

Characterizing demographic variation and contributions to population growth rate in a declining population

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Summary

1. Understanding how demographic variation translates into variation in population growth rate (λ) is central to understanding population dynamics. Such understanding ideally requires knowledge of the mean, variance and covariance among all demographic rates, allowing the potential and realized contribution of each rate to λ to be estimated. Such studies require integrated monitoring of all demographic rates across multiple years and are consequently rare, particularly in declining populations and for species with less tractable life histories.

2. We used 12 years of comprehensive demographic data from a declining ring ouzel (*Turdus torquatus*) population to estimate the mean, variance and covariance in all major demographic rates and estimate potential and realized demographic contributions to λ .

3. Population size decreased from 39 to 13 breeding pairs (−67%) and mean λ was 0.91 during 1998–2009. This decrease did not reflect a substantial concurrent decrease in any single key demographic rate, but reflected varying combinations of demographic rates that consistently produced $\lambda < 1$.

4. Basic prospective elasticity analysis indicated that λ was most sensitive to adult survival, closely followed by early season reproductive success and early brood first-year survival. In contrast, integrated elasticity analysis, accounting for estimated demographic covariance, indicated that λ was most sensitive to early brood first-year survival, closely followed by re-nesting rate, early season reproductive success, late-brood first-year survival and adult survival.

5. Retrospective decomposition of variance suggested that first-year survival contributed most to observed variation in λ .

6. However, demographic comparison with other related species suggested that adult survival, but not reproductive success or post-fledging survival, averaged lower than expected throughout the 12-year study.

7. These data demonstrate that multiple approaches, including comprehensive demographic and comparative analyses and due consideration of conflicting answers, may be necessary to accurately diagnose the demographic basis of population change.

Key-words: capture–mark–recapture, life table response experiment, life-history variation, multiple breeding attempts, sensitivity, vital rate

Introduction

Understanding which demographic rates drive variation in population growth rate (λ) is key to understanding and predicting population dynamics, and is therefore central to both fundamental and applied population ecology (Siriwardena *et al.* 2000; Sibly & Hone 2002; Coulson, Gaillard & Festa-Bianchet 2005). Two complementary approaches towards

achieving such understanding can be taken. First, prospective perturbation analysis (e.g. elasticity analysis) can be used to identify the demographic rates to which λ is most sensitive (i.e. where a relatively small change would cause a relatively large change in λ). Such analyses require knowledge of the mean of all major demographic rates comprising a species or population's life history (Benton & Grant 1999a; Sæther & Bakke 2000; Caswell 2001; Morrison & Hik 2007). Secondly, a retrospective decomposition of variance can be used to identify which demographic rates actually caused observed

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variation in λ , reflecting the magnitude of demographic variation as well as the sensitivity of λ to this variation. Such analyses additionally require knowledge of temporal variation in all major demographic rates (Benton & Grant 1999a; Wisdom, Mills & Doak 2000; Reid *et al.* 2004; Coulson, Gaillard & Festa-Bianchet 2005; Ezard, Becker & Coulson 2006; Schaub *et al.* 2006). Rigorous prospective and retrospective investigation of demographic effects on λ should also consider covariances among demographic rates, and hence the degree to which variation in one rate is concomitant with variation in another (van Tienderen 1995; Benton & Grant 1999a; Reid *et al.* 2004; Coulson, Gaillard & Festa-Bianchet 2005; Ezard, Becker & Coulson 2006). Both genetic and physiological constraints and environmental variation can generate demographic covariation, reflecting intrinsic life-history trade-offs and common environmental effects on multiple life-history components (van Noordwijk & de Jong 1986; Stearns 1992; Tavecchia *et al.* 2005). Any such positive or negative covariation acting within or across years could magnify or ameliorate the impact of variation in any single demographic rate on λ , thereby altering demographic effects on λ from those suggested by basic prospective and retrospective analyses that ignore covariation (van Tienderen 1995). Furthermore, knowledge of the mean and variance of lower-level demographic rates (e.g. reproductive rates, fecundity, short-term survival) that underlie higher-level demographic rates (e.g. total reproductive success, annual survival) is potentially key to understanding the exact demographic and ecological mechanisms driving population dynamics. Comprehensive population studies that estimate the mean, variance and covariance among all demographic rates, and corresponding potential and realized contributions to λ , are therefore required to identify general constraints on λ and understand the dynamics of specific focal populations.

Ecologists sometimes make the simplistic assumption that observed increases or decreases in population size will necessarily reflect concurrent directional changes in specific demographic rates, such as reproductive success or survival, which can then be identified and mitigated (Peach, Siriwardena & Gregory 1999; Robinson *et al.* 2004). However, increasing or decreasing population size does not require immediate directional change in any underlying rate, or indeed in λ , if the existing combination of constant and/or variable rates means that λ differs consistently from one. In this circumstance, comparative analyses can help diagnose the most likely demographic and hence ecological cause of current population change. These might ideally include comparisons of demography before and after population change began, or with other populations of the same species showing different trajectories (Siriwardena *et al.* 2000; Peery *et al.* 2004; although see Green 1999). In the absence of conspecific data, broader comparison with other species with similar life histories may prove insightful in identifying demographic rates that are consistently lower than might be expected (Green 1999; Stenhouse & Robertson 2005). Effective diagnoses of the demographic causes of population change therefore need

to be nested within, as well as contribute to, both species-specific and wider comparative frameworks.

These data requirements mean that the comprehensive studies required to identify the demographic causes of variation in λ and population size are extremely challenging, particularly for small and/or declining populations where a clear understanding of population dynamics is of immediate applied as well as fundamental value (Heppell, Caswell & Crowder 2000; Wisdom, Mills & Doak 2000). Long-term studies of reproductive success and survival of marked individuals will be necessary to robustly estimate mean rates and ensure that temporal variance and covariance are also adequately estimated (Gaillard, Festa-Bianchet & Yoccoz 1998; Gaillard *et al.* 2000; Sæther & Bakke 2000; Reid *et al.* 2004; Coulson, Gaillard & Festa-Bianchet 2005). Some demographic rates are particularly difficult to measure, forcing analysts to make simplifying assumptions that are themselves difficult to validate, or to focus on species with relatively tractable life histories (Anders *et al.* 1997; Sæther & Bakke 2000; Siriwardena *et al.* 2000; Cornulier *et al.* 2009). Specifically, while reproductive success per attempt can often be measured relatively accurately, measuring total season-long reproductive success is much more challenging for species that can breed multiple times per year, requiring accurate measurement of the frequency of multiple breeding and season length rather than just the success of a monitored sample of attempts (Martin 1995; Siriwardena *et al.* 2000; Anders & Marshall 2005; Cornulier *et al.* 2009). Despite the obvious importance of quantifying total reproductive success, this is far from always achieved (e.g. Peach, Siriwardena & Gregory 1999; Siriwardena *et al.* 2000). Indeed, the proportion of studies on birds in which multiple breeding rates were incorporated into estimates of total reproductive success actually decreased during 1987–97 (Thompson *et al.* 2001). Additionally, dispersal between an individual's natal area and area of first reproduction means that individuals marked on natal areas often cannot be located the next year even if they survive. Local first-year survival probabilities estimated using local encounter data will therefore underestimate the true first-year survival probability across the wider population (Greenwood & Harvey 1982; Payne 1991; Paradis *et al.* 1998).

Such problems can be minimized through *a priori* study design; for example, by studying resident or isolated populations of species that breed once per year (e.g. Reid *et al.* 2004; Coulson, Gaillard & Festa-Bianchet 2005; Schaub *et al.* 2006). However, this tactic would limit analyses to a biased subset of species and populations, precluding comparative analyses of demographic contributions to λ across the full life-history and ecological spectrums. Comprehensive demographic studies of populations with 'non-standard' life histories are therefore particularly valuable. Intensive season-long monitoring of the reproductive success of marked individuals is then required. Estimating first-year survival often proves the most intractable problem in such systems (Paradis *et al.* 1998; Schaub *et al.* 2006). However, substantial pre-breeding mortality can occur between fledging and dispersal from the

natal area (Anders *et al.* 1997; Thomson & Cotton 2000; Naef-Daenzer, Widmer & Nuber 2001; Rush & Stutchbury 2008). Focussed estimation of survival through this period may therefore help identify key mortality periods constraining λ . Furthermore, if variation in population size and all other demographic rates are adequately estimated, an approximate estimate of true first-year survival across the wider population can be calculated by subtraction, thereby allowing complete parameterization of prospective and retrospective analyses of broad-scale λ .

