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Delayed timing of breeding as a cost of reproduction

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Timing of breeding is a trait with considerable individual variation, often closely linked to fitness because of seasonal declines in reproduction. The drivers of this variation have received much attention, but how reproductive costs may influence the timing of subsequent breeding has been largely unexplored. We examined a population of northern wheatears *Oenanthe oenanthe* to compare three groups of individuals that differed in their timing of breeding termination and reproductive effort to investigate how these factors may carry over to influence reproductive timing and reproductive output in the following season. Compared to females that bred successfully, females that put in less effort and terminated breeding early due to nest failure tended to arrive and breed earlier in year 2 (mean advancement = 2.2 and 3.3 d respectively). Females that spent potentially more effort and terminated breeding later due to production of a replacement clutch after nest failure, arrived later than other females in year 2. Reproductive output (number of fledglings) in year 2 differed between the three groups as a result of group-level differences in the timing of breeding in combination with the general seasonal decline in reproductive output. Our study shows that the main cost of reproduction was apparent in the timing of arrival and breeding in this migratory species. Hence, reproductive costs can arise through altered timing of breeding since future reproductive success (including adult survival) is often dependent on the timing of breeding in seasonal systems.

Timing of breeding may have significant impacts on reproductive success, with seasonally breeding species often showing reduced reproductive output as the season progresses (Perrins 1965, 1970, Hochachka 1990, Öberg et al. 2014). Variation in the timing of breeding is expected to largely arise through individual differences in condition: either through constraints preventing individuals in poor condition from breeding early or through an adaptive strategy to optimize the timing of breeding in order to maximize fitness (Drent and Daan 1980, Rowe et al. 1994). Such optimal timing of breeding would be the outcome of a conflict between advantages of early breeding and advantages of delaying breeding (e.g. greater offspring value versus improved parental body condition). Differences in individual condition and thereby also timing of breeding may arise from a combination of factors such as persistent differences in individual quality (Wilson and Nussey 2010), nutritional state as determined by food availability (Drent and Daan 1980) and previous reproductive effort (Williams 1966). Because of the general feature of seasonal declines in fitness, many studies have investigated the effects of individual and environmental quality driving this relationship (Parsons 1975, de Forest and Gaston 1996, Verhulst and Nilsson 2008) and the maintenance of breeding-time variation despite strong selection pressure towards earlier breeding (Price et al. 1988). However, reproductive costs may also influence the timing of seasonal breeders (and vice versa; Nilsson and Svensson 1996, Wiggins et al. 1998, Brinkhof et al. 2002) but these relationships have been less commonly explored.

Reproductive costs may influence subsequent reproductive decisions because reproductive effort can affect individual condition (see also ‘carry-over effects’, Norris 2005, Harrison et al. 2010), or because the organism is modifying its current reproduction in relation to future reproductive output (Williams 1966, Lessells 1991, Stearns 1992). In seasonal breeders these reproductive costs may be partly driven by constraints operating on the timing of breeding: organisms breeding late in one season may not have enough time to recover their condition before the beginning of the next breeding period (Shaw and Levin 2013). This should be particularly evident in migratory species that face large energetic costs outside of breeding. In birds, for example, individuals face a series of energetically demanding stages in their yearly life cycle in addition to breeding (e.g. moulting new plumage, migration) that may limit an individual’s ability to compensate for additional or late breeding energy expenditure (Wingfield 2008, Shaw and Levin 2013). Thus, an individual that breeds late and invests more effort may be constrained to breeding later in the following season.

Trade-offs between current and future reproduction (Williams 1966, Lessells 1991, Stearns 1992) have been widely studied over the last decades by manipulating parental effort through either increased brood size or altering

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the timing of breeding to investigate reproductive costs on probability of second broods (Lindén 1988, Brinkhof et al. 2002), adult survival (Askenmo 1979, Nilsson and Svensson 1996, Brinkhof et al. 2002, Koivula et al. 2003, Golet et al. 2004, Santos and Nakagawa 2012) and/or future reproductive output (Roskaft 1985, Gustafsson and Pärt 1990, Hanssen and Erikstad 2013). However, the possibility that variation in the timing of breeding can be partly explained by variation in the cost or timing of previous reproductive events has generally not been investigated (but see Nilsson and Svensson 1996, Wiggins et al. 1998, Brinkhof et al. 2002).

