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Similar patterns of age-specific reproduction in an island and mainland population of great tits *Parus major*

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The process of ageing was long thought to be too infrequent to affect life-histories in natural populations. Long-term studies have, however, recently demonstrated ageing to be ubiquitous even in the wild, although confounding factors, such as emigration instead of mortality, or inter-population variation in rates of ageing have seldom been addressed. Here, we present analyses of female age-specific reproductive performance in a Dutch island population of great tits *Parus major*. For this population with limited connectivity to surrounding areas, we show that, between individuals, reproductive lifespan positively co-varies with recruit production, while within individuals performance improves up to 3 years of age, after which it gradually declines. We also show these patterns to be strikingly similar to those recently found in a less isolated British mainland population of great tits, characterised by different environmental conditions and life-history strategies, in particular the frequency of multiple breeding. Our results therefore suggest patterns of age-specific reproductive performance to be robust to both environmental and life-history variation.

Within-individual age-specific reproductive performance and survival probability are of growing importance to biologists, as their effect on population dynamics (e.g. Ezard et al. 2007) and life-history evolution (Bennett and Owens 2002) is becoming more and more apparent. Fortunately, while classic analyses of age-specific performance largely relied on a cross-sectional approach, and therefore could not account for selective effects via the appearance or disappearance of phenotypes from the population (Forslund and Pärt 1995), recent statistical advances have allowed for accurate estimation of within-individual age-specific trajectories from longitudinal data (van de Pol and Verhulst 2006, Nussey et al. 2008). Studies adopting this new approach have both shown that selective effects can be substantial (e.g. Nussey et al. 2006, McCleery et al. 2008, Bouwhuis et al. 2009), and provided compelling evidence for age-specificity of survival and various measures of reproductive performance (e.g. Cam et al. 2002, Brommer et al. 2007, Keller et al. 2008).

With respect to age-specific survival, the trait to study is straightforward. In the case of age-specific reproductive performance, however, the focal reproductive trait can range over the entire breeding cycle, for birds from laying date and clutch size (e.g. McCleery et al. 2008) to number of local recruits (e.g. Bouwhuis et al. 2009) or even grand-recruits (Bouwhuis et al. 2010b). This choice of trait may have consequences for detectability of age-specific performance (e.g. if age-effects increase in strength over the

breeding cycle, Bouwhuis et al. 2009), as well as its interpretation (e.g. producing fewer offspring at old age can be beneficial if these offspring are of better quality, but see Bouwhuis et al. 2010b). So far, the number of locally recruited offspring seems to be the best reproductive performance measure, since it combines offspring number and quality in terms of first-year survival. Yet, this measure only provides an unbiased estimate of reproductive senescence if emigration of offspring is independent of maternal age and reproductive lifespan. In many studies, offspring mortality and emigration are difficult to distinguish. As a solution, one can (1) use proxies for emigration to test for potential bias, such as dispersal distance (Ronce et al. 1998, Bouwhuis et al. 2009), (2) study patterns over multiple spatial scales to estimate the effect of biased dispersal (Tinbergen 2005), or (3) study isolated populations in which migration is quantitatively less important (e.g. Kluyver 1971).

Here, we adopt the latter approach and study within-individual patterns of age-specific recruit production, while controlling for between-individual heterogeneity, in a bird population that is relatively isolated: a population of great tits *Parus major* breeding on the Dutch island of Vlieland (Kluyver 1971, Verhulst and van Eck 1996, Postma and van Noordwijk 2005). A within-individual pattern of age-specific reproductive performance was recently shown for a British population of great tits at Wytham Woods (Bouwhuis et al. 2009), a population characterised by high

connectivity with the surrounding areas (Verhulst et al. 1997, McCleery et al. 2004), and a population in which offspring dispersal distance decreases with maternal reproductive lifespan (Bouwhuis et al. 2009), such that patterns of age-specific reproductive performance may be affected by differential emigration. Although populations can vary in more than one respect, and in this case connectivity, by replicating the analyses performed for the British population, we can begin to assess the robustness of age-specific patterns found.