Accordingly, we undertook a comprehensive 12-year study of a declining ring ouzel *Turdus torquatus* population to quantify the mean, variance and covariance among all major demographic rates and hence determine the potential and realized demographic drivers of λ . We quantified the change in population size across years, measured all components of season-long reproductive success and used resightings of marked individuals to quantify first-year and adult annual apparent survival rates, and hence estimated true population-wide first-year survival by subtraction. To further inform estimates of the magnitude and timing of first-year mortality, we used intensive radiotracking to measure post-fledging survival. We used prospective elasticity analysis to identify which demographic rates have the greatest potential influence on λ accounting for estimated covariance, and a retrospective analysis to decompose observed variation in λ into contributions from individual rates. We place estimated demographic rates in a cross-species comparative context, and thereby present and apply a rigorous framework for diagnosing the demographic causes of current population change.

Materials and methods

STUDY SYSTEM AND POPULATION SIZE

We studied a population of ring ouzels, a migratory multi-brooding thrush, inhabiting *c.* 22 km² of southern Glen Clunie (56°56'N 3°25'W), Braemar, Scotland, during 1998–2009. Ring ouzels also

inhabit the rest of Glen Clunie and adjacent glens, meaning that the Glen Clunie population is not isolated and estimated demographic rates can be interpreted in the context of the wider population. Demographic decomposition for such a species provides a valuable addition to existing comparative data. Furthermore, since ring ouzel is a red-listed Biodiversity Action Plan priority species in the UK (Sim *et al.* 2010), understanding demographic causes of variation in λ is also of direct applied value.

To estimate population size we systematically walked through the core study area, covering all ground to ≤ 200 m, every 1–2 weeks between mid-April and mid-July each year, and recorded the location of all ring ouzels. British ring ouzels occupy distinct breeding sites, typically separated by ≥ 240 m, with conspicuous territorial behaviour that allowed individuals to be detected at long range using binoculars. Individuals regularly make two, rarely three, breeding attempts per season (Burfield 2002). Each breeding attempt takes on average 29 days from first egg laying (3 days laying, 13 days incubation and 13 days to fledging; Burfield 2002). The number of 'early' pairs was defined as those present within 30 days of the first laying date in each year. Late pairs were defined as pairs present on or after day 31 in each year (Fig. 1). Initial sightings of pairs were substantiated by stronger evidence of breeding (e.g. nest-building, active nest, recently fledged young) in about 90% of cases. Where no further evidence of breeding was obtained, pairs were assumed to have failed early in the breeding attempt. Population size in each year (N_t) was estimated with high confidence as the maximum number of early pairs observed in that year. Resightings of marked individuals suggested that the detection rate was effectively one (see Results). Although any pairs that failed early in a breeding attempt and immediately dispersed may have gone unrecorded, any such cases were probably very rare. Estimates of N_t are therefore likely to be accurate, and population growth rate (λ) for each year during 1998–2009 was calculated as N_{t+1}/N_t .

To quantify links between demographic variation and λ , assuming an equal primary sex ratio, we used the following equation:

$$N_{t+1} = N_t((C_e R S_e \phi_{1eTrue} 0.5) + (C_l R S_l \phi_{1lTrue} 0.5) + \phi_{ad}) \quad \text{eqn 1}$$

All demographic parameters are defined in Table 1. We then attempted to estimate all demographic rates required to parameterize this equation assuming a female-based cycle and that all ouzels first bred age one.

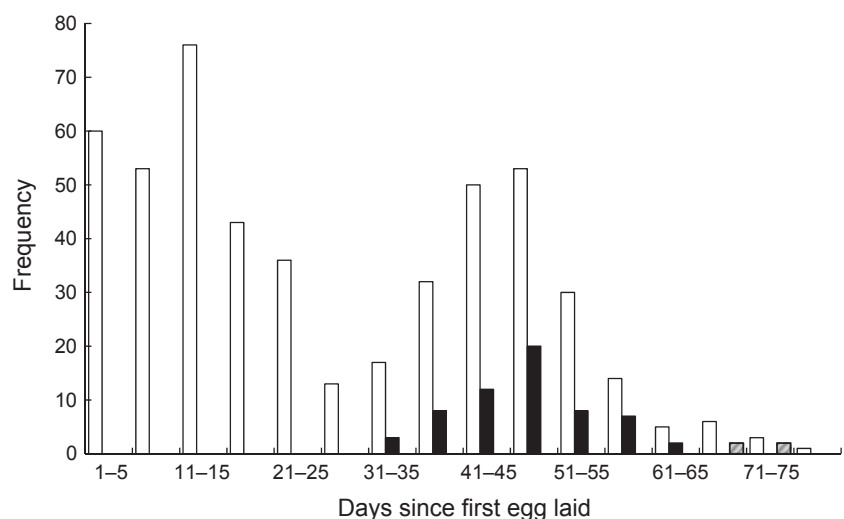


Fig. 1. Frequency distribution of laying dates, in 5-day periods since first-egg date, during 1998–2009. Open, solid and shaded bars indicate all data, known second clutches and known third clutches respectively.

Table 1. Definitions of demographic parameters

Parameter	Definition
N_t	The number of early pairs present in year t
N_{t+1}	The number of early pairs present in year $t + 1$
λ	Population growth rate (N_{t+1}/N_t)
DNSR	Daily nest survival rate: the probability of a nest surviving one day
ONSR	Overall nest survival rate: the product of the proportion of nests estimated to have survived the egg and chick stages
C_e	Proportion of females making an early breeding attempt
C_l	Proportion of females making a late breeding attempt
Y	Mean brood size at fledging in successful nests
RS_e	Early nest reproductive success
RS_l	Late-nest reproductive success
Overall RS	Number of young fledged/female/year ($RS_e + (RS_l C_l)$)
ϕ_{ad}	Apparent probability of adult survival
ϕ_f	Apparent probability of survival to 5 weeks post-fledging
ϕ_{1eApp}	Apparent probability of first-year survival of early brood chicks
ϕ_{1lApp}	Apparent probability of first-year survival of late-brood chicks
ϕ_{1eTrue}	Probability of true first-year survival, including immigration into Glen Clunie, of early brood chicks
ϕ_{1lTrue}	Probability of true first-year survival, including immigration into Glen Clunie, of late-brood chicks

REPRODUCTIVE SUCCESS

Laying dates were recorded directly from nests found during laying or hatching, estimated using known relationships between chick age and wing-length and weight (Burfield 2002), or by comparison with photographs of known-age nestlings. Nests were typically visited every 5–7 days until chicks fledged to record clutch and brood size. These regular nest visits enabled calculation of daily nest survival rates (DNSR) using the Mayfield (1975) method, which accounts for variation in the times at which nests are found, and thus in the length of the period over which they are monitored and exposed to risk of failure. As DNSR may vary through the season (Mayfield 1975), we calculated separate estimates for early and late nests, and tested for among-year variation and linear change across years in both estimates separately and combined. Overall DNSR was calculated as the product of DNSR (egg stage) and DNSR (chick stage). To calculate the proportion of nests surviving the egg and chick stages, we raised the appropriate DNSR to the powers of 16 (3 days laying plus 13 days incubation) and 13 respectively. The overall nest survival rate (ONSR) was calculated as the product of the proportion of nests surviving the egg and chick stages.

All females were assumed to make an early breeding attempt ($C_e = 1$). Two methods were used to estimate the proportion of females that made more than one breeding attempt (C_l – re-nesting rate) within each year. First, the annual proportion of individually colour-ringed females from early nests that were observed making second (or rarely third) breeding attempts was calculated directly. However, sample sizes of individually colour-ringed females were small (range 7–19 per year). Therefore, to substantiate estimates based on colour-ringed females, we calculated the ratio of the number of breeding pairs present during the late season to the early season in each year. This method lacks the precision of monitoring

individual females, but benefits from including data from the whole breeding population.

Mean RS [the number of young fledged per female, estimated as the product of mean brood size at fledging in successful nests (Y) and nest survival rate] was estimated for both early (RS_e) and late (RS_l) nests, and mean overall RS was calculated as $RS_e + (RS_l C_l)$. Standard errors were calculated following Hensler (1985):

$$\sqrt{((\text{overall DNSR})^2 \text{SE}(Y^2)) + (Y^2 \sigma(N)) + (\text{SE}(Y^2) \sigma(N))} \quad \text{eqn 2}$$

where SE is the standard error of Y^2 and $\sigma(N)$ is the variance in ONSR.

