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Site-specific dynamics in remnant populations of Northern Wheatears *Oenanthe oenanthe* in the Netherlands

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Dynamics of populations may be synchronized at large spatial scales, indicating driving forces acting beyond local scales, but may also vary locally as a result of site-specific conditions. Conservation measures for fragmented and declining populations may need to address such local effects to avoid local extinction before measures at large spatial scales become effective. To assess differences in local population dynamics, we aimed to determine the demographic drivers controlling population trends in three remaining populations of the Northern Wheatear *Oenanthe oenanthe* in the Netherlands, as a basis for conservation actions. An integrated population model (IPM) was fitted to field data collected in each site in 2007–2011 to estimate fecundity, survival and immigration. Sites were 40–120 km apart, yet first-year recruits were observed to move between some of the sites, albeit rarely. All three populations were equally sensitive to changes in fecundity and first-year survival. One population was less sensitive to adult survival but more sensitive to immigration. A life table response experiment suggested that differences in immigration were important determinants of differences in population growth between sites. Given the importance of immigration for local dynamics along with high philopatry, resulting in low exchange between sites, creating a metapopulation structure by improving connectivity and the protection of local populations are important for the conservation of these populations. Site-specific conservation actions will therefore be efficient and, for the short term, we propose different site-specific conservation actions.

Keywords: elasticity, fecundity, immigration, integrated population model, life table response experiment, survival.

Many threatened bird species occur in small populations scattered throughout a fragmented landscape. With decreasing population size, population persistence decreases (Gilpin & Soulé 1986) and, in dispersive animals, small populations sometimes persist only in the presence of a large source population or as part of a metapopulation (Hanski & Ovaskainen 2000).

Evaluating population dynamics for conservation management requires high-quality data on the demographic parameters that could be important determinants of population viability: breeding numbers, reproductive success, sex- and age-specific survival and dispersal (Ricketts 2001). Assessing which vital rates drive population

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dynamics constitutes an important step towards proposing informed conservation measures, and the spatial scale at which they operate (Caughley 1994, Schaub *et al.* 2012).

Dynamics of populations may be synchronized at large spatial scales, indicating driving forces acting beyond the scale of local sites (Blasius *et al.* 1999, Koenig 1999, Lande *et al.* 1999, Kendall *et al.* 2000, Paradis *et al.* 2000, Liebhold *et al.* 2004, Abbott 2011). However, synchrony in population dynamics decreases with decreasing population size, due to increasing demographic stochasticity (Sæther *et al.* 2007, 2011). Therefore, whereas populations of common species follow the waves of synchronized large-scale stressors (Koenig 2002, Sæther *et al.* 2011), rare species, which often occur in small and isolated populations, may require conservation interventions at a more local scale. Vital rates may be affected differentially at local scales due to site-specific conditions.

Knowing the underlying causes for large-scale population fluctuations (e.g. climate change) is important for developing long-term and international conservation strategies, but it might be equally important, and perhaps more effective in the short term, to identify the vital rates that drive local population growth, and how local populations interact (Pulliam 1988). This allows the development of evidence-based and tailored measures to safeguard local populations in the short term until positive effects of long-term, large-scale measures have become effective. Hence, to safeguard rare and localized species at a large geographical scale, it may well be necessary to identify the demographic bottlenecks of remaining local populations. Preferably, studies aimed at understanding drivers of short-term local dynamics and of long-term large-scale dynamics should be undertaken jointly to allow for effective preservation of species. However, finding the appropriate spatial scale for such conservation studies is challenging (Petranka *et al.* 2004, Schaub *et al.* 2006). One way is to include several local populations that differ in size and degree of isolation (Schaub *et al.* 2006).

The Northern Wheatear *Oenanthe oenanthe* occurs in the Netherlands in small and fragmented populations. This migratory passerine is one of the most rapidly declining breeding birds in Europe (Gregory *et al.* 2009). Since 1990, the European population has declined by over 50% (PECBMS 2012) and numbers in the Netherlands have dropped by at least 80%, from 1900–2500 breeding pairs in the 1970s to 250–290 pairs in 2011 (SOVON 2002, Boele *et al.* 2012). The species now appears on the Dutch Red List of Threatened Species. We collected data on population size and demography in three remaining populations of the species in the Netherlands, together holding almost half of the national population. The aim of the present study was to determine which demographic parameters most strongly influenced recent local population growth, as a basis for conservation actions.

We estimated vital rates (fecundity, first-year and adult apparent survival and immigration) for all three local populations by fitting an integrated population model (IPM) to field data. For each population, we performed an elasticity analysis to assess how sensitive the local population growth rate was to changes in vital rates (Jongejans & De Kroon 2005). In this way, we assessed how much the population growth rates would change if each of the vital rates was changed by a given percentage. We complemented these analyses by exploring which demographic processes drive differences in average growth rate between the populations by decomposing these into the contributions of each vital rate in a life table response experiment (LTRE; Caswell 2001) in order to determine how much each of the parameter differences contributed to the difference in population growth rates between the three sites.

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 & Bauer 1988). In lowland western Europe, numbers have been declining since the 1980s (Burfield & van Bommel 2004). Once widespread in rural areas, Northern Wheatears have all but disappeared due to agricultural intensification (Glutz von Blotzheim & Bauer 1988). For a variety of reasons, populations in (semi-) natural areas are under pressure as well.

In the Netherlands, Northern Wheatears were widely distributed until the 1980s (SOVON 2002) in sandy, oligotrophic grasslands in coastal dunes and heathlands, where they often bred in burrows of Rabbits *Oryctolagus cuniculus*. The demise of the Dutch population has been attributed to declining Rabbit populations as a result of viral disease.

