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Spring migration of Ruffs *Philomachus pugnax* in Fryslân: estimates of staging duration using resighting data

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Seasonal bird migration involves long flights, but most time is actually spent at intermediate staging areas. The duration of stay at these sites can be evaluated with mark–recapture methods that employ day-to-day local encounters of individually marked birds. Estimates of staging duration are based on two probabilities: the immigration probability, the complement of a bird's seniority to an area, and the emigration probability, the complement of the staying probability. Estimating total staging duration from seniority and staying probabilities requires validation for resighting data and here we compare three data categories of Ruffs *Philomachus pugnax* passing through The Netherlands during northward migration: (1) newly colour-ringed, (2) previously colour-ringed and (3) radio-tagged Ruffs (recorded by automated receiving stations). Between 2004 and 2008, 4363 resighting histories and 95 telemetry recording histories were collected. As sample sizes for females were low, only data for males were analysed. Possible catching effects affecting estimates of staging duration were explored. Staying probability was estimated for all data. Seniority however, could not be estimated for newly marked Ruffs; the assumption of equal 'capture' probability for reverse-time models applied to estimate seniority is violated for seasonal resighting histories starting with a catching event. Therefore, estimates of total staging duration were based on resightings of previously colour-marked birds only. For radio-tagged birds a minimal staging duration (time between tagging and last recording) was calculated. Modelling indicated that newly colour-ringed birds had a higher staying probability than previously colour-ringed birds, but the difference translated to a prolonged staging duration in newly ringed birds of only 0.4–0.5 d, suggesting a very small catching effect. The minimal staging duration of radio-tagged birds validated estimates of staging duration for colour-ringed birds in 2007 but not in 2005. In 2005 a low resighting probability resulted in underestimates of staging duration. We conclude that (1) estimates of staying probability can be affected by catching although effects on staging duration might be small, and that (2) low resighting probabilities can lead to underestimates in staging duration. In our study previously ringed Ruffs resighted in 2006–08 yielded reliable estimates of staging duration as data had sufficiently high resighting probabilities. Average staging durations varied between 19 d in 2008 and 23 d in 2006.

Key words: capture–recapture models, catching effects, colour-ringing, encounter methods, shorebird migration, staging/stopover duration, radio telemetry, resighting data

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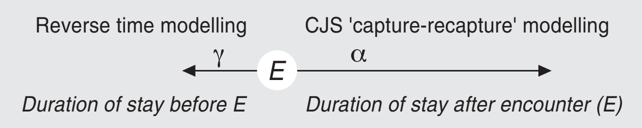
During bird migration, periods of rest and refuelling are punctuated by flight episodes (Piersma 1987). Therefore, the total duration of migration is not so much determined by the flight time as by the time in preparation of these flights, the staging duration (Hedenström & Alerstam 1997, Hedenström 2008). The use of colour-rings and radio telemetry, and the development of statistical tools, have enabled better estimations of staging duration and turnover at (re-)fuelling sites (Kersten & Smit 1984, Nebel *et al.* 2000, Schaub & Jenni 2001, Schaub *et al.* 2001, Battley *et al.* 2004, Ydenberg *et al.* 2004, Rice *et al.* 2007, Salewski *et al.* 2007, Bächler & Schaub 2007). At a staging site there is a constant flux of birds entering the site and birds that leave (Schaub *et al.* 2001). This means that counts cannot be used directly to infer population size and turnover. When individual staging duration is taken into account, however, numbers using a site can be estimated (Bishop *et al.* 2000, Frederiksen *et al.* 2001, Ydenberg *et al.* 2004, Lee *et al.* 2007).

From 2004–08 we studied the staging ecology of Ruffs *Philomachus pugnax* in Fryslân, The Netherlands (Jukema & Piersma 2000, Jukema *et al.* 2001b, Verkuil & de Goeij 2003). With 1000s of birds observed, this area ranks amongst the larger known staging areas of Ruffs in Europe (Wymenga 1999). The Ruff is a gregarious, strongly sexually dimorphic shorebird whose reproductive behaviour has been well-studied (Hogan-Warburg 1966, van Rhijn 1991, Lank *et al.* 1995, Widemo 1997, Lank & Dale 2001, Jukema & Piersma 2006), but relatively little is known about migration behaviour and demography (but see OAG Münster 1989, OAG Münster 1992, Melter & Bergmann 1996, Jukema & Piersma 2000). Ruffs breed in temperate to arctic areas ranging from Western Europe to Eastern Siberia (Zöckler 2002). Although most birds winter in the Sahel and the savannahs of eastern Africa and in India (Zwarts *et al.* 2009), a small proportion of males remain in NW Europe during winter (OAG Münster 1996).

In this paper we use three separate data categories to estimate staging duration: (1) newly colour-ringed Ruffs, (2) previously colour-ringed Ruffs returning to the area, and (3) telemetry data of newly radio-tagged Ruffs (Table 1). Based on our exploration of these categories, we present a design for using capture–resighting statistics to estimate staging duration in colour-ringed birds with long stopovers. Following Warnock (2009) we choose to use the term *staging duration* rather than *stopover duration* to emphasize that the period is much larger than the few days stopovers in songbirds. Estimates for *staging duration* were obtained by adding up the *staying time*, the time that a bird would remain in the study area after Time$_i$, and the *seniority*, the estimated time the bird was already present before Time$_i$ (Schaub *et al.* 2001, Schaub *et al.* 2004). Staying and seniority probabilities (their complements are the *emigration* and *immigration* probabilities) are estimated using survival analysis (Schaub *et al.* 2001). Birds are caught and colour-ringed, and estimates of staging duration are made based on local resightings within the same season (Kersten & Smit 1984, Ydenberg *et al.*

Table 1. Overview of possible estimations (+) of staging duration in Year$_i$ for the three data categories collected at staging location for Ruffs in The Netherlands. Notation is according Schaub *et al.* (2001): ‘α’ is *staying probability* as used to estimate *duration of stay after encounter* ; ‘γ’ is *seniority probability* as used to estimate *duration of stay before encounter*’; staging duration, the total time present at given time interval, is the sum of *duration of stay before encounter* and *duration of stay after encounter*.



