaciones repetidas, con aquellas derivadas de datos de relocalización restringidos a la misma área de captura. La duración de la parada estimada a partir de los datos obtenidos de la totalidad del sitio de parada fue dos veces mayor que la estimada a partir de los datos de recaptura y de observaciones repetidas. Aunque se obtuvieron estimaciones similares de la duración de la parada a partir de datos de relocalización cuando se utilizaron sólo datos restringidos al área de captura, la proporción de individuos transitorios fue diferente entre los dos conjuntos de datos. Las diferentes estimaciones de la duración de la parada probablemente no se debieron a la emigración local permanente, sino más bien al incumplimiento de los supuestos esenciales del modelo, como la igualdad en la probabilidad de captura o a que la probabilidad de permanecer un día adicional es independiente del tiempo que el ave ha pasado en el sitio de parada.

INTRODUCTION

Most migrating birds stop regularly at suitable sites to feed on their journeys between breeding and nonbreeding sites. The amount of time they spend at these stopover sites and resulting fuel loads in part determine the maximum flight range for the next migratory hop, and thus the spatiotemporal course of the journey. Knowledge of how long birds stay at stopover sites and factors affecting the decision to land at and depart from a stopover site are therefore crucial for understanding the ecology and evolution of migration (Jenni and Schaub 2003).

Estimating stopover duration requires repeated encounters obtained from individually marked birds during their stay at a stopover site. Birds may be encountered by recapture, resighting, or relocation (by means of telemetry). However, true stopover durations of individuals are only known when birds are marked before entering the stopover site (Iverson et al. 1996, Hake et al. 2003) and when the encounter probability (p) is 1. These conditions are not usually met in practice (Lavee et al. 1991, Kaiser 1995, Schaub et al. 2001), therefore stopover duration must be estimated from reencounter data.

Clearly, any analysis of stopover duration needs to define the stopover site. A biologically meaningful definition would be based on the spatial distribution of specific habitats, because birds usually have strong habitat preferences. In practice, however, birds are often caught at a specific trapping area within a larger stopover site with more-or-less homogenous habitat (e.g., only a small fraction of a large reed bed). Birds that move away from the trapping area are then considered to have left the stopover site, although they are still stopping over. If such permanent local emigration is frequent, stopover duration estimated from only a part of the stopover site does not reflect true stopover duration. However, the amount of this possible bias has not yet been empirically studied. This bias can be studied if the location of some individuals is known at any given time and is thus independent of the spatial scale of the study. The stopover duration estimated for these birds can then be used as a basis for comparison with estimates obtained from reencounters within the restricted trapping area. We tested whether permanent local emigration

had a significant effect on estimates of stopover duration by comparing estimates of stopover duration obtained from recapture and resighting data of individually marked birds within a restricted trapping area with estimates from the relocation data of radio-marked birds within the whole stopover site. If permanent local emigration is important, the estimated stopover duration of radio-marked birds from the whole stopover site is expected to be longer than the estimated stopover duration of recaptured and resighted birds within the trapping area.

We used Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992) to estimate the probability of a bird still being present at the site one time unit later (probability of stay; ϕ) from recapture and resighting data restricted to the trapping area and from relocation data from the whole stopover site. Using the formula for calculating the mean life expectancy (Seber 1982), an estimate of stopover duration can be obtained from the probability of stay (Schaub et al. 2001). The different techniques used to monitor the birds certainly resulted in different reencounter probabilities. An advantage of Cormack-Jolly-Seber models is that probability of stay (ϕ) and reencounter probability (p) are estimated separately, thus the estimated probability of stay should be independent of the reencounter technique. However, Salewski et al. (2007) recently provided evidence that this may not always be true—in their study, stopover duration estimated from birds that were resighted, which had a higher reencounter probability, were slightly higher than estimates from birds that were recaptured, which had lower reencounter probabilities. Therefore, to study the effect of permanent local emigration on estimates of stopover duration using birds that were followed with different encounter techniques, we had to evaluate whether the different encounter techniques resulted in different estimates of stopover duration. We thus performed an additional analysis in which we compared estimates of stopover duration based on the recapture and resighting data vs. those based on the radio-tagging data restricted to the same trapping area. This allowed us to evaluate whether the different reencounter techniques had an impact on the estimates of stopover duration, and to make better inferences about a possible effect of

permanent local emigration on estimates of stopover duration.

Stopover duration estimated by CJS models may not reflect true stopover duration because true stopover duration includes the time a bird may have already spent at the stopover site before it was caught for the first time (Schaub et al. 2001, but see Efford 2005, Pradel et al. 2005). However, it was not the aim of this study to estimate true stopover duration and we refer to the estimates derived from the probabilities of stay as “stopover duration.”

We had two main aims in this study: (1) to determine whether there was permanent local emigration from the study area and, if so, how it affected the estimation of stopover duration, and (2) to test whether estimates of stopover duration made with CJS models were the same for data sampled with two different encounter techniques.