Moreover, whereas within-species comparative studies of patterns of age-specific performance have occasionally been performed using wild-caught individuals brought into the laboratory (grasshoppers *Melanoplus sanguinipes/devastator*-Tatar et al. 1997; *Daphnia pulex-pulicaria*-Dudycha 2001; guppies *Poecilia reticulata*-Reznick et al. 2004; medflies *Ceratitis capitata*-Müller et al. 2009), we are aware of only a single replicate study in the wild. In Virginia opossums *Didelphis virginiana*, an island population having a long-term history of reduced exposure to predators was found to experience slower rates of ageing than a mainland population (Austad 1993). This is an exciting result, and similar comparative studies could shed light on whether other ecological factors underlie variation in rates of ageing between populations of the same species too. Here, we provide the first example in birds, by combining the data from the Vlieland and Wytham great tit populations. We test whether patterns of age-specific reproduction differ between these populations, which themselves differ in connectivity to the surrounding areas, environmental conditions and life-history parameters (Table 1).

Methods

Study populations and data collection

Data used here were collected as part of two long-term studies of great tits breeding in nest boxes (1) in Wytham Woods, UK, and (2) on the island of Vlieland, The Netherlands. These study populations were established in 1947 and 1955 respectively, and have been monitored continuously ever since. Each breeding season, nest boxes were checked to ascertain laying date, clutch size, hatching date, brood size and number of fledglings. Chicks were ringed when 15 days old, and parents were trapped at the nest whilst feeding their chicks. Parental age was based on

birth year for locally born birds, or plumage characteristics (Svensson 1994) at first catching for immigrants. Female immigrants comprised 45% and 22% of the Wytham and Vlieland dataset, respectively, but since most immigrants entered the population as yearlings, exact age was known for 92% and 98% of birds. For birds first captured with adult plumage, an age of 2 was assumed.

Data selection

As described previously (Bouwhuis et al. 2009), data from 1947–1960 were omitted from the Wytham dataset, because the number of nest boxes varied over this time period. Data from 1960–2008 were used, and breeding attempts were included in our dataset if: (1) the female parent was caught, (2) no experimental manipulation had occurred, (3) age and age at last reproduction (ALR) of the female parent were known, and (4) the number of local recruits produced was known. In total, this data selection resulted in 7 341 breeding attempts by 4 935 females, aged 1–9 years. For Vlieland, data from 1955–1975 and 1988–2008 were omitted because of extensive population-wide experimental manipulation during these periods. Data from 1976–1988 were used, and here, the data selection as described above resulted in 1 225 breeding years by 760 individual female great tits. Note that on Vlieland the number of recruits was summed over all broods reared in a breeding season, as Vlieland great tits regularly opted for multiple breeding (in 41% of the 1 225 breeding years; also see Verboven et al. 2001, Husby et al. 2009), whereas Wytham great tits very rarely produce a second brood (0.2% of all breeding attempts). On Vlieland, breeding age ranged from 1 to 7 years.

Statistical analysis

Patterns of age-specific recruit production have previously been analysed, and reported, for the Wytham population (Bouwhuis et al. 2009), and here we repeated these analyses for the Vlieland population. As described in Bouwhuis et al. (2009), we analysed the effect of maternal age on female recruit production using additive, cross-classified random effect models with Poisson distributed errors and a Markov chain Monte Carlo estimation algorithm with 100 000 iterations to assure mixing of parameters (Browne et al. 2007). Our model included fixed effects of (1) female status (locally-born versus immigrant, two-level class variable), (2) female age and age², (3) female ALR and ALR², and (4) interactions between female ALR and age and age². In addition, they included random effects of female identity, year, and area (there are five separate woodlands on Vlieland, which differ in size and vegetation, Kluyver 1971), to account for repeated, non-independent observations on the same bird, and spatiotemporal environmental heterogeneity, respectively. The full model (Table 2) was simplified by backward stepwise removal of least-significant terms, where significance ($p < 0.05$, two-tailed) was assessed using the Wald statistic calculated from the posterior mean and standard deviation, tested against a chi-square distribution.

Table 1. Some characteristics of the great tit populations breeding on the island of Vlieland (NL) and in Wytham Woods (UK).