Data category	State^b	Duration of stay after encounter *Staying probability* (α)	Duration of stay before encounter *Seniority probability* (γ)	Staging duration (*duration of stay before encounter+ duration of stay after encounter)*
Radio-tagged in Year$_i^a$	2	+	-	-
Colour-ringed in Year^a	2	+	-	-
Colour-ringed in Year$_{j<i}^a$	1	+	+	+

[a] Year$_i$ refers to newly colour-ringed or newly radio-tagged birds; Year$_{j<i}$ refers to previously colour-ringed birds.
[b] For model selection, previously marked (in Year$_{j<i}$) and newly marked (Year$_i$) birds are assigned different states, ‘state 1’ and ‘state 2’.

2004). Yet, seniority, which is part of staging duration, can only be calculated using individuals marked in previous years, because the assumption of equal 'recapture' probability for reverse-time modelling is violated when the encounter history starts with a catching event (Table 1). In our study system, we individually colour-marked more than 4500 individual Ruffs over five successive spring seasons, many of which returned the following years. The first encounter of returning marked birds in the new migration season is not a catch but a resighting. We were also able to compare data of returning colour-ringed Ruffs (marked in Year$_{i-1}$) with newly colour-ringed Ruffs observed in Year$_i$ of colour-ringing, which allowed us to investigate the extent and strength of a possible catching effect on the staying probability.

The capture–resighting models estimate the *resighting probability* that should be independent of marking technique (Salewski *et al.* 2007, Bächler & Schaub 2007). However, the resighting probability in colour-ring studies can be very low. This problem can be overcome with radio-tags, which give much higher reporting probabilities. Radio-telemetry, however, is costly and potentially more invasive to the birds. It certainly does not allow for large sample sizes to be accumulated over years. We applied radio-tags to a small subset of male Ruffs to verify the accuracy of estimates from colour-ring resighting data.

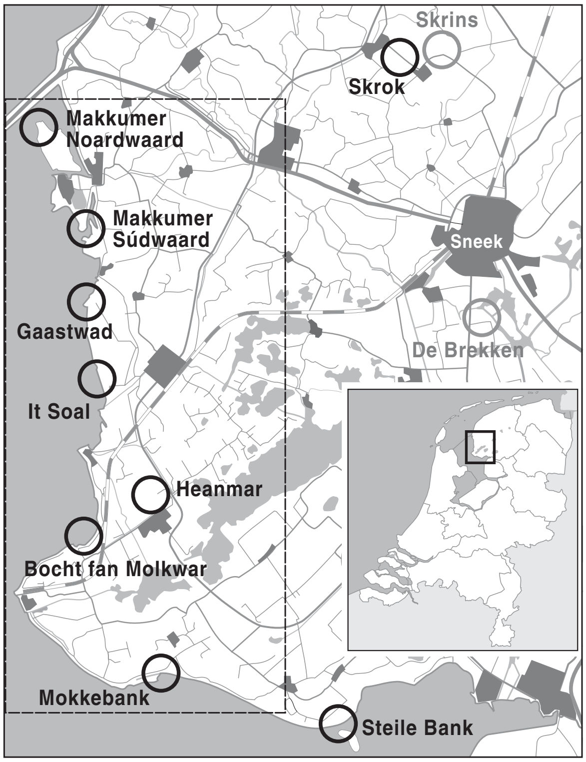


Figure 1. The study area in southwest Fryslân, The Netherlands. Indicated are the main roosting sites used by the staging Ruffs. Black circles indicate the roosts where the automated receiver stations (ARTS) tracking the radio-tagged Ruffs were placed. The box indicates the core study area (comprising c. 200 km^2) where roosts and feeding grounds were searched daily for colour-marked individuals and where the majority of catching sites was situated.

METHODS

Study area and data collection

This study was carried out at the main western European spring staging area (Wymenga 1999). During spring and autumn migration, Ruffs use the south-western part of the province of Fryslân, The Netherlands, to moult and refuel (Jukema *et al.* 1995, Verkuil & de Goeij 2003). The study area consists of grasslands intensely managed for dairy farming, and the borders of Lake IJsselmeer. The area covers c. 400 km^2 (Fig. 1). During 2004–08 staging Ruffs were studied over the entire passage periods, from the first week of March until late May. Catches were made on all days except Sundays with traditional 'wilsternets', a c. 20 m long and 3 m high clap net. The net was laid out on grassland used by foraging Ruffs and the wilsternetters used a flock of stuffed Ruffs as decoys to lure the birds near the net (Jukema *et al.* 2001a, Piersma *et al.* 2005). Each captured Ruff was marked with a unique combination of four colour rings and a coloured 'flag'. Ruffs foraged in the morning and afternoons on the grasslands and roosted at the shores of Lake IJsselmeer and along smaller lakes for a few hours at midday and at night (unpubl. data) where they were checked daily for colour rings using binoculars and telescopes. Our resighting effort of colour-ringed birds was more or less constant between 15 March and 20 May and covered all known foraging and roosting sites in the study area (Fig. 1).

Additionally, radio transmitters (BD2 transmitters, with 11 weeks guaranteed battery life time, Holohil Systems Ltd. Carp, Ontario, Canada) were issued in 2005 and 2007 to 48 and 47 adult males, respectively. The transmitters weighed 1.8 g, at most 1% of the body mass of an adult male, and were glued to the clipped feather base and skin on the plateau below the spine on the lower back using Super Glue Gel. The transmitters would fall off at the summer body moult. Individuals selected for tagging were on average 1.9 g heavier than the average population (unpubl. data). In both seasons a single transmitter was used to test equipment. These test transmitters lasted at least 10 weeks, indicating that battery life covered the migration period easily.

Automated receiving stations (ARTS) were placed close to the nine known roosting sites, covering the vast majority of Ruffs in the study area (Fig. 1). The ARTS were scheduled to collect four signals per individual at 20 min intervals, 24 hours a day. An individual was considered present if at least 3 out of 4 recordings gave a signal 1.5× stronger than the 'noise' (Green *et al.* 2002, Rogers *et al.* 2006). The ARTS recordings were collected between 25 March and 1 June each year. Minimal staging durations, the time interval between the day of tagging and the last day of recording, were calculated for each individual.

On the basis of this material we explore (1) catching effects (a comparison of staying probabilities between previously and newly captured birds), (2) age effects, (3) the occurrence of transients (transients are observed only once and therefore have a zero staying probability after an encounter at Time_i), and (4) the effect of encounter method (resightings vs. radio-detection) on resighting probability and estimates of staging duration.

