Experimental evidence of environmental effects on age-specific reproductive success: the importance of resource quality

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Age-specific access to high-quality resources (e.g. territory or nest site) might be an important determinant for improved reproductive performance with increasing age. I experimentally investigated the effects of territory quality versus other age-related improvements in breeding competence (e.g. foraging skills, breeding experience and local knowledge) on age-specific reproductive success. Territory quality (i.e. territory field layer height) was manipulated in year 2 of northern wheatears (*Oenanthe oenanthe*) that were breeding in the same territory in two consecutive years. Changing territory quality by changing field layer height had a strong effect on within-individual change in the reproductive success of wheatears. This effect was mainly due to a corresponding change in nest predation risk. When territory quality was kept constant (i.e. no between-year change in territory field layer height), within-individual reproductive success did not change between subsequent years. Thus, age-related improvements in foraging skills, breeding experience and local familiarity had no significant effect on within-individual changes in reproductive success. Increased reproductive success with increased age in northern wheatears is therefore mainly explained by an improved access to high-quality territories with increasing age. I conclude that age-dependent access to high-quality breeding resources might be a widespread phenomenon in nature.

Keywords: age; breeding experience; foraging skills; local familiarity; nest predation; reproductive success

1. INTRODUCTION

The reproductive success of first-time breeders is usually markedly lower than for older breeders, such that age often explains a large proportion of individual variation in the reproductive success of iteroparous animals (Clutton-Brock 1988; Newton 1989). There are many potential causes of age-specific reproductive performance and their relative importance might strongly affect, for example, pathways of life-history evolution (Charlesworth 1994), the evolution of mate preferences and secondary sexual traits (Andersson 1994), and population dynamics (Sutherland 1996).

Commonly suggested major causes of age-specific reproduction early in life are (i) progressive appearance or disappearance of phenotypes (e.g. differential survival), (ii) age-related improvements in competence (e.g. foraging and breeding skills), and (iii) optimization of reproductive effort (for a review, see Forslund & Pärt 1995). Factors associated with the first two explanations have been widely tested by data from long-term studies (see, for example, Clutton-Brock 1988; Newton 1989; Forslund & Pärt 1995). However, most of these studies have been observational, thus making an unequivocal separation of the effects of different age-related factors difficult or impossible. Few studies have used experimental manipulation to investigate the potential causes of patterns in age-specific reproduction (Källander 1974; Desrochers 1992a; Pärt 1995; DeForest & Gaston 1996; Catry & Furness 1999; Daunt *et al.* 1999). Although many previous studies indicate that older individuals breed on better sites than younger ones (e.g. Greenwood & Harvey 1982), no experimental study has controlled for the effects of age differences in nest site or territory quality.

Northern wheatears (*Oenanthe oenanthe*) that breed on Swedish farmland show a typical pattern of age-specific reproductive performance in which 1 year old birds do less well than older ones (Pärt 2001). Northern wheatears are short-lived, migratory birds that prefer to breed and forage in habitats dominated by a short field layer (Conder 1989; Tye 1992), with reproductive success inversely related to the height of the field layer in the territory (Tye 1992; Pärt 2001). The height of the field layer is probably the most important vegetation determinant of territory quality for breeding wheatears, because a short field layer increases prey availability and decreases nest predation risk (Conder 1989; Tye 1992; Pärt 2001). Previous results from a long-term study show that about 48% of yearling wheatears breed in territories with a permanently short field layer, whereas the corresponding figure for older birds is about 63%, and this age difference in territory field layer height is highly significant (Pärt 2001). Also, most yearlings (74%) that shifted territory between subsequent years, shifted from one with a field layer that grew tall during the incubation to nestling period, to one with a permanently short field layer (Pärt 2001). Thus, age differences in territory quality might be a major cause of the observed age-specific reproductive performance in this population (Pärt 2001).

