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# Stopover of migrating birds: simultaneous analysis of different marking methods enhances the power of capture–recapture analyses

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Abstract Analyses of stopover parameters of migrating birds with Cormack-Jolly-Seber (CJS) capture-recapture models often suffer from low precision due to sparse data sets. Low recapture rates result in low power to detect violations of the underlying assumptions and factors influencing stopover behaviour. We studied stopover behaviour of Palearctic migrant passerines in an oasis in Mauritania, West Africa. Using capture-recapture data and systematic observations of colour-ringed birds, we analysed the effect of increased sample size on probability of stay and recapture probability and the influence of a possible trap response on these parameters. We analysed capturerecapture data with the conventional CJS model and compared the results with those from a multistate model using in addition resighting data. The analyses including resighting data resulted in a higher precision of the estimates of the probabilities of stay compared

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M. Schaub Zoological Institute—Conservation Biology, University Bern, Baltzerstrasse 6a, 3012 Bern, Switzerland e-mail: michael.schaub@vogelwarte.ch to analyses using only capture-recapture data of the same individuals. Moreover, the power to detect transients was substantially enhanced. Capture had no effect on the estimates of probability to stay and recapture probability; birds did not leave the stopover site or avoid nets as a reaction to capture. The estimates of probability of stay were up to 15.7% higher when resighting data were included, probably due to the higher power to detect transients and the elimination of the bias induced by non-random temporary emigration when both data types are considered. As a consequence, stopover duration would have been underestimated when only the capture-recapture data were available. We conclude that additional resightings of colour ringed birds can produce more accurate results needed for enhancing our understanding of stopover ecology of migrants.

**Keywords** Africa · Bird migration · Colour-rings · Multistate model · Stopover duration

## Introduction

Long-distance migrating birds spend more time at stopover sites for refuelling than on actual flight bouts (Lindström 1995). Therefore, the estimation of stopover duration is fundamental for the understanding of bird migration. Recent studies have applied capture– recapture models to estimate probability of stay and seniority probability from which stopover duration can be derived (Lavee et al. 1991; Schaub and Jenni 2001; Schaub et al. 2001; Rguibi-Idrissi et al. 2003; Salewski and Schaub, submitted). However, there are two potential problems when using capture–recapture data to estimate stopover duration: low recapture rate and trap response behaviour.

Recapture rates of birds at stopover sites are usually low (Lavee et al. 1991; Chernetsov and Titov 2000; Schaub and Jenni 2001; Schaub et al. 2001). Capturerecapture models are based on probabilistic theory and use maximum likelihood for parameter estimation and are, therefore, expected to produce unbiased and precise estimates (Williams et al. 2002). However, low recapture probabilities result in low precision of the parameter estimates and low power to detect variation in parameter estimates (Burnham et al. 1987). Moreover, the power of goodness-of-fit (GOF) tests is low for sparse data sets and, therefore, the possibility to detect violations of the underlying assumptions of capture-recapture models, such as the occurrence of transients or trap-response behaviour, is limited (Pradel 1993; Pradel et al. 1997).

Birds may change their behaviour in response to capture. In some studies, migrants lost mass at stopover sites after capture (Yong and Moore 1997; Schaub and Jenni 2000) which was sometimes interpreted as a handling effect (Nisbet and Medway 1972; Lindström 1995; Schwilch and Jenni 2001). It has also been discussed that birds may depart from a stopover site as a reaction to capture (Nisbet and Medway 1972). This is difficult to confirm empirically, because emigration and non-capture are confounded. Moreover, birds may avoid nets for some time after they have been captured. This reaction might be permanent, or it may last for only a short time (immediate) and will bias the estimated probabilities of stay if not accounted for (Pradel 1993). It is not possible to confirm the occurrence of permanent trap response with capturerecapture data. If some birds leave the stopover site immediately after they have been captured or avoid completely to be captured again, estimated probability of stay will be negatively biased. In contrast, immediate trap response behaviour, where probability of stay or probability of recapture changes depending on whether or not birds have been captured at the preceding occasion, can be detected (e.g. Pradel 1993). Still, the power to detect these effects is low when recapture probabilities are low (Pradel et al. 1997) and, therefore, it is currently not known whether behavioural response to capture is a common phenomenon.