METHODS

STUDY SITE AND DATA COLLECTION

Our study area of 9 km² was situated in a dry river valley, 6 km east of Ouadâne (20°56'N, 11°37'W), in central Mauritania, West Africa. The river valley was surrounded by inhospitable sand and stone deserts. The savannah-like vegetation in the valley itself consisted of single standing *Acacia* (*Acacia tortilis*) mixed with shrubs and small trees of *Balanites aegyptiaca*, *Maerua crassifolia*, and *Leptadenia pyrotechnica* (mainly along the dry riverbed). The next suitable stopover site was located 6 km away, close to the town of Ouadâne.

The trapping area was located in the center of the river valley and covered an area of approximately 0.2 km². We placed mist nets around bushes and small trees. From 5 March to 13 May 2003 we used 19 nets with an overall length of 117 m. In 2004 we used 28 mist nets with an overall length of 177 m operated from 6 March to 8 May. These nets were placed in the same trapping area, i.e., only the number of nets within the trapping area changed, not the size of the trapping area. In both years the nets were opened daily from 06:30 to 11:00 UTC and from 16:30 to 19:30 UTC.

We chose the Orphean Warbler (*Sylvia hortensis*) for radio-tagging and banding because it was one of the most abundant species at the stopover site and birds were large enough to

carry transmitters. Orphean Warblers are trans-Saharan migrants. They breed in the Mediterranean region and winter in the dry savannahs south of the Sahara (Glutz von Blotzheim and Bauer 1991). We marked all captured individuals with a numbered aluminum band and one to three color bands for individual identification. Visual observations of the banded birds were carried out within the trapping area throughout the trapping season in 2004. These observations were made daily between 15:00 and 17:00 UTC and the observer always followed the same route. If a color-banded bird was recaptured and resighted the same day, we only considered the recapture event for data analysis.

Between 16 and 24 April 2003 nine Orphean Warblers were radio-marked. We selected birds with different fat scores, otherwise the birds were chosen randomly. Transmitters weighed 0.4 g (1.6%–2.2% of adult body weight) and had a battery life of 15–20 days (Naef-Daenzer et al. 2001, 2005). The transmitters were attached using a leg-loop harness of 0.5 mm rubber bands (Rappole and Tipton 1991). We used R1000 telemetry receivers (Communications Specialists Inc., Orange, California) with three-element Yagi antennas to relocate radio-marked individuals. The area of reception ranged from approximately 0.5–2 km. We pinpointed the position of every radio-marked individual three times a day by homing in (White and Garrott 1990). Thus, for each day we knew whether a bird was present in the trapping area, whether it was present at the stopover site (river valley), or whether it had left the stopover site. A bird was considered to have left the stopover site if no signal was received for at least three consecutive days. Departure time was defined as the night following the day of last observation. Two radio-marked birds were each recaptured once. Because of the low number of recaptures and because these recaptures did not contribute information to the probability of stay, these two recapture events were excluded from analyses. Transmitter failures were detected for two birds after 13 and 15 days, respectively. These birds were visually identified one and two days, respectively, after their transmitters failed. They were considered as having been lost on last capture in the CJS models (Pradel 1993, Schmidt et al. 2002).

TABLE 1. Definitions of Cormack-Jolly-Seber model parameters for estimating stopover durations of banded and radio-marked Orphean Warblers at a stopover site in the Sahara Desert.

Parameter	Definition
p_{CC}	Probability that a banded bird that was captured at occasion $i - 1$ is recaptured at occasion i .
p_{SC}	Probability that a banded bird that was resighted at occasion $i - 1$ is recaptured at occasion i .
p_{NC}	Probability that a banded bird that was neither captured nor resighted at occasion $i - 1$ is recaptured at occasion i .
p_{CS}	Probability that a banded bird that was captured at occasion $i - 1$ is resighted at occasion i .
p_{SS}	Probability that a banded bird that was resighted at occasion $i - 1$ is resighted at occasion i .
p_{NS}	Probability that a banded bird that was neither captured nor resighted at occasion $i - 1$ is resighted at occasion i .
φ_C	Probability that a banded bird that was captured at occasion i stayed at the stopover site until occasion $i + 1$.
φ_S	Probability that a banded bird that was resighted at occasion i stayed at the stopover site until occasion $i + 1$.
φ_N	Probability that a banded bird that was neither captured nor resighted at occasion i stayed at the stopover site until occasion $i + 1$.
φ_T	Probability that a radio-marked bird that was relocated at occasion i stayed at the stopover site until occasion $i + 1$.