Regional differences in the onset of the Northern Wheatear decline seem to be correlated with differences in the timing of Rabbit declines, with a delay of 5–10 years (Van Turnhout *et al.* 2007). Being morphologically adapted to foraging on short field layers (Kaboli *et al.* 2007), Northern Wheatears faced a deterioration of foraging habitat through grass encroachment in the absence of Rabbits. In addition, large expanses of breeding habitat were lost due to eutrophication and acidification, which stimulated growth of tall grasses, a threat to many oligotrophic systems (Bobbink *et al.* 2010). As such, the Northern Wheatear is an indicator of the quality of oligotrophic grassland and heathland ecosystems, and representative of several other ground-nesting and ground-foraging bird species (Van Turnhout *et al.* 2010).

Between 2007 and 2011, we studied three populations of Northern Wheatears in the Netherlands. The inland population at Aekingerzand (site A, 268 ha) is about 140 km from the other two populations. The coastal population at Castricum (site C, 74 ha), present for over 200 years (Nozeman 1789), is separated by 40 km from the coastal population at Den Helder (site D, 160 ha). Populations C and D breed within 1 km of the sea in coastal dunes with vegetation dominated by grasses (*Calamagrostis epigejos*, *Ammophila arenaria*), *Carex arenaria*), low scrub (*Salix repens*, *Hippophae rhamnoides*), mosses, lichens, characteristic forbs such as *Viola curtisii* and with scattered patches of vegetation-free ground. Population A breeds in heathland with drift sands. This site was previously largely forested but was restored from the 1990s by large-scale removal of trees, scrub and, locally, the upper soil layer. All sites are managed as nature reserves, and access by the public is limited to paths and roads (most restricted in D).

Long-term Northern Wheatear population trends differ strongly between sites: after large-scale removal of trees, breeding numbers (determined as the number of territorial females) at site A increased from 2–5 to 30. However, numbers in site C decreased from 165 in 1988 to 34 in 2000 and numbers in site D have fluctuated without a clear trend between 1992 and 1998 (min–max 45–69, data SOVON).

Population census and fecundity

We collected annual data on population sizes, fecundity and sex-based survival at all sites. Breeding success was not quantified for site D in 2010. Data on population size and fecundity were obtained by intensive searching for territory-holding and nesting pairs throughout the breeding season (April–July) in order to establish the number of territories, number of broods and reproductive output of individual nesting attempts. Northern Wheatears regularly produce replacement or true second broods at our study sites (Table 1). Nests were found during construction or at the egg stage by closely observing females. Nests with nestlings were easily found by following feeding parents. Nests were visited several times during a breeding attempt, with a minimum of two visits (census including ringing of nestlings and post-fledging check for dead chicks or unhatched eggs). The number of nests monitored each year was 32–67 at site A, 21–40 at site C and 33–82 at site D.

In nests situated deep inside Rabbit burrows, nest stage (nest building, eggs, young) was determined using an infra-red camera mounted on a stick, connected to a hand-held screen. Nestlings in deep nests were counted and ringed either by carefully shortening the burrow (which never resulted in abandoning the nests) or, rarely, when they appeared outside the burrow. The nest was subsequently excavated to check for any dead chicks or eggs. Families were followed after leaving the burrow to determine the presence of any unringed, and hence missed, juveniles to determine the number of fledglings. These nestlings were captured using spring-traps.

When about 10 days old, nestlings start to walk in the burrow and hence they could be out of reach at the moment of ringing. To avoid missing juveniles, we ringed most nestlings between age 5 and 9 days. As the populations were small and Northern Wheatears are easily detected, we were

Table 1. Mean annual predation rates (sd given in parentheses) by Red Foxes *Vulpes vulpes*, and re-nesting for sites A and C.

	Site A	Site C
% Predation of all nests	21.6 (14.5)	21.5 (25.0)
% Females predated	12.2 (13.8)	0
% Replacement/2nd broods	30.0 (16.6)	61.4 (6.3)

Predation at site D was rare. On average, nest predation rates by Red Foxes were equally high (22%) but females were often predated as well during a predation event at A but not at C. Predation at site C was not observed in 2008 and 2009, but greatly increased in later years.

able to determine the number of breeding females precisely. Even if successful nests were not found, they were found soon after fledging, as family groups are conspicuous and unlikely to be missed. Yearly, up to two nests were found after fledging across populations. To determine possible predation rates in our populations, we counted the numbers of predated nests and number of predated females, i.e. females not observed following a nest predation event. Unsuccessful females were not easily missed, as visits were frequent and most birds were colour-ringed: the nesting stage was known approximately for each female, and unexpected behaviour (e.g. a female spending time above ground when she was expected to be brooding, or spending time off territory) was followed by a nest check.

Capture-mark-recapture study

In 2007–2010, we individually colour-ringed 404 birds at site A (327 juveniles or nestlings and 77 adults, ≥ 1 year old), 245 at site C (221/24) and 666 birds at site D (538/128), in total 1315 birds. Most adults had already been ringed as nestlings, which explains the low numbers ringed. The sex of ringed nestlings was unknown, but all adults were sexed on the basis of plumage characters (Glutz von Blotzheim & Bauer 1988). Resightings were obtained by dedicated weekly searches in each site during the entire breeding season using telescopes. Resightings in 2007–2011 were used to estimate adult and first-year survival and movements between sites, with inclusion of occasional reports by birdwatchers from the rest of the Netherlands (Elsewhere, ‘site’ E). Most suitable breeding areas in The Netherlands, apart from our study sites, are surveyed annually as a part of the national breeding bird monitoring programme (Boele *et al.* 2012).

Integrated population model

We developed an IPM for the three populations to estimate demographic variables driving local population dynamics, including immigration, from the joint analysis of population counts, breeding success and capture-mark-recapture data. The ability to estimate immigration rates is a huge advantage of IPMs (Abadi *et al.* 2010), as immigration may be a very important variable from a conservation perspective (Schaub & Abadi 2011). The model was based on the IPM developed by Schaub *et al.* (2012). Model parameters were estimated using Monte Carlo Markov chains (MCMCs) in JAGS (Plummer 2003), derived from a script in R (R Development Core Team 2012). Three chains were run for 30 000 iterations each. After a burn-in of 10 000 iterations, every 10th remaining iteration was sampled to estimate the posterior distributions, which we summarized by their mean, standard deviation (sd) and 95% credible intervals. We used uninformative priors for all parameters, with the exception of sampling error of the count data, for which we provided a very narrow variance. The JAGS code is given in Appendix S1, and the IPM equations in Appendix S2.

