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Low immigration and high local recruitment in an isolated, coastal population of a declining grassland passerine, the Northern Wheatear *Oenanthe oenanthe*

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Abstract. The western European populations of Northern Wheatear *Oenanthe oenanthe* have halved over the past two decades. In this context of increasingly fragmented populations, a key issue is to understand the role of immigration in the maintenance of remnant populations. We characterized the local survival, fecundity, recruitment and immigration rates of a small, geographically isolated, coastal French population during a period of population stability, while the regional population was rapidly decreasing (1991–1999). Annual local adult and juvenile survival rates were estimated with capture-resighting data at, respectively, 0.463 ± 0.052 (n = 157 adults) and 0.215 ± 0.054 (n = 363 nestlings). Only 2.1 immigrants joined the population per year (7.3% of all recruits). This annual immigration rate (0.039) is lower than all 14 available estimates for small to medium-sized birds. The local population growth rate depended equally on all demographic parameters, apart from a minor influence of the immigration rate. Within-site breeding dispersal distances were low, and differed between sexes (78 ± 49 m for males, 259 ± 274 m for females). Juvenile and adult survival rates appeared lower than for populations of wheatears settled in high quality habitats, but this deficiency was compensated by high fecundity and the 2 annual immigrants. The small population size (22–27 pairs), extremely low immigration, and strong dependence on local recruits suggest that this population was demographically isolated on a patch of moderate habitat quality, with no chance of rescue by immigration in case of stochastic event. Indeed, this population went extinct in the 2000's, after a disturbance of unknown origin.

Key words: apparent survival, coastal grassland, demography, dispersal distance, habitat fragmentation, immigration, local extinction, local population dynamics, local recruitment

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INTRODUCTION

How small, geographically isolated populations go extinct or persist has long been a hot topic of research in population dynamics and conservation biology (Bowler & Benton 2005, Brook et al. 2008, Drake & Griffen 2010). As human activities increasingly fragment habitats, the connection between populations decreases (Brook et al. 2008). One of the key issues when investigating how a small, geographically isolated population can maintain a stable number of reproductive adults is to assess the role of immigration versus local recruitment in the local population dynamics (Dale 2001, Bowler & Benton 2005, Ward 2005, Schaub et al. 2006, Pradel & Henry 2007). The population size could remain stable thanks to reduced emigration because of geographic isolation (Weatherhead & Forbes 1994, Dale 2001, Bonte et al. 2012), or sufficient immigration from the rest of the metapopulation (Bowler & Benton 2005, Wilson & Arcese 2008). Although the relative importance of permanent emigration can be assessed by comparing local survival between populations, estimating the contribution of immigration to the local population dynamics is more complicated (Abadi et al. 2010). When studying population dynamics with capture-mark-recapture data, immigrants are not marked. Therefore immigrants cannot be distinguished from locally born recruits that have not been marked at birth. In such a situation, the proportion of recruits that immigrate from other populations needs to be deduced from estimates of juvenile and adult local survival rates, fecundity and population growth rate (Schaub et al. 2006, Pradel & Henry 2007, Abadi et al. 2010).

Human recreational activities alter the functioning of coastal grasslands (Coombes et al. 2008, Kerbiriou et al. 2008). The rise of tourism accelerates the fragmentation of grasslands along the coastline. And, in remaining patches, the intensification of tourism-related disturbances alters the dynamics of coastal grasslands (Kerbiriou et al. 2008) and of associated species (Kerbiriou et al. 2009). The Northern Wheatear *Oenanthe oenanthe* is one of the bird species depending on these coastal grassland habitats. The Northern Wheatear is an insectivorous, ground-foraging bird that inhabits open, grassy habitats preferentially with sparse or short vegetation, like meadows, grasslands and pastures, both in coastal and mountainous/alpine regions (Conder 1989, Pärt 2001a,b, Arlt & Pärt 2007, Arlt et al. 2008, Low et al. 2010, van Oosten 2015; for France — Ollivier 1994, Jiguet 2009). It nests in underground cavities, like rabbit burrows (Conder 1989, van Oosten 2015). Northern Wheatears are migratory, wintering in sub-Saharan Africa (Seward et al. 2013, van Oosten 2015). French coastal populations of Northern Wheatear have been decreasing since the 1980s, with extinctions over extended portions of coastline, particularly in Brittany, Picardie and Loire-Atlantique (Ollivier 1994, 1999). The densest coastal populations are now confined to the Channel's coast of Picardie and Nord-Pas de Calais, and to the sand dunes west of the Cotentin's peninsula in Normandy (Jiguet 2009). In this latter region, the decline could be quantified thanks to regular censuses (Ollivier 2009): from 100 pairs in 1985–1988, the population dropped to 40–50 pairs in 2001–2003, 15–25 pairs in 2004–2005, less than 10 in 2006–2007, and afterwards, only 2–3 pairs remaining in the Bay of the Mont Saint Michel (B. Chevalier, unpublished data; Ollivier 2009). Over all France, over the last decade, abundance of the Northern Wheatear decreased by 51% (Jiguet 2009). Not only are coastal populations in decline, but also populations in diverse habitats throughout Europe: 61% of loss between 1980 and 2012 for Europe and between 1976 and 2001 for Sweden, at least 80% between 1970 and 2011 for the Netherlands (Wretenberg et al. 2006, BirdLife International 2011, van Oosten et al. 2015).