We used generalized linear models and appropriate *post hoc* tests to test whether each component of RS (excluding DNSR, for which see above) varied among years. Error structures and link functions were Gaussian and identity for laying date (measured as Julian date from 1 April), Poisson and log for clutch and fledged brood size and binomial and logit for re-nesting rate. We tested for among-year variation in mean RS using Student's t tests with appropriate Bonferroni adjustments, following Bailey (1981). We then tested for linear increase or decrease across years in the annual means of each variable (excluding DNSR) using least squares regression. Means were weighted by annual sample size for laying date, clutch size and fledged brood size, and by the minimum annual value of DNSR and fledged brood size for RS_e , RS_l and overall RS.

ADULT APPARENT SURVIVAL

During 1999–2008, 221 adult ring ouzels marked with British Trust for Ornithology (BTO) metal rings and individual combinations of 3–4 colour rings were used to estimate ϕ_{ad} . These comprised 22 males and 23 females originally ringed as chicks within or outside Glen Clunie, and 81 male and 95 female previously unringed individuals that were trapped and ringed as breeding adults in Glen Clunie (Sim & Rebecca 2003). These adults were aged as either first-year (hatched the previous year) or adult (hatched two or more years previously) at capture (Svensson 1992). Substantial effort was made to resight all colour-ringed adults each year, both at nests during territory visits and in nearby feeding areas. Resighting effort was intensive across the study area throughout each season, resulting in a very high local resighting rate each year (see Results). Any within- or between-year dispersal between consecutive breeding attempts may result in underestimation of adult apparent survival (Paradis *et al.* 1998; Winkler *et al.* 2004). However, little dispersal was observed during opportunistic visits to nearby breeding areas, suggesting that breeding dispersal was relatively rare. Furthermore, the high annual resighting probability within Glen Clunie suggests little temporary emigration among years. To estimate ϕ_{ad} , we initially fitted a fully sex- and year-dependent Cormack–Jolly–Seber (CJS) model (Lebreton *et al.* 1992; White & Burnham 1999). This model fitted the data [goodness-of-fit tests from program RELEASE, $P = 0.93$ (male) and $P = 0.54$ (female)]. Although there was some evidence of under-dispersion ($\sum \chi^2 / \sum \text{d.f.} = \hat{c} = 0.86$), this was relatively small and we therefore set $\hat{c} = 1.0$ (Cooch & White 2008).

POST-FLEDGING SURVIVAL

To measure ϕ_f during 2006–08, chicks were fitted with 1.8 g TW4 single-celled radio tags (<http://www.biotrack.co.uk>) just prior to fledging (10–13 days post-hatch). Tags were back mounted using an elastic harness with weak link to allow tag loss after a few weeks. In 2006, 22 late nest chicks were tagged; this trial showed no detrimental

effects. A further 23 and 21 early nest chicks and 18 and 26 late nest chicks were therefore tagged in 2007 and 2008 respectively (giving totals of 44 early nest chicks from 25 broods and 66 late nest chicks from 29 broods respectively). Tags had a signal range of up to 10 km with direct line of sight, but more typically 2–3 km depending on terrain, and a battery life of up to 4 months. Tagged fledglings were located once every 2–3 days post-fledging, until the bird was found dead, shed the tag or disappeared and was assumed to have dispersed from the study area. We used the combined 2006–08 data to estimate weekly ϕ_f for chicks from early and late nests, for 5 weeks post-fledging. The signals from nine of the 110 (8.2%) tagged fledglings were lost during the first 5 weeks post-fledging. As these individuals had unknown fates (and may have dispersed), they were censored from subsequent known-fate survival analyses.

FIRST-YEAR APPARENT SURVIVAL

During 1998–2002, 805 chicks (464 from early nests and 341 from late nests), comprising 85% of those known to have fledged from the study area, were ringed with BTO metal rings and a single plastic colour ring to allow year cohort but not individual identification. During 2003–08, 581 chicks (335 from early and 246 from late nests), comprising 90% of those known to have fledged from the study area, were ringed with three or four colour rings to allow individual identification without need for recapture. It was not possible to calculate resighting probability (P) for returning chicks marked with single cohort rings during 1998–2002, as they could not be individually identified until trapped and fitted with individual colour-ring combinations in later years. However, P for returning chicks marked with individual combinations during 2003–08 was estimated to be 1.00 (see Results). Hence, we assumed a constant P of 1.00 for all first-years during 1998–2009, and estimated the apparent probability of first-year survival (ϕ_{1App}) as for ϕ_{ad} (see above).

TRUE FIRST-YEAR SURVIVAL

Estimates of ϕ_{1App} were low (see Results), probably reflecting natal dispersal away from the study area. We therefore used annual estimates of N_t , ϕ_{ad} , C and RS to estimate ϕ_{1True} (following eqn 1). The ratio of ϕ_{1eTrue} to ϕ_{1ITrue} was assumed to equal the ratio of ϕ_{1eApp} to ϕ_{1IApp} (see Results). Estimates of ϕ_{1eTrue} and ϕ_{1ITrue} therefore include immigration into Glen Clunie. Prospective and retrospective analyses based on these estimates therefore reflect demographic variation across the wider ring ouzel population (from which immigrants must originate), not across Glen Clunie specifically.

BASIC AND INTEGRATED ELASTICITIES

To quantify the expected proportional change in λ given a proportional change in each demographic rate and hence each rate's elasticity (Benton & Grant 1999a; de Kroon, van Groenendaal & Ehrlén 2000), we simulated a 5% increase in each individual rate (ϕ_{ad} , C_e , C_i , RS_e , RS_i , ϕ_{1eTrue} and ϕ_{1ITrue}) while holding the others constant and recorded the proportional change in N_{t+1}/N_t (eqn 1). This analysis assumes that all demographic rates vary independently (Benton & Grant 1999b; de Kroon, van Groenendaal & Ehrlén 2000), which may be simplistic (van Noordwijk & de Jong 1986; Stearns 1992; Tavecchia *et al.* 2005). To assess the possible degree of demographic covariation, we calculated pairwise parametric correlations between observed annual demographic rates. Correlations between ϕ_{ad} , ϕ_{1eTrue} and ϕ_{1ITrue} were calculated for 2000–09, and those between C_i , RS_e and RS_i were calculated for 1998–2009. However, ϕ_{ad} , ϕ_{1eTrue}

and ϕ_{1ITrue} during 2000–09 were correlated with C_i , RS_e and RS_i during 1999–2008 (i.e. with a 1-year lag) due to the expected effect of reproductive success in year N_t on survival to year N_{t+1} . The only correlation we could not estimate directly was that between ϕ_{1eTrue} and ϕ_{1ITrue} . As estimates of ϕ_{1App} probably underestimated ϕ_{1ITrue} (due to likely natal dispersal from the study area), the estimated correlation between ϕ_{1eApp} and ϕ_{1IApp} (–0.11) was of uncertain interpretation relative to the correlation between ϕ_{1eTrue} and ϕ_{1ITrue} . Indeed, a positive correlation between ϕ_{1eTrue} and ϕ_{1ITrue} might be expected since fledglings from early and late broods most likely experience correlated over-winter conditions. We therefore ran analyses assuming correlations of 0.25, 0.50 and 0.75 between ϕ_{1eTrue} and ϕ_{1ITrue} and assessed the sensitivity of conclusions to the assumed value.

To assess effects of demographic covariation on estimated elasticities, we calculated integrated elasticities (IEs). For a demographic rate x ,

$$IE_x = \sum_y r_{xy} e_y CV_y / CV_x \quad \text{eqn 3}$$

where r_{xy} is the correlation between rates x and y , and e_y and CV_y are the basic elasticity and coefficient of variation of y respectively (van Tienderen 1995; Sæther & Bakke 2000).

RETROSPECTIVE ANALYSIS

We estimated the realized contribution of each demographic rate to variation in λ as $e_x^2 CV_x^2$ (assuming no covariance among rates) or $IE_x^2 CV_x^2$ (assuming covariance among rates), thereby giving a variance-standardized elasticity (van Tienderen 1995). The total variance in λ can be estimated as the sum of this quantity across all demographic rates (x):

$$\text{Var}(\lambda) = \sum_x e_x^2 CV_x^2, \quad \text{eqn 4a}$$

or

$$\text{Var}(\lambda) = \sum_x IE_x^2 CV_x^2 \quad \text{eqn 4b}$$

and hence the proportional contribution of each rate x to total variation in λ (X_x ; Horvitz, Schemske & Caswell 1997; Gaillard *et al.* 2000; Caswell 2001) is:

$$X_x = e_x^2 CV_x^2 / \text{Var}(\lambda), \quad \text{eqn 5a}$$

or

$$X_x = IE_x^2 CV_x^2 / \text{Var}(\lambda) \quad \text{eqn 5b}$$

STATISTICAL ANALYSIS

We calculated CV to quantify and compare among-year variation in demographic rates that were measured on scales without upper limit (laying date, clutch size, fledged brood size and RS). However, CV is not suitable for comparing variation in proportions or probabilities since the maximum variance is constrained at $\alpha(1-\alpha)$ for a proportion α . We therefore quantified the variability in demographic rates measured as proportions or probabilities (DNSR, C_i , ϕ_{ad} , ϕ_{1App}) as the ratio of the observed variance to the maximum possible variance [i.e. variance $\alpha(1-\alpha)$; Gaillard & Yoccoz 2003; Morris & Doak 2004]. However, we additionally present CV to facilitate comparison with other studies that have used this approach.