The IPM described a pre-breeding census for each of the three sites A, C and D. The model did not incorporate direct movements between these populations, as a multistate formulation of the CMR likelihood would make it much more complex. Movements between sites were very rare. However, the IPM estimated the annual immigration rate (immigrants per female present in year $t - 1$) from the joint data. The (absolute) number of immigrants was specified by a Poisson distributed variable, with mean equal to the product of the number of females present in the previous year and the estimated immigration rate. These immigrants probably originated from populations other than those studied, possibly outside the Netherlands. Emigration was not modelled explicitly, but was included in the estimates of apparent survival rates. The IPM incorporated two age-classes: 1-year-old birds that all started breeding at this age, and older birds, for each population. Immigrants formed a third class, of unknown age (≥ 1 year). Fecundity and survival were assumed to be identical for both breeding age classes, but first-year (juvenile) survival was estimated separately. A sex ratio of 1 : 1 was assumed and the female population was modelled. Occasionally, polygynous males were found in our populations, but these were not incorporated in our female-based models.

The population size data entered in the model were the annual numbers of territory-holding and breeding females in the three sites. We modelled these assuming Poisson-distributed errors. In contrast to the IPM of Schaub *et al.* (2012), we did not use a hierarchical formulation for the demographic rates, as we considered that a 5-year study (resulting in four annual estimates) was too short reliably to separate process and sampling variation.

Fecundity (*f*) was defined for each site and year as the total number of fledged young produced per territorial female. We further decomposed this estimate into contributions of first and second clutches as

$$f = \frac{\mu_1 \times n_1 + \mu_2 \times n_2}{N}$$

where μ_1 and μ_2 are the mean number of fledglings per successful nest of first and second clutches, respectively, n_1 and n_2 the number of successful first and second clutches, and N the number of estimated territorial females. Mean number of fledglings per successful nest was estimated assuming a log-linear relationship to site, year, clutch number (first or repeat clutch) and all pairwise interactions, assuming Poisson errors. For all sites and years, the numbers of successful first and second clutches were assumed to be fixed quantities. For site D in 2010, these numbers were not available and were instead assumed to be stochastic quantities, which we estimated from the relative numbers of first and second clutches in the remaining years in D, as

$$\mathrm{P}(\text{first clutch}|n_1, n_2) \sim \text{Binomial}(B, p)$$

where B represents the number of successful broods for site D in 2010, p represents the probability that a clutch in our dataset is a first clutch, and $(1 - p)$ the probability that it is a second clutch. This allowed us to estimate n_1 and n_2 for 2010 at site D and proceed with the above equation.

We used CMR data in combination with a Cormack-Jolly-Seber model using the m-array formulation (Williams *et al.* 2002) to estimate apparent survival rates. As we were interested in possible sex differences in survival, but the sex of ringed juveniles was unknown and only those that survived could be sexed later when resighted as adults, juvenile and (sex-specific) adult survival rates were estimated from different subsets of the CMR data. First-year survival was estimated from the complete dataset, with a model including age but not sex effects on survival and resighting probability, whereas sex-specific adult survival rates were estimated from the subset of adult birds of known sex, treating the ringing event of birds ringed as adults and the first recapture as adults of birds ringed as juveniles (i.e. the first occasion on which their sex was assessed) as the first encounter. Recaptures of adults thus contribute to both sub-models, but only the adult survival and resighting rates from the second sub-model were included in the projection matrix of the IPM, and thus in the joint likelihood.

We performed prior analyses of the CMR data in program MARK (White & Burnham 1999) to identify the most parsimonious model structure (Burnham & Anderson 2002). For resighting rates, this structure included differences between yearlings and older birds, but no effects of site and year, except for a different value at site D in 2010 (lower due to less intensive fieldwork; Supporting Information Tables S1 and S5 for model selection and parameter estimation). The most parsimonious structure for adult survival included effects (with interactions) of sex and year, but not site, with the exception of a difference in survival for adult females between sites A and C/D. Survival rates of adult males did not appear in the projection matrix of the IPM, but were estimated anyway. The best model for first-year apparent survival included differences between years, but not sexes (as these were unknown) or sites (Tables S2 and S3 for model selection, Table S5 for parameter estimation). However, because we were interested in identifying which site-specific demographic variable was the most influential in driving the dynamics of each local population, we also extended this model structure to one with full site- and year-dependency in all vital rates, as well as sex- and age-dependency in apparent survival. This is almost equivalent to three separate local IPMs, with only the information on resighting probabilities being shared among sites. Convergence, as measured by the convergence diagnostic $\hat{r}$, was achieved for all parameters. The diagnostic $\hat{r}$ was 1.008 for fecundity at site A in 2007 and < 1.003 for all other parameters including the site-specific survival parameters (Gelman *et al.* 2002).

Demographic drivers of population change

To assess how annual population growth-rates are affected by proportional changes in the underlying vital rates, we calculated elasticities for vital rates (de Kroon *et al.* 2000, Caswell 2001). This prospective analysis does not reveal how the populations were affected by actual (realistic) changes in the vital rates, but shows how the populations would change if there was a future change in a demographic rate. To decompose the observed variability in population-specific growth rates as a function of variation in underlying vital rates, retrospectively, we additionally performed an LTRE (Caswell 1989). Performing prospective and retrospective analyses is worthwhile, as factors that govern annual changes and between-population differences are not necessarily the same (Gaillard *et al.* 2013).

Prospective analysis

For each population, we constructed projection matrices (Caswell 2001) parameterized with mean vital rates obtained from the IPM. The model structure is represented as:

$$\begin{bmatrix} n_j(t+1) \\ n_a(t+1) \end{bmatrix} = \begin{bmatrix} \phi_j \times \frac{f}{2} + I & \phi_j \times \frac{f}{2} + I \\ \phi_a & \phi_a \end{bmatrix} \begin{bmatrix} n_j(t) \\ n_a(t) \end{bmatrix}$$

where ϕ_j and ϕ_a denote the juvenile and adult mean yearly apparent survival, f the per-capita reproduction (fecundity) and I the per-capita immigration rate. From these models, we calculated and compared elasticity values between populations.

