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Colonial birds often demonstrate considerable breeding synchrony. In southern Sweden the semi-colonial European starling initiated the vast majority of clutches within one week. Laying dates were positively skewed so that many birds initiated clutches at similar dates early in the season. Breeding was further synchronised by a particularly strong clutch-size reduction equivalent to one third of an egg per day during the first part of the breeding season. The decline in clutch size with season also held true for separate age-classes of females, for individual females laying at different times at different years and for individual females laying at different times the same year. Trends in breeding success during nestling rearing were unlikely to explain the high degree of breeding synchrony or the seasonal decline in clutch size; nestling survival and growth were weakly related or unrelated to reproductive timing. In contrast recruitment success of fledged offspring declined sharply with season. Even within the synchronous laying period, defined as clutches initiated during the first week each year, local recruitment success declined. It is suggested that the early seasonal decline is caused by selection for synchronous fledging permitting the immediate formation of flocks after fledging, whereas the late seasonal trends may be caused by either population differences in female quality or deteriorating conditions for raising young.

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In birds the extent of breeding synchrony varies considerably both among species, among different populations of the same species and among different years in the same population (Lack 1968, Gochfeld 1980, Findlay and Cooke 1982, Ims 1990). Reproductive synchrony seems to be especially prevalent among colonial birds (Gochfeld 1980, Wittenberger and Hunt 1985, Bradbury et al. 1997). A number of hypotheses has been proposed to account for reproductive synchrony. According to the seasonal variation in food supply hypothesis, breeding synchrony is tightly coupled with resource availability to rear nestlings or fledglings (Lack 1968). According to the predation hypothesis, synchronous breeding is a way to escape predation of nestlings and fledglings, by temporarily swamping predators (Darling 1938). According to the social benefits hypothesis breeding synchrony is a way to increase breeding success by foraging in flocks (Emlen and Demong 1975) or by common defence against predators (Wittenberger and Hunt 1985). According to the mating status hypothesis breeding synchrony is a way for females to enforce social (Knowlton 1979) and genetic (Birkhead and Biggins 1987) monogamy.

Many bird species demonstrate a seasonal decline in clutch size (Klomp 1970, Price et al. 1988). It has been suggested that this seasonal decline in clutch size is adaptive because it contributes to the synchrony of the breeding season, by advancing hatching date of late layers (Finney and Cooke 1978, Karlsson 1983). However, the seasonal decline in clutch size may also be an adjustment of clutch size to seasonal changes in food availability (Lack 1966, Murphy 1986) or declining survival probabilities of fledglings (Hussell 1972, Drent and Daan 1980). It has also been argued that females in good condition or in better territories both lay earlier and produce larger clutches (Finney and Cooke 1978,

Askenmo 1982). According to recent theoretical models, a seasonal decline in clutch size can be the result of a simultaneous optimisation of laying date and clutch size, when birds or territories differ in quality (Daan et al. 1990, Rowe et al. 1994).

The European starling (*Sturnus vulgaris*) demonstrates a high degree of breeding synchrony (Karlsson 1983, Feare 1984), but with some variation both between different populations (Pinxten et al. 1990, Smith et al. 1994), and within the same population (Feare 1984, Smith and Sandell 1998). In addition, clutch size declines with season, contributing to the synchrony of breeding (Karlsson 1983). The high breeding synchrony in starlings has been attributed to defence against predators (Feare 1984) and to a strong selection to breed early to avoid the risk of becoming a secondary mated female (Smith et al. 1994). In addition it has been suggested that the seasonal decline in clutch size may be related to reduced food availability with season (Karlsson 1983) or to the competition between polygynously mated females for male parental care (Smith et al. 1994) or quality-differences between early- and late-breeding females (Christians et al. 2001). The aim of this paper is to investigate seasonal trends in reproduction that can explain the very high breeding synchrony and steep seasonal decline in clutch size in a southern Swedish population of starlings.

Methods

During 1991–1997 I studied a population of starlings breeding in the Revinge area in southern Sweden. In this area, dominated by permanent pastures, a large number of nestboxes were erected. Nestboxes were put up either solitary, or in colonies varying in size between 15 and 20 nestboxes, with nestboxes in rows with a distance of ca 8 m between boxes. Natural nest-sites in the study-area are likewise clumped to varying degrees, but may be more heterogeneous in quality than the nestboxes. To vary males' possibilities to attract secondary females additional boxes were sometimes erected ca two weeks before egg-laying, either in the same tree or in nearby trees (Smith 1995, Smith and Sandell 1998). Male starlings arrive at the colonies in early spring (February–March) and occupy one or several nestboxes. They become polygynous either by attracting several females or by taking over females from neighbouring males when these disappear. In our study area, males mate with one to four females. Females breed very synchronously, with most females initiating laying within a week (Karlsson 1983, Smith et al. 1994).