STATISTICAL ANALYSES

We used mark-recapture analysis to estimate the probability that a bird stayed in the reference area for one more day (probability of stay, φ) and to calculate the expected stopover duration. To test whether the estimated probabilities of stay differed between banded and radio-marked birds or between the trapping area and the entire stopover site, we analyzed the data with a multistate model (Lebreton and Pradel 2002), in which the states were the different reencounter techniques, and the reencounter probabilities were the transitions between and within states. Specifically, the model had the states “recaptured” (containing banded birds that were recaptured in mist nets), “resighted” (containing banded birds that were resighted), “not recaptured or resighted” (containing banded birds that were neither recaptured nor resighted), and “tagged” (containing radio-marked birds that were relocated).

Multistate models were parameterized with transition probabilities and state-specific probabilities of stay and recapture. The classical multistate model is a very flexible tool for analyzing many different study designs and biological interactions (Williams et al. 2002), as it allows fixing some parameters or reparameterizing the model. Here, we fixed the state-specific recapture probabilities (“recaptured” = “resighted” = “relocated” = 1, “not recaptured or resighted” = 0), and used the transition probabilities to estimate recapture probabilities.

The advantage of this approach is that the different reencounter protocols can be jointly analyzed and it is possible to model the reencounter probabilities as a Markovian process. The basic model is a matrix of transition probabilities and vectors of state-specific probabilities of stay (φ) and recapture:

$$\begin{bmatrix} p_{CC} & p_{SC} & p_{NC} & 0 \\ p_{CS} & p_{SS} & p_{NS} & 0 \\ 1 - p_{CC} - p_{CS} & 1 - p_{SC} - p_{SS} & 1 - p_{NC} - p_{NS} & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} \varphi_C \\ \varphi_S \\ \varphi_N \\ \varphi_T \end{bmatrix} \begin{bmatrix} 1 \\ 1 \\ 0 \\ 1 \end{bmatrix}. \quad (1)$$

The parameters in this model are explained in Table 1. Note that the reencounter probabilities of states N , C , and S sum to 1, thus only two of them (in our case C and S) need to be modeled, and that the reencounter probability of state T is 1, because radio-marked birds could always be relocated when they were present at the stopover site.

To study the effect of reencounter technique, we had to restrict the relocation data to the same area in which mark-recapture and mark-resighting data were collected, i.e., the trapping area; thus, we had to eliminate any relocations of radio-marked birds outside the trapping area. Radio-marked birds might move between the trapping and the surrounding area, and therefore be relocated within the trapping area on some days but not on others. We assumed that this kind of temporary emigration was random, and consequently resulted in a relocation probability less than 1, which needed to be estimated (Schaub, Gimenez et al. 2004). Thus,

we had to estimate the state-specific relocation rate, instead of fixing it at 1 as we did in model (1). The modified model is then written to include the vector of the state-specific recapture rates:

$$\begin{bmatrix} p_{CC} & p_{SC} & p_{NC} & 0 \\ p_{CS} & p_{SS} & p_{NS} & 0 \\ 1 - p_{CC} - p_{CS} & 1 - p_{SC} - p_{SS} & 1 - p_{NC} - p_{NS} & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} \varphi_C \\ \varphi_S \\ \varphi_N \\ \varphi_T \end{bmatrix} \begin{bmatrix} 1 \\ 1 \\ 0 \\ p_T \end{bmatrix}, \quad (2)$$

where p_T is the relocation probability.

Goodness-of-fit, transients, and immediate trap response. There is currently no goodness-of-fit (GOF) test available for our model. The recently developed GOF test for multistate models (Pradel et al. 2003) could not be used, because it cannot deal with “unobserved” states (N). Moreover, GOF tests with small sample sizes may be unreliable due to insufficient power. Therefore, we did not carry out a GOF test. Instead, we chose a conservative modeling approach and adapted our basic models to include the occurrence of transients (Pradel et al. 1997) and immediate (limited to previous capture event) trap response (Pradel 1993, Gimenez et al. 2003), because the occurrence of transients and immediate trap response behavior is known to be frequent in stopover analyses (Heuman 2004, Schaub et al. 2004). Transients are defined as birds that stay only one day at the stopover site (Pradel et al. 1997). The model can be adapted to estimate the probability that a newly captured individual is a transient and the probability of stay of the nontransients (i.e., birds that stay for more than one day at the stopover site). This is done by implementing a model with a two age-class structure to estimate the probabilities of stay (Pradel et al. 1997, Schaub et al. 2004). By definition, transients can occur in the sample of banded and radio-marked birds, but in banded birds only in state C (“recaptured”). Transients are indicated in the model notation by adding the subscript $a2$ to the corresponding probability of stay (e.g., $\{\varphi_{a2*C,S=N,a2*T}\}$ indicates that transients were accounted for in the samples of recaptured and relocated birds). Immediate trap response was modeled for the banded, but not for the radio-marked, birds. A model taking account of immediate trap response in recaptured birds constrains the two parameters $p_{SC} = p_{NC}$ to be equal but different from p_{CC} . Immediate trap response is indicated in the

model notation by adding the subscript m to the corresponding capture probability (e.g., $\{p_{m*C,S,T}\}$ indicates that immediate trap response was accounted for in recaptures).