Retrospective analysis

We decomposed differences in population growth rates into contributions from differences in the vital rates between populations. We contrasted the projection matrices of the two populations to that of the best performing population, at site D, in an LTRE. For each of the $m = 4$ vital rates θ_m, we estimated the mean $\bar{\theta}_m$ and the difference d_m between each population (k) and the reference population D (*ref*).

$$\bar{\theta}_{m,k} = \frac{\theta_{m,k} + \theta_{m,ref}}{2}$$

$$d_{m,k} = \theta_{m,k} - \theta_{m,ref}$$

Next, based on $\bar{\theta}_k$, we estimated the asymptotic growth rate $\bar{\lambda}_k$, and its sensitivity $\bar{S}_{m,k}$, to each of the vital rates. Essentially, these sensitivities reflect the slope of the population growth rate to changes in the vital rate evaluated at the midpoint between the reference and each particular population.

The differences in population growth rates can be approximated by summing over the sensitivities $\bar{S}_{m,k}$, multiplied by the differences in vital rates $d_{m,k}$:

$$\lambda_k - \lambda_{ref} = \sum_m (d_{m,k} \times \bar{S}_{m,k})$$

where $C_{m,k}$ denote the contributions of each vital rate to the difference in population growth rate between each population and the reference population.

RESULTS

All results refer to estimations derived from the fully site-specific IPM, as we were primarily interested in site-specific differences in vital rates. The rather small population sizes and conspicuous behaviour of Northern Wheatears resulted in very high annual resighting probabilities for adult birds (posterior mean for all sites and years 0.97 ± 0.01, except for site D in 2010 0.85 ± 0.05) and for first-year birds that returned (posterior mean 0.95 ± 0.02, site D in 2010 0.74 ± 0.06). This enhances the precision of our estimates of apparent survival and contributes to the estimation of other demographic parameters, including immigration. Estimated population sizes closely resembled observed population sizes (Fig. 1).

Population sizes and vital rates

Numbers and trends

The three populations contained different numbers of breeding females, site A being intermediate with on average (± 1 sd) 37.12 ± 5.12 breeding females annually in 2007–2011, population C the smallest (16.88 ± 3.42) and site D the largest (57.63± 6.31). Mean annual growth rate was negative for A, largest for C and also positive for D (Table 2).

Fecundity

Annual fecundity differed between sites and years, being highest at site D and lowest at site A (Table 2). The 95% credible intervals for the difference between sites A and D did not contain 0 (−0.962, −0.089), indicating a significant difference in fecundity. Fecundity per successful nest was highest in site A (4.50), compared with 3.98 for site C and 4.34 for site D.

Survival

First-year survival was particularly variable between years, although averages per site were very similar. Survival of adult females was lowest at site A and highest at D, with C being

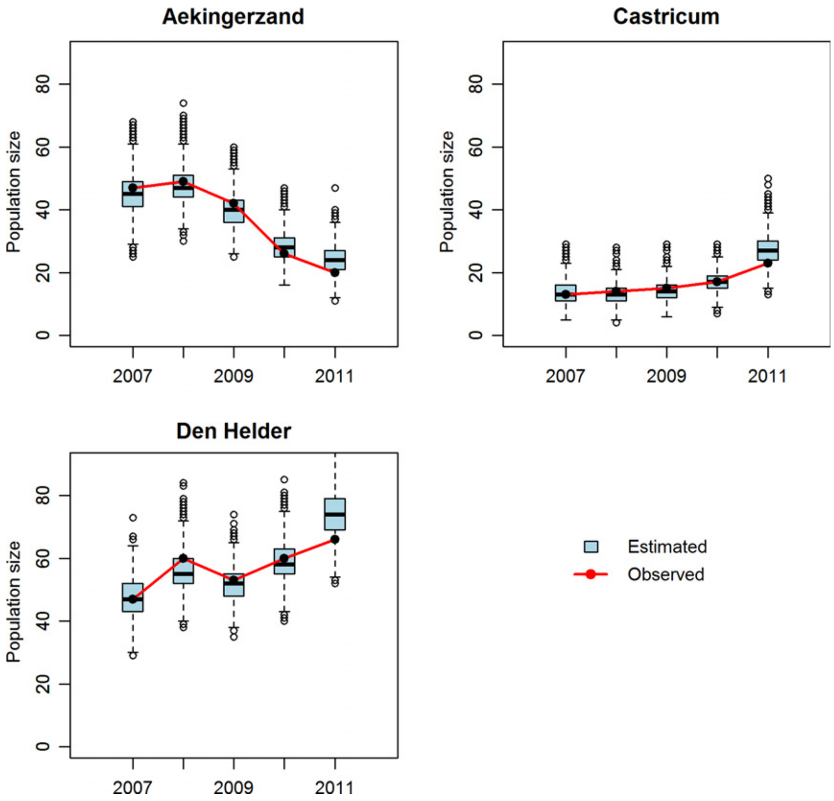

Figure 1. Population sizes (number of territorial females) in three study sites observed and estimated using IPM.

intermediate. Adult male survival was higher than adult female survival and variable between sites (Table 2). All 95% credible intervals included 0.

Immigration

The smallest population (site C) seemed to receive relatively more immigrants than sites A and D (Table 2). Average absolute numbers (± 1 sd) are 5.6 ± 2.2, 4.3 ± 0.8 and 8.6 ± 3.8 female immigrants annually at A, C and D, respectively. However, these estimates remain quite imprecise as a result of the lack of direct observational data; immigration rates were often close to 0, and nearly all 95% credible intervals for the estimated number of immigrants included 0.

