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Stage-dependent survival in relation to timing of fledging in a migratory passerine, the Northern Wheatear (*Oenanthe oenanthe*)

H. Herman van Oosten[1,2,3] · Maja Roodbergen[4,5] · Remco Versluijs[2] · Chris A. M. van Turnhout[3,4]

Abstract A better understanding of factors affecting population change is needed to explain declines of long-distance migrants. As juvenile survival is generally an important determinant of population dynamics, assessing whether juvenile survival is primarily affected either during the post-fledging stage on the natal site or during the migration and winter stages (migration-winter) is important for developing conservation strategies. Here, we assess variation in stage-dependent survival of juvenile Northern Wheatears (*Oenanthe oenanthe*), a threatened passerine in northwestern Europe. We estimate apparent survival in a Dutch coastal breeding population based on frequent resightings during the whole breeding season. We show that post-fledging survival on the natal grounds was not clearly different from survival during migration-winter and that late fledging reduces survival during both post-fledging and migration-winter. It is unknown which factors are causal to lower survival of late-fledged juveniles and this hampers effective conservation. Meanwhile, conservation measures focusing on nest protection should increase average juvenile survival in the remaining small populations in the short term because the number of successfully fledged early juveniles should increase.

Zusammenfassung

Phasenabhängiges Überleben in Bezug zum Zeitpunkt des Ausfliegens bei einem ziehenden Singvogel, dem Steinschmätzer (*Oenanthe oenanthe*)

Bestandsrückgänge bei Langstreckenziehern erfordern ein besseres Verständnis der Faktoren, die die Populationsveränderungen beeinflussen. Da das Überleben der Juvenilen im Allgemeinen eine wichtige Bestimmungsgröße für die Populationsdynamik ist, ist es für die Entwicklung von Schutzstrategien wichtig festzustellen, ob das Überleben der Juvenilen primär entweder während der Zeit nach dem Ausfliegen im Geburtsgebiet oder während des Zug- und Überwinterungszeitraumes beeinflusst wird. In dieser Studie untersuchen wir das phasenabhängige Überleben junger Steinschmätzer (*Oenanthe oenanthe*), einer bedrohten Singvogelart in Nordwesteuropa. Basierend auf regelmäßigen Beobachtungen während der gesamten Brutzeit bestimmten wir das Überleben in einer Brutpopulation an der niederländischen Küste. Wir zeigen, dass sich das Überleben in der Zeit nach dem Ausfliegen im Geburtsgebiet nicht klar unterschied vom Überleben während des Zug- und Überwinterungszeitraumes und dass ein spätes

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✉ H. Herman van Oosten
  herman_vanoosten@yahoo.co.uk

1 Oenanthe Ecologie, Wageningen, The Netherlands

2 Bargerveen Foundation, Nijmegen, The Netherlands

3 Department of Animal Ecology and Ecophysiology, Institute for Water and Wetland Research, Radboud University, Nijmegen, The Netherlands

4 Sovon Dutch Centre for Field Ornithology, Nijmegen, The Netherlands

5 Centre for Avian Population Studies, Wageningen, The Netherlands

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Flüggewerden die Überlebenswahrscheinlichkeit sowohl in der Nachbrutzeit als auch während des Zuges und der Überwinterung verringert. Es ist unbekannt, welche Faktoren das geringere Überleben der spät ausgeflogenen Jungvögel bewirken, was einen effektiven Schutz erschwert. Mittlerweile führen Schutzmaßnahmen mit Fokus auf den Schutz von Nestern kurzfristig zu einem Anstieg der durchschnittlichen Überlebenswahrscheinlich der Jungvögel in den verbliebenen kleinen Populationen, da die Anzahl der erfolgreich ausgeflogenen frühen Jungvögel ansteigt.

Introduction

After fledging, migratory songbirds pass through different stages in their first year of life, e.g. a post-fledging stage on their natal site before migration or natal dispersal (Naef-Daenzer et al. 2001; Vitz and Rodewald 2011), a migration (or dispersal) stage, and a winter stage.

In spite of juvenile survival being recognized as a major determinant of population dynamics in songbirds (Arcese et al. 1992; Saether and Bakke 2000), quantitative information on this parameter during the different stages of the avian life cycle remains scarce (Sillett and Holmes 2002; Faaborg et al. 2010; Dybala et al. 2013).

Earlier studies documented that juvenile survival is generally lowest during the first weeks after fledging (e.g. Dhondt 1979; Sullivan 1989; Thomson et al. 1999). In recent years, radiotelemetry has enabled the investigation of juvenile survival directly after fledging (e.g. Naef-Daenzer et al. 2001; Yackel Adams et al. 2006; Rush and Stutchbury 2008; Tarof et al. 2011; Vitz and Rodewald 2011; Sim et al. 2013). These studies confirmed that survival is indeed low in this period (Naef-Daenzer et al. 2001; Kershner et al. 2004; Yackel Adams et al. 2006). However, differences among species are large. For instance, fledgling survival is about 0.50 during the first 2 weeks after fledging for Hooded Warbler (*Wilsonia citrina*) (Rush and Stutchbury 2008) and Sprague's Pipit (*Anthus spragueii*) (Fisher and Davis 2011), but about 0.90 for Eastern Meadowlark (*Sturnella magna*) (Suedkamp Wells et al. 2007) and Ovenbird (*Seiurus aurocapilla*) (Vitz and Rodewald 2011). Thus, in spite of the general notion that survival is lowest during the first weeks after fledging, quantifying survival during the different phases of the yearly cycle of a songbird requires species-specific data.