In this study we specifically examine how the timing of breeding in one year influences the timing of breeding and fitness in the following year for the northern wheatear *Oenanthe oenanthe*: a species with direct links between breeding time and fitness (Öberg et al. 2014). For this we compared three categories of female wheatears that differed in their timing of breeding termination in year 1 (successful breeders [reference group], failed breeders that did not renest [early], and females that renested [late]) and returned to breed in year 2. First, we considered that if reproductive costs are expressed through changes in the timing of breeding in year 2 because of changes in effort or the timing of breeding in year 1, we expect that in comparison to successful breeders, renesters arrive and/or breed later and failed breeders arrive and/or breed earlier in year 2. Second, we examined differences in fledgling production between the groups in year 2 and considered two possibilities about how between-year reproductive costs could be expressed in the number of offspring fledged: 1) independent of the timing of breeding – i.e. once differences in the timing of breeding in year 2 were controlled for, females still showed between-group differences in fledgling production, and/or 2) dependent on the timing of breeding – i.e. between-group differences in fledgling production resulted from differences in the timing of breeding in year 2 and the subsequent change in fitness related to the seasonal fitness decline. Third, we considered costs of timing and effort of breeding on adult survival (Williams 1966) by comparing return rates for successful breeders and renesters (although not failed breeders due to confounding factors, see Methods). Finally, we considered the possibility that females that renested in year 1 already exhibited costs of reproduction in this first year during the replacement brood; thus we examined whether within-season reproductive costs were expressed in the second brood in year 1 by comparing reproductive output for these second attempts to what would be expected for a first breeding attempt at the same time of season (i.e. accounting for the seasonal decline in fitness; Öberg et al. 2014). A relatively lower reproductive output of second broods, would suggest a cost of reproduction from the first attempt.

Material and methods

Study system

The northern wheatear (hereafter 'wheatear') is an insectivorous, long-distance migratory passerine that breeds in Europe, Asia and North America and overwinters in sub-Saharan Africa. In our Swedish study area, wheatears build their nests in stone piles (80%), or under roof tiles of farm buildings (Öberg et al. 2014). Breeding pairs usually produce one brood per season, although second breeding attempts may occur after failed first attempts (~20% of all failed attempts) or after successful breeding (~5% of all successful attempts). Nest predation is the major cause of breeding failure in this system ($>85\%$ of all failures, Pärt 2001a). Wheatears are ground-foraging birds; thus, vegetation height (field layer height; FLH) is an important determinant of habitat quality (Conder 1989), with short or sparse vegetation related to higher prey availability (Tye 1992), higher reproductive success (Pärt 2001b, Öberg et al. 2014), higher adult survival (Low et al. 2010) and lower nest predation risk (Pärt 2001a, Schneider et al. 2012) than habitats characterised by tall and dense ground vegetation.

The study area (60 km^2) is in a heterogeneous agricultural landscape, southeast of Uppsala in southern central Sweden (59°50′N, 17°50′E). The area consists of a mixture of forest, crop fields, pastures, farmyards and villages where 250 territory sites have been occupied by wheatears at least once since 1993 when the yearly monitoring started, and 100–180 pairs breed in the area each year. Each year we uniquely colour-ringed chicks from ~90% of all successful nests, as well as a proportion of unmarked adults, so that, on average, ~60% of breeding adults were marked by the end of each breeding season. Adults were aged as first-year breeders or older based on plumage characteristics (Pärt 2001a). Territories were regularly visited (every 1–5 d) from arrival in early April throughout the breeding season (to the end of June). Detailed data on demographic parameters were collected from a smaller (40 km^2, 165 territory sites, 80–90 pairs yr^{-1}) central part of the study area that was visited every 1–3 d. The surrounding 2 km-wide outer part of the study area was used as a buffer zone for adult dispersal from the central area and thus visited less frequently (every 3–5 d). We did, however, collect data on site occupancy, identity of breeding individuals and nesting success in this area. Return rates are likely to reflect true survival rates because adult wheatears in our study area only disperse short distances between years (median <350 m, 90% quantile <1500 m; Arlt and Pärt 2008, Arlt et al. 2008). Furthermore, outside the 2 km buffer zone there was little suitable breeding habitat for wheatears for at least 2 km. Thus, from our dispersal data we estimate that the number of permanently emigrating adults was negligible (Low et al. 2010). Also, because wheatears move even shorter distances for renesting attempts, we were unlikely to have misclassified any renesting birds as 'failed'.