Predation

Predation by Red Foxes *Vulpes vulpes* was frequent at sites A and C (Table 1) but only occasional (one to two events per year) at site D. Females were also regularly predated at site A but not predated at all at site C (Table 1). Of all predation events leading to nest failure, 81% were due to Red Foxes at site A. Other predators included mustelids (probably Stoat *Mustela erminea*), predation of females by Eurasian Sparrowhawks *Accipiter nisus* (rings found near nest) and even mites (Acari). At site C, predation by mice was suspected twice during 2007–2011, and predation by mustelids on three occasions.

Exchange between sites

Only nine colour-ringed birds (all juveniles) were observed to have moved from one site to another. Three moved from D, and one from C to the island of Texel. Five birds moved from D to C, indicating that there was emigration from D by juveniles. No movement between A and the other sites was observed, and no adults were found to have moved between sites.

Demographic drivers of population change

Prospective analysis

Population growth-rates were equally sensitive to proportional changes in fecundity and first-year

Table 2. IPM estimates for demographic parameters by site and year, and averages per site for all years.

	2007	2008	2009	2010	2011	Average
A (Aekingerzand)						
Population size	45.647 (5.968)	47.497 (5.722)	39.739 (5.087)	28.311 (4.312)	24.415 (4.491)	37.122 (5.116)
Fecundity	2.508 (0.266)	2.767 (0.276)	3.129 (0.307)	2.347 (0.318)	5.274 (0.533)	3.205 (0.340)
Female adult survival		0.662 (0.098)	0.372 (0.081)	0.275 (0.067)	0.296 (0.092)	0.401 (0.085)
Male adult survival		0.809 (0.121)	0.611 (0.080)	0.504 (0.073)	0.612 (0.071)	0.634 (0.086)
Juvenile survival		0.182 (0.054)	0.302 (0.041)	0.323 (0.038)	0.446 (0.050)	0.313 (0.046)
Immigration		0.218 (0.182)	0.155 (0.139)	0.113 (0.107)	0.206 (0.187)	0.173 (0.154)
Annual population change		1.055 (0.170)	0.846 (0.136)	0.721 (0.127)	0.877 (0.189)	0.875 (0.156)
C (Castricum)						
Population size	13.642 (3.317)	13.344 (3.03)	13.898 (2.905)	16.820 (3.160)	26.683 (4.690)	16.877 (3.420)
Fecundity	3.236 (0.514)	3.684 (0.523)	4.683 (0.564)	3.061 (0.433)	1.871 (0.283)	3.307 (0.463)
Female adult survival		0.274 (0.129)	0.469 (0.130)	0.401 (0.116)	0.697 (0.106)	0.460 (0.120)
Male adult survival		0.552 (0.146)	0.457 (0.145)	0.589 (0.136)	0.571 (0.116)	0.542 (0.136)
Juvenile survival		0.288 (0.066)	0.215 (0.051)	0.316 (0.049)	0.441 (0.055)	0.315 (0.055)
Immigration		0.445 (0.397)	0.396 (0.365)	0.357 (0.337)	0.414 (0.384)	0.403 (0.371)
Annual population change		1.032 (0.336)	1.088 (0.316)	1.254 (0.321)	1.628 (0.368)	1.251 (0.335)
D (Den Helder)						
Population size	47.245 (6.190)	55.911 (6.193)	51.953 (5.507)	58.617 (5.943)	74.399 (7.724)	57.625 (6.311)
Fecundity	3.921 (0.417)	3.546 (0.289)	3.432 (0.278)	3.810 (0.316)	3.971 (0.359)	3.736 (0.332)
Female adult survival		0.527 (0.081)	0.562 (0.067)	0.489 (0.072)	0.441 (0.070)	0.505 (0.073)
Male adult survival		0.576 (0.082)	0.418 (0.072)	0.680 (0.084)	0.626 (0.074)	0.575 (0.078)
Juvenile survival		0.192 (0.035)	0.181 (0.027)	0.360 (0.040)	0.425 (0.044)	0.290 (0.037)
Immigration		0.337 (0.238)	0.135 (0.123)	0.141 (0.126)	0.153 (0.138)	0.192 (0.156)
Annual population change		1.202 (0.2)	0.938 (0.125)	1.138 (0.145)	1.279 (0.159)	1.139 (0.157)

Values represent site-specific posterior means with standard deviation in parentheses.

survival at all three sites, whereas the growth rate at C was slightly less sensitive to proportional changes in adult survival than at A and D (Fig. 2a). Across populations, population growth rate appeared less sensitive to changes in immigration rate than to changes in fecundity and survival, but population C was almost as sensitive to changes in immigration rate as it was to adult survival (Fig. 2a). The asymptotic population growth rates predicted by projection matrices parameterized with the site-specific mean vital rates were 0.94, 1.39 and 1.17 for A, C and D, respectively. When immigration was removed, asymptotic population growth decreased to 0.78, 0.99 and 1.00, respectively.

Retrospective analysis

Since population D has been large and stable for many years, we used it as a reference for the other two sites. Survival was in general comparable across the three populations. The largest proportional differences between populations occurred in the per-capita reproduction rate, which was clearly lower at A than in the other populations. Site C was characterized by a relatively high immigration rate (Fig. 2b). Differences between the asymptotic growth rate of A and C compared with D were dominated by different demographic processes (Fig. 2c). The relatively high growth rate at site C appears to be largely due to immigration and, to a lesser extent, first-year survival. Fecundity and especially adult survival were lower compared with site D. The lower population growth rate at site A was mostly due to lower reproduction and lower adult survival. Immigration was comparable to D and contributed only marginally to population growth. First-year survival contributed little, but positively, to population growth. The summed absolute contributions per vital rate ($f = 0.15$, $\phi_j = 0.11$, $\phi_a = -0.19$, $I = 0.22$) indicate that, compared with population D, differences in immigration were important in contributing to differences in population growth between sites. These differences were similar to or greater in importance than differences in female survival or fecundity.