Encounter histories

We collected individual encounter histories spanning a 52-day period (25 March until 15 May). In southwest Fryslân most Ruffs arrive after 15 March, and by 15 May 99% of the birds usually have left, thus our 52-day study period encompasses most of the migration. Ruffs still present in June, and Ruffs ringed at catching localities outside the core area that were not intensively searched (Fig. 1) were excluded from the analyses. Since sample sizes for females were very low, females were also excluded from the analyses. In 2004, 2005, 2006, 2007 and 2008, we obtained 855, 788, 1052, 924, and 744 encounter histories of colour-marked male Ruffs, of which up to 56% had been colour-ringed in a previous year. For radio-tagged Ruffs we collected 42 encounter histories in 2005 (four faeders – female mimics (Jukema & Piersma 2006) – were excluded from the analyses and two birds were found dead soon after release). In 2007 we obtained 47 encounter histories. Ruffs still present after 15 May were left out of the analyses as they probably were part of either the relict local breeding population or non-breeders who 'summer' in the region (in grey in Fig. 2). As capture–recapture methodology requires the number of encounter intervals to be lower than the number of encounter histories, the data were pooled per 2-day intervals to reduce number of intervals to 26. For comparison, and since observations were only made 6 days per week, the encounter histories of the colour-ringed birds were pooled in 2-day intervals as well. Pooling has the additional advantage to reduce the number of parameters in the models (White & Burnham 1999).

Survival analysis to estimate staging duration

Mark–recapture models have been developed to estimate survival (White & Burnham 1999). The global model usually applied is $\Phi_t p_t$, where Φ is the apparent survival probability, p is the resighting probability and *t* is time. Here we use mark–recapture models to estimate staging duration (Schaub *et al.* 2001). In the Schaub method, *t* is day and the 'survival' parameter Φ is the staying probability, the equivalent of day-to-day survival. During staging we assume mortality to be zero and hence true survival to be one. The staying probability (Φ) is the probability that an individual present in the population at Day_i will remain in the study area until Day_{i+1}, which is the complement to the departure or emigration probability ($1–\Phi$). To estimate total staging duration, seniority must be estimated also. Seniority (γ) is the probability that an individual was already present at the site on Day_{i-1}; the complement to seniority is arrival or immigration probability ($1–\gamma$). It is calculated by reversing the encounter history (reverse-time modelling; Schaub *et al.* 2001). γ is related to the proportion of new individuals in a time interval; if the fraction newly recruited individuals is large, then the average seniority of birds in the interval is small. Note that encounter histories can not be reversed when the assumption of equal capture rates for each interval is violated (see next section for further explanation). The staying probability Φ was estimated with the Cormack-Jolly-Seber models (CJS models, Lebreton *et al.* (1992)) or variations of this basic model structure. The seniority probability γ was estimated with the Pradel recruitment method (Pradel 1996). To calculate the total staging duration we used the program SODA which estimates the *duration of stay before encounter*, using γ and the *duration of stay after encounter*, using Φ (Schaub *et al.* 2001).

Estimating staging duration by resightings

We collected three kinds of data that yield encounter histories (Table 1). The first data category consisted of the newly colour-marked males of all ages that were released with colour-marks in Year_i. The emigration probability of these birds could be affected by catching and handling. In each year this data category contained sufficient second-calendar years to test for a possible age