Parameter	Vlieland	Wytham
Female immigration rate	22%	45%
Recruitment rate	12%	10%
Multiple breeding	yes	no
Beeches present	no	yes
Average breeding density (ha ⁻¹)	0.4	0.8
Average clutch size per season	11.8	8.7
Average brood size per season	9.5	8.1
Average nr. of fledglings per season	7.7	7.0
Average nr. of recruits per season	1.0	0.7
Average breeding age	1.8	1.8
Average reproductive lifespan	1.9	1.9

Table 2. Results from models testing the effects of age and selective disappearance (estimated using reproductive lifespan, ALR) on recruitment of offspring to the breeding population by female great tits on Vlieland. Estimates for random effects are marked by (r). Shown are parameter estimates (Est.) with standard errors, 95% CI's and significance (* for $p < 0.05$). Values for significant terms are in bold, and values for non-significant terms are presented as estimated when re-added to the minimal adequate model.

Parameter	Est.	SE	95% CI	χ^2 (DF = 1)
Age	0.202	0.112	−0.014 – 0.423	3.290
Age ²	−0.038	0.019	−0.075 – −0.002	4.046*
ALR	0.059	0.026	0.008 – 0.109	5.307*
ALR ²	−0.016	0.012	−0.037 – 0.007	1.839
ALR × age	−0.012	0.025	−0.064 – 0.036	0.209
ALR × age ²	−0.009	0.012	−0.036 – 0.015	0.499
Immigrant status	0.039	0.089	−0.215 – 0.134	0.192
Female (r)	0.122	0.039	.	.
Year (r)	0.266	0.141	.	.
Area (r)	0.078	0.160	.	.

To compare the effects of age and selective disappearance on recruitment of offspring between female great tits on the island of Vlieland and in the British population of Wytham Woods, we combined both datasets. Within the longitudinal model setup, we tested for the overall effects of immigrant status, age, age², ALR and for the effects of population, both as a main effect and in interaction with immigrant status, age, age² and ALR using the model selection described above (Table 3). The comparative model was run both using the maximal dataset for each population, and using only the data collected between 1976 and 1988 in both populations to assure that our results were not driven by the different time periods used.

All models were fitted using MLwiN v. 2.02 (Browne et al. 2001, Rasbash et al. 2005).

Results

Vlieland patterns of age-specific reproduction

We found female great tits to exhibit age-specific variation in their reproductive performance (Table 2). The significantly

negative quadratic effect of age suggests within-individual improvement in recruit production up to the average ($\pm$ SE) age of 2.91 ($\pm$ 0.04) years, after which performance declines (Fig. 1, fitted curves). The significant between-individual effect of ALR reveals a positive correlation between female reproductive lifespan and annual recruit production. This means that poor-quality breeders selectively disappear from the population, an effect masking signs of senescence at the population-level (Fig. 1, circles), as also evidenced by a poor fit between the population-level circles and individual-level curves in Fig. 1. Interactions between ALR and age, which would imply that age-effects differ between females of different reproductive lifespan, were not significant and were dropped from the model. Similarly, a quadratic effect of ALR did not explain a significant amount of variation in reproductive performance, suggesting no combined effects of selective disappearance and a trade-off between reproduction and survival, or variation in the rate of selective disappearance with age. Finally, locally-born females and females that were born elsewhere and immigrated into the Vlieland population, did not differ significantly in their annual production of local recruits.

Table 3. Results from models testing the effects of population (Vlieland vs Wytham), age and selective disappearance (estimated using reproductive lifespan, ALR) on recruitment of offspring by female great tits, using all data ($n = 8\,566$, left) and using only the years for which data were available for both populations (i.e. 1976–1988, $n = 3\,330$, right). Estimates (Est.) for random effects are marked by (r). Shown are parameter estimates with standard errors, 95% CI's and significance (** for $p < 0.01$, * for $p < 0.05$). Values for significant terms are in bold, and values for non-significant terms are presented as estimated when re-added to the minimal adequate model.

Parameter	All data				Restricted data: 1976–1988			
	Est.	SE	95% CI	χ^2 (DF = 1)	Est.	SE	95% CI	χ^2 (DF = 1)
Age	0.175	0.044	0.091 – 0.262	16.132***	0.157	0.066	0.029 – 0.290	5.712*
Age ²	−0.032	0.008	−0.047 – −0.018	17.882***	−0.029	0.011	−0.052 – −0.008	7.188**
ALR	0.046	0.012	0.022 – 0.071	13.829***	0.066	0.018	0.031 – 0.101	13.955***
Immigrant status	0.110	0.028	0.055 – 0.065	15.033***	0.122	0.047	0.032 – 0.215	6.763**
Population	0.173	0.187	−0.249 – 0.490	0.860	0.032	0.101	−0.180 – 0.225	0.098
Population × age	0.007	0.030	−0.049 – 0.066	0.055	−0.004	0.036	−0.075 – 0.067	0.014
Population × age ²	−0.009	0.018	−0.041 – 0.026	0.254	−0.013	0.022	−0.058 – 0.030	0.367
Population × ALR	0.010	0.022	−0.033 – 0.054	0.209	0.002	0.028	−0.052 – 0.056	0.005
Population × status	−0.043	0.093	−0.231 – 0.136	0.212	−0.096	0.102	−0.295 – 0.105	0.884
Female (r)	0.085	0.049	.	.	0.112	0.027	.	.
Year (r)	0.249	0.051	.	.	0.230	0.120	.	.
Area (r)	0.028	0.016	.	.	0.025	0.015	.	.