Here, I present a study that manipulates territory quality by changing territory field layer height (within the natural range) to disentangle the causes of age-specific reproductive success of northern wheatears. I used longitudinal data of individual reproductive success and I used a manipulation of territory field layer height for individuals breeding in the same territory in two consecutive years. If improvements in foraging skills, breeding experience and

knowledge of territorial resources affect individual reproductive success, within-individual reproductive success should generally improve with increasing age, and especially so for birds breeding in the same territory of a constant quality during their two consecutive breeding years. However, if age differences in territory quality are the major determinants of age-specific reproductive success, no such improvement in reproductive success would be expected, except for birds that received an experimentally improved territory quality (i.e. from tall to short field layer between years 1 and 2).

2. METHODS

(a) *Study population*

This study was conducted between 1993 and 2000 in a 60 km² study area that was situated in a farmland southeast of Uppsala, Sweden (59°50' N, 17°50' E). About 120–180 pairs of wheatears breed annually in the study area (for details, see Pärt 2001).

The northern wheatear is a small (21 g) insectivorous bird species that winters in Africa, south of the Sahara, and breeds in Europe, Asia and the northern parts of North America. In my study area, males typically arrive at the breeding grounds a few days before females; that is, from mid-April to mid-May. Older birds (≥ 2 years old) arrive, on average, a week before yearlings. Wheatears usually nest in cavities near or on the ground, often under stones, in stone piles and in stone walls. Egg-laying starts in early May, incubation lasts for 13 days and nestlings stay in the nest for about 15 days. All established males were possible to age as yearlings (brown wings) or older (black wings; Svensson 1992; Pärt 2001). About 95% of the females caught were classified as either yearlings (worn light brown remiges and coverts, worn tail feathers, pale inside of upper mandible) or older (≥ 2 years old; darker, less worn feathers; Svensson 1992; Jenni & Winkler 1994). Data on breeding females that were ringed as nestlings ($n = 70$) show that female age could be classified with a high certainty (only 7% were classified as the wrong age class). In all years, there was a strong positive association between male and female age within pairs; old males were generally mated with old females (86% of 385 old males), whereas yearling males were mated mainly with yearling females (73% of 263 yearling males; Pärt 2001).

(b) *Manipulation of territory field layer height*

All territories in this study were situated in farmland grasslands. The height of the field layer within these grasslands was estimated (visually) as the proportion consisting of short (5 cm high), medium (5–15 cm high) and high (15 cm high) dense vegetation. This visual estimate of grass height is closely correlated with an estimate based on eight random sward-stick measurements of grass height per hectare (Pearson's correlation coefficient, $r = 0.95$, $n = 18$ grasslands, $p < 0.0001$). Data on the height of the field layer were collected in late April, the first week of June, the last week of June and when the nestlings were about 10 days old. Grasslands differed markedly in the growth of the field layer because of different management regimes, and therefore territories were grouped into two distinct classes—'short' and 'tall'. In this study, all of the 'short' territories were dominated ($> 80\%$) by a field layer that was shorter than 5 cm during the whole breeding period due to grazing (pastures) or frequent mowing (farmyard lawns). In 'tall' territories all of the field layer grew to a height of at least 15 cm during the stage of

late incubation and nestling care because of the absence of grazing or continuous mowing in spring. This classification of territories encompassed most of the variation in field layer height and territory quality, as shown by its strong relationship with the reproductive success of wheatears (Pärt 2001).

Between years, however, farmers sometimes changed the management regimes for their grasslands so that managed grasslands were temporarily set aside or were grazed later in the season and vice versa. The decisions to change management regime between years were made in May, i.e. after the wheatears had chosen their territories and started to breed. Because all managed grasslands were grazed or mowed in the preceding autumn to prevent accumulation of litter or recruitment of shrubs and trees (Söderström *et al.* 2001), all territories chosen by wheatears were dominated by a short field layer ($> 90\%$ of the territory) at the time of territory establishment. Thus, when the wheatears returned to the same territory as in the previous year, they returned to a site that was visually similar as in the previous year at arrival. The between-year changes in management regimes were highly unpredictable as they were mainly based on dates of livestock release, which in turn were dependent on unpredictable factors, such as timing of spring tillage, repair of fences and sudden economic downturns (Söderström *et al.* 2001). The number of fledged young produced did not differ between manipulated territories and the other territories in the year before the manipulation (i.e. year 1: ANOVA (field layer height, manipulation); manipulation effect: $F_{1,89} = 0.08$, $p = 0.77$). I therefore viewed the manipulations of territory field layer height as random with respect to the territory-specific reproductive success of wheatears.