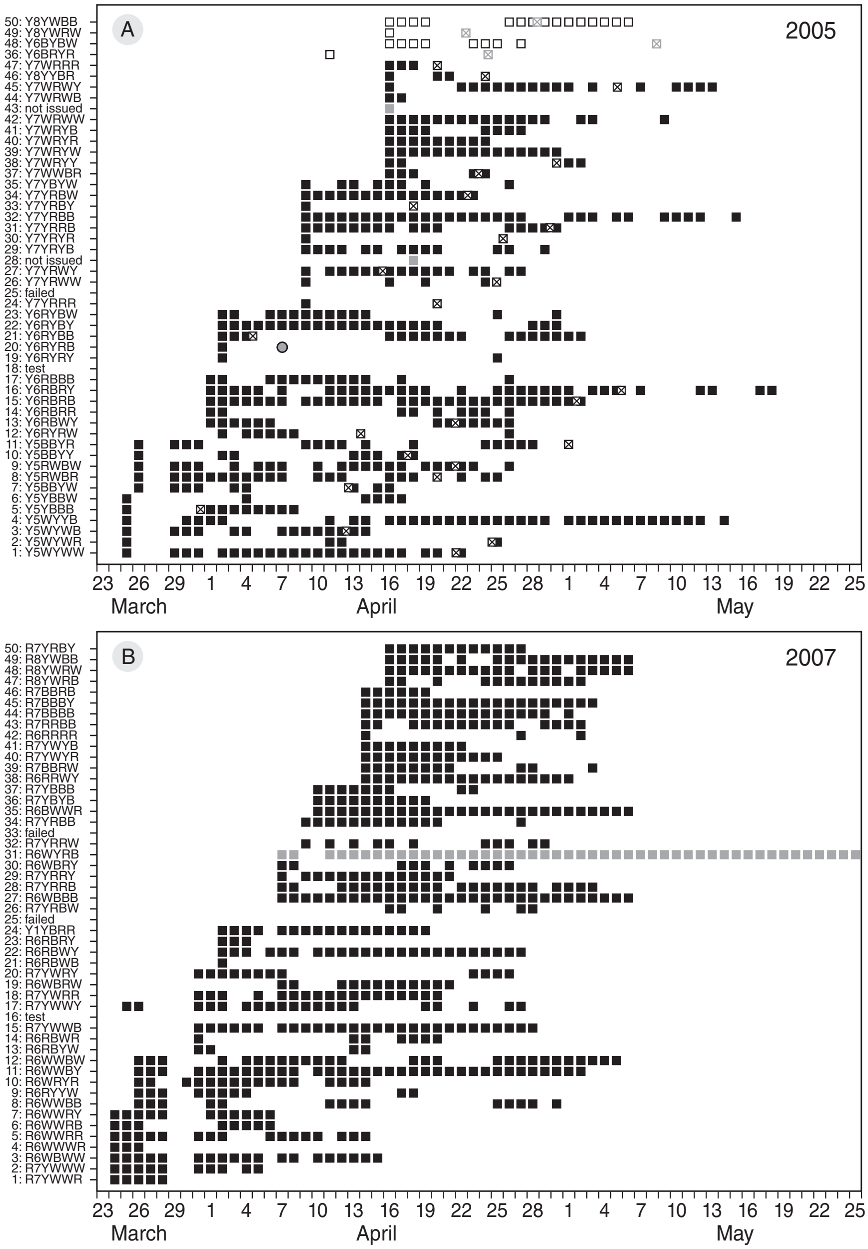


Figure 2. Encounter histories of the radio-tagged adult male Ruffs staging in southwest Fryslân, The Netherlands, during northward migration in spring in 2005 (A) and 2007 (B). Black symbols indicate ARTS recordings. Symbols with a cross indicate the last encounter by observers using hand-held receivers. Open symbols indicate faeders (female mimics). The round symbol indicates a colour-ringed resighting of a radio-tagged individual. Radio-tagged individuals left out of the analyses are indicated in grey.

affect. The second data category consisted of previously ringed birds: resighted in Year$_i$ but marked earlier in Year$_{j<i}$; all birds are adults and these previously ringed birds were not affected by catching and handling. The third category is the ARTS data set of radio-tagged adult males released and recorded in Year$_i$ (2005 and 2007). We used the staging duration of the radio-tagged birds ringed in the first two catching cohorts (caught before 2 April) as a minimum estimate of staging duration.

The staying probability can be estimated for all birds. However, the seniority probability, and hence total staging duration, can only be estimated for previously ringed birds as only for these birds all encounters are resightings. Encounter histories of newly ringed birds start with a catching event. For these newly ringed birds the calculation of seniority within the same season is not possible as the assumption of a constant recapture probability is violated. In reverse-time modelling the last interval in the reverse encounter history would lead to a catching event, which has an other probability than a resighting. For estimations we used the programs E-SURGE version 1.4.6, M7.2 (Choquet *et al.* 2009b), MARK version 4.3 (White & Burnham 1999) and SODA http://esapubs.org/Archive/ecol/E082/008/suppl-1.htm (Schaub *et al.* 2001).

Testing goodness-of-fit

To test the goodness-of-fit (GOF) of the data to the CJS models, U-CARE version 2.3, M7.2 was used (Choquet *et al.* 2009a). For the colour-marked birds, the global GOF test for the most complex model was not significant ($\chi^2_{874} = 870.41$, $P = 0.528$, $\hat{c} = 1$), indicating good fits. The subtests detected an apparent transients effect in previously ringed birds in 2006–08 (Table 2). When we left out the few individuals that were resighted very frequently (over 5 times), this transients effect disappeared. We therefore consider the apparent transients effect a consequence of somewhat stronger encounter heterogeneity in 2006–08, and excluded the possibility of transients in our migratory population which is supported by the resighting histories of the radio-tagged Ruffs (Fig. 2). We conclude that our data fit sufficiently to use the CJS model as a starting model. For the radio-tagged Ruffs a general lack of fit was indicated by the significance of the global test ($\chi^2_{72} = 181.63$, $P < 0.001$, $\hat{c} = 2.52$). The overdispersion was due to trap-dependence (Table 2). Individuals encountered at t had a higher probability to be encountered at $t+1$ than individuals not encountered at t. To account for this trap-dependence we transformed the dataset in U-CARE, and used this decomposed dataset modelled for trap-dependence in E-SURGE.

Table 2. Goodness-of-fit test results for the global model, $\Phi(t)p(t)$, for three data categories with encounter histories of Ruffs staging at a spring staging site in The Netherlands. Radio-tags were applied to adult males, and colour rings (CLR) to males of all ages. Previously ringed individuals were ringed in $\text{Year}_{j<i}$ and not recaptured but only resighted in Year_i. Newly ringed and radio-tagged Ruffs were ringed in Year_i. Newly ringed males are divided in adults and second-calendar year males (2cy). *n* is the number of individual encounter histories.

Dataset/year	$\chi^2_{\text{transient}}$	*df*	*P*	$\chi^2_{\text{trap-dependence}}$	*df*	*P*
Newly ringed CLR (adults):						
2004 (*n* = 752)	12.97	17	0.738	22.76	19	0.248
2005 (*n* = 549)	20.98	17	0.227	25.88	21	0.142
2006 (*n* = 526)	24.12	19	0.192	21.83	21	0.410
2007 (*n* = 409)	18.41	19	0.495	12.70	20	0.890
2008 (*n* = 294)	32.68	19	0.026	14.65	20	0.796
Newly ringed CLR (2 cy):						
2004 (*n* = 103)	7.53	8	0.480	0.62	10	0.999
2005 (*n* = 116)	16.79	10	0.079	5.49	10	0.856
2006 (*n* = 65)	11.66	11	0.390	6.01	13	0.946
2007 (*n* = 64)	1.95	9	0.992	3.04	11	0.990
2008 (*n* = 43)	1.87	5	0.867	2.78	7	0.904
Previously ringed birds:						
2005 (*n* = 113)	9.08	14	0.826	10.42	14	0.731
2006 (*n* = 461)	33.85	21	0.038	32.35	22	0.072
2007 (*n* = 451)	65.35	18	<0.001	25.09	19	0.159
2008 (*n* = 437)	69.51	18	<0.001	30.71	18	0.031
Radio-tagged birds:						
2005 (*n* = 42)	1.15	3	0.764	76.47	17	<0.001
2007 (*n* = 47)	1.95	4	0.745	81.52	17	<0.001

Model selection

The capture–resighting data and the radio-tagging data were analysed separately to avoid missing data issues for the years without radio-tagging. To simplify model notation, previously marked birds are referred to as *state 1* and newly marked (ringed or radio-tagged) birds as *state 2*. To test for effects of date (t), year (y), age (a) and state (s) on the staying probability Φ, we examined all hypotheses on additive and interactive effects of these four parameters. This resulted in 37 models to be tested for colour-ringed birds and 13 models for radio-tagged birds (which contained only adults and a single state, *state 2*).