Survival analyses were run in program MARK 5.1 (White & Burnham 1999) using the nest survival (DNSR), known fate (ϕ_f)

and recapture (ϕ_{ad} and ϕ_{1App}) models. Goodness-of-fit tests were not necessary for the DNSR and ϕ_f models as the saturated models fitted the data perfectly (Cooch & White 2008). For all models Akaike's Information Criterion, adjusted for small sample size (AICc), was used to identify the best supported model that included the survival parameters of interest (Burnham & Anderson 2002). The model with the lowest AICc is the best supported model, and provides the best description of the data given the balance between over-fitting (hence loss of precision) and under-fitting (hence bias, Burnham & Anderson 2002).

We first tested for year effects on P , and then year effects on ϕ . Random effects models were used to estimate process variance in ϕ_{ad} and generate shrunk estimates (Burnham & White 2002; Loison *et al.* 2002). All other analyses were run in SAS v8 (SAS Institute 2001). Means are presented as ± 1 standard error (SE). Summaries of all main results and parameter estimates are presented in the main text. Further details of survival models and annual sample sizes are provided in Supporting information. To provide comparative context, estimated mean demographic rates were compared with published data from related species (see Discussion).

Results

POPULATION SIZE

The number of breeding pairs (N_t) decreased from 39 in 1998 to 13 in 2009 (-67% , Fig. 2). There was a particularly large decrease (-37%) from 27 pairs in 2004 to 17 pairs in 2005 (Fig. 2). Mean population growth rate (λ) was 0.91 (range 0.63–1.00, SE = 0.03) during 1998–09, and N_t never increased from one year to the next.

REPRODUCTIVE SUCCESS

Estimates of the mean, among-year variation and linear change across years in components of RS are described in Table 2 and Fig. 3. Sample sizes are given in Table S1 (Supporting information). In summary, early nest laying date varied significantly among years (being earlier in 2005 than in

2007 or 2008), whilst among-year variation in late-nest laying date approached significance. However, there was no significant tendency for either to become progressively earlier or later through the study period (Table 2, Fig. 3a). For clutch and fledged brood size, only early nest fledged brood size varied significantly among years (being smaller in 2006 than in 1998), and also showed a marginally non-significant tendency to decrease through the study period (Table 2, Fig. 3b,c). Although there was moderate support for models indicating greater early nest DNSR than late-nest DNSR, and that late-nest DNSR increased across years ($\Delta AICc = 1.0$ – 1.5), the best supported model included constant DNSR across all nests (Table S2, Supporting information). Mean ONSR was 0.65 ± 0.04 (early nests) and 0.57 ± 0.05 (late nests; Fig. 3d).

The mean proportion of colour-ringed females recorded re-nesting was 0.64, while the mean ratio of the number of pairs present during the late vs. early season was 0.63 (Table 2, Fig. 3e). These two measures of re-nesting frequency were closely correlated across years (Spearman $r_{11} = 0.76$, $P = 0.007$), suggesting that the latter provides a good measure of the overall re-nesting rate (C_1). Over 12 years, only five females were observed to make three breeding attempts in a season: one reared three broods, two reared two broods, and two reared one brood. Triple brooding therefore contributed little to λ . Re-nesting rate did not vary significantly among years, or increase or decrease significantly across years (Table 2, Fig. 3e).

Due to these patterns of variation in the lower level rates, both RS_e and RS_l varied significantly among years (being higher in 1998 than 2000, and in 2009 than 2000 respectively, Table 2, Fig. 3f). Overall RS also varied among years, being significantly higher in 1998 than in 2000 and 2008, and significantly higher in 2005 and 2009 than in 2000. Neither RS_e , RS_l nor overall RS increased or decreased significantly across years (Table 2, Fig. 3f,g). RS_l varied more among years than RS_e , followed by early laying date, late fledged brood size and early fledged brood size (Table 2).

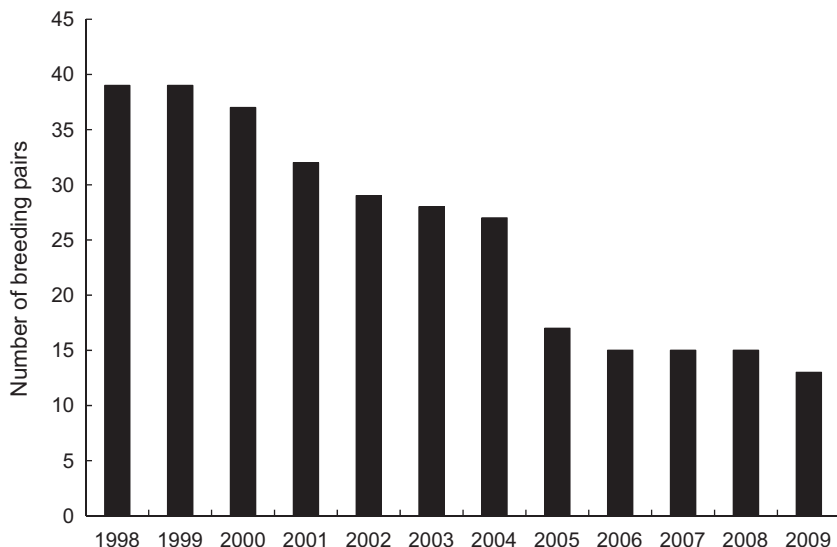


Fig. 2. The estimated number of early breeding ring ouzel pairs in the core study area during 1998–2009.

Table 2. Mean, variance, coefficient of variation (CV), proportion of the maximum possible variance (P_{\max} , the ratio of observed variance to maximum possible variance), test of among-year variation and regression coefficients of estimated linear change across years (β) for key demographic rates. Positive ΔAICc scores indicate reduced support for survival models that included among-year or across-year variation. Rate codes are defined in Table 1

Variable	Mean	Variance	CV	P_{\max}	Among-year variation	β
Early laying date	28 April	48.1	0.24		$F = 3.13 \pm 0.40, P = 0.001$	$+0.045 \pm 0.20, P = 0.83$
Late laying date	1 June	79.7	0.14		$F = 1.74 \pm 0.59, P = 0.07$	$+0.058 \pm 0.23, P = 0.80$
Early clutch size	4.0	0.12	0.09		$\chi^2 = 0.14 \pm 0.002, P = 0.71$	$-0.0003 \pm 0.002, P = 0.85$
Late clutch size	4.0	0.32	0.14		$\chi^2 = 0.10 \pm 0.003, P = 0.75$	$+0.0006 \pm 0.004, P = 0.88$
Early fledged brood size	3.6	0.64	0.22		$\chi^2 = 7.05 \pm 0.004, P = 0.008$	$-0.011 \pm 0.006, P = 0.07$
Late fledged brood size	3.7	0.68	0.23		$\chi^2 = 0.32 \pm 0.005, P = 0.57$	$-0.0006 \pm 0.008, P = 0.95$
Early DNSR	0.985	0.0001		0.004	$\Delta\text{AICc} = 6.2$	$0.019 \pm 0.04, \Delta\text{AICc} = 2.8$
Late DNSR	0.982	0.0001		0.003	$\Delta\text{AICc} = 14.9$	$0.029 \pm 0.02, \Delta\text{AICc} = 1.5$
C_1	0.63	0.01		0.025	$\chi^2 = 0.37 \pm 0.03, P = 0.55$	$-0.020 \pm 0.03, P = 0.54$
RS_e	2.32	0.38	0.27		$t = 4.19, P < 0.05$	$+0.012 \pm 0.02, P = 0.62$
RS_l	2.10	0.46	0.32		$t = 3.89, P < 0.05$	$+0.041 \pm 0.02, P = 0.10$
Overall reproductive success	3.64	0.73	0.20		$t = 3.81\text{--}4.63, P < 0.05$	$+0.015 \pm 0.02, P = 0.49$
Adult male ϕ	0.47	0.02	0.26	0.06	$\Delta\text{AICc} = 12.1$	$-0.050 \pm 0.06, \Delta\text{AICc} = 1.3$
Adult female ϕ	0.37	0.02	0.35	0.07	$\Delta\text{AICc} = 8.5$	$+0.009 \pm 0.05, \Delta\text{AICc} = 2.0$
ϕ_{ad}	0.42	0.01	0.21	0.03	$\Delta\text{AICc} = 10.9$	$-0.019 \pm 0.04, \Delta\text{AICc} = 1.8$
$\phi_{1e\text{App}}$	0.05	0.0007	0.50	0.01	$\Delta\text{AICc} = 10.2$	$-0.037 \pm 0.05, \Delta\text{AICc} = 0.1$
$\phi_{11\text{App}}$	0.02	0.0003	0.87	0.02	$\Delta\text{AICc} = 15.3$	$-0.034 \pm 0.10, \Delta\text{AICc} = 0.5$