The experiment created three groups of territories with respect to between-year changes in field layer height: (i) short to tall, (ii) tall to short, and (iii) no change. The 'no change' group acted as a control and included territories that had a field layer that was permanently short ($n = 49$) or that grew tall ($n = 19$) during both years. All territories used in this study were spatially separated (> 500 m apart) and the three groups were highly interdispersed spatially and temporally.

(c) *Data selection and statistics*

I only used data for birds that bred in two consecutive years in the same territory. For individuals with breeding records from more than 2 years, I selected the first 2 year observation to avoid pseudoreplication. In total, 40 individuals were yearlings and 52 were 2 years or more old (i.e. old) in their first year of observation. Most old birds were probably 2 years old in their first year of observation, as very few individuals recruit to the population at ages older than 2 years (3 of 150 locally born recruits). Because age differences in birds are usually most marked during the first 2 years of life (see, for example, Forslund & Pärt 1995), age class at first observation was included in the analyses (i.e. yearling versus older). In all analyses, sexes were combined. If both sexes of a pair survived and bred on the same territory in two subsequent years, I selected only the youngest in the pair to be included in the analyses to avoid pseudoreplication. Sex effects in age-specific reproduction were not considered because I found no significant effects of sex in the initial analyses ($p > 0.20$ in all tests), although the sample size was too small to investigate small effects of sex on age-specific reproduction. Furthermore, a cross-sectional analysis on a larger dataset ($n = 724$ pairs) showed no significant sex differences in patterns of age-specific reproductive success ($p > 0.30$, T. Pärt, unpublished data). The number of fledged young was standardized for

Table 1. The effect of an experimental change in territory field layer height (i.e. short to tall, tall to short and no change) and age class (1 year and ≥ 2 years old at the first year of observation) on within-individual change in number of fledglings by northern wheatears breeding on the same territory in two consecutive years.

	d.f.	sum of squares	<i>F</i>	<i>p</i>
change in field layer height (<i>a</i>)	2	169.89	9.05	0.0003
age class (<i>b</i>)	1	14.36	1.53	0.22
<i>a</i> $\times$ <i>b</i>	2	14.04	0.75	0.48
error	86	806.80	—	—

yearly differences (mean = 0), and within-individual change in fledgling production was analysed by an ANOVA. Within-individual changes in breeding success (i.e. 0 or 1) could obtain values of -1 , 0 and $+1$, and were analysed with ordinal logistic regression. The models presented here had statistically significant effects ($p < 0.01$). All tests were done in JMP v. 3.2 (SAS 1999) on balanced datasets.

3. RESULTS

The manipulation of territory quality by changing field layer height of individuals that bred in the same territory in two consecutive years showed that a change in field layer height strongly affected within-individual change in fledgling production (tables 1 and 2). Individual reproductive success improved when the territory field layer height was manipulated from tall to short, whereas it decreased when the field layer was changed from short to tall (figure 1, table 2). Within-individual change in fledgling production did not differ between young and old individuals (i.e. yearling or older in the first year of observation, respectively; table 1). Furthermore, the response to the manipulation of field layer height did not differ between age classes, as the interaction term was not significant (table 1). Within-individual changes in breeding success (i.e. failed versus successful, mainly reflecting nest predation; Pärt 2001) explained most (68%) of the variation in within-individual change in the number of fledged young (see table 2). Manipulating territory field layer height had a strong effect on within-individual change in breeding success (ordinal logistic regression (age class, change in field layer height); change in field layer: $\chi^2_2 = 15.6$, $p = 0.0004$; age class: $\chi^2_1 = 0.22$, $p = 0.64$).