Despite this sharp, global decline of the species, the demography of the Northern Wheatear has been studied in only three sets of populations: a large and stable population from farmlands of inland Sweden (Pärt 2001a,b, Arlt & Pärt 2007, 2008, Arlt et al. 2008, Low et al. 2010, Pärt et al. 2011), an island, declining population from Scotland (Seward et al. 2013), and two coastal and one isolated inland populations from the Netherlands (van Oosten 2015, van Oosten et al. 2015). These studies documented two main ecological causes of population decline: low habitat quality and geographic isolation. Low habitat quality decreases all demographic parameters: fecundity — through low food availability and reduced foraging efficiency of adults (Pärt 2001a,b, Arlt et al. 2008, Pärt et al. 2011), adult local survival — through an increased cost of parental care and increased predation (Arlt et al. 2008, Low et al. 2010, van Oosten et al. 2015), juvenile local survival — through condition-dependent mortality (Arlt et al. 2008, Seward et al. 2013), or emigration and immigration — through decreased habitat attractiveness (Pärt et al. 2011). Conversely, geographic isolation is more likely to decrease immigration as less prospectors reach the most isolated populations (Bowler & Benton 2005, Ward 2005, Schaub et al. 2006, Wilson & Arcese 2008, van Oosten et al. 2015), and to increase local juvenile survival, since returning yearlings would have reduced opportunities of finding another population where to settle (Weatherhead & Forbes 1994, Dale 2001, Wilson & Arcese 2008, Foerschler et al. 2010, Bonte et al. 2012; but see Dale 2001 for the opposite prediction).

The aim of the present study is to document the demography of a small, geographically isolated, French coastal population of Northern Wheatears. This population went extinct 5 years after the end of our demographic survey. We attempt to infer the respective role of adult survival, local fecundity, local recruitment, and immigration in the fate of this population. We analyse the demographic data of this population for a period of stable population size (1991–1999). We compare estimates of the demographic parameters of our population with those of other stable populations (Arlt et al. 2008, Low et al. 2010, Seward et al. 2013, van Oosten et al. 2015), used as references, in search of demographic weaknesses that may have facilitated extinction. The small size of our population (22–27 pairs) alone was already indicative of a high vulnerability to extinction through environmental and/or demographic stochasticity (Drake & Griffen 2010). But we hypothesize that supplementary demographic deficiencies could have been (i) a low annual, adult local survival rate, (ii) a deficient recruitment of locally born individuals caused by true low juvenile survival and/or high natal dispersal (emigration), (iii) low reproductive output, and/or (iv) a low recruitment of immigrating, new breeding adults. If the ecological weakness was low habitat quality, we predict that all four parameters could have low values, whereas in case of critical geographic isolation, immigration should be particularly low, and local survival particularly high.

METHODS

Study area and population

Between 1991 and 1999, we monitored a population of Northern Wheatears, made of 22–27 breeding pairs (Fig. 1), from the French coastal stronghold south-west of the Cotentin's peninsula, in Normandy. The study area (100–120 ha) was located on the 4 km long, 500 m wide peninsula of the Havre de la Vanlée (Bricqueville-sur-Mer, France; 48°55'00"N 01°33'47"W). The habitat was composed of a large, sandy dune fixed with European Marram Grass *Ammophila arenaria* parallel to the shore, covered with Annual Seablite *Suaeda maritima* (see Ollivier 1997, 1999, Ollivier et al. 1999, for more details). The nearest breeding population was at 12 km north in the 1980s (Debout 1992), and 30 km north and south in the 2000s (Ollivier 2009). From 1991 to 1999, visits started on March 18th ± 14 (s.d.) days (range: March 2nd–April 10th), and ended on June 20th ± 23 (May 26th–July 29th). The first wheatears were observed on March 22nd ± 11 (March 9th–April 10th). The monitoring effort was higher in the years 1993–1995, with 19 ± 3.6 visits throughout the breeding season (to achieve a precise temporal characterization of breeding events), and when we managed to mark ca. 81% of known nestlings and ca. 88% of observed adults (respectively, number of ringed nestlings divided by the number of observed 14–18 day old fledglings, and total number of marked adults, newly marked or resighted, divided by the number of paired and non-paired adults observed per season). In 1991–1992, and after 1995, the study site was visited 5.5 ± 2.6 times per breeding season. This reduced field effort was sufficient to achieve the same resighting probability as in 1993–1995 (i.e. models with resighting probability that could differ between the two study periods had lower $QAIC_c$ than models assuming constant resighting probability; results not shown). A visit lasted 12 hours, and effort was equally distributed throughout the study site. Marked individuals were identified using binoculars (magnification ×10) or a telescope (×30). Between 1991 and 1995, 100 adults (46 males, 54 females) and 363 nestlings were captured and individually marked with a unique combination of three colour-rings. Fifty-seven juveniles returned to the study site (24 males, 33 females), 45 were first resighted after one year (yearling), six after two years, and six after three years. Unmarked adults were captured at their nest, with an automated clap net, when provisioning their chicks with food. Among these birds, we could not distinguish yearlings from older individuals. Sex was determined according to adult plumage dimorphism. Nestlings were captured by hand in the nest for marking at 7–10 days old. Over the whole study period, adults generated 268 informative capture-resighting data points (i.e., sums of Ri values of the corresponding m-array, Lebreton et al. 1992; 144 for males, 124 for females) and nestlings generated 449 data points (363 for the first year of life, 86 as yearlings or older). Per year, it corresponded, on average, to 41.6 ± 7.5 marked adults (newly marked and returning individuals) and 90.8 ± 34.8 marked nestlings.