Candidate models. We formulated a priori hypotheses according to our main questions and translated each of them into a model. We used an information-theoretic approach to assess support for each of the models (Burnham and Anderson 1998). We did not examine time effects because of a rather small sample size and the resulting low power to detect these effects.

Our first hypothesis was that the probability of stay depended on the spatial scale. To test this, we considered two models, one in which the probability of stay for the banded and radio-marked birds was equal $\{\varphi_{C=S=N=T}\}$ and one in which it was different $\{\varphi_{C=S=N,T}\}$. These two models were applied to the data set including the relocations from the whole stopover site. To test the second hypothesis, that estimates of stopover duration were independent of encounter technique, we fitted the same two models to a restricted data set that included only the relocations within the trapping area. We combined each of these two models with the four possible combinations for occurrence of transients in the samples of recaptured and relocated birds, resulting in eight models for probability of stay (Table 2). It was obvious a priori that reencounter probabilities were different among states, but it was not clear whether immediate trap responses were apparent. Thus, to estimate reencounter probabilities we considered models with immediate trap response on both recapture and resighting probabilities, immediate trap response for only one reencounter probability, and no immediate trap response (Table 2). These four models were used in combination with each of the eight models for probability of stay, thus we examined 32 models in total for each data set (relocation data from the entire stopover site and restricted to the trapping area).

We used program MARK 4.1 (White and Burnham 1999) to fit our models, and based parameter estimation and model selection on Akaike’s information criterion corrected for small sample sizes (AIC_c ; Burnham and Anderson 1998). We also calculated derived parameters and their associated standard errors from the most parameterized models (the models in

TABLE 2. Notation and descriptions of the Cormack-Jolly-Seber models evaluated for estimating stopover durations of banded and radio-marked Orphean Warblers at a stopover site in the Sahara Desert. The symbol ϕ denotes probability of stay, and p denotes the reencounter probability; subscript $a2$ refers to transients (birds that stay for only one day at the stopover site), subscript m refers to immediate trap response (different reencounter probability for previous reencounter event), subscript C denotes banded birds that were recaptured, subscript S denotes banded birds that were resighted, subscript N denotes banded birds that were neither captured nor resighted, and subscript T denotes radio-marked birds that were relocated.

Notation	Description
$\phi_{a2^*C=S=N,a2^*T}$	Probability of stay of banded birds is different from probability of stay of radio-marked birds; the model accounts for transients in both banded and radio-marked samples.
$\phi_{a2^*C=S=N, T}$	Probability of stay of banded birds is different from probability of stay of radio-marked birds; the model accounts for transients in the sample of banded birds.
$\phi_{C=S=N,a2^*T}$	Probability of stay of banded birds is different from probability of stay of radio-marked birds; the model accounts for transients in the sample of radio-marked birds.
$\phi_{C=S=N, T}$	Probability of stay of banded birds is different from probability of stay of radio-marked birds; the model does not account for transients.
$\phi_{a2^*C=S=N=a2^*T}$	Probabilities of stay of banded and radio-marked birds are identical; the model accounts for transients in both banded and radio-marked samples.
$\phi_{a2^*C=S=N=T}$	Probabilities of stay of banded and radio-marked birds are identical; the model accounts for transients in the sample of banded birds.
$\phi_{C=S=N=a2^*T}$	Probabilities of stay of banded and radio-marked birds are identical; the model accounts for transients in the sample of radio-marked birds.
$\phi_{C=S=N=T}$	Probabilities of stay of banded and radio-marked birds are identical; the model does not account for transients.
$p_{m^*C,m^*S,T}$	Reencounter probabilities for recaptured, resighted, and relocated birds are different; the model accounts for immediate trap response on both recapture and resighting probabilities.
$p_{m^*C,S,T}$	Reencounter probabilities for recaptured, resighted, and relocated birds are different; the model accounts for immediate trap response on recapture probability.
$p_{C,m^*S,T}$	Reencounter probabilities for recaptured, resighted, and relocated birds are different; the model accounts for immediate trap response on resighting probability.
$p_{C,S,T}$	Reencounter probabilities for recaptured, resighted and relocated birds are different; the model does not account for immediate trap response.

which all the parameters were estimated separately and where transients and immediate trap response were accounted for). These parameters were the stopover duration, $S = -1/\ln(\phi)$, and the probability that a newly captured individual was a transient, $\tau = 1 - \phi_{a1}/\phi_{a2}$, where ϕ_{a1} is the probability of stay of the first age class (transients) and ϕ_{a2} is the probability of stay of the second age class (nontransients; Pradel et al. 1997). The standard errors of the derived parameters were calculated with the delta method (Seber 1982). All data are presented as mean \pm SE unless otherwise noted.