Survival during the remainder of the pre-migration juvenile period remains little studied (Faaborg et al. 2010, but see Sim et al. 2013). In this period, juveniles must prepare for southbound migration by an energy-consuming post-juvenile moult and by strongly increasing fat reserves

(Berthold 1996; Bauchinger and Biebach 2001) to be able to fly long distances and cross barriers such as the Mediterranean Sea, the Gulf of Mexico, the Great Lakes, the Sahara Desert or the deserts east of the Caspian Sea (Moreau 1972; Gauthreaux 1999; Deppe and Rotenberry 2005; Newton 2008; Holmes 2007). Thus, failure to prepare may carry-over to affect survival during migration (Berthold 1996; Bauchinger and Biebach 2001).

Few studies have aimed to disentangle survival at the natal site from winter survival (Tarof et al. 2011; Grüebler et al. 2014). Tarof et al. (2011) estimated survival during a post-fledging period until the onset of migration and during the migration and winter stages (migration-winter) for Purple Martins (*Progne subis*). They found post-fledging survival to be much lower than survival during migration and winter, as did Grüebler et al. (2014) for Swiss Barn Swallows (*Hirundo rustica*). It is clear that more data from multiple species are needed to improve our understanding of the influence of post-fledging and migration-winter periods on population dynamics of migratory birds, in order to enhance effective targeting of conservation efforts (Sillett and Holmes 2002).

The difficulty in estimating survival away from the natal and/or breeding grounds is that it is virtually impossible to individually track birds once they disperse or leave for migration, unless satellite transmitters or global positioning system loggers are used. These, however, can only be used for relatively heavy species, though these devices are quickly becoming lighter (currently ca 1 g). This technique can therefore as yet not be applied to small songbirds.

One way to deal with this problem in mark-recapture studies is to include an 'unobservable state' in multi-state models for stage-dependent survival (Kendall and Nichols 2002). These models split survival into different states and estimate state-specific survival and resighting probabilities, as well as transition rates between the states. When several resightings are performed at the observable state, survival in an unobservable state can be estimated by making additional assumptions.

Survival of juveniles fledged early in the breeding season is often higher than that of juveniles fledged later in the season, which is hypothesized to be due to higher food abundance, lower predation pressure and/or because parents breeding early may be of higher quality and provide more food (Smith et al. 1989; Naef-Daenzer et al. 2001; Verhulst and Nilsson 2008; Vitz and Rodewald 2011 but see Anders et al. 1997; Yackel Adams et al. 2006). Early fledglings may also arrive earlier at stopover and wintering sites and thereby experience more favourable conditions and gain competitive advantage on non-breeding sites, resulting in increased survival rates.

Seward et al. (2013) found that supplementary fed fledglings of Northern Wheatears (*Oenanthe oenanthe*)

experienced increased juvenile annual survival rates. They predict that juveniles leaving the natal grounds in a better condition will also experience higher survival rates in non-breeding areas. However, they did not measure such an effect, as this requires intensive resighting or remote tracking of juveniles.

Here we use mark-resight data to test the hypotheses that in Northern Wheatears (*O. oenanthe*):

1. Post-fledging survival on the natal grounds is lower than migration-winter survival.
2. Post-fledging survival on the natal grounds is higher for early fledged juveniles than for late-fledged juveniles.
3. Survival during the migration-winter period is also higher for early fledged juveniles than for late-fledged juveniles, resulting in higher first-year survival of early fledged juveniles than of late-fledged juveniles.

If all three hypotheses were true, this would indicate that conditions on the natal sites are a bottleneck in the life cycle of Northern Wheatears, not only affecting juvenile survival on natal sites but also during migration-winter.

Methods

Study species and sites

The Northern Wheatear is an insectivorous long-distance migrant breeding from Eastern Canada and Greenland across Eurasia to Western Alaska (Glutz von Blotzheim and Bauer 1988). The species ranks among the top ten most strongly declining common species in Europe (Gregory et al. 2009). Since 1990 the European population has declined by over 50 % (PECBMS 2013). Reasons for these strong declines include agricultural intensification, afforestation and less intense use of heathlands leading to increasing vegetation height, aggravated by the effects of atmospheric nitrogen deposition and declining rabbit (*Oryctolagus cuniculus*) populations (Glutz von Blotzheim and Bauer 1988). In the Netherlands, Northern Wheatears occur in heathlands and sandy, oligotrophic grasslands in coastal dunes where they often breed in burrows of rabbits.

Between 2007 and 2011, we intensively studied three populations of Northern Wheatears in the Netherlands by colour-ringing nestlings and adults (Van Oosten et al. 2015): the inland population at Aekingerzand (268 ha; 52°55′N, 6°18′E); the coastal population at Castricum (74 ha; 52°33′N, 4°36′E), and the nearby coastal population at Den Helder (160 ha; 52°52′N, 4°43′E). Sites are described in more detail in Van Oosten et al. (2015). Except for a few single pairs elsewhere the three populations are the remaining mainland breeding populations of

Northern Wheatears in the Netherlands, i.e. this is not a study of three sites within homogeneous breeding habitat (or a larger continuous population) but rather a study of three more or less isolated sites.

Early and late broods

Northern Wheatears regularly produce replacement clutches after failure and also true second broods following a successful first attempt, defined as at least one chick having fledged. This leads to two distinct peaks in hatching phenology during the breeding season (Fig. S1). Juveniles were grouped by fledging period, which was known for all nestlings: young fledged either 'early', before 18 June or 'late', on or after 18 June (Fig. S1).

Second and repeat broods are regularly seen in the populations, with up to 60 % of all females involved. However, the fraction of true second broods and repeat clutches varies strongly between years, since nest predation rates also vary. In years with high nest predation rates, later broods are mostly repeat broods. In addition, predation rates are site specific. Therefore, the number of true second versus repeat clutches also varies between sites. We lumped together second and repeat broods but we acknowledge that differences in survival may exist between them.