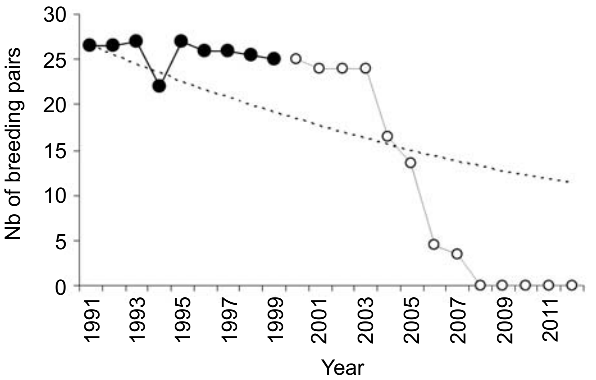

Fig. 1. Annual variations in the number of breeding pairs of Northern Wheatear during the present study (black dots), and subsequently, until the extinction of the population (white dots; censuses made by B. Chevalier). The dotted line indicates the theoretical trajectory of the population size in absence of immigration, i. e. according to the computed population growth rate using local survival and fecundity values and ignoring the recruitment of immigrants ($\lambda_{no\ immig.}$ = 0.960, see Methods for more details).

The number of first breeding attempts observed per year is considered as the number of breeding pairs. During each visit, all nests were precisely located on a map. Distances between nest sites were used to quantify local natal and breeding dispersal. Differences in natal dispersal between sexes were tested with t-tests adjusted for unequal variances, and in breeding dispersal with a linear mixed effect model on log-transformed distances, including a random term for between-individual variation and a residual variance term to account for unequal variances between sexes. Females laid their first eggs on April 25th ± 11 (range: April 5th–May 28th; n = 76), and incubated for 12–16 days (Ollivier 1997, Ollivier et al. 1999). Over all monitored broods, clutch size was 5.5 ± 1 eggs (n = 89) and brood size was 4.8 ± 1.5 fledglings (n = 68). 52 of 76 first broods (68.4%) were successful, producing 5.2 fledglings per successful brood. Fifteen of 52 successful reproductive pairs (28.9%) engaged in a second brood, whereas 12 of 24 pairs that failed with their first breeding attempt re-laid (50%). The reproductive success of second broods was 82.3% (n = 34), producing 3.6 fledglings per successful brood (n = 31). Chicks fledged at an age of 14–18 days. Reproduction lasted until late June.

Local survival and resighting probabilities

Annual local survival rates were estimated with Cormack-Jolly-Seber (CJS) models fitted to capture-recapture data (Lebreton et al. 1992). Resightings are treated as recaptures. Models were fitted with the software MARK v. 5.1 (White & Burnham 1999). Data were analysed in two steps. First, we analysed capture-resighting data of adults only, and evaluated the variation in annual, local survival (φ) and/or resighting probabilities (p) between years (time effect) and sexes. The annual, local (or apparent) survival probability is the probability that a marked individual survives and returns to the study site from one breeding season to the following one. The resighting probability is the probability to locate and identify a marked individual in the study site during a given breeding period. Second, we analysed all data, including nestlings, and evaluated the effects of year and age. *Age* was defined as a two-level factor, distinguishing juveniles (i.e. from nestling to yearling) from adults, or a three-level factor (noted age_3): juvenile (i.e. from nestling to 2nd calendar year) versus yearling (from 2nd to 3rd calendar year) versus 'other adults' (a mixture of birds in their 3rd calendar year or more, and unmarked yearlings that we could not distinguish from unmarked older adults). The effects of year, sex, age, and their interactions, on survival or resighting probabilities were assessed with modified Akaike's information criteria, adjusted for small sample size and overdispersion ($QAIC_C$, adults only: $\hat{c} = 2.782$; all ages: $\hat{c} = 2.934$, median $\hat{c}$ values were obtained by boostrap, with 500 simulations, with the simplest, final model for each analysis, see Table 1; Burnham & Anderson 1998). Adequate fits to the data of general models, accounting for the effects of group (i.e., *sex* or *age*) and time (noted *t*, i.e. year) and their interactions on both parameters [noted φ (*group***t*) p(*group***t*)], were verified with U-CARE v.2.2.5 (Choquet et al. 2009). Construction of age-effects, by constraining parameters to be equal between groups of age at marking (nestlings versus adults) followed Lebreton et al. (1992). For the analysis of adults only, the fit was satisfactory ($\chi^2 = 17.84$, df = 21, p = 0.66, without trap-dependency nor transience). All possible models were then fitted. For the analysis including all individuals, i.e. juveniles and adults, a significant lack of fit was detected ($\chi^2 = 34.40$, df = 20, p = 0.02, without trap-dependency). This global lack of fit was largely attributable to the heterogeneity in survival probability between juveniles and adults within the group of individuals marked as nestlings, resulting in an apparent transiency of individuals for this group (test 3.SR, standardized log-odds ratio statistic for transience = 2.86, p = 0.002; Lebreton et al. 1992). There may have been also some heterogeneity in resighting probability between age classes (cf. Results). These heterogeneities were accommodated for by including a true age effect in most models considered in the model selection (Lebreton et al. 1992; Table 1). In both analyses, we also allowed for a linear trend in logit-transformed survival probability on year [noted φ (*T*)]. The model with the lowest $QAIC_C$ was retained as the best model, i.e. the one achieving the best compromise between parsimony (number of parameters in the model) and fit to the data (deviance). A difference in $QAIC_C$ of less than two points from the best model identified models that received statistical support. To discuss the plausibility of these alternative models, we relied on $QAIC_C$ weights (w_i). A $QAIC_C$ weight gives the probability that a model correctly reflects the mechanism generating the data, assuming that the correct model is among those considered in model selection (Burnham & Anderson 1998). The relative importance of explanatory variables is assessed with the sums of weights of the models that include these variables (Σw_i; Burnham & Anderson 1998). Estimates, standard errors and 95% confidence intervals of survival and resighting probabilities were obtained either with the most relevant model, i.e. one of the models within 2 points from the best model, or with a model averaging procedure (where the estimates are weighted by the $QAIC_C$ weight of each model to produce estimates accounting for uncertainty in model selection; Burnham & Anderson 1998).