Breeding time categories

We divided breeding birds for which we had breeding records in two consecutive years (hereafter year 1 and year 2) into three categories that varied in their reproductive effort and timing of breeding termination; 1) 'successful' females successfully fledged chicks with their first and only breeding attempt in year 1. These birds were used as a reference group in terms of amount of reproductive effort and timing of breeding termination (mean ± SE relative to 1 May: day 57.6 ± 0.22) compared to the other two groups. Young were assumed to be independent at ~25 d old (Öberg et al. 2015). 2) 'Failed' females lost their brood in the first week after hatching and did not renest. Thus, these birds invested less, and terminated their breeding at an earlier time than the successful group (day 48.8 ± 0.84). 3) The 'renest' group consisted of females that failed early with their first attempt, often during incubation, and laid a replacement clutch, typically within 2–4 weeks and were subsequently successful; thus renesters invested more effort than failed females and terminated their breeding at a time later than other females (day 78.8 ± 1.67).

Between season costs of reproduction

We measured costs of reproduction in terms of effects on arrival time, timing of breeding and the arrival-breeding interval in year 2. Arrival time to the breeding grounds was defined as the date (relative to 1 May) an individual was first observed in the study area. We included observations of arrival during years (1993–1998 and 2002–2012) and areas when monitoring was every 1–3 d (mean = 2.2) during the arrival period (mid April to 25 May). Observations were excluded if the first observation of an individual was <7 d before its egg-laying date as this is the minimum time required to build the nest and start egg laying (Conder 1989, Moreno 1989). Timing of breeding was defined as the date the first egg was laid (egg-laying date 'ELD', relative to 1 May), and was estimated for all breeding attempts based on chick hatching dates (88% of all breeding attempts) or observations of breeding behaviour (12% of all breeding attempts, Öberg et al. 2014). We only used dates for first breeding attempts in year 2 ($\text{ELD} \leq 31$, Öberg et al. 2014) because we were primarily interested in the effects on the timing of the initial breeding attempt. The arrival-breeding interval was the number of days between arrival and egg laying. We were interested in the arrival-breeding interval because individual condition influences the recovery time from migration to the start of breeding (shown for capital breeders, Bêty et al. 2003), which could be one way reproductive costs are expressed.

We also considered costs of reproduction in terms of the number of chicks fledged in year 2 relative to the timing of breeding by considering: 1) that the additional reproductive effort or late breeding in year 1 may deplete internal resources available for breeding in year 2, independent of the timing of breeding (i.e. breeding output is lower than expected in year 2), and/or 2) that any differences between groups in their reproductive output in year 2 was simply a result of differences in the timing of breeding and the related seasonal reproductive decline (Öberg et al. 2014).

Adult return rates

We compared return rates for successful breeders and renesters to look for potential trade-offs between reproductive timing/effort and survival. Return rates are unlikely to be systematically biased for the different groups because: 1) between-year resighting rates in this population are very high and not influenced by factors that might differ between the groups (FLH, egg-laying date or female age, Low et al. 2010, Öberg et al. 2014), and 2) between-year adult dispersal has little effect on 'true' adult survival estimates in this population (for details see Arlt and Pärt 2008, Arlt et al. 2008, Low et al. 2010). Because female wheatears are often killed on the nest during nest failure predation events (Low et al. 2010), we could only meaningfully compare the return rates of females that were successful with their first attempt (n = 789) to those that renested and were successful with their second attempt (n = 56). Including any birds whose nests failed and did not renest in the same year would confound over-winter survival by direct on-nest predation.

Within season costs of reproduction

Although it is clear that failed birds invest less in reproduction than successful females and renesters, it is not clear whether renesters invest more than successful birds. This is because renesters may express costs of reproduction in their renesting attempt in year 1, meaning they reduce their reproductive output in the second brood to compensate for the effort expended in their first. If so, renesters could invest similar (or even less) in reproduction than successful birds in year 1, with implications for the interpretation of between-group differences in year 2. Thus, we compared reproductive output of the renesters' second brood to the expected reproductive output of a bird attempting its first breeding at the same time of season while accounting for other factors known to affect reproductive output in this system: female age and territory quality (Pärt 2001a, b, Arlt and Pärt 2007, Low et al. 2010, Öberg et al. 2014).