An option to enhance recapture probabilities and thus to increase the power to detect heterogeneity such as transients or trap-response behaviour is to resight birds which were marked individually with colour rings (e.g. Rock 1999). This sampling scheme has the advantage that, from the same random sample of birds, a data set with low (capture–recapture data only) and one with high (additional resightings) recapture probabilities are obtained, allowing an examination of the impact of varying recapture rates on the estimated stopover parameters. However, conventional capture– recapture models can only be used to analyse either capture–recapture data or capture-resighting data because recapture and resighting probabilities differ. Analysing the data in conjunction is possible with a specially designed multistate model.

We set up a constant effort mist-netting site in Ouadâne, Mauritania, West Africa, in spring 2003 and 2004 and marked birds with an aluminium ring and an individual combination of colour rings. We then searched for colour-ringed birds systematically. The resulting capture-recapture and capture-resighting data were analysed simultaneously with a multistate capture-recapture model. The aims of our analyses were: (1) to test empirically how much the precision of estimated capture-recapture parameters (survival, recapture probability) increases when re-encounter rates increase; (2) to test whether the enhanced re-encounter rate has an impact on the probability to detect transients; (3) to test whether capture alters stopover behaviour of birds; (4) to test whether recapture and re-observation rates depend on whether the birds were recaptured or re-observed, respectively, on the preceding day; and (5) to discuss the potential benefit of colour ring data for the study of stopover behaviour of migrating birds.

# Methods

Study area and data collection

Birds were mist-netted between 22 March and 15 May 2003 and between 7 March and 8 May 2004 in Ouadâne (20°54'N, 11°35'W), an oasis in the western Sahara, central Mauritania. Mist nets were set up between Balanites aegyptiaca, Maerua crassifolia and Acacia tortilis trees fringing a dry riverbed approximately 5 km northeast of the village of Ouadâne. In total, 19 nets  $(6 \times 2.5 \text{ m each})$  were set up in 2003 and 29 nets 2004. The nets were operated daily throughout the period with the exception of 3 days with strong winds in 2003. Nets were opened at sunrise at about 0600 hours and closed at about 1100 hours. In the evening, nets were operated from about 1630 to sunset at about 1900 hours. Nets were checked for birds in 30-min intervals. All birds captured were marked with an aluminium ring and an individual combination of colour rings.

In 2003, colour-ringed birds were searched for (by V.S.) whenever there was time between checking the

nets and handling captured birds. In April and early May, the vicinity of the nets was searched for colourringed birds for about 3 h in the early afternoon about every second day. In 2004, daily standardised searches for colour-ringed birds in the netting area were performed by M.T. in the late afternoon.

# Species analysed

There were sufficient captures (>40) and subsequent re-encounters (>10%) for the analysis of three species in both years (subalpine warbler *Sylvia cantillans*, common whitethroat *S. communis* and orphean warbler *S. hortensis*). In 2004, there were also sufficient data for eastern olivaceous warbler *Hippolais pallida* and willow warbler *Phylloscopus trochilus*.

# Data analysis

Stopover duration can be calculated from estimates of the probabilities of stay and seniority by simple transformations (Schaub et al. 2001). Here, we focus on the probability of stay only, because it was recently questioned whether the seniority probability needs to be included for getting estimates of stopover duration (Efford 2005; Pradel et al. 2005). We first analysed the capture-recapture data to estimate mean and variance of the probabilities of stay and recapture, respectively. We also tested whether a significant proportion of transients (defined in a statistical sense as individuals whose probability of stay is zero, i.e. leave the study site after 1 day) occurred. These estimates were compared with estimates from the re-encounter data (i.e. capture-recapture data including resightings) of the same birds analysed with a multistate model to address our aims 1 (precision of estimates) and 2 (occurrence of transients). We then used the re-encounter data analysed by the multistate model to test whether probability of stay immediately after a capture differs from the probability of stay without immediate preceding capture (aim 3, capture effect on stopover behaviour). We also tested whether immediate trapresponse behaviour was apparent and thus addressed topic 4 (capture effect on re-encounter probability). All analyses were performed with program MARK (White and Burnham 1999).