I determined laying dates, clutch sizes and hatching dates for all active nests (Smith et al. 1994, Smith et al. 1995, Sandell and Smith 1996). Since laying and hatching dates were heavily skewed to the right (see below) I

calculated relative laying-dates and hatching-dates by subtracting the earliest laying date or hatching date in the study area for the particular year. Nestlings were ringed and measured when 13–15 days old. After nest-leaving, nests were inspected for remains of nestlings, to determine fledging success. When calculating fledging success, I excluded total nest-failures. This was because total nest-failures were mostly due to disparate reasons not related to mating status (e.g. human interference, poor locking of nestbox roofs resulting in predation by pine-martens or cats, destruction of nestboxes by cows). Males were captured from their arrival onwards and females during the nestling rearing period. Each captured bird was individually marked with an aluminium ring and a unique combination of three colour rings.

Parents were assigned to nests by observing them building nests, incubating eggs or providing nestlings with food. Males do not always assist their secondary females and, thus, for some males the criterion that they defended the nestbox just prior to laying was used (Smith et al. 1994). When most males in a study colony were known, mating status was assigned to the females. It was assumed that laying order reflected mating order, which seems to be generally true in this population (Smith et al. 1994, Sandell and Smith 1996). If no male was observed during nestling feeding during more than 60 min of observation, the female at the nest was assumed to be a secondary female (Sandell et al. 1996).

A number of experiments have been performed in the study population. In this study most nestboxes that were affected by the experiments were excluded. Cases in which the male was given an extra nestbox before breeding were not excluded. Neither were twelve nest-boxes given supplemental food during the incubation period, since this experiment did not affect breeding success (Smith et al. 1993). When any of a polygynous male's nests was affected by an experiment, all nests of that male were excluded from analyses. The only exception was simple cross-fostering experiments, in which neither brood size nor nestling age was changed, in which case only the nests involved in the cross-fostering experiment was excluded, since a male's other nests were assumed to be unaffected. In addition, a small number of repeat and second clutches were excluded, except when otherwise stated.

When data were approximately normally distributed, I used general linear methods with type 3 sums-of-squares. When including random factors, I used mixed models. Fledging and recruitment success were analysed assuming binomial error distribution and a logit link-function (Crawley 1993). To handle small amounts of overdispersion, I used the deviance divided by the degrees of freedom as a scale parameter and tested significance with an F-test. When data were not overdispersed a likelihood-ratio test was used. Non-normal data were analysed with non-parametrical methods (Siegel and

Castellan 1988). Statistical analyses were performed with SYSTAT 5.02 and SAS 8.02. In all analyses, year was used as a factor when it significantly improved the fit of the model. Unless otherwise stated, interactions were excluded when they did not significantly improve the fit of models.

Many tests demonstrate that reproductive success decreases with the advancement of laying/hatching-date (see below). To test if early clutches experienced reduced breeding success (i.e. selection for breeding synchrony), I tested if a quadratic term significantly improved the fit of models.

Earlier studies have demonstrated that secondary females may be constrained in when they can lay their eggs (Eens and Pinxten 1995, Eens and Pinxten 1996, Sandell and Smith 1996, Sandell 1998). Therefore I repeated several of the analyses, using only monogamous and primary females, which are assumed to be less socially constrained in when they can lay their eggs.

Results

Laying dates

Laying was very synchronous with 73–93% (mean 87%) of females initiating laying within the first week after the first egg was laid in the population studied (hereafter called the synchronous period, Fig. 1). Secondary females may be constrained in when they can lay their eggs because of the behaviour of already mated females (Eens and Pinxten 1996, Sandell 1998). The analysis was therefore restricted to monogamous and primary females. Overall 93% of these females laid their first egg during the synchronous period. Variation in laying date
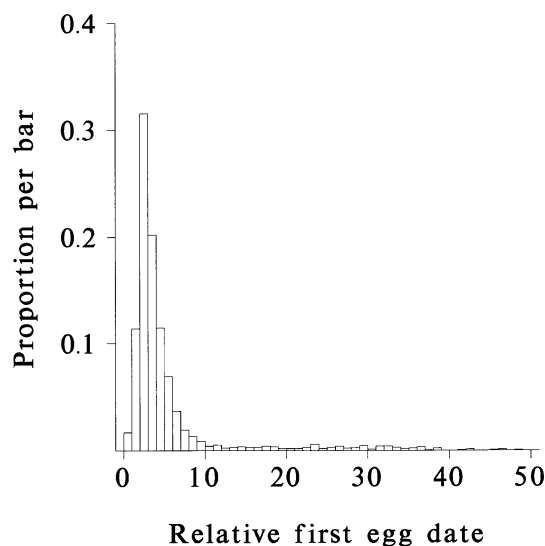
for monogamous and primary females significantly differed between years (Levene's test, $F_{6,931} = 25.11$, $p < 0.001$), because in 1996 a lower proportion of females laid their first egg during the first week (84%), whereas in the remainder of the years 94–97% of the females did so. The distribution of laying dates was skewed to the right (Fig. 1). This skew may depend on inclusion of females laying repeat clutches after undetected breeding failure, e.g. outside the study area. However, the distribution was skewed to the right also when only clutches initiated during the first week were included (skewness $= 0.59$, $t_{\infty} = 9.28$, $p < 0.001$).