Statistical analysis

Between-season effects

We examined group-level differences for the relative change in arrival ($n_{\text{successful}} = 132$, $n_{\text{renest}} = 12$, $n_{\text{failed}} = 12$), egg-laying date ($n_{\text{successful}} = 275$, $n_{\text{renest}} = 13$, $n_{\text{failed}} = 20$) and the arrival-breeding interval ($n_{\text{successful}} = 174$, $n_{\text{renest}} = 12$, $n_{\text{failed}} = 12$). For this we included factors from the first year's breeding attempt known to influence reproductive effort and/or timing (FLH and female age (first-year versus older); Pärt 2001a, Öberg et al. 2014). In addition, because we were investigating the relative change in the timing of arrival and breeding, we needed to account for the ability of a bird to advance or delay from one season to the next. A bird that breeds late in one year, by chance will tend to breed earlier in another year, and vice versa (regression to the mean, Galton 1886). Thus, in all reproductive timing models we included a standardised date expressing the deviation of each individual from the population mean in the first year (see also Barnett et al. 2005). For the arrival-breeding interval, we included the arrival date in year 2, to account for the possibility that later arriving individuals will be under greater time pressure to begin breeding and so the arrival-breeding interval will be a function of arrival date (Potti 1999, Bêty et al. 2003).

We examined the group-level differences in the number of fledglings produced in year 2 ($n_{\text{successful}} = 217$, $n_{\text{renest}} = 16$, $n_{\text{failed}} = 20$). This was modelled as a zero-inflated Poisson (logit link binomial and log link Poisson) with factors known to influence nesting success (egg-laying date and FLH) included in the binomial component and factors that influence fledging success (egg-laying date, FLH and female age, Öberg et al. 2014) in the Poisson. From these model estimates we produced two sets of predictions. First, we examined the group-level predictions for fledgling production if egg-laying dates for each group were the same in the second year (i.e. searching for evidence of a cost of reproduction independent of the timing of breeding). Second, we compared fledgling production for each group when the different group-level egg-laying dates were included in the prediction of fledgling production (i.e. we allowed differences in the seasonal timing of breeding to influence reproductive output).

Within-season effects

We compared reproductive fitness components (clutch size, number of fledglings, and number of recruits per nest) for birds that undertook a single breeding attempt (i.e. successful or failed; n = 362) to the second breeding attempt of renesters (n = 16). Because the birds in our system demonstrate a strong seasonal reproductive decline in fitness (Öberg et al. 2014), and because second attempts were initiated later in the season, we directly compared model predictions from the time period where first and second attempts overlapped (i.e. days 20–30; where 1 = 1 May). Models included factors known to influence reproductive output in this system (Öberg et al. 2014): egg laying date, FLH (short vs tall) and female age (first year vs older); the fledging and recruit models also included nest location (roof vs ground nests). Clutch size and recruit models used a log-link (Poisson distribution) and the number fledged was modelled as a zero-inflated Poisson (combined binomial [logit link] and Poisson [log link] distribution model) to account for excess zeros resulting from predation-induced nest failure (Öberg et al. 2014). All models fitted year as a random effect on the intercept.

We used a Bayesian framework for generating estimates from generalized linear mixed models (using the Gibb's sampler 'JAGS' [Plummer 2003] called from R [R Development Core Team]). This approach allowed us to directly calculate probabilities for between-group differences (reported as *Pr*(group comparison) = %) from the posterior distributions for these group differences. For all models we used 100 000 draws without thinning, a burn-in of 10 000 and ran 3 chains with different initial values to ensure convergence (convergence was checked by visual inspection of the chains and the Gelman and Rubin diagnostic). All priors were 'non-informative' for analyses of the timing of breeding and reproductive output (model parameter beta estimates dnorm ~ (0, 0.0001), for precision (tau) estimates dgamma ~ (0.001, 0.001), for BUGS-code of all models see Supplementary material Appendix 1). For analyses of female return rates we used 'non-informative' priors for the between group comparison.

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.1f240> (Low et al. 2015).