We used the Cormack–Jolly–Seber (CJS) model to estimate local survival rates from the capture–recapture data (Lebreton et al. 1992). These estimates are viewed as the probability of stay at stopover sites, because it can reasonably be assumed that mortality is insignificant during the rather short stopover duration (Schaub et al. 2001; Schaub and Jenni 2001). The CJS model estimates two parameters: the probability that a marked individual that is present at the stopover site on day *i* is still present at the stopover site on day i+1(probability of stay,  $\Phi_i$ ), and the probability that a marked individual that is present at the stopover site on day *i* is recaptured on day *i* (recapture probability,  $p_i$ ). Heumann (2004) analysed a subset of our data and found no time variation for probabilities of stay and recapture. Therefore, we always considered for recapture a model structure with constant parameters across time. For the probability of stay, we also considered a model structure with constant parameters across time and a further one in which transients were accounted for (Pradel et al. 1997; Schaub et al. 2004a). These model parts were combined resulting in two candidate models (see electronic appendix 1a). We used Akaike's information criterion (AIC) to rank the models (Burnham and Anderson 1998). We evaluated the GOF of a model that does account for transients using tests implemented in U-CARE (Choquet et al. 2003). These tests were only possible with the recapture data.

For the analysis of the re-encounter data (i.e. capture-recapture and capture-resighting data), we formulated a multistate model (Nichols et al. 1992). The model consists of the states "recaptured" (containing colour-ringed birds that were recaptured in mist-nets), "resighted" (containing colour-ringed birds that were resighted) and "not recaptured or resighted" (containing colour-ringed birds that were neither recaptured nor resighted). Multistate models are parameterised with state-specific transition, survival and recapture probabilities. Here, we fixed the statespecific recapture probabilities ("recaptured" = "resighted" = 1, "not recaptured nor resighted" = 0), and instead used the transition probabilities to estimate recapture probabilities. The model is written by a matrix of transition probabilities and by a vector of state-specific probabilities of stay, and the states "recaptured" (C), "resighted" (S), and "not recaptured nor resighted" (N) are from left to right and from top to down:

$$\begin{bmatrix} p_{\rm CC} & p_{\rm SC} & p_{\rm NC} \\ p_{\rm CS} & p_{\rm SS} & p_{\rm NS} \\ 1 - p_{\rm CC} - p_{\rm CS} & 1 - p_{\rm SC} - p_{\rm SS} & 1 - p_{\rm NC} - p_{\rm NS} \end{bmatrix} \begin{bmatrix} \phi_{\rm C} \\ \phi_{\rm S} \\ \phi_{\rm N} \end{bmatrix}.$$

The multiplication of the two elements results in the state transition probability from 1 day to the next.

The parameters in the model are the reencounter probabilities  $p_{AB}$  (probability that a bird that was

encountered with method A at occasion i-1 is encountered with method B at occasion *i*, given that it is still at the stopover site at i) and the probabilities of stay  $\Phi_A$  (probability that a bird that was encountered with method A at occasion i is still at the stopover site at occasion i+1). The subscript C refers to capture, subscript S to resighting and subscript N to non-reencounter (neither recaptured nor resighted).