In staging areas with seasonally peaked abundances, the emigration probabilities will increase over the season; this makes Φ date-specific (t). In this study the number of observers increased each year leading to an increase in resighting rates; this makes p year dependent. Hence the model $\Phi_t p_y$ was considered the biologically relevant initial model. Subsequently several models with additive and interactive effects between date and year were tested. Next, the interactive effects of age and state ($\Phi_{(t+y).a}$ or $\Phi_{(t+y).s}$) were considered. Also models that assumed age and state effects to be additive to the year and date effect ($\Phi_{t+y+.a+s}$) were considered. And it was examined how sensitive the supposed effects of state and age on staying probability were to differences in resighting probabilities between these groups, by examining various models with interactive and additive effects of the four parameters (e.g. $p_{t.y.(s+a)}$, $p_{(t.y)+s+a}$). As there were no young birds in the state 'previously ringed', the interaction between s and a could not be estimated.

The candidate models were ranked according to the modified Akaike Information Criterion (AIC), and corrected for $\hat{c}$ values of the global models to account for overdispersion and sample size (QAIC$_c$) (Burnham & Anderson 1998).

As the bootstrapping procedure in SODA was run for each year separately, model selection was repeated for each year. SODA also estimates the time present before encounter, so we needed to select models for both Φ and γ. For all years, except 2005, the most parsimonious models were $\Phi_t p_t$ and $\gamma_t p_t$. In 2005 the resighting probability was constant, with $\Phi_t p$ and $\gamma_t p$ being the most parsimonious models.

Estimates of staging duration

In SODA, for each of the 26 time intervals within each year, 300 estimates for *duration of stay before encounter* (for previously ringed birds only) and *duration of stay after encounter* (for each method in each year) were obtained by bootstrapping (Schaub *et al.* 2001). As the estimates converged at 200 iterations after testing 50, 100, 200 iterations, the number of iterations was set safely to 300. The estimates obtained followed a normal distribution. In all years the intervals 20–26 (4–15 May) had less than 10 resightings and to prevent overestimating total staging duration, all estimates for the period from 4 May onwards were left out (Morris *et al.* 2006).

RESULTS

Encounter rates

In newly ringed and previously ringed Ruffs, the proportion of individuals resighted after the initial catch or after the initial resighting after returning was not significantly different ($\chi^2_3 = 4.77$, $P = 0.11$), being 22% in 2004, 26% in 2005, 47% in 2006, 43% in 2007 and 36% in 2008. The most parsimonious model did not include the state parameter (s) in the resighting probability (p) term (Tables 1 and 3), indicating that p was not significantly different between newly ringed and previously ringed Ruffs. Over the 2-day intervals p was on average 0.14 for all birds. For adult males only, mean p over all 26 time interval was 0.11 (95% CI 0.03–0.19) in 2004, 0.13 (0.02–0.21) in 2005, 0.17 (0.13–0.22) in 2006, 0.15 (0.12–0.18) in 2007, and 0.15 (0.09–0.21) in 2008.

The proportion of radio-tagged birds re-encountered after release was 99%; only one individual was never reported and many individuals were recorded daily (Fig. 2) and often several times per day. The resighting probability over the 2-day intervals was 0.67 (0.61–0.71) in 2005 and 0.80 (0.75–0.83) in 2007; the difference between the years was significant (Table 4). This is most likely a consequence of birds spending more time at the roosts during day-time in 2007 compared with 2005 (unpubl. data).

Staying probabilities and catching effects

The staying probability Φ of the colour-ringed birds varied significantly with date, year, state (newly or previously marked) and age (Table 3). The additive models including year and date (Φ_{y+t}) were more strongly supported than the interactive models ($\Phi_{y.t}$) (Table 3). This indicates that there were annual differences in the overall staying probabilities, but no annual differences in the seasonal pattern of emigration. The staying probability declined with date, which means that emigration rates increased over the season (Fig. 3).

By comparing newly colour-ringed with previously ringed Ruffs, we detected indications of a catching ef-

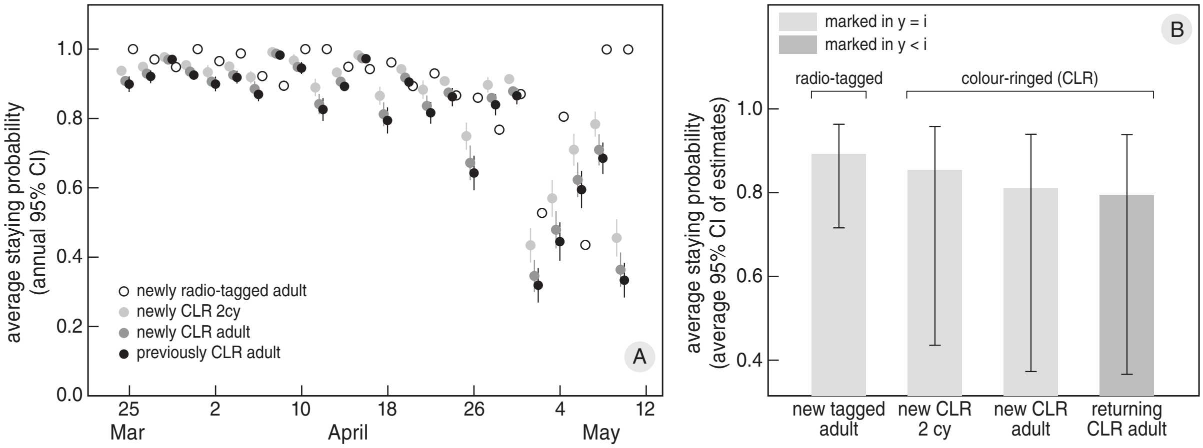


Figure 3. (A) Seasonal changes in staying probability (Φ) for four different groups: newly radio-tagged adult males, newly colour-ringed (CLR) second-calendar (2cy) year males, newly colour-ringed adult males, and previously colour-ringed adult males. 95% CIs are calculated over years. (B) Differences in staying probability between the four groups as obtained from the most parsimonious models using the program E-SURGE. 95% CIs are means for each time interval. Data meeting the requirements to estimate the total staging duration (see text) indicated in dark grey.

Table 3. Model selection for staying and resighting probabilities of colour-ringed male Ruffs at a spring staging site in The Netherlands, with respect to date and year (2004–08), age (second-calendar year and adult) and data category (state, newly and previously ringed). See Fig. 3 for graphical representation of parameter differences in estimations of Φ. To lead the eye, the initial models including date and year only are indicated with *. Indicated are the deviance, the number of estimated parameters in the model (NP), QAIC$_c$, ΔQAIC$_c$ and QAIC$_c$ weights.