Figure 1. Age-specific reproductive performance in 760 female great tits on Vlieland. Circles show the population-level average number of recruits produced with standard errors and sample size; the dotted line shows the overall mean. Curves are calculated from the minimal adequate model (Table 2), such that lines represent birds of different reproductive lifespan, and the shape of the curves reflects within-individual improvement and senescence. Note that the poor fit between the curves and circles represents the effect of selective disappearance of poor-quality breeders from the breeding population, an effect masking signs of senescence at the population level.

Inter-population comparison

Combining the Vlieland and Wytham datasets resulted in a total of 8 566 breeding years by 5 695 individual females, whose age ranged from 1–9, averaging 1.81. Our analyses of recruit production confirmed that, overall, female great tits exhibit age-specific variation in their reproductive performance, and experience selective disappearance of poor-quality breeders from the breeding population (Table 3). Despite the immigrant status effect being non-significant for Vlieland (see above), there was a significant overall effect of female immigrant status that did not differ significantly between the populations, showing that locally-born females outperform immigrant females.

Moreover, the effects of female age, age² and ALR on recruit production did not differ between the Vlieland and Wytham populations, as evidenced by the population parameter never reaching statistical significance, either as a main effect, or in interaction with female age, age² or ALR (Table 3). The similarity of age effects of reproductive performance was also confirmed by a strong correlation between age-specific recruit production for ages 1–7 in the two populations: for the population-level averages (Pearson's $r = 0.884$, Fig. 2 solid circles), as well as the fitted values for birds of average ALR from the minimal adequate models (Pearson's $r = 0.999$, Fig. 2 open circles).

Restricting the dataset to breeding events from the years for which data were available for both populations, i.e. 1976–1988, did not alter the qualitative conclusions of the models (Table 3).

Figure 2. Correlation between age-specific recruit production of female great tits in two populations: Vlieland (NL) and Wytham Woods (UK). Solid circles represent population-level average recruit production, whereas open circles are fitted values from individual-level minimal adequate models for birds of average reproductive lifespan (i.e. 1.9 years, which is why points are below the population-level average values). Numbers are the age classes to which the data points belong.

Discussion

Our analyses of age-specific reproductive performance in a Dutch island population of great tits led to two main findings: between-individual heterogeneity in survival and reproductive performance, and, after accounting for this heterogeneity, within-individual age-specificity of recruit production. Moreover, our inter-population comparison showed these patterns to be statistically indistinguishable from the patterns found in a British population of great tits.

Between-individual heterogeneity was revealed by a positive correlation between female reproductive lifespan (measured as age at last reproduction, ALR) and annual recruit production. A similar pattern has previously been found for kittiwakes *Rissa tridactyla* (Cam et al. 2002), and was suggested to reflect differences in individual quality (but see Wilson and Nussey 2010). Alternatively, a positive correlation between female reproductive lifespan and recruit production could arise if females which are poor survivors, or are more prone to disperse between breeding events and leave the study area, produce offspring which are more likely to emigrate. For the Wytham population, the likelihood of this option was previously assessed by testing for a relation between maternal ALR and offspring natal dispersal distance (Bouwhuis et al. 2009), although the factors determining dispersal distance within a woodland may differ from the factors determining whether or not individuals emigrate from a woodland altogether (Verhulst et al. 1997). Females with a longer reproductive lifespan produced offspring that dispersed less far within the study (maternal ALR: -0.320 ± 0.124 , $\chi^2_1 = 6.633$, $p = 0.010$), suggesting one of these mechanisms may be at work if dispersal distance also reflects the emigration process.