Local population dynamics

To assess the degree to which the stability of the population size during the period 1991–1999 (Fig. 1) was due to the recruitment of individuals born locally versus immigration, we proceeded as follows. Since one-year old individuals are mature, we assumed that all adults could reproduce (Conder 1989, Low et al. 2010). First, we computed the local, geometric population growth rate without immigration ($\lambda_{no\ immig.}$) with a simple pre-breeding census, female-based matrix model with one age class (simplified from Legendre et al. 1999, i.e. assuming that all recruits were born locally). Then, we added an immigration rate parameter to the matrix model, ω (following Schaub et al. 2012), which is defined as the ratio between the number of immigrants in year *t* and the number of adults in the population in year *t*-1 (assuming an equal sex-ratio), and searched for the value of ω that allowed the population growth rate in presence of immigration ($\lambda_{with\ immig.}$) to equal the observed value of population growth rate at our study site for the period 1991–1999 ($\lambda_{obs.}$, mean of annual ratios of population sizes, N_{t+1}/N_t). We also computed the recruitment rate (R), defined as the proportion of adults that are new to the local breeding population on a given year, computed according to the formula: $R = 1 - (\varphi / \lambda_{with\ immig.})$ (Abadi et al. 2010). We computed the percentage of change of the population growth rate induced by a 1% increase of each demographic parameter to identify the relative contribution of each trait to the trend of the population (i.e., elasticity of $\lambda_{with\ immig.}$ to each demographic parameter; Legendre et al. 1999, Arlt et al. 2008).

RESULTS

Local adult survival

The most parsimonious CJS model (Table 1A) indicated that survival and resighting probabilities could be considered as constant through time, and independent of sex (Fig. 2). The annual local survival rate of adults was 0.463 ± 0.052 (95% confidence interval: 0.364–0.565), with an annual resighting rate of 0.873 ± 0.074 (95% CI: 0.651–0.962). However, the best model ($w_i = 0.40$) was only two times more likely than the two models with a $\Delta QAIC_C < 2$. These competing models suggest that males may have survived better than females (Σw_i for sex effect = 0.21; respectively, 0.480 ± 0.075, 95% CI: 0.339–0.625, and 0.449 ± 0.070, 95% CI: 0.318–0.587; estimated with model φ (sex) p(.)), and that the local survival of adults may have decreased throughout the study period ranging from 0.484 ± 0.080 (95% CI: 0.334–0.636) in 1991 to 0.440 ± 0.089 (95% CI: 0.278–0.615) in 1998 (estimated using model-averaging; Σw_i for linear year effect = 0.23; Fig. 2).

Age-dependency of local survival

The model with the lowest $QAIC_c$, φ (*age*) p(*age*$_3$), indicates that both survival and resighting probabilities most likely depended on age (Table 1B). Annual local survival rates differed between age classes (Σw_i of models with an age effect on survival = 0.99). With the best model, the local survival was lower for juveniles (0.215 ± 0.054, 95% CI: 0.127–0.338) than for adults (Fig. 2). The local survival of yearlings did not strongly differ from that of adults, since the three-class age effect (φ (*age*$_3$) p(.)) was 2.6 times less likely than the two-class age effect (φ (*age*) p(.)). Again, there was some support for a linear trend through years in local survival (Σw_i = 0.23), but this trend would not differ between juveniles and adults (w_i = 0.05 for model φ (*age*T*) p(.)). Resighting probability, using the best model, was estimated at 0.577 ± 0.143 (95% CI: 0.303–0.811) for yearlings, 0.591 ± 0.162 (95% CI: 0.280–0.843) for second-time breeders and 0.895 ± 0.075 (95% CI: 0.640–0.976) for adults (this last category mixing older adults and some, unmarked yearlings). When pooling the two first age classes, the resighting probability of first- and second-time breeders was 0.583 ± 0.117 (95% CI: 0.352–0.782).