Results

Between-season effects

Birds that invested less in reproduction and terminated breeding earlier in year 1 (failed breeders) tended to arrive earlier, had a shorter arrival-breeding interval, began egg laying earlier in year 2 and thus produced more fledglings when compared to birds in the 'successful' or 'renest' groups (Fig. 1; Table 1). Birds that invested more in breeding and terminated breeding later (renesters) in year 1 tended to arrive later than other birds in year 2; however, there was no clear evidence that this resulted in a later date of egg-laying in comparison to 'successful' birds (Fig. 1; Table 1). Evidence for a between-group difference in the number of chicks fledged in year 2 only had reasonable support if the between-group differences in breeding time were included in the predictions of fledgling output (Table 1; Fig. 1). This indicates that between-group differences in fledgling output were largely driven by differences in the timing of breeding in year 2. There was a tendency that renesters had lower adult female survival between years 1 and 2 compared to breeders of the successful group (Table 1).

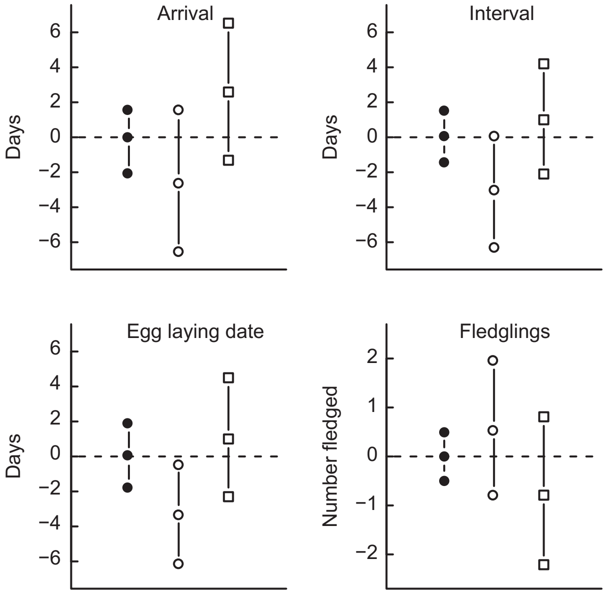

Figure 1. Relative differences in the timing of arrival to the breeding grounds, interval between arrival and egg laying, initiation of egg laying and number of chicks fledged ('Fledglings + date' in Table 1) for first breeding attempts in year 2 in the three groups: 'successful' – filled black circles; 'failed' – open circles; 'renest' – open squares, with the 'successful' group as the reference group. Ranges show the 95% credible intervals and the central tendency (median) from the posterior distribution of the models' predictions. Probabilities of between-group differences are given in Table 1.

Within-season effects

Renesters generally laid fewer eggs during their second breeding attempt compared to their first (first: 6.5 ± 0.19, second: 5.6 ± 0.29 eggs); however, the decline in clutch size, number of fledglings and recruits per nest between breeding attempts followed the expected seasonal decline in reproduction. This can be clearly seen by comparing the overlap between late first broods and early second broods (days 20–30; Fig. 2).

Discussion

Despite breeding time being generally acknowledged as an important factor influencing fitness in seasonal breeding organisms, studies investigating between-year effects of reproductive costs often neglect the role of changes in the timing of breeding in the following season and its impact

Table 1. Estimated median and 95% credible interval (CI) range for female reproductive and survival parameters in year 2 for the three groups. Group differences are sampled directly from the posterior distribution of the difference between the two groups and show: 1) the probability that one group mean is smaller than another (where group1 < group2 = 0.50 indicates identical group means), and 2) the mean, standard deviation (SD) and 95% CIs for this posterior distribution of the difference between the two groups (i.e. effect size). 'Fledglings only' assumes groups do not differ in their breeding time in year 2, 'Fledglings + date' includes the different group-level breeding times in the estimated number of fledglings per nest.