Model	NP	Deviance	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ weight
$\Phi_{t+y+a+s}\ p_{(t.y)+a}$	158	25170.1	25493.2	0.00	0.42
$\Phi_{t+y+a}\ p_{(t.y)+a+s}$	158	25171.5	25494.6	1.46	0.20
$\Phi_{t+y+a+s}\ p_{(t.y)+a+s}$	159	25169.7	25494.9	1.69	0.18
$\Phi_{t+y+a+s}\ p_{t.y}$	157	25174.7	25495.8	2.58	0.12
$\Phi_{t+y+a}\ p_{t.y}$	156	25178.7	25497.6	4.42	0.05
$\Phi_{t+y+s}\ p_{t.y}$	156	25180.4	25499.3	6.14	0.02
*$\Phi_{t+y}\ p_{t.y}$	154	25186.6	25501.4	8.18	0.01
$\Phi_{t+y}\ p_{(t.y)+a+s}$	157	25184.0	25505.0	11.82	0.00
*$\Phi_{t}\ p_{t.y}$	150	25199.6	25506.0	12.81	0.00
$\Phi_{(t+y).s}\ p_{t.y}$	184	25139.3	25517.0	23.78	0.00
$\Phi_{(t+y).a}\ p_{t.y}$	184	25160.6	25538.2	45.05	0.00
$\Phi_{t+y+a+s}\ p_{t.y.s}$	254	25038.6	25565.1	71.97	0.00
*$\Phi_{t.y}\ p_{t.y}$	239	25088.3	25582.7	89.56	0.00
$\Phi_{t+y+a+s}\ p_{t.y.a}$	268	25048.7	25605.4	112.23	0.00
*$\Phi_{t.y}\ p_{t+y}$	154	25468.4	25783.1	289.94	0.00
*$\Phi_{t+y}\ p_{t+y}$	59	25730.7	25849.7	356.51	0.00
*$\Phi_{t}\ p_{y}$	31	25954.6	26016.9	523.75	0.00
*$\Phi_{t}\ p$	25	26226.8	26276.9	783.77	0.00

Applied are multistate logit models corrected for the number of parameters and with state transition set to zero. 37 models were tested; only the 18 most parsimonious models are shown. Model notation: 'Φ' staying probability, 'p' resighting probability, 't' 26 time intervals of two days each, 'y' study years, 'a' age groups, and 's' state: 0 = not encountered, 1 = encountered and newly ringed, 2 = encountered and previously ringed. No transitions between states were allowed.

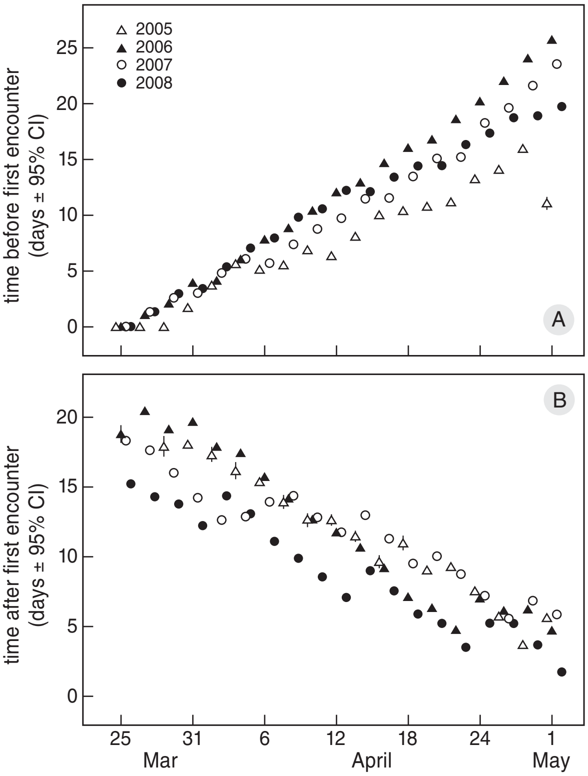


Figure 4. Estimates of staging duration of male Ruffs at a spring staging site in The Netherlands between 2005 and 2008. Based on resightings of Ruffs marked in a previous year. Estimates (mean ± 95% CI of bootstrap estimates) were obtained by running 300 iterations per interval in the program SODA. (A) Duration of stay before encounter estimated with the seniority probability (γ); (B) Duration of stay after encounter as estimated with the staying probability (Φ). Note that 95% CI's are very small, except in 2005.

fect on staying probability (Table 3, Fig. 3). The model separating the two states (newly or previously ringed) had a better fit, although the confidence intervals of the estimates overlapped (Fig. 3B). Throughout the season, the newly ringed adults had on average a 1.9% higher staying probability than the previously ringed adults. The radio-tagged adult males had on average 9.4% higher staying probabilities than the previously ringed adult males, and this probability did not vary between years (Table 4).

Each year approximately 15% of newly caught males were second-calendar year males. That models including age fitted better (Table 3) suggests a significant age effect. The second-calendar year birds had a 4.9% higher staying probability than newly caught adults and 6.9% higher staying probability than returning adults (Fig. 3), which means that young males had a 4.9% longer staging duration than adults and that the catching and handling effect increased staging duration with 2%.

Estimates of staging duration

The average total staging duration of colour-ringed birds in 2006 was 23.2 ± 2.8 days, 21.1 ± 3.0 d in 2007 and 18.5 ± 3.9 d in 2008. The estimated *duration of stay before encounter* increased over the season and *duration of stay after encounter* decreased as the season progressed (Fig. 4). In 2005, the staging duration estimate was very low (14.0 ± 3.5 d). Especially the estimates of *time before encounter* were considerably lower than in other years, while the *time after encounter* fell within the distribution of the other years. In contrast, minimal staging durations of radio-tagged birds were similar in 2005 and 2007 (see below). The low resight-

Table 4. Model selection for staying and resighting probabilities of radio-tagged male Ruffs at a spring staging site in The Netherlands, with respect to date and year (2005 and 2007). See Fig. 3 for graphical representation of parameter differences in estimates for Φ. Indicated are the deviance, the number of estimated parameters in the model (NP), $QAIC_c$, $\Delta QAIC_c$ and $QAIC_c$ weights.