Capture–mark–recapture study

Northern Wheatears are strongly philopatric and very conspicuous in their open habitat, a combination which allows for very high annual resighting probabilities between years (Van Oosten et al. 2015). This provides an excellent setting to study survival in more detail.

During the period 2007–2010, we marked 1018 nestlings with individual combinations of three coloured leg rings and an aluminium ring from the Dutch Centre for Avian Migration and Demography (Table 1). Nestlings were measured and marked when between 6 and 12 days old. We used wing length to predict nestling age, since wing length is least influenced by changing environmental conditions such as food abundance (Boag 1987; Dahdul and Horn 2003). Indeed, wing length appeared to predict age (days 6–12) of 49 nestlings from 12 broods of known age with a very high accuracy ($R^2 = 0.94$). Fledging success was determined by observing young after fledging and included a control of the nest after fledging to check for remaining dead eggs or nestlings. Resightings in the study sites in the period 2008–2011 were used to estimate annual first-year survival. The most suitable breeding areas in the Netherlands are being surveyed as part of the ongoing national breeding bird monitoring program (Boele et al. 2014). About half of the Dutch breeding population is

Table 1 Numbers of Northern Wheatears marked as 'early' and 'late' nestlings per study site in the Netherlands in the period 2007–2010

	Aekingerzand		Castricum		Den Helder	
	Early juveniles	Late juveniles	Early juveniles	Late juveniles	Early juveniles	Late juveniles
2007	34	13	28	14	117	8
2008	94	12	37	15	149	22
2009	93	19	45	24	164	3
2010	48	14	39	11	70	5
Total	269	58	149	64	500	38

monitored and colour-ringed, with requests to other observers to carefully check for colour-ringed Northern Wheatears in the remaining half resulting in $n = 5$ reports. Only occasionally do colour-ringed birds establish territories or breed elsewhere. To conclude, we are confident that our apparent survival estimates are close to true survival rates. Resighting effort was high, especially during the peak of the breeding season (May–June): all areas were visited several days a week in this period. To investigate first-year survival in more detail we used a subset of 2 years (2009 and 2010) with more intensive field observations from one study site, Castricum. In 2009 and 2010 a total of 119 juveniles were marked in Castricum (69 in 2009, 50 in 2010). This site is small, and in these 2 years observations were made on at least 2 days (usually more) per week, during the entire breeding season, using telescopes and covering the whole study area in search of missing individuals. Observations continued until juveniles were no longer observed at the natal site, presumably either because they died or because they had left for migration (Fig. S2). Northern Wheatears have never been observed at the study site after the first week of September.

Survival analyses

Annual juvenile survival in relation to fledging period

Cormack–Jolly–Seber models, as implemented in Program MARK (Lebreton et al. 1992; White and Burnham 1999), were used to estimate annual survival of juveniles. We used Akaike's information criterion corrected for small sample sizes (AIC$_c$) (Burnham and Anderson 2002) to select the best-supported models among a set of biologically plausible, a priori formulated, models (Table 2). Models were formulated based on our knowledge of Northern Wheatears and on the literature. Models with a ΔAIC$_c$ (difference in AIC$_c$ value between a given model and the best model) <2, were considered equally supported by the data.

We first selected the best model for resighting probability (p), using the most detailed model for survival rate (Φ), which included site (Aekingerzand, Castricum or Den Helder), maturity (juvenile and adult; we use the term 'maturity' instead of 'age' to avoid confusion with age effects within the juvenile stage) and year. The next step was to select the best model for survival rate, including only second-order interactions which we presumed could be relevant, to avoid problems with estimability. The resulting best model including site was used in further analyses testing for effects of fledging period. We chose the best model with site, since we previously showed that juvenile and adult survival differs between the three sites (Van Oosten et al. 2015), as does timing of fledging.

Hypotheses 2 and 3 (early fledged juveniles have higher survival rates than late-fledged juveniles) were tested using the best basic model, and then adding the factor fledging period (early or late). If the AIC$_c$ of this model improved by >2 after including an effect of fledging period, and parameter estimates for this effect showed higher survival of early fledged young compared to late-fledged young, we accepted hypothesis 2, if not, the hypothesis was rejected.

Goodness-of-fit (GOF) was assessed for the most general model with an additive effect of the grouping factor fledging period, using parametric bootstrap procedures. The variance inflation factor, $\hat{c}$, was calculated by dividing the observed model deviance by the mean deviance from the simulations. The bootstrap method (1000 simulations) showed that the model fitted the data sufficiently well ($P = 0.18$, with estimated $\hat{c} = 1.12$).

Stage-dependent juvenile survival in relation to fledging period

To be able to separate survival on the natal site from survival during migration-winter, we used multi-state models (e.g. Hestbeck et al. 1991) in program MARK, including an unobservable state. These models are able to separate mortality from departure for migration. 'State' refers to the stages as used throughout the paper. A schematic overview of the multi-state survival model is provided in Fig. S3.