RESULTS

In 2003, we captured a total of 75 Orphean Warblers. We fitted nine with radio-transmitters, and the remaining 66 birds were considered for mark-recapture analysis. Of these, 60 were never recaptured, five were recaptured once, and one individual was recaptured twice. We did not carry out visual observations in

2003, thus there is no resighting data from this year. In 2004 we captured 178 Orphean Warblers and all were color-banded. Of these, 157 were never recaptured, 20 were recaptured once, and one bird was recaptured twice. In addition, we resighted 60 individuals; 30 individuals were resighted once, 16 were resighted twice, three individuals were resighted three times, and 11 individuals were resighted more than three times. The seasonal pattern of first captures for both years is shown in Figure 1.

Modeling recapture and resighting data vs. relocation data from the entire stopover site provided strong evidence that probabilities of stay differed (Table 3). The four top-ranked models with a summed Akaike weight (w_i) of 0.80 included different probabilities of stay for banded and radio-marked individuals. Based on the most parameterized model ($\phi_{a2^*C=S=N,a2^*T}; p_{m^*C,m^*S}$), stopover duration estimated from relocation data from the entire stopover site was 13.9 ± 5.7 days ($n = 9$; Fig. 2). This

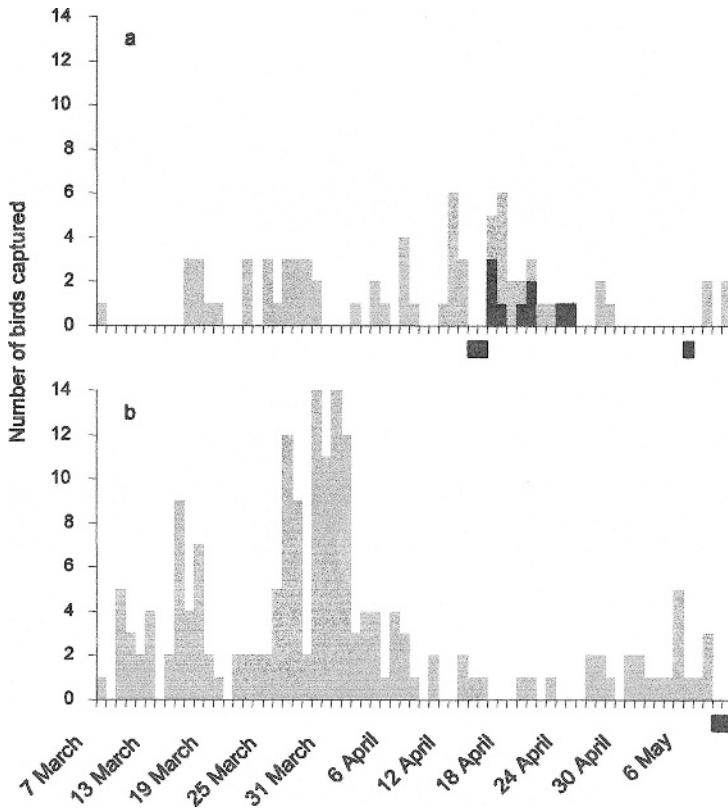


FIGURE 1. The seasonal pattern of first captures of Orphean Warblers in 2003 (a) at a stopover site in the Sahara Desert shows that most birds were captured between 12 and 17 April. Nine birds were radio-marked between 16 and 24 April (indicated by the vertical black bars). In 2004 (b) most of the birds were captured two weeks earlier than in 2003. Days when mist nets were closed are indicated by black bars below the time axis.

was twice as long as stopover duration estimated from the recapture and resighting data (6.4 ± 0.9 days, $n = 244$; Fig. 2). All top-ranked models included a term for transients for the recaptured and resighted birds (Table 3). The proportion of transients for the most parameterized model was estimated at 0.46 ± 0.08 . Although the summed Akaike weight from models with two different age classes was 0.43 (Table 3), there was no support for the occurrence of transients in the sample of radio-marked birds. This is because all radio-marked birds stayed at the stopover site for at least two days, therefore the probability of stay for the first age class was 1.

The results from modeling recapture and resighting data vs. relocation data restricted to the trapping area were rather ambiguous (Table 4). The summed Akaike weight of models including a difference in the probability

of stay between banded and radio-marked birds was slightly lower ($w_i = 0.46$) than the summed Akaike weight of models in which probabilities of stay were identical ($w_i = 0.54$). Based on the most parameterized model ($\phi_{a2^*C=S=N,a2^*T;Pm^*C.m^*S,T}$), estimated stopover duration of the radio-marked birds when analysis was restricted to the trapping site was 13.7 ± 7.9 days ($n = 9$, number of relocated birds = 5) and thus similar to the estimate obtained when the data from the entire stopover site were used.