Model	NP	Deviance	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight
$\Phi_t\ p_{y.m}$	32	1357.5	1423.0	0.00	0.72
$\Phi_{t+y}\ p_{y.m}$	33	1357.4	1425.0	1.96	0.27
$\Phi_{t+y}\ p_{(t+y).m}$	61	1306.9	1434.2	11.23	0.00
$\Phi_{t.y}\ p_{y.m}$	59	1313.2	1436.2	13.19	0.00
$\Phi_t\ p_m$	31	1373.9	1437.3	14.25	0.00
$\Phi_t\ p_{t.m}$	57	1318.8	1437.4	14.44	0.00
$\Phi_{t+y}\ p_{t.y.m}$	85	1264.8	1445.2	22.23	0.00
$\Phi_{t.y}\ p_{t.y.m}$	102	1226.7	1446.0	22.95	0.00
$\Phi_y\ p_{t.m}$	32	1409.1	1474.6	51.58	0.00

Applied are trap-dependent logit models assuming an interactive trap-effect, corrected for the number of parameters. 13 models were tested; only the nine most parsimonious models are shown. The models assuming an additive trap effect had very low rankings and are not shown. Model notation: 'Φ' staying probability, 'p' resighting probability, 't' 26 time intervals of two day each, 'y' study years, 'm' trap-dependance.

ing probability and low sample size in 2005 may have created a false signal of recruitment and hence an underestimate of the seniority. We conclude that in 2005 *time before encounter* was underestimated due to the low resighting rates and low samples size and we consider estimates of total staging duration obtained from colour-ringed birds in 2005 unreliable.

Minimal staging duration of radio-tagged birds was not significantly different between years ($F_{1,82} = 0.71$, $P = 0.40$); however, the interaction between tagging cohort and year was significant ($F_{3,82} = 2.65$, $P = 0.05$) with minimal staging duration estimates in the first two cohorts being higher in 2005 than in 2007 (Fig. 5). We consider the staging duration of the first cohorts to be a close approximation of the total staging duration as birds were tagged soon after arrival. The staging duration of these first cohorts was 24 days in 2005 and 19 days in 2007 (Table 5, Fig. 5).

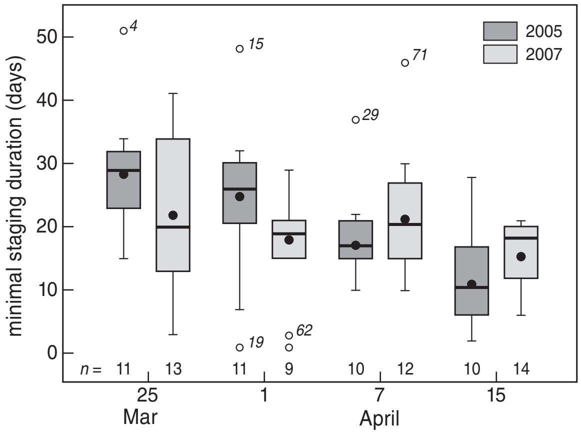


Figure 5. Minimal staging duration (the time interval between tagging and the last recording) of adult male Ruffs radio-tagged in 2005 and 2007. Sample sizes are indicated below box plots. Boxes represents the 95% CI intervals, horizontal lines represent the median, bars represent the range, solid dots are mean values and open dots are outliers.

Table 5. The minimal staging duration of radio-tagged Ruffs (mean ± SD), which is the time interval between the day of tagging and the last day of recording as presented in Fig. 2. The minimal staging duration is given for three groups. The birds tagged before 2 April are supposed to belong to the first arrival cohort. *n* is sample size.

Tagging group	2005	*n*	2007	*n*
All tagged birds	21.1 ± 11.3	42	19.1 ± 9.7	47
All but summer birds	19.2 ± 9.2	39	18.5 ± 9.1	46
Tagged before 2 April	24.2 ± 8.7	20	19.2 ± 11.3	22

DISCUSSION

We explored possible catching and handling effects on staging duration of staging Ruffs in The Netherlands. Models allowing newly and previously colour-ringed birds to have different staying probabilities had better fits (Table 3) and subsequent comparison of model estimates showed that the staying probability was highest in newly ringed and radio-tagged Ruffs (Fig. 3). However, as the confidence intervals overlap (Fig. 3) it remains to be seen whether these differences are relevant. Here we explore what our findings would mean for staging duration if true. Model estimates indicated that staging durations of newly colour-ringed adult males were 0.4–0.5 days longer than birds ringed in previous years. This longer time span might represent the time needed to recover from capture and handling and given the average total staging duration of 18.5–23.3 days this cost is rather small. The second-year birds would stay 1.0 days longer than adults, which is biologically relevant as younger, inexperienced birds might need more time to accumulate new body stores.

The 9% difference in staying probability between adult males radio-tagged in Year$_i$ and adult males colour-ringed in Year$_{j<i}$, would translate in an estimated prolonging of the staging duration by 1.8–2.3 d. Subtracting the value we found above for the time cost of capture and handling indicates that the effects of the radio transmitter would add 1.4–1.8 d to the staging duration. Is there any indication why radio-tagged birds would increase their staging duration more than colour-ringed birds? The weight of the tag added only 1% to the adult males' body mass and we do not expect them to compensate for this weight gain. However, radio-tagged birds were brought to the field station to be processed and thus were handled for longer than birds that only received colour-rings who were mostly processed in the field. We suggest that this longer time-lag between catching and release could lead to a longer staging duration. In Dunlin *Calidris alpina* on northward migration a similar effect was found when the length of stay at marking sites was compared with more northerly staging sites (Warnock *et al.* 2004). However, part of this particular variation might be attributed to faster migration later in spring and/or a much lower probability to re-encounter a bird during later stages of migration (Warnock *et al.* 2004). In summary, the detected catching effects were very small and might be insignificant to Ruffs.

As we did not find significant transient effects in the newly ringed birds, captured Ruffs did not seem to emigrate from the catching area soon after the event

(Table 2). We did not find indications for higher mortality rates in newly ringed birds or radio-tagged birds. The staying probability Φ is a parameter with two components: the site fidelity, Φ_f, the probability to remain in the study area, and the true survival Φ_s. A high mortality rate of new catches (a low Φ_s) can not be detected when it is obscured by a extended staging duration of survivors (a high Φ_r). However, the proportion of birds resighted after the first encounter was equal in newly and previously ringed Ruffs, and 99% of the radio-tagged males were detected after release, which suggest that mortality due to catching was low for colour-ringed and radio-tagged Ruffs.