We distinguished two stages: post-fledging stage at natal site (N) and migration-wintering stage away from natal site (W). Juveniles departing for migration to their wintering grounds switch from stage N to stage W; those returning

Table 2 Summary statistics of the candidate models assessing the influence of different variables on resighting rate and annual survival

No.	Model	k	AIC_c	ΔAIC_c	w_i	Deviance
Model selection for resighting probability						
A1[a]	Φ (site × maturity × year) p (maturity + D10)	27	2337.53	0.00	0.92	2282.65
A2	Φ (site × maturity × year) p (site + maturity)	28	2342.87	5.34	0.06	2285.93
A3	Φ (site × maturity × year) p (site × maturity)	30	2346.06	8.53	0.01	2284.98
Model selection for survival, without factor fledging period						
B1	Φ (maturity × year) p (maturity + D10)	11	2323.92	0.00	0.54	2301.77
B2[a]	Φ (site × maturity + maturity × year) p (maturity + D10)	15	2326.69	2.77	0.13	2296.42
B3	Φ (maturity + year) p (maturity + D10)	8	2326.87	2.95	0.12	2310.78
B4	Φ (site + maturity × year) p (maturity + D10)	13	2327.52	3.59	0.09	2301.31
B5	Φ (site × maturity + year) p (maturity + D10)	12	2328.07	4.15	0.07	2303.90
B6	Φ (site + maturity + year) p (maturity + D10)	10	2330.55	6.63	0.02	2310.42
B7	Φ (site × year + site × maturity + maturity × year) p (maturity + D10)	21	2331.94	8.02	0.01	2289.40
B8	Φ (site × year + maturity × year) p (maturity + D10)	19	2332.53	8.60	0.01	2294.09
Model selection for survival, factor fledging period included						
C1	Φ (site × maturity + maturity × year + fperiod) p (maturity + D10)	16	2316.15	0.00	0.73	2283.83
C2	Φ (site × maturity + maturity × year + site × fperiod) p (maturity + D10)	18	2319.22	3.08	0.16	2282.83
C3	Φ (site × maturity + maturity × year + fperiod × year) p (maturity + D10)	19	2320.56	4.41	0.08	2282.12

Only models with Akaike's information criterion corrected for small sample sizes (AIC_c) weights (w_i) >0.001 are shown

k Number of parameters, *maturity* juvenile/adult, *D10* resighting probability in Den Helder in 2010 (when less frequent visits were made to this site), *fperiod* fledging period (early/late)

[a] Starting models in the next selection step (see text)

from migration to their natal sites switch from stage W to stage N. In stage W no observations were made. Therefore, stage W was an 'unobservable state' (Kendall and Nichols 2002). We assumed that a missing but alive juvenile (resighted the following year as an adult) at the end of the natal post-fledging period could represent either a bird which was still present at the natal site but was not seen, or a bird which had already departed for migration. Resighting data were summarized per 2-week interval, resulting in seven distinct 2-week intervals during the natal post-fledging period (21 May–27 August) and eight encounter occasions. This assumption is in concordance with our field observations, since we just once observed one juvenile after 27 August at the study site. To make sure all living juveniles departed for migration, the last encounter occasion at the natal site (occasion 8) was set at zero for all juveniles. In the following year, individuals returning as adults to the breeding grounds were recorded soon after their arrival (median arrival date 2010–2011 was 18 April); the last interval (the unobservable state migration-wintering) therefore consisted of fifteen 2-week intervals.

The encounter histories file thus included (1) nine encounter occasions—eight after fledging in the natal year (1st calendar year) and one in the next year (2nd calendar year), and (2) eight intervals—seven 2-week intervals at the natal site and one 30-week interval at all migration-wintering sites together. The effective sample size was 496

fledgling/interval combinations. We again used AIC_c values to select the best-supported models among a set of a priori formulated models (Table 3).

In these models, survival rate (S), resighting probabilities (p) and/or transition rates (ψ; the probability that an individual departs from one stage to the next, e.g. from the natal site to migration-wintering site) were formulated as a function of:

1. Interval at natal site (7 two-week intervals).
2. Juvenile age (two age classes: 0–4 weeks after fledging and >4 weeks after fledging).
3. Cohort (eight cohorts—encounters in which nestlings were marked and fledged, thereby entering the marked population); cohorts were used to be able to vary the timing of the onset of migration (see below).
4. Fledging period (early—fledglings that fledged during the first 6 weeks of the fledging season, cohorts 1–3; late—fledglings that fledged after the sixth week of the fledging season, cohorts 4–8).
5. Year (2009 and 2010).
6. Stage (N and W).

Our models assume that juveniles cannot depart for autumn migration from the natal site before the 4th interval (before 15 July, $\psi_{NW} = 0$ during the first three intervals), that all juveniles have departed during the 7th interval (before 27 August, $\psi_{NW} = 1$ during the second-last

Table 3 Summary statistics of the candidate models assessing resighting rate and stage-dependent juvenile survival