Clutch size

Clutch size decreased significantly with the advancement of laying (ANCOVA with year as a factor, the effect of laying date, $b = -0.068$, $F_{1,1333} = 354.88$, $p < 0.001$; Fig. 2). However, the slope of the relationship differed significantly between years ($F_{6,1327} = 6.78$, $p < 0.001$), although it was significantly negative in all years ($p < 0.001$ in all cases). However, clutch size declined with season in a non-linear fashion (ANCOVA, the effect of adding a quadratic component, $F_{1,1332} = 147.45$, $p < 0.001$), because of a slower rate of decline late than early in the season. Restricting the analyses to clutches initiated during the synchronous period, the decline in clutch size was 0.32 eggs per day ($F_{1,1189} = 490.89$, $p < 0.001$) and did not differ between years ($p > 0.9$), whereas the decline was weak for the remainder of the

Fig. 1. Frequency distribution of laying date in European starlings in the Revinge area, southern Sweden, 1991–1997.
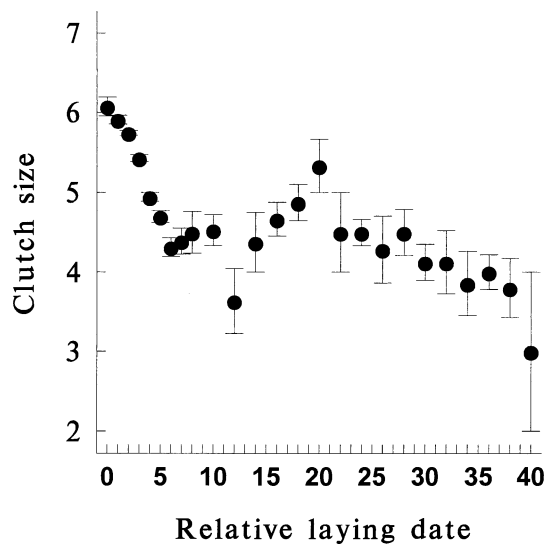

Fig. 2. Clutch size in relation to laying date. Day 0 = the first day an egg was produced in the studied population each year. For day > 8 data pooled to every second day and for day > 39 all data pooled to day = 40, to avoid small sample sizes. Mean ± standard error shown.

season (b = -0.02, $F_{1,148} = 4.70$, p = 0.032) and did not differ between years (p > 0.4).

The reduction of clutch size with advancement of laying could be caused by either females of lower 'quality' or 'condition' laying late and producing smaller clutches, or because clutch size is adjusted to laying date per se. Although a non-experimental study cannot control for female condition altogether, some sources of variation in female condition can potentially be controlled for. Female age is thought to affect the ability of birds to gather energy to egg-laying and nestling feeding (Klomp 1970, Forslund and Pärt 1995). The above analyses were therefore repeated for one year old females and older females separately. For both one year old females (b = -0.29, $F_{1,141} = 76.13$, p < 0.001) and for older females (b = -0.26, $F_{1,539} = 110.10$, p < 0.001), clutch size decreased with advancement of laying during the synchronous period. Another possibility to control for variation in female 'quality' or 'condition' is to investigate the pattern of clutch size change for individual females breeding at different dates in different years. Since repeatability of relative laying date is low (0.16, Smith, unpubl.), there is much between-season variation in individual females' laying dates. For individual females older than one year producing clutches in more than one breeding season, clutch size depended on laying date (mixed model with female identity as a random factor, the effect of relative laying date, b = -0.27, $F_{1,229} = 42.36$, p < 0.001). Finally, females demonstrated a clutch size decline also within the same season. In the study area, there were five known cases in which repeat clutches followed a failed breeding attempt not subject to any experimental manipulation. Those repeat clutches were laid 16 to 43 days later than the first clutch. Clutch size decreased with the advancement of laying (b = -0.078, $F_{1,4.11} = 75.30$, p < 0.001).