This general model needs to be constrained to test our hypotheses. To test whether the probability of stay is independent of whether a bird has been captured requires to constrain the three probabilities of stay to be equal  $(\Phi_C = \Phi_S = \Phi_N)$ . The model referring to the alternative hypothesis that the probability of stay is influenced by the preceding capture only needs the constraint that  $\Phi_S$  and  $\Phi_N$  are equal  $(\Phi_C, \Phi_S = \Phi_N)$ . Re-encounter probabilities may also differ depending on whether or not the individual has been encountered on the previous occasion (immediate trap response); it might be apparent only for physical capture, only for resighting, for both or for none of them. A model referring to the hypothesis that an immediate trap response is apparent for physical capture requires the constraint  $p_{SC}=p_{NC}$  versus  $p_{CC}$ , a model referring to the hypothesis that immediate trap response is apparent for resightings requires the constraint  $p_{CS}=p_{NS}$ versus  $p_{SS}$ , and models without immediate trap responses requires the constraints  $p_{\rm CC}=p_{\rm SC}=p_{\rm NC}$  for capture and  $p_{CS}=p_{SS}=p_{NS}$  for resighting, respectively. Different combinations of these model parts were used to define the set of candidate models (see electronic appendix 1b).

The probability that newly-caught individuals are transients and the probabilities of stay of non-transients can be estimated by fitting a model with an agedependent structure with the first age class spanning 1 day (Pradel et al. 1997). The probability that a newlycaught individual is a transient is then  $\tau = 1 - \Phi_1 / \Phi_2$ , where  $\Phi_1$  is the estimate of the probability of stay of the first and  $\Phi_2$  the estimate of the probability of stay of the second age class. Because our birds need all to be captured before they can eventually be resighted, transients can only occur in the state "recaptures". Thus, in the transient models, only the parameters  $\Phi_{\rm C}$ have an age-dependent structure. If the probabilities of stay are the same in all states and there are transients, the probability of stay of the second age class in the state "recaptured" is the same as the probabilities of stay of the other states.

# Results

# Modelling recaptures

The proportion of recaptured birds (Table 1) ranged from 2.3% (willow warbler) to 15.5% (common whitethroat). Individual birds were recaptured up to four times (subalpine warbler in 2004). Only one willow warbler was recaptured, hence CJS models could not be applied. The GOF tests were never significant indicating no violation of the model assumptions (Table 2).

Transients were detected in two out of seven analvses (willow warbler excluded; see electronic appendix 2a and 3a). In subalpine warbler and common whitethroat in 2003, there was high uncertainty about whether transients occurred since both relevant models had similar support. Capture probabilities (Table 3) were generally low and ranged from 0.023 (eastern olivaceous warbler in 2004) to 0.173 (common whitethroat in 2004). The precision of these estimates was rather poor as indicated by high coefficients of variation, which ranged from 28.2% (subalpine warbler, 2004) to 76.0% (common whitethroat, 2003). Probability of stay of non-transients ranged from 0.775 (common whitethroat, 2003) to 0.864 (eastern olivaceous warbler, 2004), and the corresponding coefficients of variation from 3.2% (subalpine warbler, 2004) to 8.8% (common whitethroat, 2004; Table 4).

#### Modelling reencounters

The proportion of the birds that were re-encountered (Table 1) ranged from 17.2% (common whitethroat,

Table 1 Number of individuals of six species caught, percentage of individuals recaptured and reencountered at least once, and the maximal number of times an individual has been recaptured and reencountered

Species	Year	п	% recaptured	% re-encountered	Max no. recaptures	Max. no. re-encounters
Subalpine warbler	2003	125	8.8	31.2	2	13
Common whitethroat	2003	71	15.5	23.9	3	8
Orphean warbler	2003	66	12.1	43.9	2	11
Eastern olivaceous warbler	2004	80	11.2	33.7	2	11
Subalpine warbler	2004	336	9.8	30.4	4	15
Common whitethroat	2004	93	5.4	17.2	3	5
Orphean warbler	2004	178	12.1	29.3	2	13
Willow warbler	2004	45	2.3	26.7	1	5