	Model	k	$QAIC_c$	$\Delta QAIC_c$	w_i	Q deviance
Model selection for resighting probability						
A1	S (state × year + state × fperiod + age × fperiod) p (·)	10	475.21	0.00	0.53	103.66
A2	S (state × year + state × fperiod + age × fperiod) p (y)	11	477.28	2.07	0.19	103.64
A3	S (state × year + state × fperiod + age × fperiod) p (t)	15	477.59	2.38	0.16	95.49
A4	S (state × year + state × fperiod + age × fperiod) p ($y + t$)	16	478.25	3.04	0.12	94.02
A5	S (state × year + state × fperiod + age × fperiod) p ($y × t$)	21	483.56	8.35	0.01	88.51
Model selection for stage-dependent survival						
B1	S (state + fperiod)	5	465.75	0.00	0.15	104.53
B2	S (fperiod)	4	466.49	0.74	0.10	107.31
B3	S (state + juv age + fperiod)	6	467.55	1.81	0.06	104.29
B4	S (state × fperiod)	6	467.79	2.04	0.05	104.53
B5	S (state + year + fperiod)	6	467.80	2.05	0.05	104.53
B6	S (state)	4	468.06	2.31	0.05	108.88
B7	S (juv age + fperiod)	5	468.47	2.72	0.04	107.25
B8	S (year + fperiod)	5	468.53	2.78	0.04	107.31
B9	S (constant)	3	468.73	2.98	0.03	111.59
B10	S (state + juv age × fperiod)	7	469.15	3.40	0.03	103.82
B11	S (state + juv age)	5	469.51	3.77	0.02	108.30
B12	S (state × fperiod + juv age)	7	469.59	3.84	0.02	104.27
B13	S (state + year + juv age + fperiod)	7	469.61	3.86	0.02	104.29
B14	S (state × year + fperiod)	7	469.81	4.06	0.02	104.49
B15	S (state × fperiod + year)	7	469.85	4.10	0.02	104.53
B16	S (state + year)	5	470.01	4.26	0.02	108.79
B17	S (year)	5	470.01	4.26	0.02	108.79
B18	S (juv age × fperiod)	6	470.18	4.43	0.02	106.92
B19	S (year + juv age + fperiod)	6	470.51	4.77	0.01	107.25
B20	S (juv age)	4	470.76	5.02	0.01	111.59
B21	S (state × fperiod + juv age × fperiod)	8	471.11	5.36	0.01	103.72
B22	S (state + year + juv age × fperiod)	8	471.21	5.46	0.01	103.82
B23	S (state + year + juv age)	6	471.47	5.72	0.01	108.20
B24	S (state × year + juv age + fperiod)	8	471.64	5.89	0.01	104.25
B25	S (state × fperiod +year + juv age)	8	471.66	5.91	0.01	104.27
B26	S (state × year + state × fperiod)	8	471.88	6.13	0.01	104.49
B27	S (state × year)	6	471.98	6.23	0.01	108.71
B28	S (year + juv age × fperiod)	7	472.24	6.49	0.01	106.91

For ψ_{NW}, being the departure probability [i.e. transition from post-fledging stage at the natal site to the migration and winter stages (migration–winter)], model 7 is used in all models (all individuals depart for migration at the latest during the seventh interval, but the first two cohorts may depart earlier (cohort 1 during the 5th and 6th interval and cohort 2 during the 6th interval; Table S1). Only models with w_i >0.001 are shown

State Natal post-fledging (N)/migration-winter (W), *juv age* two age classes (≤4 and >4 weeks after fledging); for other abbreviations, see Table 2

interval) and that all surviving juveniles return to the natal site for breeding in the following year ($\psi_{WN} = 0$ for the first seven intervals and 1 during the last interval). When selecting the best model for ψ_{NW} for the remaining intervals, we varied the cohort-interval combinations at which juveniles had equal probabilities of departure from the natal grounds, as we expected earlier cohorts to be able to depart earlier than later cohorts (Table S1; see also Fig. S2).

First, the best-supported model for departure probability (i.e. transition from post-fledging stage at the natal site to the migration-winter stage ψ_{NW}) was selected, using the most parsimonious model for survival during the breeding season [S_N (year × fledging period × juvenile age)], a

simpler model without age effects for survival outside the breeding season [S_W (year × fledging period)] and a model with year and interval effects for recapture probability p at the natal site, [p_N (year × interval); $p_W = 0$, W being the unobservable state).

Next, the best model for resighting probability on the natal site (p_N) was selected, using the starting models for survival during the breeding season (S_N) and during migration-winter (S_W), with only the most relevant second-order interactions (stage × year, stage × fledging period and juvenile age × fledging period), to improve estimability of parameters and the best model for ψ_{NW}. As the number of visits to the study site differed between intervals, we tested whether p_N differed substantially between intervals and years: (1) p_N(year × interval). (2) p_N(year + interval), (3) p_N(year), (4) p_N(interval), and (5) p_N(·).

Finally, using the best-supported models for ψ_{NW} and p_N, the best-fitting model for S (stage-dependent survival) was selected. In the model for survival we included main effects of stage [post-fledging stage at natal site (N) and migration-wintering stage away from natal site (W)], year, juvenile age and fledging period (early and late), and the most relevant interactions stage × year, stage × fledging period and juvenile age × fledging period. As we were specifically interested in when the additional mortality of late-fledged juveniles (cohorts >3) occurred, in comparison with early fledglings (hypotheses 2 and 3), we also included the interaction term stage × fledging period. Other interactions were not included, to avoid problems with estimability.

Hypothesis 1 is accepted if survival at the natal site proves lower than that at the migration-wintering sites. Hypotheses 2 and 3 are accepted if survival of early fledged juveniles is higher than that of late-fledged juveniles, at both the natal and the migration-wintering sites, respectively.

As in interval-specific models S and p of the last interval are confounded, we assumed a value of 0.93 for p_N for this interval, resulting from the above analyses of first-year survival. In addition, we decided not to test for interval-dependent survival in state N (i.e. we assumed constant survival for intervals 1–7), as this resulted in many inestimable parameters. As the juvenile age class 0–4 weeks was only present during the breeding season, we could only test for juvenile age effects in S_N, not in S_W.

To make sure that all parameters in the final models were estimable, we substituted, one by one, the parameters of the most parsimonious model for S and best models for p and ψ (model A1 in Table 3) by fixed but slightly different values. As this always caused the model deviance to slightly change, we concluded that all estimated parameters were indeed estimable.

GOF was assessed for the most parsimonious model for S with relevant interactions [S (stage × year + stage × fledging period + juv age × fledging period)] and p_N (year × interval) and the best model for ψ_{NW} using the bootstrap method. The GOF test showed a near lack of fit of the most parsimonious model ($P = 0.085$). However, the dispersion parameter was small, $\hat{c} = 1.20$. Therefore, we corrected the AIC$_c$ values with this parameter to correct for the possible lack of fit.