If clutch size was affected by the risk of losing male parental care to a secondary female mated to the same male, I would expect first mated females to lay earlier and/or show a steeper decline of clutch size with season as a way of competing with the second mated females. First mated females on average laid earlier than monogamous females (relative laying date 2.18 vs 4.27, $F_{1,858} = 15.69$, p < 0.001), but this may be a simple consequence of early laying females being mated to males with a higher probability of attracting secondary females. The slope of the clutch size–laying date relationship during the first week did not differ between monogamous and primary females ($F_{1,747} = 0.002$, p = 0.96). Furthermore, monogamous females mated to a male with only one nestbox and therefore not risking that their male become polygynous did not lay later ($F_{1,172} = 2.52$, p = 0.11) but tended to show a shallower seasonal trend compared to monogamous females mated to a male with two nestboxes (b = -0.18 vs -0.36, $F_{1,108} = 3.47$, p = 0.065; the analysis restricted to 1993–1997 when both categories existed, males with boxes ≤ 2.1 m apart were excluded since they normally do not manage to attract additional mates (Smith and Sandell 1998). However, this result was the result of the first group containing a higher number of late breeding females; when restricting the analysis to the synchronous period, no difference was found ($F_{1,106} = 0.23$, p = 0.63).

The reduction of clutch size during the first week resulted in an increased synchronisation of hatching dates as compared to laying dates (the slope of the regression of hatching date on first egg date, b = 0.63, significantly differs from one, $F_{1,1141} = 185.96$, p < 0.001).

Seasonal effects on reproductive success

Twenty-four nests predated during nestling rearing, 5 nests predated during incubation and 13 nests predated during laying did not differ in timing from the remainder of the nests (p > 0.6 in all cases). Furthermore, nests laid during the first synchronous week were not more prone to predation during laying, incubation or nestling rearing than nests laid later (Mantel-Haenzel test which test the association between two binary variables while controlling for another variable, p > 0.5 in all three cases).

Fledging success (fledglings/hatchling) declined with the advancement of hatching during the first two weeks, to improve again later in the season (generalised linear model with binomial error and a logit link-function and year as a factor, the effect of hatching date: b = -0.17, $F_{1,647} = 19.71$, p < 0.001, hatching date squared: b = 0.0051, $F_{1,647} = 16.48$, p < 0.001), but the model showed a significant lack-of-fit (Hosmer and Lemeshow goodness-of-fit test, $\chi^2_8 = 27.03$, p = 0.0007). Restricting the analysis to clutches produced during the synchronous period, fledgling success decreased with hatching date (b = -0.28, $F_{1,567} = 24.86$, p < 0.001; goodness-of-fit, $\chi^2_8 = 12.81$, p = 0.12) with no quadratic relationship ($F_{1,566} = 0.46$, p = 0.50). This negative relationship did not differ between years ($F_{6,561} = 1.03$, p = 0.40). When restricting the analysis to monogamous and primary females, no effect of hatching date could be detected ($F_{1,470} = 1.66$, p = 0.20). There was also no quadratic relationship ($F_{1,469} = 2.33$, p = 0.13). Restricting the analysis to breeding attempts where both mating status and hatching date was known, a model including mating status as a predictor better fitted data than a model including hatching date as a predictor (Akaike Information Criterion 1495.1 vs 1508.9). This suggests that the reduced fledging success with advanced hatching date could arise because secondary females, receiving less assistance from males, generally breed later.

The lack of seasonal decline in fledging success could be because females adjust clutch size to changing food

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conditions. To control for the effect of clutch size, the production of fledglings was related to hatching date for the four most common clutch sizes separately. For clutches laid during the synchronous period, fledgling production did not depend on laying date for clutches of four ($F_{1,30} = 1.07$, $p = 0.31$) and seven ($F_{1,38} = 0.33$, $p = 0.57$), but did for clutches of five ($b = -0.31$ nestlings/day, $F_{1,216} = 49.02$, $p < 0.001$) and six ($b = -0.19$, $F_{1,267} = 8.06$, $p = 0.0049$, Fig. 3).

Mean nestling mass tended to decrease with the advancement of hatching date (ANCOVA with year as a factor, $b = -0.051$ g/day, $F_{1,607} = 3.73$, $p = 0.054$), but the effect differed between years ($F_{6,601} = 5.89$, $p < 0.001$) because the relationship was only significantly negative in three years out of seven ($p < 0.01$ in all three cases). For none of these years was there a significant quadratic relationship ($p > 0.14$ in all cases). Restricting the analyses to clutches laid during the synchronous period, there was no effect of hatching date on nestling mean mass ($F_{1,511} = 0.50$, $p = 0.48$). Also for monogamous and primary females, there tended to be a decline in nestling mass with advancing hatching date ($b = -0.067$ g/day, $F_{1,442} = 3.62$, $p = 0.058$), but the slope differed between years ($F_{6,435} = 3.60$, $p < 0.002$) because the relationship was only significantly negative in two years out of seven ($p < 0.05$ in both cases). For both these years a quadratic component was significant ($p < 0.02$ in both cases), because of a few late clutches with very low mass contributing to a steeper decline late in the season.