ADULT APPARENT SURVIVAL

Estimates of the mean, among-year variation and linear change across years in survival are described in Table 2 and Fig. 4a. The annual resighting probability (P) was estimated as 0.98 ± 0.02 . The probability that a returning adult would remain undetected was therefore low. The best supported model included year-independent but sex-specific ϕ_{ad} (Tables 2 & S3, Fig. 4a). However, four further models received moderate support ($\Delta\text{AICc} = 1.3\text{--}2.0$), including linear decreases in male and/or female ϕ_{ad} , or among-year variation in female ϕ_{ad} (Table S3, Supporting information).

POST-FLEDGING SURVIVAL

The best supported model included week-independent ϕ_{f} that differed between fledglings from early (0.88 ± 0.03) and late (0.74 ± 0.03) nests (Table S4, Supporting information Fig. 4b). However, two further models received moderate support ($\Delta\text{AICc} = 0.9\text{--}1.3$), including among-week variation in ϕ_{f} of fledglings from early or late nests (Table S4, Supporting information). ϕ_{f} across the first 5 weeks post-fledging was 0.57 ± 0.08 and 0.22 ± 0.06 for early and late-nest fledglings respectively.

FIRST YEAR APPARENT AND TRUE SURVIVAL

Of 805 chicks ringed with single cohort colour rings during 1998–2002, 35 returned as adults, of which 26 were trapped and individually identified. Of these, 21 (81%) and five (19%) were from early and late nests respectively. The best supported model for $\phi_{1\text{App}}$ included linear decreases in both $\phi_{1e\text{App}}$ ($0.01/\text{year}$) and $\phi_{11\text{App}}$ ($0.004/\text{year}$) during 1999–2009 (Table S5, Supporting information Fig. 4c). However, a

model with no change across years received almost as much support ($\Delta\text{AICc} = 0.6$, Table S5, Supporting information), and suggested that mean $\phi_{1e\text{App}}$ (0.053 ± 0.008) was higher than mean $\phi_{11\text{App}}$ (0.022 ± 0.006). Mean estimated $\phi_{1\text{True}}$ during 2000–09, calculated from eqn 1, was 0.36 ± 0.04 (early broods) and 0.15 ± 0.02 (late broods, assuming that $\phi_{1e\text{True}} = 2.4 \times \phi_{11\text{True}}$, as observed for $\phi_{1e\text{App}}$). However, estimates of $\phi_{1\text{True}}$ will be sensitive to error in estimates of other demographic rates and N_t , and process variance cannot be estimated (see Discussion).

ELASTICITIES

Basic elasticities indicated that λ was most sensitive to ϕ_{ad} , followed by RS_e and $\phi_{1e\text{True}}$, and was relatively insensitive to C_1 , RS_l and $\phi_{11\text{True}}$ (Table 3). Population stability ($\lambda = 1.0$) would require increases in either ϕ_{ad} to 0.51 (21%), RS_e to 2.83 (22%), $\phi_{1e\text{True}}$ to 0.42 (22%), RS_l to 4.20 (100%) or $\phi_{11\text{True}}$ to 0.27 (100%) over the mean observed rates. Increasing C_1 to the maximum possible value of 1.0 would result in $\lambda = 0.96$.

There were strong negative correlations between estimated $\phi_{1e\text{True}}$ and RS_e , and ϕ_{ad} and estimated $\phi_{1e\text{True}}$, and strong positive correlations between ϕ_{ad} and RS_l , and C_1 and RS_e (Table 3). Integrated elasticities indicated that λ was most sensitive to $\phi_{1e\text{True}}$, closely followed by C_1 , RS_e , $\phi_{11\text{True}}$ and ϕ_{ad} . $\text{IE}(\phi_{1e\text{True}})$ was qualitatively robust to changing the assumed correlation between $\phi_{1e\text{True}}$ and $\phi_{11\text{True}}$, but $\text{IE}(\phi_{11\text{True}})$ was less so (Table 3).

RETROSPECTIVE ANALYSIS

Assuming basic elasticities, $\phi_{1e\text{True}}$ was estimated to account for most variance in λ , followed by RS_e and ϕ_{ad} (Table 3). Assuming integrated elasticities, $\phi_{1e\text{True}}$ accounted for by far

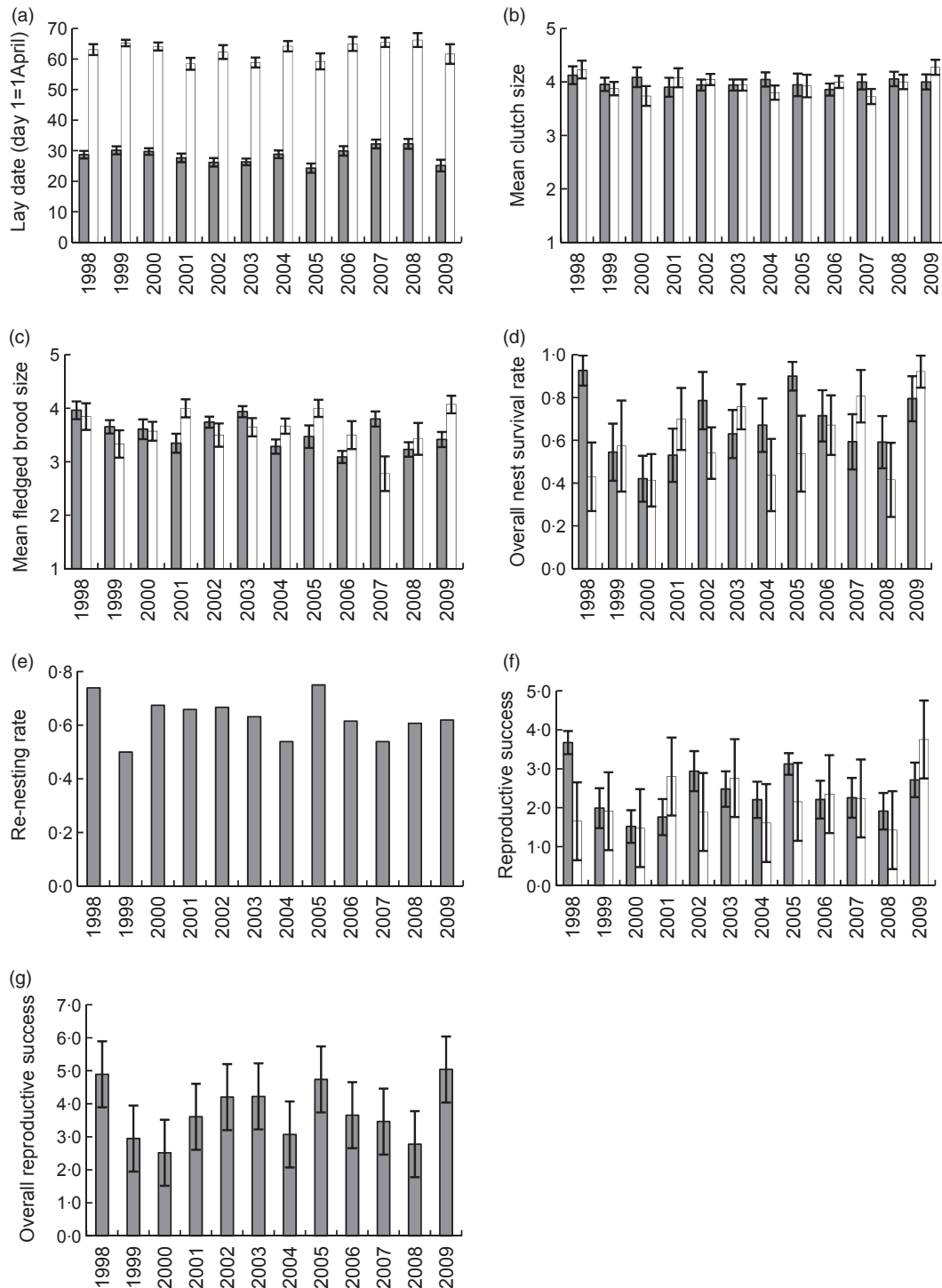


Fig. 3. Mean (± 1 SE) (a) laying date, (b) clutch size, (c) fledged brood size, (d) overall nest survival rate, (e) re-nesting rate (C_1), (f) reproductive success per brood and (g) overall reproductive success during 1998–2009. Shaded and open bars indicate early and late nests respectively.

the most variance in λ , regardless of the assumed correlation between ϕ_{1eTrue} and ϕ_{1lTrue} . However, the estimated contribution of ϕ_{1lTrue} was sensitive to this assumption (Table 3).