Local population dynamics

The average local geometric population growth rate without immigration ($\lambda_{no\ immig.}$) was computed assuming that the population consisted of 27 females (as counted in 1991), a juvenile local survival rate of 0.215, an adult local survival rate of 0.463, a primary sex-ratio of 1:1, and an annual female fecundity of 4.63 fledglings per year (accounting for brood size, brood failure, fledging success per breeding attempt, and frequency

Table 1. Model selections to assess year-dependency, and (A) sex- and (B) age-dependency of local survival and resighting probabilities of Northern Wheatears (in bold: retained models). Samples sizes are given as number of marked individuals and total number of informative capture-resighting data points (in individual*year). Overdispersion factors (ĉ) were used to adjust model deviances (QDEVIANCE) and QAIC$_C$ for overdispersion. Abbreviations: np, number of intrinsically estimable parameters in the model (following Viallefont et al. 1998); QAIC$_C$ — Akaike's information criteria adjusted for small sample size and overdispersion; ΔQAIC$_C$ — difference in QAIC$_C$ between the model and the model with the lowest QAIC$_C$; φ — local survival probability; p, resighting probability; *t* — factorial effect of time, *T* — linear effect of time, (.), constancy; *sex* — two-level sex factor; *age* — two-level age factor (juvenile *versus* adult); age_3 — three-level age factor (juveniles versus yearling versus adult); subscripts ad and juv, respectively, adult and juvenile; *, interaction of terms.

Model	QAIC$_C$	ΔQAIC$_C$	QAIC$_C$ weight	Np	QDEVIANCE
A — Adults only, 70 males (144 individual*years), 87 females (124 individual*years), ĉ = 2.782					
φ (.) p(.)	**154.80**	**0.00**	**0.40**	**2**	**31.08**
φ (*T*) p(.)	**155.86**	**1.06**	**0.24**	**3**	**30.10**
φ (*sex*) p(.)	**156.75**	**1.95**	**0.15**	**3**	**30.99**
φ (.) p(*sex*)	156.82	2.02	0.15	3	31.06
φ (*sex*) p(*sex*)	158.75	3.96	0.06	4	30.93
φ (*t*) p(.)	166.29	11.50	0.00	9	27.93
φ (.) p(*t*)	166.94	12.15	0.00	9	28.58
φ (*sex*+*t*) p(.)	168.33	13.54	0.00	10	27.81
φ (*t*) p(*sex*)	168.44	13.64	0.00	10	27.91
φ (.) p(*sex*+*t*)	168.87	14.08	0.00	10	28.35
φ (*sex*) p(*t*)	168.99	14.20	0.00	10	28.47
φ (*sex*+*t*) p(*sex*)	170.46	15.67	0.00	11	27.76
φ (*sex*) p(*sex*+*t*)	170.69	15.89	0.00	11	27.99
φ (*t*) p(*t*)	177.65	22.86	0.00	15	26.08
φ (*sex*+*t*) p(*t*)	179.78	24.98	0.00	16	25.94
φ (*t*) p(*sex*+*t*)	179.90	25.10	0.00	16	26.06
φ (*sex*+*t*) p(*sex*+*t*)	182.00	27.20	0.00	17	25.88
φ (*sex***t*) p(.)	182.60	27.80	0.00	17	26.48
φ (.) p(*sex***t*)	182.95	28.16	0.00	17	26.84
φ (*sex*) p(*sex***t*)	184.63	29.84	0.00	18	26.22
φ (*sex***t*) p(*sex*)	184.83	30.04	0.00	18	26.42
φ (*t*) p(*sex***t*)	194.71	39.91	0.00	23	24.51
φ (*sex***t*) p(*t*)	194.82	40.02	0.00	23	24.62
φ (*sex*+*t*) p(*sex***t*)	196.97	42.18	0.00	24	24.37
φ (*sex***t*) p(*sex*+*t*)	197.08	42.29	0.00	24	24.48
φ (*sex***t*) p(*sex***t*)	209.82	55.03	0.00	30	22.31
B — All individuals, 363 nestlings, 100 adults (268 individual*years, including 86 individual*years for individuals marked as nestlings), ĉ = 2.934					
φ (*age*) p(age_3)	**288.55**	**0.00**	**0.29**	**5**	**31.62**
φ (*age*) p(.)	**289.13**	**0.58**	**0.21**	**3**	**36.25**
φ (*age*) p(*age*)	**289.69**	**1.14**	**0.16**	**4**	**34.79**
$φ_{ad}(.)φ_{juv}(T)$ p(.)	290.64	2.09	0.10	4	35.73
φ (age_3) p(.)	291.01	2.46	0.08	4	36.11
φ (*age*+*T*) p(.)	291.05	2.50	0.08	4	36.15
φ (*age***T*) p(.)	292.13	3.58	0.05	5	35.20
$φ_{ad}(.)φ_{juv}(t)$ p(.)	293.95	5.40	0.02	6	34.98
φ (.) p(*age*)	296.95	8.40	0.01	3	44.07
φ (*age*) p(*t*)	298.25	9.70	0.00	9	33.12
φ (*age*+*t*) p(.)	300.76	12.21	0.00	10	33.57
φ (*age*) p(*age*+*t*)	301.33	12.78	0.00	11	32.07
φ (*age*+*t*) p(*age*)	301.49	12.94	0.00	11	32.22
φ (*age*) $p_{ad}(.)\ p_{juv}(t)$	303.35	14.80	0.00	11	34.09
φ (.) p(.)	306.90	18.35	0.00	2	56.05
φ (*age***t*) p(*age***t*)	363.10	74.55	0.00	43	23.82