Nestling tarsus length was unrelated to hatching date ($F_{1,609} = 0.28$, $p = 0.60$), but the effect differed between years ($F_{6,603} = 5.25$, $p < 0.001$) because the relationship was significantly negative in two years out of seven ($p < 0.001$ in both cases) and marginally positive in one year ($p < 0.05$). In one of the years with a negative trend, there was a marginally non-significant quadratic relationship ($p = 0.055$) because of some late very small broods. In the two other years a quadratic component was not significant ($p > 0.6$ in both cases). Restricting the analysis to the synchronous period, there was no effect of hatching date on nestling mean tarsus length ($F_{1,507} = 0.43$, $p = 0.51$). For monogamous and primary females, there was no overall seasonal relationship ($F_{1,446} = 2.49$, $p = 0.12$), but the relationship differed between years ($F_{6,440} = 3.14$, $p = 0.005$) because it was significantly negative in three years out of seven ($p < 0.05$ in all three cases). In all these years a quadratic component was significant because of a few clutches with small nestlings produced late in the season contributing to a faster decline with date late in the season ($p < 0.05$ in all cases).

Lack of relationship between hatching date and nestling size could be explained by females adjusting clutch size to prevailing conditions. However, there were no significant relationships between nestling tarsus length (ANCOVA with year as factor and clutch size as covariate, the effect of hatching date, $F_{1,498} = 0.84$, $p = 0.36$) or nestling mass ($F_{1,502} = 1.83$, $p = 0.17$) and hatching date for synchronous females.

Recruitment success

Recruitment success is based on a total number of 65 recruits from 653 broods that produced between zero and two recruits each. Dispersal distance for both males and females was unrelated to relative hatching date (H. G. Smith, unpubl.), suggesting that local recruitment is a reasonable measure of survival. Recruitment was negatively affected by both fledgling condition as measured by tarsus length (H. G. Smith, unpubl.) and by advancement of hatching date ($\chi^2 = 6.13$, $n = 649$, $p = 0.013$). Therefore the effect of year, mean nestling tarsus length and hatching date were analysed simultaneously. For all broods, recruitment probability declined with season ($b = -0.19$, $\chi^2 = 7.76$, $n = 538$, $p = 0.005$; goodness of fit, $\chi_8^2 = 6.02$, $p = 0.64$; Fig. 4). A quadratic component was not significant ($\chi^2 = 0.01$, $p = 0.92$). The relationship did not differ between years ($\chi^2 = 6.42$, $p = 0.27$). The decline in recruitment probability with season also held true when analysing only monogamous and primary females' broods ($b = -0.31$, $\chi^2 = 6.75$, $n = 391$, $p = 0.009$; goodness of fit, $\chi_8^2 = 10.10$, $p = 0.25$). When analysing only synchronous females, the result was not significant ($\chi^2 = 3.19$, $n = 443$, $p = 0.07$; goodness of fit,
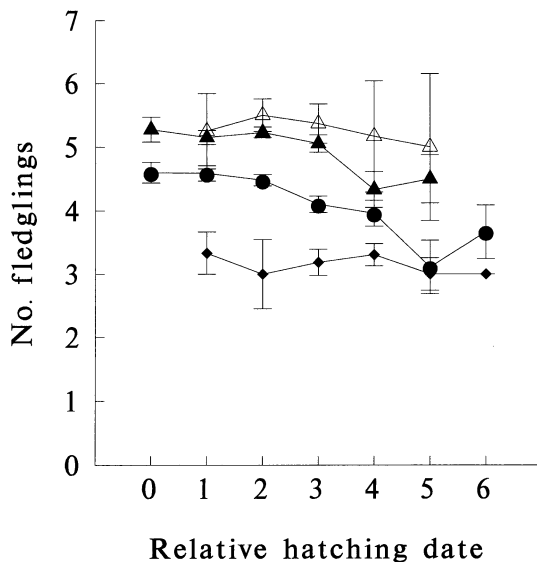

Fig. 3. Number of fledglings produced by synchronous females in relation to relative hatching date for females laying clutches with 4 (◆), 5 (●), 6 (▲) and 7 (△) eggs. Day 0 = the first day a clutch in the studied population hatched each year. Mean ± standard error shown. Two observations at hatch = 7 not included.
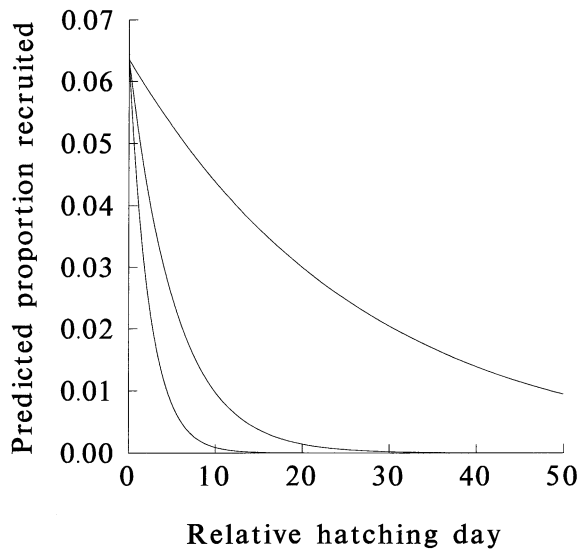
Fig. 4. Predicted proportion recruited according to generalized linear model including year, tarsus length and hatching date of offspring. Results given for arbitrary year (1993) and average sized offspring. 95% confidence limits computed on the profile likelihood function given.