Results

Annual survival in relation to fledging period

First-year annual survival of early fledged juveniles was 0.31 ± 0.09 SD, compared to 0.17 ± 0.06 for late-fledged juveniles and 0.53 ± 0.03 for adults, averaged across sites for 2007–2011. Figure 1 shows the yearly survival estimates for early and late juveniles, and includes also adults for comparison. Resighting probability was generally high and differed between juveniles and adults [juveniles 0.93 (95 % CI 0.86–0.96), adults 0.97 (0.93–0.99)], and was lower for study area Den Helder in 2010 [juveniles 0.70 (0.54–0.82), adults 0.87 (0.75–0.94)], due to lower observation effort (Table 2).

The best-supported model (ΔAIC$_c$ <2) for survival without the factor fledging period (early and late), included maturity (juvenile and adult), year and their interaction, but not site (Table 2). However, since previous analyses showed that juvenile and adult survival differ among sites (Van Oosten et al. 2015) and fledging date also differed among the three sites (general linear model in SPSS 21.0,
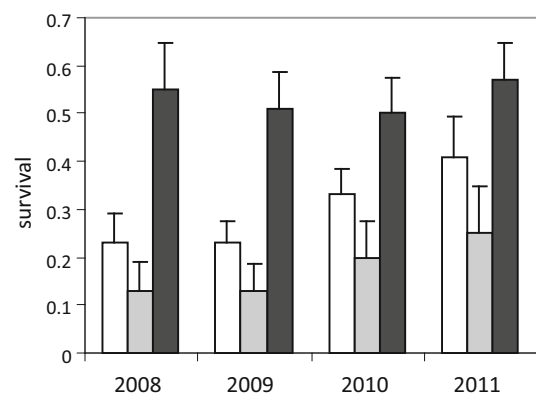

Fig. 1 First-year annual survival for early (*white bars*) and late (*grey bars*) broods, with adult annual survival (*black bars*) shown as a reference. Estimates based on the best-supported model for survival which includes site and maturity (juvenile/adult) and their interaction, and maturity and year and their interaction, as well as an additive effect of fledging factor (early/late; Table 2). Values (mean and SD) shown per year for all three sites combined

$F = 46.30$, $df = 2$, $P \leq 0.0001$), we used a starting model that did include site when testing for effects of fledging period. The best-supported model for survival with site effects consisted of the main effects of site and maturity and their interaction, and of year and its interaction with maturity (Table 2), and was used as the starting model for testing effects of fledging period. The inclusion of the factor fledging period did improve the starting model significantly (compare starting model B2 without fledging period with model C1 with fledging period; $\Delta AIC_c = 10.54$; Table 2). Adding interaction terms of site or year with fledging period (models C2 and C3, respectively) did not further improve the model.

Stage-dependent juvenile survival in relation to fledging period

The two best models ($\Delta AIC_c < 2$) for transition probabilities from natal site to migration-winter sites (ψ_{NW}) were models 6 and 7 (see table S1). As model 7 was slightly better (ΔAIC_c of model 6 is 0.64) and contained fewer parameters, we used this model to analyse stage-dependent survival. For resighting rate the best model was the model with constant resighting rate (see Table 3).

We further explored first-year survival by dividing between stages: natal post-fledging (N) and migration-winter (W). Survival during the migration-winter stage did not differ significantly from survival during the post-fledging period at the natal site (compare models B2 and B9 without state effects with corresponding models B1 and B6 with state effects; $\Delta AIC_c = 0.74$ and 0.67, respectively; Table 3). When comparing early and late fledglings, average survival per 2-week interval appears higher for early fledglings than for late fledglings, both during the natal post-fledging period (early/late fledglings 0.932 ± 0.015 SE/0.878 ± 0.032) and during migration-winter (early/late fledglings 0.959 ± 0.007/0.924 ± 0.017; Fig. 2). Including juvenile age (≤ 4 vs. > 4 weeks after fledging) only increased the AIC_c value of the model for survival, and thus did not significantly improve the model (Table 3, compare model B3 with age effects to the corresponding model B1 without age effects). However, the model including an age effect in addition to effects of stage and fledging date was among the three best models with $\Delta AIC_c < 2$, and although its effect was small, it agreed well with the expectation that survival is lower in the first few weeks after fledging (0.926 ± 0.019 SE vs. 0.940 ± 0.021 in early fledglings and 0.871 ± 0.037 vs. 0.895 ± 0.043 in late fledglings). The probability of leaving for migration was similar for the first cohort of fledglings during the 5th and 6th interval and the second cohort during the 6th interval, and amounted to 0.59 ($\psi_{NW} = 0.587 \pm 0.071$ SE) for all cohorts during the 7th interval.
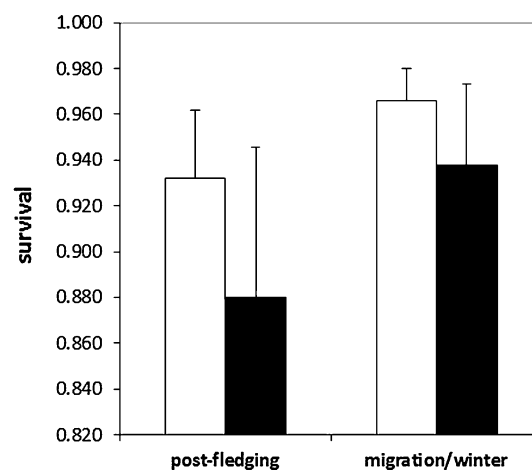
Fig. 2 Natal post-fledging and migration-winter survival of early fledglings (*white bars*) and late fledglings (*black bars*) from the best model, given as average (SE) survival per 2-week interval. The best-supported model includes additive effects of state (natal post-fledging vs. migration-winter) and fledging period (early vs. late); Table 3