Groups	Group median (95% CIs)	Group difference probability	Group difference mean ± SD (95% CIs)
Arrival			
successful	−4.82 (−6.5, −2.8)	failed < success = 0.87	2.2 ± 1.9 (−1.7, 6.1)
renest	−1.84 (−5.7, 2.1)	success < renest = 0.94	2.9 ± 1.8 (−0.7, 6.6)
failed	−7.02 (−11.1, −2.9)	failed < renest = 0.97	5.2 ± 2.6 (0.1, 10.3)
Arrival-breeding			
successful	17.6 (16.2, 19.1)	failed < success = 0.98	3.1 ± 1.5 (0.7, 6.1)
renest	18.7 (15.5, 21.8)	success < renest = 0.75	1.0 ± 1.5 (−4.0, 2.0)
failed	14.4 (11.3, 17.7)	failed < renest = 0.97	4.1 ± 2.1 (−0.05, 8.3)
Egg laying			
successful	13.7 (11.9, 15.6)	failed < success = 0.99	3.3 ± 1.2 (0.8, 5.8)
renest	14.8 (11.4, 18.2)	success < renest = 0.75	1.1 ± 1.5 (−4.0, 2.0)
failed	10.4 (7.5, 13.3)	failed < renest = 0.99	4.4 ± 1.9 (0.5, 8.2)
Fledglings only			
successful	4.0 (3.5, 4.5)	success < failed = 0.55	0.1 ± 0.7 (−1.5, 1.4)
renest	3.3 (1.9, 4.8)	renest < success = 0.80	0.7 ± 0.8 (−0.9, 2.1)
failed	4.1 (2.7, 5.6)	renest < failed = 0.77	0.8 ± 1.0 (−1.3, 2.7)
Fledglings + date			
successful	4.0 (3.5, 4.5)	success < failed = 0.76	0.5 ± 0.7 (−2.0, 0.9)
renest	3.2 (1.8, 4.8)	renest < success = 0.83	0.8 ± 0.7 (−0.8, 2.2)
failed	4.5 (3.2, 6.0)	renest < failed = 0.90	1.3 ± 1.0 (−0.8, 3.3)
Return rates			
successful	0.45 (0.41, 0.49)		
renest	0.39 (0.27, 0.52)	renest < success = 0.83	0.06 ± 0.06 (−0.1, 0.2)
failed	–		

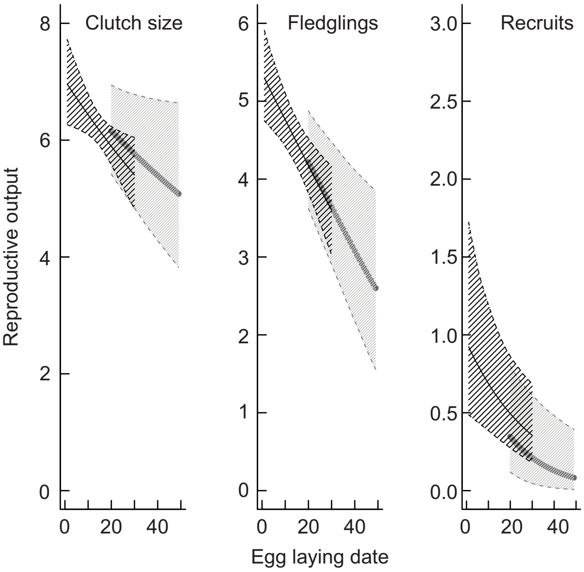

Figure 2. Reproductive output relative to egg-laying date (ELD 1 = 1 May) for birds undertaking their first breeding attempt in a season (black: ELD range from 0–30) and those undertaking their second attempt (grey: ELD range 20–50). The overlap between groups occurs between days 20 and 30 and shows no clear evidence of the reproductive output of second breeding attempts being smaller than that predicted by a seasonal decline in reproduction (*Pr*(clutch size: second attempt < first attempt) = 39%; *Pr*(number fledglings: second attempt < first attempt) = 49%; *Pr*(number recruits from successful nests: second attempt < first attempt) = 80%). Shaded areas indicate the 95% credible intervals and the central tendency (median) from the posterior distribution of the models' predictions.

on fitness. In northern wheatears, females that exerted less breeding effort and terminated breeding earlier in the previous season (failed breeders), tended to arrive earlier and breed earlier in the following year when compared to other breeders. We assume that causes of failure (primarily predation) are not systematically biasing our sample; however, if birds that fail and do not renest are generally of lower quality than other birds (O'Brien and Dawson 2013) then our results are probably conservative and the cost of reproduction effects are even greater than we report here. This potential conservatism in our estimates of fitness benefits to failed breeders also relates to the possibility that their reduced breeding effort resulted in increased survival to the following year (Williams 1966), a measure we were unable to quantify because of on-nest predation rates confounding these estimates. Similarly, females spending more effort and terminating breeding later (renesters) tended to arrive later in the following season when compared to birds that only had one breeding attempt. Thus reproductive costs were expressed as reduced fledgling production resulting from changes in the timing of breeding in year 2 and its relationship to seasonal declines in reproductive output (Öberg et al. 2014). However, as with most experimental studies of reproductive costs that simultaneously manipulate timing of breeding termination and reproductive effort in year 1 (Verhulst and Nilsson 2008), we cannot separate the relative importance of these effects on the timing of reproduction in year 2.