$\chi^2_8 = 5.35$, p = 0.72). However, the statistical test was very conservative because data were underdispersed (deviance/df = 0.42). If correcting for underdispersion by using deviance divided by the degrees of freedom as a scale parameter (Wilson and Hardy 2002), the result was significant ($F_{1,435} = 7.51$, p = 0.006). Out of 541 broods producing fledglings within the synchronous period, 60 (11.1%) produced at least one recruit, whereas only 2 out of 108 (1.9%) broods after the synchronous period produced any recruits (stratifying by year, Mantel-Haenzel $\chi^2 = 7.59$, p = 0.006).

Discussion

Synchronous breeding

Starlings in the Revinge area bred synchronously. 87% of the females laid their first egg within 14% of the available breeding season as judged by laying-dates observed (Karlsson 1983). Already mated females may constrain the possibilities for secondary females to lay (Eens and Pinxten 1995, 1996, Sandell and Smith 1996, 1997, Sandell 1998), forcing them to lay at a time that does not maximise their fitness. Restricting the analysis to monogamous and primary females, which may be less socially constrained in when they can lay, demonstrated that 93% bred within 15% of the available days. In addition, the very strong reduction in clutch size with the advancement of laying (− 0.31 eggs per day) during the synchronous period resulted in an increased synchronisation of hatching dates. Hence, the reduction of clutch

size with season could be a mechanism whereby females synchronise their reproductive timing with other females (Finney and Cooke 1978, Karlsson 1983).

The synchronous breeding in this population of starlings could be explained in two different ways. First, there could be selection for synchrony per se (Gochfeld 1980, Ims 1990), penalising both early and late breeding attempts. The positive skew in laying dates may suggest that some females delay their laying to synchronise breeding (Gochfeld 1980). That this may occur was suggested by an aviary study where starlings in visual contact with food constrained starlings (which therefore delayed breeding) bred later than starlings with no such visual contact (Meijer and Langer 1995). Furthermore, in a food supplementation study, the effect of laying date was much smaller when only a part rather than a whole colony was food supplemented (Källander and Karlsson 1993). In this study, different measures of reproductive success decreased continuously with season (or were unaffected), suggesting that there is no stabilising selection for synchronous breeding. However, if starlings with the potential to breed very early delayed laying or laid large clutches to delay hatching so that many starlings started breeding simultaneously, there will be no asynchronous starlings early in the breeding season and the effect would be impossible to detect. Hence, there may be a cost of breeding asynchronously per se, which is hidden because no females nest asynchronously with other females early in the season. Because of the proportional low number of recruits, the power to detect a quadratic effect may also be low. Second, selection for early breeding combined with a small variation between females in when they are able to start laying could result in synchronous breeding (Lack 1968). The starling is a semi-colonial bird that does not defend feeding territories (Feare 1984). Since in the study area, the variation in laying date is present within the colonies, variance in laying dates cannot be because of variation in food availability (Davies and Lundberg 1985, Martin 1987, Nager 1990). Thus, mainly individual differences in quality should contribute to variation in hatching date. A strong penalty of delaying breeding could also result in that low-quality females that would otherwise lay late, advance laying at some cost (e.g. reduced fecundity or survival).

There are several factors that may select for synchronous or early breeding. First, the penalty of delaying reproduction could be high, because of deteriorating feeding conditions during the nestling period (Dunnet 1955). For example, many studies of temperate zone birds have demonstrated reduced nestling survival (Hatchwell 1991, Spear and Nur 1994, Verhulst et al. 1995) or growth (Sedinger and Flint 1991, Barba et al. 1995, Siikamäki 1998) with season. In the starling it seems unlikely that declining foraging conditions with season select for synchrony. Important foods for star-

lings such as leatherjackets, caterpillar larvae and earth-worms (Dunnet 1955, Tinbergen 1981, Whitehead et al. 1996) do not show a dramatic seasonal decline during the starlings' breeding season (Laughlin 1967, Tinbergen 1981, Sjöstedt 1986). The hypothesis that a rapid decline in food availability caused most birds to breed during the first week is difficult to reconcile with the fact that broods produced much later in the season have reason-ably high reproductive success (87% vs 86% fledging success for monogamous and primary females hatching their broods within and after the synchronous period). The significant but weak relationship between nestling size and hatching date for monogamous and primary females found in this study may instead be attributed to quality differences between birds (Perrins and Moss 1975, Rowe et al. 1994) and was in fact due to a very small number of broods (< 2%) produced more than a month after the start of the breeding season.