Discussion

Comprehensive understanding of population dynamics requires a thorough understanding of which demographic

rates could, and do, cause variation in population size (Sæther & Bakke 2000; Caswell 2001; Reid *et al.* 2004; Coulson, Gaillard & Festa-Bianchet 2005; Ezard, Becker & Coulson 2006; Schaub *et al.* 2006; Morrison & Hik 2007). This in turn requires comprehensive knowledge of the mean, variance and covariance among these rates, presenting a major empirical challenge, particularly in small and/or declining populations of species where such knowledge is of

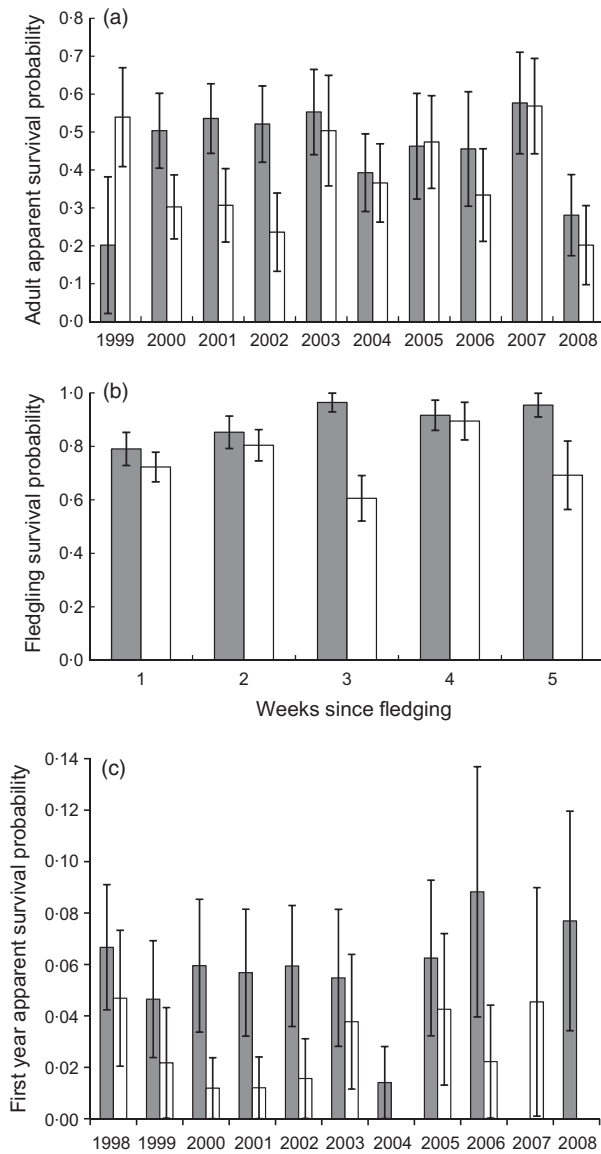


Fig. 4. Mean (± 1 SE) estimates of (a) ϕ_{ad} of males (shaded bars) and females (open bars), (b) ϕ_f of fledglings from early (shaded bars) and late (open bars) nests during 2006–2008 combined and (c) ϕ_{1Aapp} of chicks fledged from early (shaded bars) and late (open bars) broods. X-axis labels indicate the start of each survival period.

specific as well as general value. The most robust possible inference requires as rigorous estimation of demographic parameters as feasible, consideration of the sensitivity of conclusions to assumptions regarding parameters that can only be poorly estimated, and appropriate comparison with other systems. Such multi-faceted studies, however, remain rare.

Our study population of ring ouzels decreased by 67% during 1998–2009, mirroring decreases observed across the UK more widely (Sim *et al.* 2010). Comprehensive investigation of the demographic causes of this decrease showed that it did not simply reflect a substantial concurrent decrease in any single key demographic rate, as often assumed and observed (Gaillard, Festa-Bianchet & Yoccoz 1998; Robinson *et al.* 2004). Rather, it reflected varying combinations of demographic rates that consistently produced $\lambda < 1$. More subtle analysis of the potential and realized consequences of demographic variation is therefore required to evaluate the causes of population change and potential routes to recovery.

PROSPECTIVE ANALYSIS

Basic elasticities indicated that λ was most sensitive to variation in ϕ_{ad} , closely followed by RS_e and ϕ_{1eTrue} . These results are broadly consistent with previous studies of relatively long-lived vertebrates, which reported that λ was most sensitive to variation in ϕ_{ad} (e.g. Gaillard, Festa-Bianchet & Yoccoz 1998; Gaillard *et al.* 2000; Sæther & Bakke 2000; Reid *et al.* 2004; Ezard, Becker & Coulson 2006; Morrison & Hik 2007). However, basic elasticities do not consider covariation between demographic rates, which can account for a significant proportion of total variation in λ (Coulson, Gaillard & Festa-Bianchet 2005; Ezard, Becker & Coulson 2006). Calculating integrated elasticities, which do incorporate covariation, requires data describing the degree to which all demographic rates are constrained to covary. Demographic covariation is generally estimated across short time series from observational studies, and hence with substantial uncertainty over magnitude and causation (Reid *et al.* 2004; Ezard, Becker & Coulson 2006). However, integrated elasticities estimated from such data are still valuable in indicating whether conclusions based on basic elasticities are likely to be

Table 3. Basic (e) and integrated elasticities (IE) of each rate, the estimated percentage contribution to variation in λ estimated from e (X_e) and IE (X_{IE}), and the matrix of pairwise correlation coefficients among demographic rates. Rate codes are defined in Table 1. Values for IE, IE^2CV^2 and X_{IE} , assuming correlations between ϕ_{1eTrue} and ϕ_{1lTrue} ($r_{assumed}$) of 0.25, 0.50 and 0.75, are presented (see Methods)

	Correlation matrix									$r_{assumed} = 0.50$		$r_{assumed} = 0.25$			$r_{assumed} = 0.75$			
	e	CV	e^2CV^2	X_e	ϕ_{ad}	ϕ_{1eTrue}	ϕ_{1lTrue}	C_1	RS_e	IE	IE^2CV^2	X_{IE}	IE	IE^2CV^2	X_{IE}	IE	IE^2CV^2	X_{IE}
ϕ_{ad}	0.46	0.21	0.0097	21.2						0.208	0.002	6.0	0.208	0.002	4.8	0.208	0.002	7.4
ϕ_{1eTrue}	0.44	0.32	0.0202	44.0	-0.57					0.404	0.017	51.8	0.428	0.019	46.0	0.380	0.015	56.2
ϕ_{1lTrue}	0.10	0.32	0.0010	2.1	-0.57	0.50				0.232	0.006	17.1	0.343	0.012	29.4	0.122	0.002	5.8
C_1	0.10	0.12	0.0001	0.3	-0.07	-0.08	-0.08			0.369	0.002	6.3	0.369	0.002	4.9	0.369	0.002	7.7
RS_e	0.44	0.27	0.0139	30.3	0.30	-0.66	-0.66	0.55		0.294	0.006	18.8	0.294	0.006	14.9	0.294	0.006	23.0
RS_l	0.10	0.32	0.0010	2.1	0.64	-0.35	-0.35	0.03	-0.03	0.001	0.000	0.0	0.001	0.000	0.0	0.001	0.000	0.0

robust; yet remarkably few empirical studies have estimated integrated elasticities despite the clear need to do so (van Tienderen 1995; Coulson, Gaillard & Festa-Bianchet 2005).