Fig. 2. Model-averaged estimates of local survival probabilities per year, illustrating the stability throughout the study period, the weak difference between sexes, and the low local survival of juveniles. Error bars represent 95% confidence intervals (upper bound for females, lower bound for males). No juvenile was marked after 1995.

of first and second broods). This resulted in a $\lambda_{no\ immig.}$ of 0.960, indicating that, without immigration, this population should have been decreasing (Fig. 1). To achieve the observed stability of the population size (mean annual $\lambda_{obs.}$ for the period 1991–1999 = 0.998), the immigration rate ω is computed to be 0.039, corresponding to 2.1 immigrants per year, or 7.3% of the annual recruits being immigrants. The annual recruitment rate R was 0.536. The growth rate of the population size was equally sensitive to a 1% change in juvenile local survival, number of fledglings per successful nest, adult local survival or reproductive success (respectively, 43.5, 43.5, 40.5 and 39.5% of change of $\lambda_{with\ immig.}$) but relatively insensitive to a 1% change in immigration rate (3.4%).

Local dispersal between nest sites

The local dispersal of adults between consecutive breeding events (i.e., between nest sites within the study area) was lower in males than in females ($F_{1,48}$ = 6.7, p = 0.013). The mean distance between nests used in consecutive years was 78 ± 49 m for males (median: 70; 10–90% quantiles: 20–150 m, maximum: 300 m; n = 24), and 259 ± 274 m for females (median: 150 m; 10–90% quantiles: 25–600 m, maximum: 1200 m; n = 26). The local natal dispersal of yearlings (i.e., the distance between their birth nest and their first nest as adults) did not differ significantly between sexes ($t_{22.1}$ = -1.37, p = 0.184): 583 ± 321 m for males (median: 580 m; 10–90% quantiles: 170–1000 m; maximum: 1220 m; n = 13) and 436 ± 249 m for females (median: 380 m; 10–90% quantiles: 200–860 m; maximum: 1100 m; n = 17).

DISCUSSION

Normal adult local survival

In our coastal, apparently geographically isolated population of Northern Wheatear, the local annual survival rate of adults (0.463) was the same as for the Scottish, island population (0.477, Seward et al. 2013), but it was lower than for food-supplemented adults in the Scottish population (0.528, Seward et al. 2013) and for adults from Dutch populations (0.543, after excluding a low survival rate for females highly exposed to predation, van Oosten et al. 2015). Our estimate also falls in between average estimates for 'bad' (0.366) and 'good' (0.525) habitats for the Swedish population (Arlt et al. 2008, Low et al. 2010). All these estimates are supposed to be close to true adult survival rate because of the large study area with the use of a buffer zone (60 km^2; Arlt et al. 2008, Low et al. 2010), or because of population isolation and high adult philopatry (Seward et al. 2013, van Oosten 2015). The rate observed at our site is 3 to 15% lower than in other stable or 'good habitat' populations, suggesting that local habitat was good, although not ideal, for the species. Considering that Swedish and Scottish populations were stable with an average local adult survival rate very close to the one observed in our study population, the adult survival rate can be considered as sufficiently high to secure population stability at our study site (given that fecundity was high; cf. hereafter). Faithfulness of adults to their former breeding site is the rule in many birds, including migratory species (Greenwood & Harvey 1982, Ward 2005). As our study site was 60 times smaller than the Swedish study site, surviving adults were much more faithful to their breeding population than in Sweden. Between-year median dispersal distances were short (70 and 150 m for males and females, respectively), markedly less than in the Swedish population (308 m and 352 m, respectively; Arlt & Pärt 2008). This breeding dispersal pattern supports a high fidelity of experienced breeders to our study site. Adult annual survival rates of both sexes were very close (0.449 for females, 0.480 for males). The observed difference in survival (6.5% lower for females than for males) is intermediate between the difference for the Scottish population (2.1%, Seward et al. 2013) and for the Swedish (16%, Low et al. 2010) and Dutch populations (12.1%, 15.1%, 36.8%, van Oosten et al. 2015). Lower survival of females is attributed primarily to their higher exposure to predators during incubation, and a greater workload than males during the chick rearing period (Low et al. 2010, van Oosten 2015, van Oosten et al. 2015). Hence, female predation at nest and/or habitat-dependent female work load were not a problem in our population, indicative of a relatively good habitat for female survival. Overall, during the period of population stability, there was no indication that our study population suffered from unsustainably high mortality or emigration rates of local breeders.