For Vlieland, which is more isolated than Wytham, we expect emigration to be quantitatively less important (Kluyver 1971). Nevertheless, an analysis of offspring natal dispersal distance revealed a quantitatively similar, although non-significant, effect of maternal ALR ($-0.382 \pm 0.267 \text{ m}^{0.5} \text{ yr}^{-1}$, $\chi^2_1 = 2.052$, $p = 0.152$). Combination of the Wytham and Vlieland dataset confirmed the relationship to be similar (population*ALR: -0.090 ± 0.252 , $\chi^2_1 = 0.129$, $p = 0.719$) and the overall ALR effect to be significantly negative (-0.324 ± 0.116 , $\chi^2_1 = 7.865$, $p = 0.005$). Therefore, if emigration is indeed less important on Vlieland, we may expect natal dispersal distance to reflect processes other than emigration (also see Verhulst et al. 1997), and the positive correlation between reproductive lifespan and recruit production to mainly reflect female and offspring survival, i.e. individual quality differences. More work on the origin of individual quality (e.g. Hamel et al. 2009a, Hamel et al. 2009b), and on the genetic basis of longevity and dispersal (e.g. McCleery et al. 2004, Doligez and Pärt 2008), may provide mechanistic support for this idea.

Controlling for between-individual heterogeneity is crucial for estimation of average within-individual change with age from longitudinal data (van de Pol and Verhulst 2006). Here, while accounting for reproductive lifespan our analyses of Vlieland great tits revealed a significant quadratic effect of female age on recruit production. These analyses showed that the average female improves in reproductive performance up to the age of three years, due to improved skills or optimisation of reproductive effort (Forslund and Pärt 1995), after which performance deteriorates, most likely due to senescence (Williams 1957, Hamilton 1966; but see McNamara et al. 2009). Again, this pattern is statistically indistinguishable from that found in the British population, where recruit production also showed a quadratic relationship with age, and also peaked at three years of age (Bouwhuis et al. 2009). Based on the absence of a population-effect on patterns of age-specific reproduction, and the similarity of age-specificity as shown in Fig. 2, we can therefore conclude that the great tits on Vlieland and in Wytham show strikingly similar patterns of improvement and deterioration in reproductive performance with age, and thus that patterns of age-specific reproductive performance are robust.

Whereas females immigrating into the population of Vlieland are known to lay larger clutches than locally-born females (Verhulst 1995, Postma and van Noordwijk 2005), we found no significant difference between residents and immigrants in terms of recruit production. This agrees with previous analyses of lifetime reproductive success (LRS) in these birds, which was 0.6 recruits lower in immigrants (i.e. 37%, Verhulst and van Eck 1996), not due to a difference in recruit production, but due to immigrant females experiencing reduced local survival. In the Wytham population, immigrants are known to suffer from reduced LRS as well (0.4 recruits, i.e. 15%, Bouwhuis et al. 2010a), but there it originates from impaired reproductive performance rather than survival. This explains why the female immigrant status effect is significant in analyses of age-specific reproductive performance for Wytham (Bouwhuis et al. 2009), but not for Vlieland, although analyses of the combined datasets does not indicate the immigrant status effect to significantly differ between the populations, and

show that overall immigrant females produce fewer recruits annually than resident females.

Finally, our finding of strikingly similar patterns of age-specific reproductive performance in a Dutch island and British mainland population of great tits suggests the numerous demographic, environmental and life-history differences between these two bird populations (Table 1) to have no pronounced effect on age-specific patterns of reproduction. In accordance with this idea, both populations are characterised by very similar average breeding age (Table 1), which was recently found to explain most variation in rates of ageing between species (Jones et al. 2008). Hence it may not be coincidental that both average breeding age and the rate of senescence are strikingly similar in our two study populations. We hope future work, employing similar analytical techniques, will broaden the scope of the work presented here, allowing more extensive comparative analyses of rates of reproductive ageing in birds.

In conclusion, our analyses of a Dutch island population of great tits, characterised by relatively low migration rates and relatively high local recruitment rates, have revealed between-individual heterogeneity, and within-individual age-specificity of reproductive performance. Both patterns are strikingly similar to recent findings in a British population of great tits, and although our analyses increase the population sample size merely from one to two, they strongly suggest that the patterns found are robust under varying levels of connectivity, environmental conditions and concomitant differences in life histories.

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