DISCUSSION

To provide a scientific basis for conservation measures on a national scale, we elucidated demographic bottlenecks for three populations of the threatened Northern Wheatear. By applying an

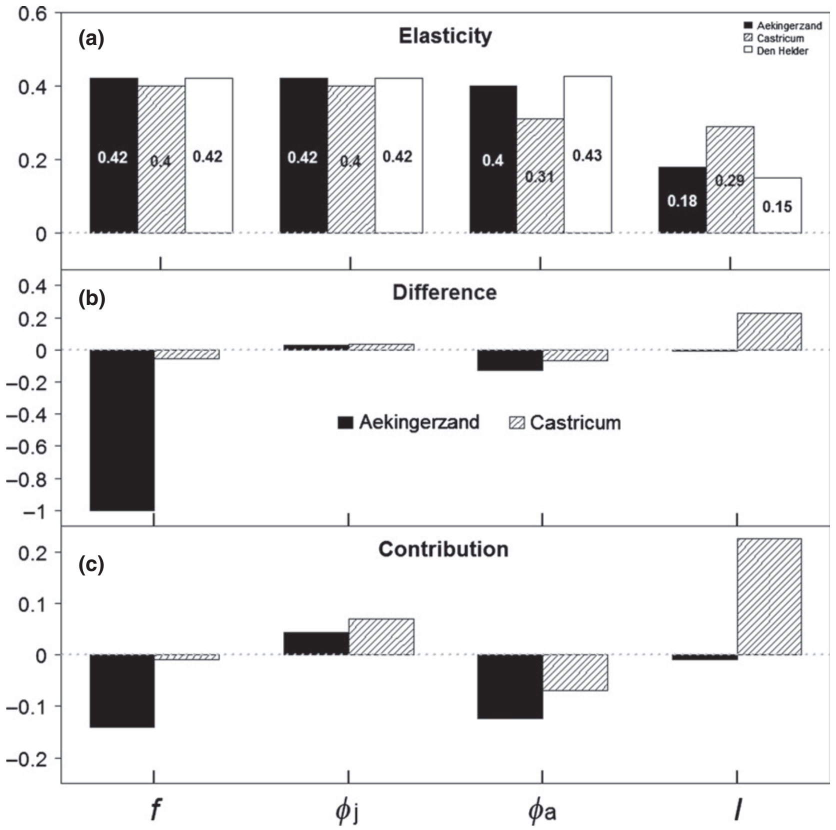

Figure 2. (a) Elasticities of asymptotic population growth rate to changes in fecundity (*f*), first-year survival (ϕ_j), adult survival (ϕ_a) and immigration rate (*I*). Bars include the corresponding value. (b) Absolute differences in vital rate estimates between populations A, C and reference population D. (c) Contributions of differences in vital rates to the difference in population-specific growth rates, between populations A, C and reference population D.

IPM we were able not only to estimate survival and reproduction but also to obtain estimates of immigration rates which, given the often scattered nature of contemporary populations, could well determine their viability (Ward 2005, Schaub *et al.* 2010, 2013), and were indeed found to be a factor of importance. The link with conservation management is direct: by combining an IPM with an elasticity and LTRE analysis we show that each population is sensitive to different vital rates, which may be most effectively altered by conservation measures. We show that to safeguard a large-scale (national) population, it is important to safeguard several local populations, each with its own dynamics, with tailored site-specific measures. Furthermore, as immigration contributes strongly to differences in population growth, connectivity between populations should be improved to enhance the likely viability of the populations (Hernández-Matías *et al.* 2013).

Variation between populations

The three populations differed in numbers, trends and vital rates. Moreover, the populations appeared to be controlled by different vital rates and functioned as either a sink or a source. As our fully site-specific model was not favoured over a reduced model with only partial site-effects on survival based on the DIC, estimated site differences should be interpreted with care, but most can be plausibly explained by differences in conditions at the sites.

Only the Aekingerzand (A) population showed a yearly decline during the study period. The LTRE indicated that low fecundity and below-average adult female survival contributed most to this poor performance. Nest predation by Red Foxes was frequent, which also led to predation of breeding females at this site. In spite of equally regular nest predation, no females were lost during such events at site C. At site C (and D, where nest predation occurs only occasionally) females bred in vacated burrows of Rabbits and could move deeper into the burrows during an attack by any predator. However, females at site A breed in shallow cavities among the roots of decaying trunks left after tree removal, and are trapped during a predation event. Given the strong population decline observed over the study period, we suggest that the habitat restoration project at this site created an ecological trap for Northern Wheatears: the short and sparse vegetation following tree removal is suitable for foraging and the decaying tree trunks provide plentiful, but dangerous, nesting sites.

Immigration becomes more important in small populations because the same number of immigrants will make a proportionally higher contribution to fluctuations in population size. Additionally, immigration is also important in conditions with lower than average fecundity and adult survival, as is the case for site A. However, the estimated immigration rates and elasticity to immigration were low compared with the other two sites. This might indicate that this inland population is more isolated than the coastal populations, which may prove to be connected to remnant populations on the Dutch Wadden Sea islands. The estimated six immigrant birds may well have originated from adjacent breeding sites in Germany, where small populations still persist (Stiftung Vogelmonitoring Deutschland & DDA, in preparation).

The coastal dune population near Castricum (C) is the smallest of the three, but showed the strongest population growth during the study period. The LTRE analysis suggested that immigration is the main explanation for the higher population growth of C than the other populations. Population C would be very vulnerable to stochastic events without immigration, due to its small size and area of suitable habitat. Although the estimated mean annual number of immigrants was only four, the population is more sensitive to immigration than populations A and D and would not have grown without these immigrants. Despite similar mean nest predation rates at A and C, replacement or second clutches were twice as common at C. Perhaps the high incidence of females predated by Red Foxes precludes production of repeat clutches at A, whereas females were rarely predated at C. The relatively large population at Den Helder (D) escaped the 1990s decline of Rabbits and has been stable for many years (SOVON). D had the highest average fecundity of the three populations. Therefore it could potentially function as a source population for adjacent coastal dune areas. Indeed, population D supplied site C with emigrant birds almost annually, despite there being 40 km between the two sites.