Second, breeding synchrony may be a way to escape predation on parents or nests (Darling 1938, Robertson 1973, Westneat 1992). As a social forager, starlings may benefit from reproductive synchrony by having to spend less time vigilant (Powell 1974, Jennings and Evans 1980) or from social food finding (Tinbergen and Drent 1980). Synchronous starlings may also be able to benefit from communal mobbing of predators (Shields 1984). How-ever, in studies were adults birds were followed over the breeding season, loss of parents was rare (H. G. Smith, unpubl.). Furthermore, nest-predation was rare and not related to reproductive synchrony. Therefore predation on parents and nests seems unlikely to be the main selective agent behind reproductive synchrony.

Third, synchronisation could be a way for females to compete for male parental care. A number of studies have demonstrated that males allocate their paternal care in relation to the hatching date of his different females' broods, providing more care to early hatched broods (Slagsvold and Lifjeld 1994, Bruun et al. 1997). Hence, by delaying breeding, a female risk that another female might outcompete her. However, monogamous females did not lay earlier when their males had access to an extra nestbox to which he could attract an additional female. Neither did monogamous females mated to males with an extra nestbox have a different seasonal clutch size trend. Thus, competition for parental care may not be the main cause of reproductive synchrony in the starling.

Fourth, females may breed synchronously to avoid intra-specific competition in the form of conspecific brood parasitism or extra-pair matings (Birkhead and Biggins 1987), although it has also been suggested that breeding synchrony may increase female opportunities for extra-pair matings (Stutchbury and Morton 1995). However, conspecific brood-parasitism is a consequence of some females being constrained from breeding early and therefore using brood-parasitism as a secondary

reproductive strategy while awaiting possibilities to breed (Sandell and Diemer 1998), rather than a selective pressure causing early breeding. The frequency of extra-pair offspring does not show any seasonal trend and will thus not select for early breeding (H. G. Smith, unpubl.). In the starling, extra-pair matings also seems to occur only after female solicitation (Eens and Pinxten 1990). Hence, the occurrence of males available for mating may not be a cost to the female (Eens and Pinxten 1990). Hence, it is unlikely that reproductive synchrony is caused by females avoiding intra-specific brood-parasit-ism or extra-pair mating attempts.

Lastly, breeding synchrony may result from the very steep reduction in the reproductive value of independent young with the advancement of season. In this starling population, the reduction in reproductive value with the advancement of season was extraordinarily strong compared to other studies of survival of independent offspring (see below). In the absence of clear effects of timing of breeding on other reproductive parameters, seasonal variation in the reproductive value of young remains the most likely candidate that selects for reproductive synchrony.

Seasonal trends in clutch size

Starlings in this population demonstrated a very strong reduction of clutch size with the advancement of laying date, especially during the first week after the first egg in the population was laid a particular year. A reduction in clutch size with season is a common phenomenon in temperate zone birds (Klomp 1970, Price et al. 1988), although often not as dramatic as in this starling population (Findlay and Cooke 1982, Stutchbury and Robertson 1988, Hochachka 1990, Winkler and Allen 1996). Recently a number of models have been proposed that may explain a seasonal decline in clutch size. These models differ in if they consider laying date to be constrained (Price et al. 1988, Price and Liou 1989) or optimized (Daan et al. 1990).

When birds or their territories differ in quality, simultaneous optimisation of laying date and clutch size can result in a decline of clutch size with season (Daan et al. 1990, Rowe et al. 1994). If there is a conflict between an advantage of breeding early, because of greater offspring value, and an advantage of delaying breeding, because of greater accumulated condition and hence an ability to lay a larger clutch, this will result in individuals in poor condition laying later and laying smaller clutches. This model could explain both the breeding synchrony and the sharp decline of clutch size with season in this study as the result of a strong decline in offspring value with season. An important property of the model is that an enforced delay of laying should result in the production of a larger clutch (unless the

enforcement affects condition). Although the sample size is small, females laying repeat clutches demonstrated a seasonal decline in clutch size between their first and their second clutch, suggesting that date per se rather than condition is affecting clutch size. However, it cannot be excluded that condition was lower in females laying repeat clutches. However, Christians et al. (2001) did not find any relationship between female condition and clutch size in starlings.

If laying date is constrained (sensu Price et al. 1988), optimisation of clutch size to a decline in offspring value with season would result in a reduction of clutch size with season (Hussell 1972, Murphy 1986). Such an interpretation is compatible with the combination of a strong seasonal decline in clutch size and recruitment probability found in this study. In contrast to the previous one, this hypothesis cannot directly explain why breeding is so synchronous in this population of the starling (see above).