There are a number of mechanisms that could explain changes in the timing of breeding for birds returning in year 2. For migrating birds, breeding is often immediately followed by two major and energetically demanding life-cycle events, moult and migration (Fero et al. 2008, Alerstam 2011). Individuals that terminate breeding early have more time to prepare their physiology and condition before migration (Mitchell et al. 2012a, b) and to avoid an overlap between breeding and moult (Nilsson and Svensson 1996, Siikamäki 1998, Mitchell et al. 2012b) which, in turn, is expected to improve condition and/or survival during and post-migration (Nilsson and Svensson 1996). Also, individuals that arrive early to the wintering grounds may be at a competitive advantage to those arriving later and thus be able to start earlier when it is time to migrate back to the breeding grounds in the following year (Marra et al. 1998, Norris et al. 2004). Another factor in this system is the potential for improvement in territory quality from one year to the next because individuals that fail and do not renest have the opportunity of prospecting for the remainder of that season. Failed breeders in year 1 that prospect, increase their probability of settling on a high quality territory in year 2 and yielding higher reproductive and survival outcomes (Pärt et al. 2011). This could explain why failed birds were able to not only arrive earlier (e.g. relatively better winter territories) but also reduce their arrival-breeding interval (e.g. relatively better breeding territory).

Adult female return rates suggested only very weak differences between survival of successful birds and renesters with a high degree of uncertainty in the estimates. Because the survival of failed birds that did not renest was confounded with adult on-nest predation (Low et al. 2010), without an experimental approach we were unable to determine the potential survival benefit effect of failure, which further reduces our ability to interpret – and potentially underestimates – the impact of effort/timing in year 1 on survival to year 2. However, assessing the degree to which an organism trades off survival for reproduction by simply examining survival to year 2 as a function of reproductive effort in year 1 is likely to underestimate the cost of reproduction in any case. This is because: 1) females with higher reproductive effort/later breeding in year 1, breed later in year 2, 2) later breeding females in year 2 are more likely to fail because of increasing seasonal nest predation risk (Öberg et al. 2014), and 3) nest predation is tightly linked to predation of breeding females (Low et al. 2010). Thus, although a bird might survive from year 1 to 2 despite higher reproductive costs in year 1, the trade-off with survival might not be immediately apparent. This is because the survival cost is not expressed in reduced return rates, but rather reduced survival during the year 2 breeding season because delayed breeding in year 2 increases adult predation risk in that year. To our knowledge this carry-over effect on survival because of changes in the timing of breeding in year 2 has rarely, if ever, been explicitly considered.

The within-season analysis of renesters showed that the decline in reproductive output from first to second attempts of three fitness component measures (clutch size, numbers of fledglings, number of recruits) was at a rate consistent with the expected seasonal declines in fitness in this population (Fig. 2). This indicates that females spent the expected effort relative to their timing of breeding breeding and seemed to not compensate for any costs from the first attempt by reducing effort in the second; assuming that there were no confounding effects of persistent differences in quality of individuals relative to the timing of breeding (reviewed by Verhulst and Nilsson 2008). Despite the lack of an experimental approach to explicitly disentangle confounding effects, our interpretation is likely to be valid because of evidence that seasonal declines in reproductive output in this system mainly result from changes in environmental quality, rather than the quality of individuals or breeding territories (Öberg et al. 2014, Pärt et al. unpubl.).

Although the production and provisioning of dependent young should be influenced by past reproductive effort ('the cost of reproduction', Williams 1966, Stearns 1992), the mechanism through which it operates is rarely linked to changing the timing of breeding. Here we show that individual decisions on the timing of breeding are influenced by previous breeding history. Our results also imply that carry-over effects from one season to the next may influence the decision on whether to renest after failure or not. Although renesting individuals have the fitness benefits of producing a replacement clutch, it also comes at a cost of delayed breeding (and possibly reduced survival) in the following year, while failed individuals are able to arrive and breed earlier in the next season with the potentially higher fitness it entails. Costs of producing a replacement clutch hence need to be weighed against benefits of earlier breeding in the next season. Our study is one of the few to highlight the importance of future impacts on the timing of breeding as a potential cost of reproduction since future reproductive success (including adult survival) may be highly dependent on the timing of breeding in seasonal systems.

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Supplementary material (Appendix JAV-00623 at <www.avianbiology.org/readers/appendix>). Appendix 1.