Conservation implications

The fact that all three populations appeared to have their own independent population dynamics has important ramifications for conservation interventions at larger scales. As such, this study may serve as a case study for the many other species that occur in small and often isolated populations. Importantly, we show that dispersal between remaining breeding populations was rare. This may mean that recolonization of sites where the species has become locally extinct will be a slow process. The importance of immigration for small populations was emphasized by the fact that differences in immigration rate contributed the most to differential population growth rates in our study.

Our study further shows that even if measures that cope with large-scale stressors are translated into practical conservation actions, these may be too late or too general for small populations and those with differential demographic bottlenecks. This is particularly true in populations that exhibit a high degree of natal and breeding philopatry. Elucidating demographic bottlenecks for several populations provides opportunities to implement measures that may be effective in the short term. We emphasize the importance of conserving small, relict populations which may, or may not, be connected by mutual migration. Designing conservation plans for several populations requires more extensive funding and time budgets. Indeed, it would be most efficient to plan specific conservation strategies for species at the very onset of decline, when populations are still relatively robust to stochasticity and are more densely spaced, which may allow more frequent migration between sub-populations.

As an illustration of how local demographic studies can result in tailored conservation measures, we briefly present actions to safeguard local populations of Northern Wheatears. For site A we would focus on increasing both fecundity and adult survival. To enhance both vital rates simultaneously, nest protection measures have been implemented since 2010 (wire-mesh covers to prevent excavating of nests by predators). This seems to have been very successful: during the first complete season of applying nest protection, fecundity was 5.27, compared with 2.60 on average for 2007–2010, and no nests or females were predated by Foxes. We also expect that female survival will recover in the coming years. Preservation of the immigration-sensitive population C requires the safeguarding of population D. Because population C may be prone to stochastic effects due to low breeding numbers and being restricted to a small remaining fragment of suitable habitat, it would be beneficial to increase the area of suitable habitat, both adjacent and very close to the existing population. The absence of dominating demographic drivers at site D may indicate a sound balance between fecundity, survival and migration and therefore be indicative of population stability. This is supported by the stability of the population since at least the early 1990s and may be due to the sustained presence of high Rabbit densities. As long as habitat quality remains in its current state, population D seems the most secure of the studied populations. Therefore, we do not recommend high-impact conservation measures in this site yet.

In the longer term, more sustainable conservation actions may encompass rehabilitating natural processes by increasing the effects of aeolian activity (Arens & Geelen 2006). However, we emphasize the joint importance of effective short-term measures and the restoration of such natural processes, as these may become effective only after time periods that exceed the endurance of the remaining populations in the contemporary setting.

CONCLUSIONS

In spite of a national and international decline, our results suggest that the remaining local Northern Wheatear populations in The Netherlands are driven by different vital rates. As many other threatened species also occur in scattered populations, we advocate implementing multi-site studies, with populations of different sizes and different degrees of isolation, in order to elucidate conservation actions that can operate locally and in the short term. By safeguarding several local populations one thereby protects the overall population on a larger geographical scale.

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REFERENCES

Abadi, F., Gimenez, O., Ullrich, B., Arlettaz, R. & Schaub, M. 2010. Estimation of immigration rate using integrated population modeling. *J. Appl. Ecol.* **47**: 393–400.

Abbott, K.C. 2011. A dispersal-induced paradox: synchrony and stability in stochastic metapopulations. *Ecol. Lett.* **14**: 1158–1169.

Arcese, P. & Smith, J.N.M. 1988. Effects of population density and supplemental food on reproduction in song sparrows. *J. Anim. Ecol.* **57**: 119–136.

Arens, S.M. & Geelen, L.H.W.T. 2006. Dune landscape rejuvenation by intended destabilisation in the Amsterdam water supply dunes. *J. Coastal Res.* **22**: 1094–1107.

Atkinson, P., Buckingham, D. & Morris, A. 2004. What factors determine where invertebrate-feeding birds forage in dry agricultural grasslands? *Ibis* **146**: 99–107.

Blasius, B., Huppert, A. & Stone, L. 1999. Complex dynamics and phase synchronization in spatially extended ecological systems. *Nature* **399**: 354–359.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L. & De Vries, W. 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecol. Appl.* **20**: 30–59.

Boele, A., Van Bruggen, J., Van Dijk, A.J., Hustings, F., Vergeer, J.-W., Ballering, L. & Plate, C.L. 2012. *Broedvogels in Nederland in 2010*. Nijmegen: SOVON Vogelonderzoek Nederland.

Burfield, I. & van Bommel, F. 2004. *Birds in Europe: Populations Estimates, Trends and Conservation Status*. Cambridge: BirdLife International.

Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York: Springer.

Caswell, H. 1989. Analysis of Life Table Response Experiments 1: decomposition of effects on populations-growth rate. *Ecol. Mod.* **46**: 221–237.

Caswell, H. 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*, Vol. 2. Sunderland, MA: Sinauer Associates.

Caughley, G. 1994. Directions in conservation biology. *J. Anim. Ecol.* **63**: 215–244.

Gaillard, J.-M., Hewison, A.J.M., Klein, F., Plard, F., Douhard, M., Davison, R. & Bonenfant, C. 2013. How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of constrasted populations of roe deer. *Ecol. Lett.* **16**: 48–57.

Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. 2002. *Bayesian Data Analysis*. Boca Raton: Chapman & Hall.

Gilpin, M.E. & Soulé, M.E. 1986. Minimum viable populations: processes of species extinction. In Soulé, M.E. (ed.) *Conservation Biology: the Science of Scarcity and Diversity*: 19–34. Sunderland, MA: Sinauer Associates Inc.

Glutz von Blotzheim, U.N. & Bauer, K.M. 1988. *Handbuch der Vögel Mitteleuropas*. Wiesbaden: AULA-Verlag.

Gregory, R., Willis, S., Jiguet, F., Vorisek, P., Klvanova, A., van Strien, A., Huntley, B., Collingham, Y., Couvet, D. & Green, R. 2009. An indicator of the impact of climatic change on European Bird Populations. *PLoS ONE* **4**: e4678.