The stage-dependent survival model that had most support from the data (smallest $QAIC_c$ value; Table 3) includes juvenile survival as a function of stage (post-fledging stage at natal site N and migration-wintering stage away from natal site W) and fledging period (early and late). The model with an additive effect of stage (N or W) and fledging period (early or late) was marginally better than the model that also included the interaction of the two (Table 3). This suggests that survival per 2-week interval differed in a similar way for early and late-fledged juveniles at the natal site (fledging—end of August) and during migration-winter (September–March). However, differences in $QAIC_c$ values between subsequent models were small, and the models for survival with an additive effect of stage, fledging period and age (model B3) and with an effect of fledging date only (model B2) explained the data equally well. As these models all had $\Delta QAIC_c < 2$ we used model averaging to obtain robust estimates for survival; parameter estimates are given in Table 4.

Discussion

We used mark-resight data to test three hypotheses that in Northern Wheatears (*O. oenanthe*): (1) post-fledging survival on the natal grounds is lower than migration-winter survival, (2) post-fledging survival on the natal grounds is higher for early fledged juveniles than for late-fledged juveniles, and (3) survival during the migration-winter period is also higher for early fledged juveniles than for late-fledged juveniles, resulting in higher first-year survival of early fledged juveniles than late-fledged juveniles.

Table 4 Averaged estimates of survival parameters of the best-supported three models (Table 3) of the post-fledging and migration-wintering juvenile survival analysis

State	Fledging period	Age	Interval[a]	Estimate	SE	Unconditional SE
N	Early (cohorts 1–3)	≤4 weeks	1–7	0.936	0.013	0.016
N	Early (cohorts 1–3)	>4 weeks	1–7	0.939	0.013	0.016
N	Late (cohorts 4–8)	≤4 weeks	1–7	0.886	0.030	0.034
N	Late (cohorts 4–8)	>4 weeks	1–7	0.891	0.031	0.034
W	Early (cohort 1–3)	All	8	0.955	0.008	0.010
W	Late (cohort 4–8)	All	8	0.919	0.021	0.022

Survival is per 2-week interval

Age Weeks after fledging, *Early* fledged during the first 6 weeks of the fledging season (cohorts 1–3), *Late* fledged after the 6th week of the fledging season (cohorts 4–8); for other abbreviations, see Table 3

[a] Two-week intervals at natal site (*7*); 30-week interval spanning migration-winter (*1*)

We did not find proof to accept hypothesis 1: post-fledging survival on the natal grounds was not clearly different from survival during the migration-winter period (all three top models have ΔQAIC$_c$ <2). Hypotheses 2 and 3 are accepted, since we showed that post-fledging survival on the natal grounds was higher for early fledglings than for late fledglings (hypothesis 2) and that 2-week survival during the migration-winter period was also higher for early than for late-fledged juveniles (hypothesis 3). Together they resulted in higher annual survival for early fledged juveniles than for late-fledged juveniles.

First-year survival in relation to fledging period

First-year survival of late-fledged Northern Wheatears was much lower than that of early fledged birds. Survival of fledglings could have been underestimated due to permanent emigration out of the natal site. This could be especially true for late fledglings: to avoid competition with early fledglings and adults, they may choose to prepare for moult and migration away from the natal site and choose to breed at the novel site the next spring. Fortunately, Northern Wheatears show a very high degree of (natal) fidelity in our (Van Oosten et al. 2015) and other study populations, such as in Sweden (Arlt et al. 2008), on Fair Isle, UK (Seward et al. 2013) and in France (Henry and Ollivier 2015). This is a common pattern in many bird species (Maness and Anderson 2013), and also other factors (covarying with fledging date) could explain the patterns found here.

Factors reported to influence juvenile survival include size, weight, sex, brood size and hatchling growth (Maness and Anderson 2013). Some or all of these factors may be responsible for the patterns observed here.

Stage-dependent survival

Average 2-week survival rate of juvenile Northern Wheatears on the natal grounds was not clearly different from survival during the migration-winter stage. This is an unexpected result because survival of juveniles in songbirds is typically lowest in the first weeks after fledging (e.g. Naef-Daenzer et al. 2001; Vitz and Rodewald 2011; Sim et al. 2013; reviewed in Cox et al. 2013), although survival varies greatly among species and the survival model including an age effect was among the top-three survival models in our study. This may indicate that, if there is a difference between these two stages, it is too small to be detectable with current sample sizes. Apart from a lack of power due to small sample sizes, we may not have found support for differential survival on the natal sites compared to the migration-winter period because the relatively high natal post-fledging survival of Northern Wheatears equalled the summed (putatively lower) migration and (putatively higher) winter survival. Sillett and Holmes (2002) show that survival of the Neotropical Black-throated Blue Warbler (*Dendroica caerulescens*) during migration is at least 15 times lower than survival in the stationary periods (summer and winter). Grüebler et al. (2014) show for Barn Swallows that survival of juveniles after the first 3 weeks post-fledging is similar to adult survival. Being able to estimate over-winter survival in the African Sahel would yield much more insight into survival between the different periods and locales during the annual cycle.

Average 2-week survival rates during post-fledging at natal sites were high compared to other studies on juvenile passerines (reviewed in Cox et al. 2013): only Purple Martin *Progne subis* [0.939 for resighted colour-ringed juveniles (Tarof et al. 2011)] and Eastern Meadowlark *Sturnella magna* [0.944, including juveniles with unknown fate (Kershner et al. 2004)] show survival rates similar to our Northern Wheatears (0.932 for early fledglings and 0.878 for late fledglings). This indicates that post-fledging survival may strongly differ between species. Also, field-work methodology in combination with sample sizes may partly influence the findings: post-fledging survival of Purple Martins as determined by radio-telemetry was

0.868, but based on resightings of colour-ringed birds was 0.939 (Tarof et al. 2011).