**Table 2** Goodness of fit tests of the model that does account for transients using only the recapture data

Species/year	Year	GOF test		
		$\chi^2$	df	Р
Subalpine warbler	2003	0.70	5	0.98
Common whitethroat	2003	1.87	8	0.98
Orphean warbler	2003	0.94	4	0.92
Eastern olivaceous warbler	2004	0.00	3	1.00
Subalpine warbler	2004	15.53	40	1.00
Common whitethroat	2004	0.01	4	1.00
Orphean warbler	2004	0.01	11	1.00
Willow warbler	2004	NA	NA	NA

The test-statistics of the overall test are shown with the degrees of freedom (df) and the significance level (P). For one data set, the tests could not be computed (NA)

2004) to 43.9% (orphean warbler, 2003). Individuals were reencountered up to 15 times (subalpine warbler, 2004). Moreover, due to the resighting activity, there were sufficient records of willow warblers for an analysis.

Models taking transients into account were the most parsimonious ones in four out of seven analyses (willow warbler excluded; see electronic appendix 2b and 3b). Compared to the recapture data, transients were detected in three more cases (subalpine warbler and common whitethroat in 2003, orphean warbler in 2004). Additionally, in eastern olivaceous warblers, the second best model including transients was very close to the best one, indicating that there may have been transients as well (see electronic appendix 3b). The summed weights of models including transients was generally higher with re-encounter data compared to when only recaptures were considered (see electronic appendix 2b and 3b) indicating that the power to detect transients was higher when the reencounter probability was enhanced. In the common whitethroat in 2004, the recapture data indicated transients, but not the reencounter data (see electronic appendix 3b).

There was evidence for an immediate trap response due to resighting in six out of eight analyses, but only in two was there evidence for an immediate trap response due to recapture (see electronic appendix 2b and 3b). All immediate trap responses were positive. Thus, birds that were seen (or captured) at occasion i-1 had a higher chance of being resighted (or recaptured) at occasion i than individuals that were not seen (or captured) at occasion i-1 (Table 3). In all analyses, the resighting probability was distinctly higher than the recapture probability (Table 3).

Capture generally had no impact on the immediate decision of birds to depart from the stopover site (see electronic appendix 2b and 3b). An exception was the eastern olivaceous warbler in 2004, where the probability of stay was reduced immediately following a capture event (Table 4).

The probabilities of stay based on re-encounter data were higher than the estimates from the recapture data, with the exception of the common whitethroat in 2004 (Table 4), but confidence intervals were often overlapping. Consequently, stopover duration after first capture was estimated to be higher using reencounter data compared to the use of recapture data alone (Fig. 1). Probabilities of stay estimated using

**Table 3** Recapture, resigning and reencounter probabilities (p), standard error (SE) and coefficient of variation in % (CV) of p of the most parsimonious CJS and multistate models