There were substantial correlations among ring ouzel demographic rates, albeit across only 10–12 years and reflecting uncertain biological mechanisms. ϕ_{ad} was strongly positively correlated with RS_e and RS_l , while ϕ_{1True} was strongly negatively correlated with ϕ_{ad} , RS_e and RS_l . Given all provisos, integrated elasticities indicated that λ was most sensitive to variation in ϕ_{1eTrue} , closely followed by C_l , RS_e , ϕ_{1lTrue} , and ϕ_{ad} , but insensitive to variation in RS_l . Given the inevitably large uncertainty over the covariance structure, the integrated elasticities are perhaps best interpreted qualitatively rather than quantitatively. However, the substantial differences between basic and integrated elasticities emphasize the potential importance of accounting for demographic covariation, and the integrated elasticities suggest increased potential for variation in first-year survival to drive variation in λ compared to that predicted by basic elasticities.

Compared to the few other studies that have considered demographic covariation, all of which are subject to similar provisos to our study, our results contrast with Sæther & Bakke (2000), where λ was most elastic to variation in ϕ_{ad} in seven of eight bird species, and Reid *et al.* (2004) where λ was most elastic to variation in ϕ_{ad} , followed by pre-breeding ϕ and RS in red-billed choughs (*Pyrrhonorax pyrrhonorax*). A similar pattern has emerged in mammals, with integrated elasticities generally remaining highest for ϕ_{ad} (van Tienderen 1995; Coulson, Gaillard & Festa-Bianchet 2005), although in red deer (*Cervus elephas*) λ was most elastic to variation in RS (Benton, Grant & Clutton-Brock 1995).

RETROSPECTIVE ANALYSIS

The degree to which any demographic rate causes population change depends on the rate's variability as well as the sensitivity of λ to this variation (Gaillard, Festa-Bianchet & Yoccoz 1998; Gaillard *et al.* 2000; Sæther and Bakke 2000). In ring ouzels, ϕ_{1eTrue} , ϕ_{1lTrue} and RS_l varied most (Table 2). Notwithstanding the uncertainty around the estimated variance of ϕ_{1True} and the associated covariance structure, ϕ_{1True} apparently contributed most to variation in λ based on both basic and integrated elasticities. Previous studies of both avian (Reid *et al.* 2004; Robinson *et al.* 2004; Ezard, Becker & Coulson 2006; Schaub *et al.* 2006) and mammalian (Gaillard, Festa-Bianchet & Yoccoz 1998; Gaillard *et al.* 2000; Coulson, Gaillard & Festa-Bianchet 2005) demography also concluded that ϕ_1 contributes most to variation in λ , suggesting that variation in first-year or sub-adult survival may be a common demographic cause of population dynamics.

COMPARATIVE DEMOGRAPHY

There has been debate about whether the demographic rates to which λ is most sensitive, or those which account for most recent variation, are the most appropriate targets for population management (e.g. Benton & Grant 1999a; Wisdom,

Mills & Doak 2000; Sibly & Hone 2002; Coulson, Gaillard & Festa-Bianchet 2005). However, when $\lambda < 1$ throughout a demographic study, the demographic changes responsible for population decline may pre-date the study period used to directly inform either prospective or retrospective analysis. The most elastic and/or variable rates as currently observed may consequently differ from those which have changed since previous periods of population stability, or could change again in the future. In this situation, demographic comparisons with other appropriate populations and species can help identify rates that were lower than expected given a population's current life history (Peery *et al.* 2004).

Table S6 (Supporting information) compares our estimates of mean ring ouzel demography with those from other studies of ring ouzels and related species. These species comprise two closely related European species (blackbird *Turdus merula* and song thrush *Turdus philomelos*), and three closely related North American long-distance migrant species (wood thrush *Hylocichla mustelina*, ovenbird *Seiurus aurocapilla* and Swainson's thrush *Catharus ustulatus*). All data were collected using similar methodology to ours, and thus constitute the most relevant comparative data.

Our estimates of mean clutch and fledged brood size, RS_e , RS_l and ONSR lie within the ranges recently observed in other UK ring ouzel populations (Table S6, Supporting information). These data suggest that these components of reproductive success were not unduly low in our study population, although the comparative data are also from declining populations. Blackbird and song thrush have similar clutch and fledged brood sizes to ring ouzels, but substantially lower ONSR and hence lower RS per attempt (Table S6, Supporting information). However, while female song thrushes in a declining population had overall RS of 2.7, those in a stable population had overall RS of 4.0 (Thomson & Cotton 2000). Thus, our estimate of overall ring ouzel RS (3.6 young fledged/female/year) compares favourably with this stable song thrush population. One challenging component of RS to measure is the re-nesting (or multiple breeding) rate. Although few rigorous comparative data are available, the mean observed re-nesting rate (0.63) was similar to that recorded in wood thrushes (0.61, Friesen *et al.* 2000). Overall, therefore, there is little compelling evidence that the overall RS observed in our declining ring ouzel population was substantially less than might be expected for such a species.

Our survival probabilities estimated from radiotracking suggested weekly and 5-weekly ring ouzel ϕ_r were similar to those estimated for all song thrush broods from British ringing recoveries (Table S6, Supporting information). In addition, our ring ouzel ϕ_r estimates also lie within those obtained from radiotracking fledgling ovenbird, Swainson's thrush and wood thrush (Table S6, Supporting information). Our results are thus consistent with previous studies suggesting that ϕ_r is often a key component of avian ϕ_{1True} (Anders *et al.* 1997; Naef-Daenzer, Widmer & Nuber 2001; Rush & Stutchbury 2008), but do not suggest that ring ouzel ϕ_r was unusually low.

Mean estimated ϕ_{ad} was considerably lower than for British blackbirds and song thrushes (Table S6, Supporting information). However, British breeding populations of these species are largely sedentary and therefore not exposed to the same costs of migration as migratory ring ouzels (Wernham *et al.* 2002). Song thrushes breeding in Russia and Finland and wintering in southern Europe, and migratory wood and Swainson's thrushes and ovenbirds, also had higher ϕ_{ad} than ring ouzels (Table S6, Supporting information). Thus, our estimate of ϕ_{ad} for ring ouzel is substantially lower than for migratory species with otherwise relatively similar life histories.

Conclusions

Comprehensive prospective and retrospective analyses of 12 years of demographic data highlighted first-year survival as one key rate causing variation in λ in ring ouzels. However, comparison with available demographic data from species with similar life histories suggested that adult survival averaged lower than might be expected across the whole study period, and may therefore be at least partly responsible for the observed population decline. These analyses therefore emphasize that multiple approaches, and due consideration of conflicting answers, may be necessary to accurately diagnose the demographic causes of population change.

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References

Anders, A.D. & Marshall, M.R. (2005) Increasing the accuracy of productivity and survival estimates in assessing landbird population status. *Conservation Biology*, **19**, 66–74.

Anders, A.D., Dearborn, D.C., Faaborg, J. & Thompson, F.R. (1997) Juvenile survival in a population of neotropical migrant birds. *Conservation Biology*, **11**, 698–707.

Bailey, N.T.J. (1981) *Statistical Methods in Biology*. Edward Arnold, London.

Benton, T.G. & Grant, A. (1999a) Elasticity analysis as an important tool in evolutionary and population ecology. *Trends in Ecology and Evolution*, **14**, 467–471.

Benton, T.G. & Grant, A. (1999b) Optimal reproductive effort in stochastic, density-dependent environments. *Evolution*, **53**, 677–688.

Benton, T.G., Grant, A. & Clutton-Brock, T.H. (1995) Does environmental stochasticity matter? Analysis of red deer life-histories on Rum. *Evolutionary Ecology*, **9**, 559–574.

Burfield, I. (2002) *The breeding ecology and conservation of the ring ouzel Turdus torquatus in Britain*. Unpublished PhD thesis, University of Cambridge, Cambridge.

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

Burnham, K.P. & White, G.C. (2002) Evaluation of some random effects methodology applicable to bird ringing data. *Journal of Applied Statistics*, **29**, 245–264.

Caswell, H. (2001) *Matrix Population Models*. Sinauer, Sunderland, USA.

Cooch, E. & White, G.C. (2008) *Program MARK: A Gentle Introduction*. Available at: <http://www.phidot.org/software/mark/docs/book/>.

Cornulier, T., Elston, D.A., Arcese, P., Benton, T.G., Douglas, D.J.T., Lambin, X., Reid, J., Robinson, R.A. & Sutherland, W.J. (2009) Estimating the annual number of breeding attempts from breeding dates using mixture models. *Ecology Letters*, **12**, 1184–1193.

Coulson, T., Gaillard, J.M. & Festa-Bianchet, M. (2005) Decomposing the variation in population growth rate into contributions from multiple demographic rates. *Journal of Animal Ecology*, **74**, 789–801.