High juvenile local survival

Annual, local survival probability of juveniles (0.215), i.e. resulting from first-year survival and natal philopatry, was particularly close to the estimate for the isolated, island Scottish population (0.184, Seward et al. 2013), and was somewhat smaller than for the Swedish (weighted mean across habitat types: 0.270, range: 0.168–0.316, Arlt et al. 2008) and Dutch populations (0.306, van Oosten et al. 2015). Knowing that local juvenile survival rate in migratory species is usually less than 0.05 (Weatherhead & Forbes 1994, Ward 2005), these estimates suggest that natal philopatry is particularly high for studied populations of Northern Wheatears. But these high rates of natal philopatry may have different explanations. The Swedish study area was large (60 km^2) and stratified (core, central area of 8 km^2) so that most dispersal events occurred within the study area (Arlt et al. 2008). Hence, at this site, juvenile survival was close to true juvenile survival rate. At the contrary, for other populations, the high proportion of returning yearlings would better be explained by geographical isolation: returning yearlings would have had limited opportunities of settling elsewhere than in their natal population (Seward et al. 2013, van Oosten et al. 2015). Note again that our study area was 60 times smaller than the Swedish study area, whereas the local juvenile survival rate was only 1.26 times lower. Such an increased natal philopatry in case of geographic isolation is well known from remote island populations, where dispersal is strongly counter-selected (Bowler & Benton 2005, Bonte et al. 2012), and has also been suggested in some bird metapopulations (Schaub et al. 2006, Wilson & Arcese 2008, Foerschler et al. 2010). Overall, the high local juvenile survival rate, particularly for a migratory species, supports that our study population was likely to be geographically isolated, although the proportion of emigrants and/or juvenile mortality was higher than in remnant, Dutch populations.

The age-dependence of resighting probabilities suggests that it was difficult for yearlings to acquire a good territory, and to have a good reproductive success, potentially because of the competition with elder adults (Pärt 2001a,b). Yearling and second-time breeders had a lower resighting probability (0.583) than older adults (0.873; also observed by D. Arlt in litt., van Oosten et al. 2015, but not in Seward et al. 2013). Note that the true difference must have been even larger since the 'older adult' class included some yearlings (see Methods). If this difference in resighting probability is due to temporary emigration (i.e., $p = 0$), it means that 33% of these young adults had not settled yet on the study site during their first and second years of breeding. Conversely, if these birds were actually present in the study area (i.e. $p > 0$), they must have exhibited a reproductive behaviour different from older individuals, making them less prone to be resighted. A greater rate of nest failure than for older adults (Arlt et al. 2008), resulting in floating behaviour (Pärt et al. 2011) and earlier post-breeding dispersal (Arlt & Pärt 2008), could potentially explain this reduced resighting probability for younger adults.

Normal fecundity

Reproductive performances were very similar between our population and other studied populations (Ollivier 1997, Arlt et al. 2008). Reproductive success of first broods (i.e., the proportion of broods producing fledglings) was estimated at 69% (Ollivier 1997) versus 73% in other studies (weighted average across habitat types from estimates in Arlt et al. 2008; 71% in Pärt 2001a; 53–75% in Buchmann 2001 for German populations). In our population, 25% of pairs laid a second brood, in line with other populations at the same latitude (Conder 1989; 30–60% in van Oosten et al. 2015), whereas second broods were rare in Sweden (Arlt et al. 2008). Mean number of fledglings per successful breeding attempt were 5.17 and 3.58, respectively for first and second broods, resulting in a mean annual female fecundity of 4.63 fledglings. In Dutch populations, the mean number of fledglings per successful nest (3.98–4.50) and annual female fecundity (3.21–3.74) were markedly lower (van Oosten et al. 2015). The demographic balance of our population was similar to that of the isolated, island Scottish population, and differed from Dutch populations by its high fecundity that almost compensated for slightly lower juvenile and adult survival rates. All these isolated or remnant populations had an equal sensitivity of the population growth rate to reproductive and survival parameters (Seward et al. 2013, van Oosten et al. 2015, present study), the sensitivity of the population growth rate to fecundity parameters being higher than in the large, inland Swedish population (elasticities in the range 40–44% versus 6–29% in Arlt et al. 2008). Overall, there was no indication of a poor reproductive output in our population.

Very low immigration

The proportion of recruits per year compensated adult mortality, with 54% of new breeders per year. But only 7% of these recruits (2.1 individuals per year) would have been immigrants, i.e. born in other populations. This immigration rate did contribute to the stability of population size (Fig. 1), but it was so low that its influence on the population growth rate (elasticity) was 10 times smaller than for other demographic parameters. Indeed, over the study period (1990's), the regional population size of Northern Wheatears halved, what reduced the number of potential immigrants. This low immigration rate is surprising for a migratory species that could prospect much more, and more distant, sites than sedentary species (Ward 2005). Out of available estimates of annual immigration rate for small and medium-sized birds (Table 2), our estimate is indeed the lowest (0.039), corresponding to one immigrant for every 12.8 breeding pairs in year *t*-1. In the three remnant Dutch wheatear populations, immigration was higher (van Oosten et al. 2015). Dutch coastal populations received 4.3 and 8.6 immigrants per year, respectively, what represented a major source of recruits (ω = 0.315 and 0.192), and was responsible for population growth. And the most isolated, inland population still received 5.6 immigrants per year (ω = 0.173), although this immigration was insufficient to halt population decline due low fecundity and female survival. The next lowest value of immigration rate was for a ca. 30-pair, isolated population of Little Owl *Athene noctua*, that ultimately became extinct (Schaub et al. 2006). Despite drastic, geographic isolation, the Swiss population of migratory Eurasian Hoopoe *Upupa epops* that thrives at 250–350 km from the nearest population of similar size, maintained a immigration rate 7 times higher than in our population (Schaub et al. 2012). All other estimates (Table 2; see also Ward 2005) concur to suggest that immigrants usually constitute an important fraction of adult population size (ω range: 0.12–0.56; Table 2), with a relative contribution of immigration to population growth equal to, or even higher than, that of local recruitment. In our population, geographical isolation combined with rapid regional decline of the species (nearest population at 12–30 km; Ollivier 2009) would have led to a particularly strong shortage of immigrants, as observed in other highly isolated bird populations (Ward 2005, Schaub et al. 2006, Wilson & Arcese 2008; with the exception of hoopoes in Schaub et al. 2012).