Species and model		р	SE	CV
2003				
Subalpine warbler				
CJS model	р	0.034	0.013	38.2
Multistate model	$p_{\rm CC} = p_{\rm SC} = p_{\rm NC}$	0.030	0.009	30.0
	$p_{\rm CS} = p_{\rm NS}$	0.198	0.026	13.1
	$p_{SS}$	0.566	0.044	7.8
Common whitethro	pat			
CJS model	p	0.075	0.057	76.0
Multistate model	$p_{\rm CC} = p_{\rm SC} = p_{\rm NC}$	0.118	0.032	27.1
	$p_{\rm CS} = p_{\rm NS} = p_{\rm SS}$	0.173	0.037	21.4
Orphean warbler	100 110 100			
	р	0.034	0.016	47.1
	$p_{\rm CC} = p_{\rm SC} = p_{\rm NC}$	0.021	0.007	33.3
	$p_{\rm CS} = p_{\rm NS}$	0.112	0.020	17.9
	$p_{SS}$	0.512	0.064	12.5
2004				
Eastern olivaceous	warbler			
CIS model	n	0.023	0.010	43 5
Multistate model	P $p_{CC} = p_{SC} = p_{NC}$	0.026	0.009	34.6
	$p_{CC} = p_{NC}$	0.225	0.031	13.8
	Des Pins	0.450	0.053	11.8
	F 55			
Subalpine warbler		0.071	0.000	•••
CJS model	р	0.071	0.020	28.2
Multistate model	$p_{\rm CC}$	0.073	0.020	27.4
	$p_{\rm SC} = p_{\rm NC}$	0.035	0.006	1/.1
	$p_{\rm CS} = p_{\rm NS},$	0.233	0.019	8.2
	$p_{SS}$	0.466	0.050	0.1
Common whitethro	oat			
CJS model	р	0.173	0.079	45.7
Multistate model	$p_{\rm CC} = p_{\rm SC} = p_{\rm NC}$	0.028	0.011	39.3
	$p_{\rm CS} = p_{\rm NS} = p_{\rm SS}$	0.040	0.014	35.0
Ornhean warbler				
CIS model	n	0.034	0.010	294
Multistate model	P $p_{cc} = p_{cc} = p_{Nc}$	0.041	0.009	22.0
manificate model	$p_{CC} = p_{NC} = p_{NC}$	0.176	0.025	14.2
	PCS = PNS	0.386	0.052	13.5
	P 33	0.000	0.002	1010
Willow warbler		0.000	0.000	100
Multistate model	$p_{\rm CC}$	0.028	0.028	100
	$p_{\rm SC} = p_{\rm NC}$	< 0.001	<0.001	22.0
	$p_{\rm CS} = p_{\rm NS}$	0.073	0.024	52.9
	pss	0.327	0.113	34.6

<b>Table 4</b> Parameter estimates from the most parsimonious	Species and model	Transients	Probability of stay				
CJS and multistate models		Estimate (SE)	Estimate (SE)	CV			
	2003						
	Subalpine warbler						
Shown are the probability that a newly caught individual is a transient (SE), the probability of stay (SE) and	CJS model	-	0.778 (0.053)	6.8			
	Multistate model	0.52 (0.014)	0.900 (0.016)	1.8			
	Common whitethroat	· · /					
	CJS model	-	0.775 (0.057)	7.4			
	Multistate model	0.62 (0.085)	0.874 (0.040)	4.6			
	Orphean warbler	× /					
	CJS model	-	0.817 (0.058)	7.1			
	Multistate model	-	0.879 (0.019)	2.2			
	2004						
	Eastern olivaceous warbler						
	CJS Model	-	0.864 (0.045)	5.2			
	Multistate model (after capture)	-	0.471 (0.072)	15.3			
	Multistate model (not after capture)	-	0.925 (0.017)	1.8			
	Subalpine warbler						
	CJS model	0.62 (0.103)	0.834 (0.027)	3.2			
	Multistate model	0.54 (0.077)	0.876 (0.012)	1.4			
	Common whitethroat						
	CJS model	0.87 (0.065)	0.822 (0.072)	8.8			
	Multistate model	_	0.780 (0.042)	5.4			
	Orphean warbler						
	CJS model	-	0.794 (0.040)	5.0			
	Multistate model	0.47 (0.071)	0.859 (0.020)	2.3			
the coefficient of variation in	Willow warbler						
% (CV) of the probability of	Multistate model	-	0.853 (0.035)	4.1			

re-encounter data were always more precise than the estimates from the recaptures alone (Table 4). The coefficient of variation (CV) varied between 1.4% (subalpine warbler, 2004) and 5.4% (common whitethroat).