Ezard, T.H.G., Becker, P.H. & Coulson, T. (2006) The contributions of age and sex to variation in common tern population growth rate. *Journal of Animal Ecology*, **75**, 1379–1386.

Friesen, L.E., Wyatt, V.E., Cadman, M.D., Mackay, R.J., Cheskey, E.D., Allen, M.L. & Ramsay, D. (2000) Extent of double-brooding and seasonal movement of nesting females in a northern population of wood thrushes. *Wilson Bulletin*, **112**, 505–509.

Gaillard, J.M., Festa-Bianchet, M. & Yoccoz, N.G. (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, **13**, 58–63.

Gaillard, J.M. & Yoccoz, N.G. (2003) Temporal variation in survival of mammals: a case of environmental canalization? *Ecology*, **84**, 3294–3306.

Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toïgo, C. (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.

Green, R.E. (1999) Applications of large scale studies of demographic rates to bird conservation. *Bird Study*, **46**, S279–S288.

Greenwood, P.J. & Harvey, P.H. (1982) The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*, **13**, 1–21.

Hensler, G.L. (1985) Estimation and comparison of functions of daily nest survival probabilities using the Mayfield method. *Statistics in Ornithology* (eds B.J.T. Morgan & P.M. North). Springer, Berlin. *Lecture Notes in Statistics*, **29**, 289–302.

Heppell, S.S., Caswell, H. & Crowder, L.B. (2000) Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology*, **81**, 654–665.

Horvitz, C., Schemske, D.W. & Caswell, H. (1997) The relative 'importance' of life-history stages to population growth: prospective and retrospective analyses. *Structured-Population Models in Marine, Terrestrial and Freshwater Systems* (eds S. Tuljapurkar & H. Caswell), pp. 247–271. Chapman & Hall, New York.

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

Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67–118.

Loison, A., Sæther, B.-E., Jerstad, K. & Røstad, O.W. (2002) Disentangling the sources of variation in the survival of the European dipper. *Journal of Applied Statistics*, **29**, 289–304.

Martin, T.E. (1995) Avian life history evolution in relation to nest sites, nest predation and food. *Ecological Monographs*, **65**, 101–127.

Mayfield, H. (1975) Suggestions for calculating nest success. *Wilson Bulletin*, **87**, 456–466.

Morris, W.F. & Doak, D.F. (2004) Buffering of life histories against environmental stochasticity: accounting for a spurious correlation between the variabilities of vital rates and their contribution to fitness. *American Naturalist*, **163**, 579–590.

Morrison, S.F. & Hik, D.S. (2007) Demographic analysis of a declining pika *Ochotona collaris* population: linking survival to broad-scale climate patterns via spring snowmelt patterns. *Journal of Animal Ecology*, **76**, 899–907.

Naef-Daenzer, B., Widmer, F. & Nuber, M. (2001) Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology*, **70**, 730–738.

van Noordwijk, A.J. & de Jong, G. (1986) Acquisition and allocation of resources: their influence on variation in life-history traits. *American Naturalist*, **128**, 137–142.

Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R.D. (1998) Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology*, **67**, 518–536.

Payne, R.B. (1991) Natal dispersal and population structure in a migratory songbird, the Indigo Bunting. *Evolution*, **45**, 49–62.

Peach, W.J., Siriwardena, G.M. & Gregory, R.D. (1999) Long-term changes in over-winter survival rates explain the decline of reed buntings *Emberiza schoeniclus* in Britain. *Journal of Applied Ecology*, **36**, 798–811.

Peery, M.Z., Beissinger, S.R., Newman, S.H., Burkett, E.B. & Williams, T.D. (2004) Applying the declining population paradigm: diagnosing causes of

- low reproductive success in Marbled Murrelets. *Conservation Biology*, **18**, 1088–1098.
- Reid, J.M., Bignal, E.M., Bignall, S., McCracken, D.I. & Monaghan, P. (2004) Identifying the demographic determinants of population growth rate: a case study of red-billed choughs *Pyrrhocorax pyrrhocorax*. *Journal of Animal Ecology*, **73**, 777–788.
- Robinson, R.A., Green, R.E., Baillie, S.R., Peach, W.J. & Thomson, D.L. (2004) Demographic mechanisms of the population decline of the song thrush *Turdus philomelos* in Britain. *Journal of Animal Ecology*, **73**, 670–682.
- Rush, S.A. & Stutchbury, B.J.M. (2008) Survival of fledgling hooded warblers (*Wilsonia citrina*) in small and large forest fragments. *The Auk*, **125**, 183–191.
- Sæther, B.-E. & Bakke, Ø. (2000) Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, **81**, 642–653.
- SAS Institute. (2001) *SAS/STAT Users' Guide, Version 8*. SAS Institute Inc., Cary, NC.
- 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.
- Sibly, R.M. & Hone, J. (2002) Population growth rate and its determinants: an overview. *Philosophical Transactions of the Royal Society of London*, **357**, 1153–1170.
- Sim, I.M.W. & Rebecca, G.W. (2003) Catching methods and biometrics of breeding Ring ouzels *Turdus torquatus torquatus* in northeast Scotland. *Ring-ing & Migration*, **21**, 163–168.
- Sim, I.M.W., Rollie, C., Arthur, D., Benn, S., Booker, H., Fairbrother, V., Green, M., Hutchinson, K., Ludwig, S., Nicoll, M., Poxton, I., Rebecca, G., Smith, L., Stanbury, A. & Wilson, P. (2010) The decline of the Ring Ouzel in Britain. *British Birds*, **103**, 229–239.
- Siriwardena, G.M., Baillie, S.R., Crick, H.Q.P. & Wilson, J.D. (2000) The importance of variation in the breeding performance of seed-eating birds in determining their population trends on farmland. *Journal of Applied Ecology*, **37**, 128–148.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Stenhouse, I.J. & Robertson, G.J. (2005) Philopatry, site tenacity, mate fidelity and adult survival in Sabine's gulls. *The Condor*, **107**, 416–423.
- Svensson, L. (1992) *Identification Guide to European Passerines*. L. Svensson, Stockholm.
- Tavecchia, G., Coulson, T., Morgan, B.J.T., Pemberton, J.M., Pilkington, J., Gulland, F. & Clutton-Brock, T.H. (2005) Predictors of reproductive cost in Soay sheep. *Journal of Animal Ecology*, **74**, 201–213.
- Thompson, B.C., Knadle, G.E., Brubaker, D.L. & Brubaker, K.S. (2001) Nest success is not an adequate comparative estimate of avian reproduction. *Journal of Field Ornithology*, **72**, 527–536.
- Thomson, D.L. & Cotton, P.A. (2000) Understanding the decline of the British population of song thrushes *Turdus philomelos*. *Ecology and Conservation of Lowland Farmland Birds* (eds N.J. Aebischer, A.D. Evans, P.V. Grice & J.A. Vickery), pp. 151–155. British Ornithologists' Union, Tring, UK.
- van Tienderen, P.H. (1995) Life cycle trade-offs in matrix population models. *Ecology*, **76**, 2482–2489.
- Wernham, C.V., Toms, M.P., Marchant, J.H., Clark, J.A., Siriwardena, G.M. & Baillie, S.R. (eds) (2002) *The Migration Atlas: Movements of the Birds of Britain & Ireland*. T & A.D. Poyser, London.
- White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**(supplement), 120–138.
- Winkler, D.W., Wrege, P.H., Allen, P.E., Kast, T.L., Senesac, P., Wasson, M.F., Llambias, P.E., Ferretti, V. & Sullivan, P.J. (2004) Breeding dispersal and philopatry in the tree swallow. *The Condor*, **106**, 768–776.
- Wisdom, M.J., Mills, L.S. & Doak, D.F. (2000) Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology*, **81**, 628–641.

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Supporting Information

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

Table S1. Sample sizes for the variables shown in Fig. 3. Figures given are for the whole study area, whereas the number of early breeding pairs presented in Fig. 2 was accurately assessed annually from a core area, comprising approximately 80% of the whole study area. Thus, sample sizes for some years are higher than the number of early breeding pairs monitored in the core area. Rate codes are defined in Table 1.

Table S2. Models used to estimate daily nest survival rates (DNSR).

Table S3. Capture–mark–recapture models used to estimate adult annual apparent survival probabilities (ϕ_{ad}).

Table S4. Known fate models used to estimate post-fledging weekly survival probabilities (ϕ_f).

Table S5. Capture–mark–recapture models used to estimate first-year annual apparent survival probabilities (ϕ_1).

Table S6. Comparison of mean estimates of reproductive success (RS) and survival for ring ouzels in Glen Clunie with those from other studies on ring ouzels and other related species.

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