In a study of North American starlings, starlings experimentally forced to lay replacement clutches demonstrated no seasonal decline in clutch size, contrasting with the population trend (Christians et al. 2001). This suggests that the seasonal decline in clutch size is caused by low-quality females laying late in the season. However, if the strong early season decline in clutch size is caused by selection for synchrony, the experimental delay in that study may have caused replacement clutches to be produced so late that any selection for synchrony is no longer relevant. Thus, only an experimental study delaying laying within the synchronous period can verify if individual females adjust clutch size to laying date within this period. The weak decline in clutch size with laying-date late in the season found in this study, may be related to factors other than selection for synchrony, for example population variation in female quality or seasonal variation in conditions to raise young (Christians et al. 2001).

Seasonal trends in recruitment success

Although a decline in recruitment with advancement of hatching date is commonly observed in birds (Perrins 1965, Cooke et al. 1984, Newton and Marquiss 1984, Daan et al. 1990, Hochachka 1990, Spear and Nur 1994, Brinkhof et al. 1997), the decline in this starling populations may be stronger than in most other bird populations studied. The decline also seems to be unrelated to seasonal variation in food supply to nestlings, since there was no comparable trend in nestling condition and since the seasonal trend in recruitment success also held true when controlling for nestling tarsus length (which is a predictor of post-fledging survival, H.G. Smith, unpubl.). A difference in the recovery-rate of males and females combined with

seasonal variation in offspring sex ratio can produce apparent seasonal trends in recruitment. However, there seems to be no seasonal trend in offspring sex-ratios in starlings (Kessel 1957, Bradbury et al. 1997).

Recruitment could decline rapidly with hatching date in this starling population because of a decline in the food supply so that late fledged nestlings are unable to find enough food. Although there may be a dramatic decline in food availability when leatherjackets emerge in August (Laughlin 1967), food availability in the form of soil dwelling invertebrates in the Revinge area does not change dramatically during the time between fledging and migration (Sjöstedt 1986).

In some species the reduction of recruitment probability with the advancement of hatching date has been attributed the fact that late fledged juveniles become sub-dominant to early-fledged ones and therefore become sub-dominant in flocks (Eden 1987, Nilsson and Smith 1988), are forced to disperse (Nilsson and Smith 1988, Stickland 1991) or migrate (Gauthreaux 1978, Smith and Nilsson 1987). In such cases, survival rate of a fledged young may depend on the number of already fledged juveniles (Kluyver 1971, Tinbergen et al. 1985). However, dominance because of prior residency has been tied to territorial behaviour (Piper 1997) and starlings do not defend territories post-fledging but move around in large flocks (Feare 1984, Krementz et al. 1989). Hence, it is unlikely that social dominance because of prior residency is the factor causing the seasonal decline in recruitment probability in starlings.

Dunnett (Dunnet 1955) suggested that synchronisation of breeding was to permit the immediate formation of flocks after fledging. Juvenile starlings form flocks immediately after fledging (Feare 1984). These flocks move around in the general breeding area, but within a few weeks of fledging juvenile starlings start to migrate south (Roos 1984, Rasmussen and Zuschlag 1989). Late-fledged young with poorer flying and foraging ability (Marchetti and Price 1989) may have problems following these flocks. Since the flocks offer protection from predation (Powell 1974, Jennings and Evans 1980, Feare 1984), it might be a considerable cost not being able to join these flocks. Interestingly, starling fledglings in an area where the starlings are less synchronous and stay in the local area for a prolonged time after breeding did not show a similar seasonal trend in survival (Krementz et al. 1989).

A reason for the early migration of juvenile starlings, may be that local food resources are partly depleted (Whitehead et al. 1996) and may also become inaccessible because of summer-drought (Feare 1984). Although the reduction in food availability may not be large enough to explain the sharp decline in recruitment with hatching date, it may cause starlings to migrate. If so, late-hatched starlings may either be left behind or be forced to follow the migrating flocks at a less mature

stage. In both cases, increased mortality might be the consequence.

Conclusion

This study demonstrates the importance of studying post-reproductive phenomenon to understand life-history decisions taken by parents during the reproductive period. The parameters measured during the reproductive season were unlikely to solely explain either the extraordinarily large breeding synchrony or the decline in clutch size with season. Instead it is likely that a drastic decline in fledgling survival probability with advancement of hatching force parents to breed as early as possible, possibly at the expense of fecundity causing the seasonal decline in clutch size. The strong seasonal decline in recruitment probability could be caused by the adaptive value of joining juvenile migrating flocks soon after fledgling. If so, it may also pay early females to delay laying to synchronise breeding with other females, contributing to the reproductive synchrony in starlings.

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