CONCLUSION

The potential demographic weaknesses of our population would have been its small population size and geographic isolation, resulting in an extremely low number of immigrants per year and the consequent strong dependence on local recruitment. This isolation would have prevented the population from being rescued by immigration in case of local demographic or environmental accident. Between 2003 and 2006, during the abrupt, linear decline of the number of breeding

Table 2. Estimates of annual immigration rates (ω) for small to medium-sized birds. Ranges report the extent of variation between populations (minimum, maximum) for multi-site studies. Apart from Little Owl and Willow Tit, all species are long-distance migrants. Methods for estimating the immigration rate can be inference from local demographic parameters ('inferred', Schaub et al. 2006) or the use of integrated population models ('IPM', Abadi et al. 2010).

Species	ω	Method	Reference
Northern Wheatear *Oenanthe oenanthe*	0.04	Inferred	Present study
Little Owl *Athene noctua*	0.16 (0.09, 0.29)	Inferred	Schaub et al. 2006
Red-backed Shrike *Lanius collurio*	≥ 0.20	Inferred	Hemerik et al. 2015
Willow Tit *Poecile montanus*	0.22	Inferred	Lampila et al. 2006
Eurasian Wryneck *Jynx torquilla*	0.25	IPM	Schaub et al. 2012
Northern Wheatear *Oenanthe oenanthe*	0.26 (0.17, 0.40)	IPM	van Oosten et al. 2015
Eurasian Hoopoe *Upupa epops*	0.28	IPM	Schaub et al. 2012
Golden-cheeked Warbler *Setophaga chrysoparia*	0.33	IPM	Duarte et al. 2015
Red-backed Shrike *Lanius collurio*	0.43 (♂), 0.56 (♀)	IPM	Schaub et al. 2013

pairs (Fig. 1), the population lost on average 13 individuals per year. According to our computations, a complete cut-off of immigration and the trend for a reduced adult survival would have accounted for a loss of only 4.3 individuals per year. An additional disturbance must have directly affected the study population between the end of our study (1999) and 2004. Rabbit density and vegetation cover did not markedly change. The only change we can think of is the increase in frequency of spring or summer droughts, starting with a historical heat wave in the year 2003 (Jiguet et al. 2011), which could have reduced habitat suitability for wheatears. The sudden decline in population size could also be due to the specialization of a local predator on wheatears (van Oosten 2015), or degrading wintering conditions, but we do not have any element to discuss the plausibility of these alternative hypotheses.

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STRESZCZENIE

[Niska imigracja i wysoka lokalna rekrutacja w izolowanej populacji białorzytki]

Zachodnioeuropejskie populacje białorzytki zmniejszyły się o połowę w ciągu ostatnich dwóch dekad. W kontekście coraz bardziej rozproszonych populacji, kluczową kwestią jest zrozumienie roli imigracji w ich utrzymaniu.

W pracy scharakteryzowano parametry demograficzne: przeżywalność, rozrodczość, rekrutację i imigrację w niewielkiej (22–27 par lęgowych), izolowanej geograficznie populacji białorzytki. Badania prowadzono w latach 1991–1999, w okresie stabilnej liczebności populacji (Fig. 1), gdy populacja na poziomie regionu dość szybko malała. Dorosłe i młode były indywidualnie znakowane, w kolejnych sezonach poszukiwano ich w terenie, aby na tej podstawie określić ich powracalność i przeżywalność. W analizach przeżywalności uwzględniono m.in. płeć i wiek ptaków oraz rok obserwacji (Tab. 1).

Roczną lokalną przeżywalność dorosłych oraz młodych oszacowano odpowiednio na 0,463 ± 0,052 i 0,215 ± 0,054. Przeżywalność ptaków dorosłych była podobna dla obu płci i nie różniła się między latami (Tab. 1, Fig. 2). Oszacowano także, że w badanym okresie do populacji włączało się 2,1 imigranta na sezon (co stanowi 7,3% wszystkich rekrutów). Wyliczony roczny wskaźnik imigracji (0,039) jest niższy niż wszystkie szacunki dostępne do tej pory dla 14 gatunków małych i średniej wielkości ptaków (Tab. 2). Dystans dyspersji lęgowej w obrębie badanej populacji był niewielki i różnił się pomiędzy płciami.

Przeżywalność zarówno dorosłych, jak i młodych osobników była niższa niż stwierdzana w populacjach zamieszkujących siedliska wysokiej jakości, ale była ona kompensowana wysoką rozrodczością i imigracją. Uzyskane wyniki sugerują, że badana populacja gniazdowała w siedlisku umiarkowanej jakości i była odizolowana od innych populacji, przez co nie miała szans na odbudowę w przypadku zdarzeń losowych. W istocie, populacja ta zanikła w roku 2000 roku, z nieznanych bliżej powodów (Fig. 1).