### Discussion

stay

The use of resighting data in conjunction with the capture-recapture data resulted in considerably more

Fig. 1 Estimated stopover duration after first capture and 95% confidence intervals calculated from the probabilities of stay ( $\Phi$ ) from the most parsimonious multistate (dots) and CJS models (circles). For the multistate model of eastern olivaceous warbler, the lower value is the estimated stopover duration immediately after capture and the upper value immediately after resighting or nondetection. The dotted line separates the results of 2003 and 2004

precise estimates of the probability of stay, and in a higher power to detect transients compared to the results based only on capture-recapture data. Furthermore, capture had no immediate impact on behaviour: the probability of stay and the probability to be recaptured immediately after capture did not generally differ compared to the probabilities of stay and recapture not immediately following a capture event. Including resightings can be considered as an increase of the sample size, leading to increased precision of the parameter estimates as shown in this study because



residual variance gets smaller (Burnham and Anderson 1998). Higher precision of parameter estimates increases the power to test hypotheses on these parameters.

When only recapture data were considered, there was a high uncertainty whether transients occurred in some analyses (subalpine warbler and common whitethroat in 2003). When the resighting data were added, there was a clear indication that transients were present in these species. In contrast, in the common whitethroat in 2004 the opposite was true: only the inclusion of the resightings showed that there were no transients, which had been concluded when only the recaptures would have been considered. The probability of a failure to detect transients, although they are present, is high in studies with low recapture rates (Pradel et al. 1997). A consequence of the failure to detect transients is that the probability of stay and, thus, the estimate of stopover duration, is underestimated. Because the occurrence of transients is common in migrants (e.g. Titov 1999; Schaub and Jenni 2001; Schaub et al. 2004b) it is suggested that many capture-recapture studies which analysed data sets with low recapture rates underestimated stopover duration of migrating birds.

It was previously discussed that migrants might alter their stopover behaviour due to handling stress. Migrants could either prolong their stay, because their fuel deposition is negatively influenced by capture (Schwilch and Jenni 2001), or migrants could shorten their intended stay when a stopover site is regarded as dangerous (Nisbet and Medway 1972; Fransson and Weber 1997). In this study, the probabilities of stay were not influenced by capture. The only exception was the eastern olivaceous warbler in 2004 whose probability of stay decreased immediately following a capture event. Thus, in six out of seven analyses (willow warbler excluded), birds did not alter their behaviour due to capture with respect to stopover duration. We also had no evidence that birds that were still present at the stopover site avoided mist-nets as a response to previous capture. Therefore, data gained from mist netting studies can reveal unbiased results about probability of stay and stopover duration.

In six out of eight analyses, the resighting probability on day i + 1 of birds that were seen already on day i was higher than that of the birds that were not seen on day i. There are two possible explanations for this effect. First, observers may have been more attentive at places where they had previously noticed marked birds. Second, it may result from temporary emigration by floaters (Winker 1998) or individuals with spatially changing activity centres. These are found to be frequent in populations of migrants on wintering grounds and stopover sites (Zahavi 1971; Wood 1979; Davies and Houston 1981; Stünzner-Karbe 1996; Bächler and Schaub, submitted). Our data sets are too small to test which possibility is the case, but we think that the second one is the more likely explanation.

The probability of stay estimated with the recapture data was generally lower than the estimates with the re-encounter data. We expected that these two estimates should be the same, because they stem from exactly the same individuals. For statistical reasons, the estimates must be identical because we accounted for the additional resightings with the multistate model. Therefore, one or more assumptions underlying the capture-recapture models must have been violated. First, there may have been transients that were not detected with the recaptures. Consequently, probabilities of stay were biased low compared to probabilities of stay of non-transients estimated with the reencounter data. Second, when only recaptures were considered, there may be non-random temporary emigration (i.e. birds foraging above the 2.5-m high nets but not leaving the study area) resulting in slightly biased estimates of the probability of stay (Kendall et al. 1997; Schaub et al. 2004a). Third, the model assumption that the probabilities of stay are independent of the time the birds have already spent at the stopover site may have been violated. The GOF tests for capture-recapture models (Lebreton et al. 1992) are sensitive to all of the discussed violations. However, the power of the GOF tests is low when data are sparse (Pradel et al. 1997; Schaub et al. 2004a; Williams et al. 2002). This study suggests, therefore, that probabilities of stay can be underestimated when capture probabilities are low and that migrants may stay longer on stopover sites than estimated with conventional CJS analyses.