In contrast to the relocation data from the whole stopover site, there was considerable support for the occurrence of transients in the relocation data restricted to the trapping area. The four top-ranked models included a term for transients (summed $w_i = 0.79$; Table 4) and, under the most parameterized model, the probability that a newly caught individual was

TABLE 3. Model selection results for probability of stay (ϕ) and recapture probability (p) of Orphean Warblers at a stopover site in the Sahara Desert, based on recapture, resighting, and relocation data, when relocations from the entire stopover site were considered. Model selection was based on the difference in Akaike's information criterion corrected for small sample sizes between each candidate model and the best model (ΔAIC_c), and Akaike weights (w_i). Also presented are the number of estimated parameters (K) and the model deviance. Only models with $w_i > 0.01$ are shown. For model descriptions see Table 2.

Model	Deviance	K	ΔAIC_c^a	w_i
$\Phi_{a2^*C=S=N,T;PC,m^*S}$	840.49	6	0.00	0.27
$\Phi_{a2^*C=S=N,T;Pm^*C,m^*S}$	838.82	7	0.39	0.22
$\Phi_{a2^*C=S=N,a2^*T;PC,m^*S}$	839.27	7	0.84	0.17
$\Phi_{a2^*C=S=N,a2^*T;Pm^*C,m^*S}$	837.60	8	1.23	0.14
$\Phi_{a2^*C=S=N,a2^*T;PC,m^*S}$	843.62	6	3.13	0.06
$\Phi_{a2^*C=S=N,a2^*T;Pm^*C,m^*S}$	841.63	7	3.20	0.05
$\Phi_{a2^*C=S=N,T;PC,m^*S}$	846.16	5	3.62	0.04
$\Phi_{a2^*C=S=N,T;Pm^*C,m^*S}$	844.11	6	3.62	0.04

^a The AIC_c value for the best model was 1106.46.

a transient was estimated at 0.40 ± 0.18 . Thus stopover duration estimates from the two sets of relocation data were similar, but the proportion of transients was different.

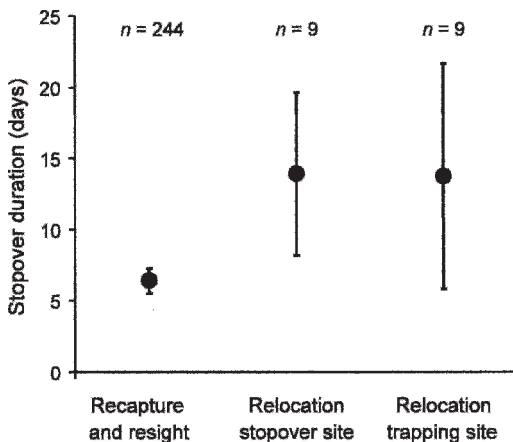


FIGURE 2. Mean stopover duration estimated with Cormack-Jolly-Seber models from radio-marked Orphean Warblers at a stopover site in the Sahara Desert was twice as long as when estimated from recapture and resighting data. Mean stopover duration estimated from radio-marked birds in the entire stopover site did not differ substantially when the data set was restricted to the trapping area. Stopover durations were estimated from nontransients (birds that stayed more than one day at the stopover site) only. Error bars indicate standard errors.

TABLE 4. Model selection results for probability of stay (ϕ) and recapture probability (p) of Orphean Warblers at a stopover site in the Sahara Desert, based on recapture, resighting, and relocation data, when only relocations within the trapping area were considered. Model selection was based on the difference in Akaike's information criterion corrected for small sample sizes between each candidate model and the best model (ΔAIC_c), and Akaike weights (w_i). Also presented are the number of estimated parameters (K) and the model deviance. Only models with $w_i > 0.01$ are shown. For model descriptions see Table 2.

Model	Deviance	K	ΔAIC_c^a	w_i
$\Phi_{a2^*C=S=N,a2^*T;PC,m^*S,T}$	858.42	8	0.00	0.22
$\Phi_{a2^*C=S=N,a2^*T;Pm^*C,m^*S,T}$	860.67	7	0.17	0.21
$\Phi_{a2^*C=S=N,a2^*T;Pm^*C,m^*S,T}$	858.85	8	0.43	0.18
$\Phi_{a2^*C=S=N,a2^*T;Pm^*C,m^*S,T}$	856.77	9	0.43	0.18
$\Phi_{a2^*C=S=N,T;PC,m^*S,T}$	864.56	6	2.00	0.08
$\Phi_{a2^*C=S=N,T;Pm^*C,m^*S,T}$	862.88	7	2.38	0.07
$\Phi_{a2^*C=S=N,T;PC,m^*S,T}$	864.47	7	3.97	0.03
$\Phi_{a2^*C=S=N,T;Pm^*C,m^*S,T}$	862.81	8	4.39	0.02

^a The AIC_c value for the best model was 1134.10.