If reproductive success improves with increasing age, owing to improved skills in foraging and breeding activities, one would expect fledgling production to be higher in the second year as compared with the first year of breeding, for birds that bred in territories with a constant quality between years. However, individuals did not improve their reproductive success with increasing age when territory field layer height was kept constant between years (paired *t*-test: mean difference (year 2 – year 1) $\pm$ s.e. = -0.36 ± 0.51 , -0.50 ± 0.54 , and -0.45 ± 0.38 , for young, old, and age classes pooled, respectively; $p > 0.25$ in all tests). To test whether age-related skills might be revealed only in particular environmental conditions, I investigated whether within-individual

Table 2. Number of fledglings (mean $\pm$ s.e.) and breeding success (per cent successful) of northern wheatears breeding on the same territory in two subsequent years. Raw data are presented for each experimental group (i.e. in relation to a manipulation in territory field layer height in year 2).

	<i>n</i>	year 1		year 2	
		mean	s.e.	mean	s.e.
number fledged					
tall to short	8	2.75	0.88	4.57	0.92
same	68	4.79	0.26	4.26	0.30
short to tall	16	5.26	0.41	2.06	0.61
breeding success					
tall to short	8	62.5	—	87.5	—
same	68	85.3	—	80.9	—
short to tall	16	93.7	—	43.8	—

change in fledgling production differed depending on whether birds were breeding in permanently good or poor territories. However, within-individual change in fledgling production did not differ between birds that bred in territories with short and tall field layer in both years (ANOVA (age class, field layer height); field layer height effect: $F_{1,65} = 0.37$, $p = 0.54$).

4. DISCUSSION

Northern wheatears show a marked age difference in reproductive performance between 1 and 2 years of age and this is partly due to an age difference in nest predation risk (Pärt 2001). Old wheatears potentially have better access to high-quality territories than yearlings due to an earlier arrival at the breeding grounds and a better knowledge of where to find the best territories (Pärt 2001). Furthermore, unsuccessful yearlings improve their choice of future territory by choosing a new territory on the basis of field layer height and conspecific reproductive success in the summer a year before the next breeding attempt (T. Pärt, unpublished data). Yearlings have also been shown to shift to better territories in the next year, and observational data indicate that age differences in territory quality might be a major factor causing this age-specific pattern of reproductive success (Pärt 2001). However, because high-quality individuals are expected to select the best sites, such observational data might be confounded by quality differences between individuals.

By manipulating territory quality after territory establishment of individuals breeding in the same territory in two subsequent years, I was able to elucidate the direct effects of territory quality on individual reproductive success. The results of the experiment were strikingly clear. A manipulation from tall to short field layer improved reproductive success, whereas a manipulation from short to tall field layer decreased individual reproductive success (figure 1). Thus, territory field layer height had a strong effect on individual reproductive success. By contrast, there was no tendency for increased reproductive success with increasing age when changes in territory quality were controlled for.

Figure 1. Within-individual change in fledgling production (year 2 – year 1) in relation to an experimental change in territory field layer height in year 2 of northern wheatears breeding on the same territory in two consecutive years. *n*-values, least-squares means (see model in table 1) and standard error (s.e.) bars are shown for each experimental class. *p*-values refer to contrasts from the model presented in table 1.

Several previous studies have shown that first-time breeders on average breed on poorer sites than older ones (e.g. Greenwood & Harvey 1982; Møller 1991; Newton 1991, 1992; Holmes *et al.* 1996), but this is the first, to my knowledge, experimental investigation of the importance of resource quality on age-specific reproduction. The strong effect of territory field layer height combined with a lack of other age effects on reproductive success indicate that resource quality, and especially age-specific acquisition to high-quality resources, might be a major determinant of age-specific patterns of reproductive performance.