In conclusion, there are several advantages when resightings of colour-ringed birds are included in capture-recapture studies on stopover behaviour of migrating birds. The sample size can be increased by resightings in cases where capture and recapture rates cannot be increased. Due to increased sample size, the power to detect endogenous (e.g. age, sex) and environmental (e.g. season, weather) effects on stopover behaviour (Schaub and Jenni 2001; Rguibi-Idrissi et al. 2003; Schaub et al. 2004b) or violations of model assumptions are enhanced, which allows the making of more rigorous inferences and the obtaining of more precise estimates. Another advantage is that the analyses become more flexible and allow the testing of more hypotheses that are otherwise difficult to assess (e.g. temporary emigration due to vertical movements). Moreover, resightings could easily be extended to the area surrounding the capture area, allowing the testing of whether local permanent emigration is important (Bächler and Schaub, submitted). Therefore, additional colour ring data analysed with appropriate statistical methods can produce more precise results needed for the understanding of stopover ecology of migrants compared to mere capture– recapture studies.

# Zusammenfasung

Rastplatzökologie von Zugvögeln: Die simultane Anwendung verschiedener Markierungsmethoden erhöht die Genauigkeit der Schätzungen von Fang - Wiederfangmodellen

(Überlebenswahr-Schätzungen von Parametern scheinlichkeit=Wahrscheinlichkeit am Rastplatz zu bleiben, Rastdauer) zur Rastplatzökologie von Zugvögeln mittels Cormack-Jolly-Seber (CJS) Fang-Wiederfang Modellen leiden oft unter kleinen Datensätzen. Niedrige Wiederfangraten führen z.B. dazu, dass Verletzungen der Annahmen, die solchen Modellen zugrunde liegen oder Faktoren, die das Rastverhalten von Zugvögeln beeinflussen, nicht erkannt werden. untersuchten das Rastverhalten Wir paläarktischer Singvögel in einer Oase in Mauretanien, Westafrika. Mit Hilfe von Fang-Wiederfangdaten und systematischer Beobachtungen individuell farbberingter Vögel analysierten wir die Auswirkungen, die ein erhöhter Datensatz auf Schätzungen der Überlebenswahrscheinlichkeit und der Wiederfangwahrscheinlichkeit hat, sowie den Einfluss einer möglichen Fangreaktion der Vögel auf diese Parameter. Wir analysierten Fang-Wiederfangdaten mit einem einfachen CJS Modell und verglichen die Ergebnisse mit denen eines multistate Modells, welches zusätzlich die Wiederbeobachtungen derselben Individuen berücksichtigten. Die Analysen, die Wiederbeobachtungen einschlossen, führten zu einer höheren Präzision der Schätzungen der Überlebenswahrscheinlichkeit im Vergleich zu den Analysen, die nur Wiederfänge berücksichtigten. Darüber hinaus wurde die Wahrscheinlichkeit Transients (Vögel, die nur einen Tag am Fangplatz bleiben) festzustellen erhöht. Der Fang hatte keinen Einfluss auf die Schätzungen der Überlebens- oder der Wiederfangwahrscheinlichkeit, was zeigt, dass Vögel infolge des Fanges nicht den Rastplatz verlassen oder die Netze vermeiden. Die Schätzungen der Überlebenswahrscheinlichkeit waren

im Vergleich zu den Fang-Wiederfangdaten bis zu 15,7% erhöht, wenn multistate Modelle angewendet wurden. Dies könnte durch die höhere Wahrscheinlichkeit Transients zu entdecken bedingt sein, wodurch Schätzfehler vermieden werden. Die Rastdauer von Vögeln würde somit unterschätzt werden, wenn nur Fang-Wiederfangdaten analysiert werden. Beobachtungen farbberingter Vögel führen daher zu genaueren Schätzungen von Rastdauern, welche unerlässlich für das Verständnis der Rastplatzökologie von Zugvögeln sind.

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