Recapture probability was 0.04 ± 0.01 and there was no support for an immediate trap effect. In contrast, the resighting probability for a bird that was observed the previous day was 0.38 ± 0.05 , while it was only 0.17 ± 0.02 for a bird not seen the previous day. This might indicate that the observer looked harder for birds in places where they had been seen the previous day.

DISCUSSION

Estimates of stopover duration of Orphean Warblers at a desert stopover site obtained from relocation data collected over the entire stopover site were higher than estimates of stopover duration obtained from recapture and resighting data collected at a trapping area covering only a small portion of the entire stopover site. There are three conceivable reasons for this difference: (1) artifacts due to the sampling design, (2) permanent local emigration, and (3) violations of the CJS model assumptions.

EVIDENCE FOR ARTIFACTS DUE TO THE SAMPLING DESIGN

The relocation and resighting data were collected in different years (2003 and 2004, respectively), thus a difference in stopover duration between the two encounter techniques

could reflect differential stopover durations between years. However, there was no difference in the probability of stay between the two years when only recapture data were analyzed (Appendix), suggesting that stopover duration was the same in both years.

Relocation data were only collected from 16 April to 11 May, while resighting and recapture data were collected from 5 March to 13 May. If stopover duration increased over the course of the season, this could explain the observed discrepancy. To test for a possible seasonal effect, we fitted a model to the recapture and resighting data similar to the most parsimonious model but with an additional linear trend of time of season. This model had more support than the model without the linear time trend ($\Delta AIC_c = 2.08$), but the trend was negative (ϕ at first encounter occasion = 0.91, ϕ at last encounter occasion = 0.75). Therefore, the discrepancy cannot be explained by seasonal change in stopover duration.

Alternatively, the transmitters may have affected the behavior of the birds (Calvo and Furness 1992, Murray and Fuller 2000). For example, feeding time, and consequently fat deposition rate, could have been reduced, which might have resulted in prolonged stopover durations. Although we found no studies investigating the effect of radio-tagging on stopover duration, it is known from other studies that transmitters can alter the feeding behavior of birds (Massey et al. 1988, Pietz et al. 1993). However, there are also many studies that report no negative effects on feeding and other behavior (Hill and Talent 1990, Neudorf and Pitcher 1997, Naef-Daenzer et al. 2001). Chernetsov (2005) radio-marked smaller birds with proportionately heavier transmitters (3.2%–5.3% of body mass) than we did and found significantly shorter median stopover durations (1.6–3.4 days), which does not support a transmitter effect. We tried to minimize possible effects of radio-tagging by using very lightweight transmitters and an appropriate transmitter attachment technique.

Lastly, it could be argued that the large difference in stopover duration between banded and radio-marked birds simply reflects a small sample bias. However, despite the small sample size and corresponding large variation in stopover duration, the summed Akaike weight of the models that supported a difference in

stopover duration between radio-marked and banded birds was four times higher than the summed Akaike weight of the models supporting no difference. Therefore, we think that small sample bias did not affect our results.

EVIDENCE FOR PERMANENT LOCAL EMIGRATION

The main difference between the models using data from radio-marked birds in the entire stopover site and those restricted to the trapping area was the occurrence of transients in the latter. The high percentage of transients (40%) among the radio-marked birds within the trapping area seems not to be an effect of small sample size, as the same percentage of transients was estimated in the much larger data set of recaptured and resighted birds. The mean stopover durations of the nontransient birds were very similar, regardless of whether data from the entire stopover site or from only a fraction of it were used. This was because any permanent local emigration occurred immediately after first capture. Chernetsov and Titov (2000) revealed a similar result: reduction of the trapping area increased the number of transients, but stopover duration of the nontransients was not affected. Thus, accounting for transients appeared to be successful in adjusting for permanent local emigration. If, however, permanent local emigration occurs after two or more days, it is not possible to correct for the bias with the currently available models.

EVIDENCE FOR VIOLATIONS OF CORMACK-JOLLY-SEBER MODEL ASSUMPTIONS

Based on the most parameterized model, the mean stopover duration of radio-marked birds from the trapping area was about two times higher than the mean stopover duration of the banded birds within the same area. However, due to model selection uncertainty, it was not clear whether this difference was real or due to the different recapture rates of the data sampling methods. The use of CJS models should ensure that recapture probability does not affect estimates of stopover duration. However, this may not always be the case (Salewski et al. 2007) due to violations of assumptions underlying the CJS model. Any violation of these assumptions can result in biased estimates (Burnham et al. 1987). There are two assumptions underlying the CJS model

which we believe are likely to have been violated.