Hanski, I. & Ovaskainen, O. 2000. The metapopulation capacity of a fragmented landscape. *Nature* **404**: 755–758.

Hernández-Matías, A., Real, J., Moleón, M., Palma, L., Sánchez-Zapata, J.A., Pradel, R., Carrete, M., Gil-Sánchez, J.M., Beja, P., Balbontín, J., Vincent-Martin, N., Ravayrol, A., Benítez, J.R., Arroyo, B., Fernández, C., Ferreiro, E. & García, J. 2013. From local monitoring to a broad-scale viability assessment: a case study for the Bonelli's Eagle in western Europe. *Ecol. Monogr.* **83**: 239–261.

Jongejans, E. & De Kroon, H. 2005. Space versus time variation in the population dynamics of three co-occurring perennial herbs. *J. Ecol.* **93**: 681–692.

Kaboli, M., Aliabadian, M., Guillaumet, A., Roselaar, C.S. & Prodon, R. 2007. Ecomorphology of the wheatears (genus *Oenanthe*). *Ibis* **149**: 792–805.

Kendall, B.E., Bjørnstad, O.N., Bascompte, J., Keitt, T.H. & Fagan, W.F. 2000. Dispersal, environmental correlation, and spatial synchrony in population dynamics. *Am. Nat.* **155**: 628–636.

Koenig, W.D. 1999. Spatial autocorrelation of ecological phenomena. *Trends Ecol. Evol.* **14**: 22–26.

Koenig, W.D. 2002. Global patterns of environmental synchrony and the Moran effect. *Ecography* **25**: 283–288.

de Kroon, H., van Groenendael, J. & Ehrlen, J. 2000. Elasticities: a review of methods and model limitations. *Ecology* **81**: 607–618.

Lande, R., Engen, S. & Saether, B.E. 1999. Spatial scale of population synchrony: environmental correlation versus dispersal and density regulation. *Am. Nat.* **154**: 271–281.

Liebhold, A., Koenig, W.D. & Bjørnstad, O.N. 2004. Spatial synchrony in population dynamics. *Annu. Rev. Ecol. Evol. Syst.* **35**: 467–490.

Nozeman, C. 1789. *Nederlandsche Vogelen; Volgens Hunne Huishouding, Aert en Eigenschappen Beschreeven*. Amsterdam: Jan Christiaan Sepp.

Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R.D. 2000. Spatial synchrony in populations of birds: effect of habitat, population trend and spatial ecology. *Ecology* **81**: 2112–2125.

PECBMS 2012. *Trends of Common Birds in Europe. 2012 update*. Prague: PECBMS.

Petranka, J., Smith, C. & Scott, A. 2004. Identifying the minimal demographic unit for monitoring pond-breeding amphibians. *Ecol. Appl.* **14**: 1065–1078.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In 3rd International Workshop on Distributed Statistical Computing. Vienna.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. *Am. Nat.* **132**: 652–661.

R Development Core Team 2012. *A Language and Environment for Statistical Computing*. Vienna. Available at: http://www.R-project.org.

Ricketts, T.H. 2001. The matrix matters: effective isolation in fragmented landscapes. *Am. Nat.* **158**: 87–99.

Sæther, B.E., Engen, S., Grøtan, V., Fiedler, W., Matthysen, E., Visser, M.E., Wright, J., Møller, A.P., Adriaensen, F., van Balen, H., Balmer, D., Mainwaring, M.C., McCleery, R.H., Pampus, M. & Winkel, W. 2007. The extended Moran effect and large-scale synchronous fluctuations in the size of great tit and blue tit populations. *J. Anim. Ecol.* **76**: 315–325.

Sæther, B.E., Grøtan, V., Engen, S., Noble, D.G. & Freckleton, R.P. 2011. Rarity, life history and scaling of the dynamics in time and space of British birds. *J. Anim. Ecol.* **80**: 215–224.

Schaub, M. & Abadi, F. 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. *J. Ornithol.* **152**: 227–237.

Schaub, M., Ullrich, B., Knotzsch, G., Albrecht, P. & Meisser, C. 2006. Local population dynamics and the impact of scale and isolation: a study on different Little Owl populations. *Oikos* **115**: 389–400.

Schaub, M., Aebischer, A., Gimenez, O., Berger, S. & Arlettaz, R. 2010. Massive immigration balances high anthropogenic mortality in a stable eagle owl population: lessons for conservation. *Biol. Conserv.* **143**: 1911–1918.

Schaub, M., Reichlin, T.S., Abadi, F., Kery, M., Jenni, L. & Arlettaz, R. 2012. The demographic drivers of local population dynamics in two rare migratory birds. *Oecologia* **168**: 97–108.

Schaub, M., Jakober, H. & Stauber, W. 2013. Strong contribution of immigration to local population regulation: evidence from a migratory passerine. *Ecology* **94**: 1828–1838.

SOVON 2002. *Atlas van de Nederlandse Broedvogels 1998–2000*. Leiden: KNNV.

Van Turnhout, C., Aben, J., Beusink, P., Majoor, F., van Oosten, H. & Esselink, H. 2007. Breeding success and feeding ecology of the declining Dutch Wheatear *Oenanthe oenanthe* population. *Limosa* **80**: 117–122.

Van Turnhout, C.A.M., Foppen, R.P.B., Leuven, R., Van Strien, A. & Siepel, H. 2010. Life-history and ecological correlates of population change in Dutch breeding birds. *Biol. Conserv.* **143**: 173–181.

Ward, M.P. 2005. The role of immigration in the decline of an isolated migratory bird population. *Conserv. Biol.* **19**: 1528–1536.

White, G. & Burnham, K. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**: 120–139.

Williams, B.K., Nichols, J.D. & Conroy, M. 2002. *Analysis and Management of Animal Populations*. San Diego: Academic Press.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. JAGS code, with information from all populations.

Appendix S2. State-space equations of the IPM.

Tables S1–S5. Model selection and parameter estimations of age-, year- and site-dependency of survival and resighting probabilities in a Cormack-Jolly-Seber formulation.