Improvements in foraging skills, breeding experience and local knowledge (at the spatial scale of a territory) are generally acknowledged as being important determinants of improved reproductive performance with increasing age (Newton 1989; Forslund & Pärt 1995). Foraging skills clearly improve over the earliest, juvenile, stages of life (for reviews, see Marchetti & Price 1989; Wunderle 1991). Whether foraging skills and other skills continue to improve among reproductive age classes is generally not known, because experiments are rarely used when testing hypotheses of age-specific reproductive performance (Forslund & Pärt 1995). Two experiments using food supplementation indicate that food availability and possibly age-related foraging skills might be important determinants for age-specific reproductive success, mainly because of an advanced timing of breeding (Källander 1974; Desrochers 1992*a,b*; but see Lundberg & Davies (1985) for no effects). However, two other experiments directly manipulated the breeding time of young and old pairs (old pairs generally bred earlier than young pairs) and showed that age differences in breeding time were not responsible for the observed age difference in nestling survival (DeForest & Gaston 1996; Daunt *et al.* 1999). Last, an experiment that manipulated age of first breeding, and thus breeding experience, indicated no

effects of breeding experience on age-specific reproductive success in a short-lived bird species (Pärt 1995). In most of these studies, age-specific foraging skills have been used as a default explanation for the unexplained variation in reproductive success (see also Catry & Furness 1999), but none of them fully controlled for age differences in the acquisition of defended resources. It is possible, therefore, that some of the above results might have been confounded by age differences in resource quality. For example, other studies of the same species or species with similar ecology, as investigated in the above-mentioned studies, indicate that territory or nest-site quality might be an important determinant of reproductive success (e.g. Shaw 1986; Møller 1991; Hatchwell *et al.* 1996; Danchin *et al.* 1998).

Studies of colonial, long-lived bird species, such as many seabirds, often show starvation of nestlings as a major component of age-specific reproductive performance, implying that foraging skills and breeding experience constrain reproductive success (e.g. DeForest & Gaston 1996; Daunt *et al.* 1999, and references therein). However, nest-site quality also varies in colonial species, especially in relation to nest predation risk (e.g. Danchin *et al.* 1998). Nest predation risk might in itself affect incubation behaviour and nestling food provisioning rates (e.g. Martin *et al.* 2000), and consequently produce results that are superficially similar to those expected under foraging or breeding experience constraints. Thus, although improved competence in foraging and breeding activities are likely to influence the reproductive performance of long-lived species (e.g. Daunt *et al.* 1999; Catry & Furness 1999), the effects of an age-dependent change in such intrinsic capacities might have been inflated by a corresponding change in nest-site quality.

5. CONCLUSIONS

My study highlights the need to invoke age-specific variation in the quality of defended resources when investigating the causes of age-specific reproductive performance. This is because older individuals generally have better access to high-quality resources than do young individuals because of age differences in dominance, timing of resource acquisition and better prior knowledge of where to find the best resources (Danchin *et al.* 1998). In species that show a resource-defence mating system (e.g. many birds), age-specific variation in reproductive success is likely to be at least partly caused by a corresponding age variation in access to high-quality, defended resources. Future experimental studies, including the effects of resource quality, will hopefully reveal whether improved skills in foraging and breeding actually affect age-specific patterns of reproductive performance and whether the relative importance of such skills differs in relation to the life history of the organism.