One of these assumptions is that of “equal catchability.” The CJS model assumes that encounter probability at time i (p_i) is the same for all individuals present at time i . However, factors like sunlight, wind, visibility, bird behavior (e.g., habitat use, vertical height distribution, spacing system, flight distance, flight frequency, ability to avoid nets, activity level, and search and settling time), bird size and condition, environment (e.g., vegetation structure and resource distribution), and mesh size and tension of the mist nets are all known to produce heterogeneity in recapture or resighting probability (MacArthur and MacArthur 1974, Buckland and Hereward 1982, Fitzgerald et al. 1989, Pardieck and Waide 1992, Jenni et al. 1996, Remsen and Good 1996, Anderson 2001, Dunn and Ralph 2004), and heterogeneity in encounter probability can result in negatively biased probabilities of stay (Carothers 1979, Buckland 1982). In contrast, relocation data are not affected by these factors because a radio-marked bird with an intact transmitter can always be encountered when it remains within range of telemetry equipment. Therefore, there is far less heterogeneity in the reencounter probability of relocation data than in the reencounter probability of recapture or resighting data.

In addition, biased estimates of departure probability can emerge if an inappropriate model is used. Our model assumed that the probability of stay was independent of the time a bird had already spent at the stopover site. This may be an unrealistic assumption in migrating birds. It is more likely that the probability of stay decreases with the time a bird has already spent at the site. If this is true and data are analyzed with CJS models, the probability of stay is negatively biased, and the bias increases the smaller the recapture probability becomes (MS, unpubl. data). This behavior agrees qualitatively with our results. Such violations of the CJS model should be detected with a goodness-of-fit test, although with a small data set the power may not be sufficient.

In conclusion, our study suggests that permanent local emigration had no significant effect on the estimates of probability of stay, because the permanent local emigrants left the trapping area immediately after first capture

and could therefore be accounted for with models that included transients. Inference about transients, however, should be made with caution, because in mark-recapture and resighting studies covering only a fraction of an entire stopover area, it is not possible to distinguish between transients in a biological sense and permanent local emigrants.

Our estimated mean stopover duration tended to be higher when the reencounter probability was enhanced. This result is supported by another study with larger sample sizes in which different encounter techniques were used (recapture vs. recapture and resight; Salewski et al. 2007). Therefore, we believe that the main reason for the discrepancy we found is due to the violation of model assumptions or the application of an inappropriate model. More research is needed in this area and we suggest two lines: (1) development of new models. These models should be capable of estimating “arrival-dependent” probabilities of stay, even if arrival is not observed. This is equivalent to modeling age-dependent survival when the age at first encounter is unknown. Such models would need to include information from the complete capture history, not only from the first encounter onwards (Manske and Schwarz 2000). However, more complex models would need larger sample sizes, and sample size is often a limiting factor in the analysis of mist-net data (Kendall et al. 2004); and (2) improvement of encounter techniques. Anderson et al. (2003:304) stated that, “sophisticated analysis methods do not mitigate poor-quality data.” Many data sets from mist-net capture (and, to a lesser extent, also resighting data) are of rather poor quality, due to the low recapture probability (Schaub et al. 2001, this study). Moreover, the assumption of equal catchability is likely to be violated in many mark-recapture studies. We therefore recommend the use of data sampling techniques that ensure a high rate of encounter and minimize recapture heterogeneity. Efforts should also be made to develop such encounter techniques.

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APPENDIX. To check whether probabilities of stay (ϕ) and recapture (p) differed between the two years of study (2003 and 2004), we fitted a simple Cormack-Jolly-Seber model to the recapture data and used year (y) as grouping variable. The following four models were tested: no differences between years in capture probability or probability of stay $\{\phi.; p.\}$, difference in probability of stay but not capture probability between the two years $\{\phi_y; p.\}$, difference in capture probability but not probability of stay between the two years $\{\phi.; p_y\}$, differences in probability of stay and capture probability between the two years $\{\phi_y; p_y\}$. These four models were extended to the occurrence of transients (Pradel et al. 1997), resulting in eight models. The most parsimonious model was the one with no difference in the probabilities of stay and recapture between years, which had about 2.6 times more support than the models with year-specific differences in capture probability and probability of stay. There was only weak support for the occurrence of transients among the recaptured birds. Model selection was based on the difference in Akaike's information criterion corrected for small sample sizes between each candidate model and the best model (ΔAIC_c), and Akaike weights (w_i). Also presented are the number of estimated parameters (K) and the model deviance.

Model	Deviance	K	ΔAIC_c^a	w_i
$\phi.; p.$	207.15	2	0.00	0.38
$\phi_{a2}; p.$	206.82	3	1.71	0.16
$\phi.; p_y$	207.03	3	1.92	0.15
$\phi_y; p.$	207.13	3	2.02	0.14
$\phi_{a2}; p_y$	206.70	4	3.65	0.06
$\phi_y; p_y$	206.74	4	3.69	0.06
$\phi_{a2}^*; p.$	205.95	5	4.98	0.03
$\phi_{a2}^*; p_y$	205.87	6	6.99	0.01

^a The AIC_c value for the best model was 322.99.