The second goal of this paper was to assess methodological caveats in estimations of staging duration by comparing data categories of colour-marked and radio-tagged Ruffs. Firstly, we want to stress that when applying the method implemented in SODA to estimate the *time before encounter*, resightings of newly captured birds have to be omitted at each time interval, as the encounter history cannot contain different encounter methods with different probabilities (Schaub *et al.* 2001). If newly marked individuals are not excluded, they create a false signal of recruitment or immigration in the population, which will lead to an underestimation of the seniority probability. This implies that for analyses of staging duration using resightings, newly marked birds cannot be used. However when after initial capture, the subsequent encounters are captures as well, there is no problem (Schaub & Jenni 2001, Schaub *et al.* 2004).

Secondly, we confirmed with empirical data that estimates of staging duration are sensitive to a low resighting probability, which is in line with a sensitivity analysis for a general case (Calvert *et al.* 2009). In 2005 the sample size of 113 previously colour-ringed birds was insufficient to yield reliable estimates of seniority, which led to low estimates of the duration of stay which were incongruent with telemetry data. In 2007, when p had increased, the colour-ring data yielded estimates that were comparable to other years and to the telemetry data. One of the basic assumptions of capture–recapture analyses is that the resighting probability should not affect estimates of Φ and γ. Note that it has been suggested before that very large sample sizes are required to overcome a low resighting probability (Sandercock 2003, Calvert *et al.* 2009).

The methods as implemented in the software SODA (Schaub *et al.* 2001) and the MARK and E-SURGE model selection (White & Burnham 1999, Choquet *et al.* 2009b) are useful for ecologists to estimate staging duration, but have their shortcomings. SODA does not yet allow for capture–recapture models that incorporate strong heterogeneity in encounter rates that is not due to transients but to variance in 'trap-happiness'. Another problem is that SODA assumes a normal distribution of staging durations and when staging duration follows alternative distributions this may result in large overestimates (up to 100%) (Efford 2005). However, as shown by an extensive sensitivity analysis on Red Knots *Calidris canutus*, the Schaub method is relatively insensitive to different cohorts within the passage population and estimates of staging duration were fairly robust between scenarios (Gillings *et al.* 2009).

We therefore conclude that (1) estimates of staging duration can be affected by catching, ringing and radio-tagging, and that (2) low resighting probabilities can lead to underestimates in staging duration. For our study system, we conclude that the colour-mark data of the previously ringed Ruffs from 2006–08 yield biologically reliable estimates of staging duration as the data had sufficiently high resighting probabilities to meet the available mark–recapture model assumptions and estimates were not affected by catching/handling.

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SAMENVATTING

Langeafstandstrekkers onderbreken onderweg vaak de trek om nieuwe lichaamsreserves op te slaan. De tijd die wordt doorgebracht op de rustplaatsen bepaalt in belangrijke mate de snelheid waarmee de hele trekweg wordt afgelegd. Wij hebben in 2004–08 met behulp van de 'merk–terugvangst' methode van Schaub et al. (2001) een schatting gemaakt van de tijd die Kemphanen *Philomachus pugnax*, die in grote aantallen hun voorjaarstrek in Friesland onderbreken, op de Friese pleisterplaatsen verbleven. Met de Schaub-methode wordt de totale verblijfsduur geschat door twee kansen te berekenen: (1) de zogenaamde senioriteit, de kans dat de vogel al aanwezig was voor de vangst of waarneming (gelijk aan 1–immigratiekans) en (2) de blijfkans, de kans dat een vogel na de vangst of waarneming blijft (1–emigratiekans). In totaal werden 4363 manlijke Kemphanen van kleurringen voorzien (voor de schaarse vrouwtjes en faren werden onvoldoende waarnemingen verzameld: deze zijn hier verder buiten beschouwing gelaten). In 2005 en 2007 werden bovendien 95 mannetjes van een zendertje voorzien. We vergelijken in ons artikel drie sets met gegevens: (1) waarnemingen aan Kemphanen die in het betreffende voorjaar van kleurringen waren voorzien (de nieuw-gekleurringde groep), (2) waarnemingen aan Kemphanen die in voorafgaande jaren waren gemerkt en opnieuw Friesland aandeden (de reeds-gekleurringde groep) en (3) de geautomatiseerde registraties (van negen vangstations) van Kemphanen met zenders (de gezenderde groep). Voor de gezenderde vogels werd de minimale verblijfsduur berekend (de tijdsperiode tussen het aanbrengen van de zender en het laatste vastgelegde signaal). Deze minimale verblijfsduur werd gebruikt om de verblijfsduurschattingen van de vogels met kleurringen te evalueren. Voor nieuw-gekleurringde vogels kon de totale verblijfsduur niet worden bepaald omdat de senioriteit niet kan worden geschat. De blijfkans na vangst of waarneming kan wel voor beide groepen worden bepaald. De blijfkansmodellen detecteerden een vangeffect: nieuw-gekleurringde vogels hadden een grotere blijfkans dan de reeds-gekleurringde vogels. Het verschil, omgerekend naar de duur van het verblijf na vangst of waarneming, was echter slechts 0,4–0,5 dagen. Het vangeffect was dus heel klein. In 2007 was de minimale verblijfsduur van de gezenderde vogels (19,1 ± 9,7 dagen) iets lager dan de totale verblijfsduur van de reeds-gekleurringde vogels (21,1 ± 3,0 dagen). In 2005 was de minimale verblijfsduur van de gezenderde vogels echter veel hoger (21,1 ± 11,3 dagen tegen 14,0 ± 6,3 dagen). In 2005 was de waarnemingskans van vogels met kleurringen echter laag en de steekproef klein. Dit leidde tot lage waarden voor de aanwezigheidsduur. De totale verblijfsduur van 2005 is daarom hoogstwaarschijnlijk een onderschatting. We concluderen dat voor het beschrijven van de totale verblijfsduur van Kemphanen in Friesland alleen de reeds-gekleurringde vogels van 2006–08 betrouwbare schattingen van de verblijfsduur (19–23 dagen) hebben opgeleverd.

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