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REFERENCES

- Andersson, M. 1994 *Sexual selection*. Princeton, NJ: Princeton University Press.
- Catry, P. & Furness, R. W. 1999 The influence of adult age on territorial attendance by breeding great skuas *Catharacta skua*: an experimental study. *J. Avian Biol.* **30**, 399–406.
- Charlesworth, B. 1994 *Evolution in age-structured populations*. Cambridge University Press.
- Clutton-Brock, T. H. 1988 *Reproductive success*. Chicago, IL: University of Chicago Press.
- Conder, P. 1989 *The wheatear*. London: Christoffer Helm.
- Danchin, E., Boulinier, T. & Massot, M. 1998 Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* **78**, 2415–2428.
- Daunt, F., Wanless, S., Harris, M. P. & Monaghan, P. 1999 Experimental evidence that age-specific reproductive success is independent of environmental effects. *Proc. R. Soc. Lond. B* **266**, 1489–1493.
- DeForest, L. H. & Gaston, A. J. 1996 The effect of timing on breeding and reproductive success in the thick-billed murre. *Ecology* **77**, 1501–1511.
- Desrochers, A. 1992a Age-related differences in reproduction by European blackbirds: restraint or constraint? *Ecology* **73**, 1128–1131.
- Desrochers, A. 1992b Age and foraging success in European blackbirds: variation between and within individuals. *Anim. Behav.* **43**, 885–894.
- Forslund, P. & Pärt, T. 1995 Age and reproduction in birds—hypotheses and tests. *Trends Ecol. Evol.* **10**, 374–378.
- Greenwood, P. J. & Harvey, P. H. 1982 The natal and breeding dispersal of birds. *A. Rev. Ecol. Syst.* **13**, 1–21.
- Hatchwell, B. J., Chamberlain, D. E. & Perrins, C. M. 1996 The demography of blackbirds *Turdus merula* in rural habitats: is farmland a sub-optimal habitat? *J. Appl. Ecol.* **33**, 1114–1124.
- Holmes, R. T., Marra, P. P. & Sherry, T. W. 1996 Habitat specific demography of breeding black-throated blue warblers: implications for population dynamics. *J. Anim. Ecol.* **65**, 183–195.
- Jenni, L. & Winkler, R. 1994 *Moult and ageing of European passerines*. London: Academic.
- Källander, H. 1974 Advancement of laying of great tits by the provision of food. *Ibis* **116**, 365–367.
- Lundberg, A. & Davies, N. B. 1985 The influence of food on time budgets and timing of breeding of the dunnoek *Prunella modularis*. *Ibis* **127**, 100–110.
- Marchetti, K. & Price, T. 1989 Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. *Biol. Rev. Camb. Phil. Soc.* **64**, 51–70.
- Martin, T. E., Martin, P. R., Olson, C. R., Heidinger, B. J. & Fontaine, J. J. 2000 Parental care and clutch sizes in North and South American birds. *Science* **287**, 1482–1485.
- Møller, A. P. 1991 Clutch size, nest predation, and distribution of avian unequal competitors in a patch environment. *Ecology* **72**, 1336–1349.
- Newton, I. 1989 *Lifetime reproduction in birds*. London: Academic.
- Newton, I. 1991 Habitat variation and population regulation in sparrowhawks. *Ibis* **133** (Suppl. 1), 76–88.
- Newton, I. 1992 Experiments on the limitation of bird numbers by territorial behaviour. *Biol. Rev.* **67**, 125–173.
- Pärt, T. 1995 Does breeding experience explain increased reproductive success with age? An experiment. *Proc. R. Soc. Lond. B* **360**, 113–117.
- Pärt, T. 2001 The effects of territory quality on age-dependent reproductive performance in the northern wheatear (*Oenanthe oenanthe*). *Anim. Behav.* **62**, 379–388.
- SAS 1999 *JMP v. 3.2 statistics*. Cary, NC: SAS Institute, Inc.
- Shaw, P. 1986 Factors affecting the breeding performance of Antarctic blue-eyed shags *Phalacrocorax atriceps*. *Ornis Scand.* **17**, 141–150.
- Söderström, B., Pärt, T. & Linnarsson, E. 2001 Grazing effects on between-year variation of farmland bird communities. *Ecol. Appl.* **11**, 1141–1150.
- Sutherland, W. 1996 *From individual behaviour to population ecology*. Oxford University Press.
- Svensson, L. 1992 *Identification guide to European passerines*, 4th edn. Stockholm, Sweden: Märstatryck.
- Tye, A. 1992 Assessment of territory quality and its effects on breeding success in a migrant passerine, the wheatear. *Ibis* **134**, 273–285.
- Wunderle, J. R. Jr 1991 Age-specific foraging proficiency in birds. In *Current ornithology* (ed. D. M. Power), pp. 273–324. London: Plenum.