Post-fledging survival is often strongly affected by high predation rates of juveniles with still limited locomotion and foraging abilities (e.g. Sullivan 1989; Anders et al. 1997; Naef-Daenzer et al. 2001; Sim et al. 2013). Unfortunately, we have no information about predation pressure on fledglings for our Northern Wheatear populations. However, predation rates of Northern Wheatear fledglings in our study population may be relatively low since post-fledging survival rate is high compared to that of other passerines (Cox et al. 2013). Post-fledging survival is further influenced by food availability (Seward et al. 2013) and intra-specific competition (Arcese and Smith 1985). Together they may affect body condition and therefore may carry-over to also affect survival during the migration-winter stage. This may explain why survival was not clearly different in both stages.

Most if not all studies show a dip in daily survival during the first few days after fledging (Sullivan 1989, Anders et al. 1997; Sim et al. 2013; Kershner et al. 2004; Tarwater et al. 2011 ; Yackel Adams et al. 2006; Naef-Daenzer et al. 2001; Dybala et al. 2013). In addition, some studies show a second dip after the nestlings have become independent (Sullivan 1989; Anders et al. 1997; Sim et al. 2013) although others do not (Kershner et al. 2004; Tarwater et al. 2011; Yackel Adams et al. 2006; Naef-Daenzer et al. 2001). We divided survival into two periods (≤4 and >4 weeks after fledging) and found some support for differential survival between them. However, we found no strong evidence that post-fledging survival differs from migration-winter survival in Northern Wheatears. This may indicate that the survival dip immediately after fledging is small in Northern Wheatears, resulting in overall post-fledging survival not differing from migration-winter survival. Dividing the post-fledging period into daily or weekly survival would shed more light on the magnitude of age-related survival, but this needs more frequent resightings in the field.

Stage-dependent survival in relation to fledging period

In particular, post-fledging survival of late fledglings may be lower that of than early fledglings because food availability may decline during the breeding season, such as reported for temperate, deciduous forests (Feeny 1970; Southwood et al. 2004; Both et al. 2010). However, other ecosystems such as marshes harbor relatively high densities of arthropods throughout the season (Halupka et al. 2008; Both et al. 2010). Data on changes in food abundance throughout the breeding season are largely unavailable for coastal dunes in Western Europe. Nevertheless, since the

post-fledging period of early compared to late-fledged Northern Wheatears shifts in time, different prey species or stadia (larva, imago) are available to them, as a result of differences in prey phenology. Seward et al. (2013) supplemented Northern Wheatears after fledging with extra food, which increased their annual survival compared to non-fed individuals. Although study sites could conceivably differ greatly in natural food abundance, Seward et al.'s (2013) work shows that food is potentially limiting Northern Wheatear populations. If food availability is lower at the end of the breeding season, it may affect body condition of late fledglings which may then carry-over to also affect migration-winter survival, more than for early fledglings.

Aggressive interactions among fledglings were frequently observed in the field, and fledglings are known to defend territories against conspecifics as early as during the post-fledging period (Glutz von Blotzheim and Bauer 1988; Conder 1989). Perhaps both post-fledging and migration-winter survival are lower for late fledglings because of theoretically more intense intraspecific competition: late fledglings do not only have to compete with adults, but also with remaining early fledged juveniles on the natal site (Fig. S1). This may hamper foraging effectiveness, as shown for other passerines (Arcese and Smith 1985; Merilä and Svensson 1997). This may also indicate that the lack of early fledged, thus stronger, conspecifics in years of high rates of nest predation may alleviate intra-specific competition (e.g. accessibility to food, foraging time) for late fledglings and hence, increase their first-year survival (Tinbergen et al. 1985). In corroboration with this idea, Both et al. (1999) show that being heavy has a positive effect on survival, especially in years with a high juvenile density, probably because heavier fledglings can better withstand competition with early fledglings. Still, the negative effect of fledging period on juvenile survival was found for all three sites and 4 study years. This may indicate that post-fledging survival is not strongly affected by fluctuations in density. Alternatively, the years of research may have been 'benign' years, whereas there may be years when a high number of fledglings coincides with low food availability. In the latter scenario, post-fledging survival (and migration-winter survival) may be affected by intraspecific competition.

Conclusions and implications for conservation

First, we have shown that post-fledging survival of Northern Wheatears on the natal grounds and survival during the migration-winter stage do not clearly differ. Second, post-fledging survival on the natal grounds was higher for juveniles fledged early in the breeding season compared to late-fledged juveniles. Third, survival during

the migration-winter stage was also higher for early fledged juveniles than for late-fledged juveniles. Higher survival during both the post-fledging stage and migration-winter stage resulted in higher annual survival rates for early fledglings (0.31), compared to late fledglings (0.17). From these results it follows that conservation strategies should focus in the short term on improving nest success of early broods since early offspring have a higher annual survival than late offspring. Population growth rate may be doubly affected by high nest predation rates: first through low reproductive output caused by low nest success and second through low juvenile survival of fledglings from late replacement clutches.

Differences in survival between early and late fledglings that pertain during the migration-winter stage strongly suggest that conditions at the natal sites are important since they may well carry-over to influence survival during later stages. Therefore, improving conditions at natal sites can have long-lasting effects which increase survival during later stages. In the longer term, the identification of factors causing the lower (post-fledging and migration-winter) survival of late fledglings than of early fledglings should be the subject of studies as a first step towards mitigating their negative effects.

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