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AGE AND REPRODUCTION IN LESSER SPOTTED WOODPECKERS (*DENDROCOPOS MINOR*)

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ABSTRACT.—We examined the influence of female age, male age, and pair-bond duration on start of egg-laying, clutch size, and number of young fledged in the Lesser Spotted Woodpecker (*Dendrocopos minor*). We also attempted to disentangle the relative influence of individual age and pair-bond duration on reproduction, because the effect of those factors may be confounded. Breeding performance improved with age in that old females started egg-laying earlier and old males raised more young than yearlings, and old pairs both started egg-laying earlier and raised more young than new pairs. Clutch size was not affected by age, but showed a strong negative relation with laying date. Late-laying yearling females experienced a lower survival, and the survival of yearling males showed a positive relation with fledgling production. That differential survival was a likely mechanism explaining the differences in reproductive performance between yearling and old birds. Several analyses suggested that pair-bond duration had independent positive effects on reproduction. Benefit of long-term pair-bonds appeared to depend upon repeated breeding with a particular partner. The mechanisms behind the benefit of remating with a particular partner remain unclear, however. We postulate that much of the patterns of age effects on reproduction in the Lesser Spotted Woodpecker may be caused by constraints posed by the territorial system and effects of territory quality, although effects of individual quality can not be excluded.
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A COMMON PATTERN IN BIRDS is an improvement of breeding performance with age (Klomp 1970, Sæther 1990). The improvement may concern one or several different measures of breeding success, for example start of egg-laying, clutch size, egg size, hatching success, fledging success, and fledgling brood size (Sæther 1990). In short-lived species, the improvement may be apparent only between the first and second year (Dhondt 1989), whereas in longer-lived species an improvement may occur also beyond the second year (Ollason and Dunnett 1988, Newton 1989, Wooller et al. 1990). Because individual age often explains a substantial part of the interindividual variation in reproductive success (Clutton-Brock 1988, Newton 1989), an understanding of the mechanisms behind the patterns of age-specific reproduction is important for an understanding of behavioural strategies, life histories, and population dynamics (Clutton-Brock 1988, Forslund and Pärt 1995).

A number of hypotheses have been advanced to explain patterns of age-specific improvement of reproductive performance. Two hypotheses focus on changing proportions of phenotypes within a population. First, by a progressive disappearance of poor reproductive performers ("Bad-quality birds hypothesis," Curio 1983; or "Selection hypothesis," Nol and Smith 1987). If poor reproductive performers also have lower survival than good ones, the proportion of good reproductive performers will increase in older age-classes of a population. Second, by a progressive appearance of good reproductive performers ("Delayed breeding hypothesis," Hamann and Cooke 1987). If good reproductive performers enter the breeding population at an older age than poor ones, the proportion of good reproductive performers will increase in older age-classes.

A third hypothesis relates to improvements of competence of individuals. ("Constraint hypothesis," Curio 1983; or "Maturation hypothesis," Hamann and Cooke 1987). As they age, individuals improve in skills that positively affect reproductive performance. Consequently, individuals are expected to be better reproductive performers when they enter older age-classes. Examples are experience of breeding as such; foraging ability; knowledge about predators, competitors, mates, territories and mi-

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gration routes; and access to better territories due to earlier arrival or higher social status.

A fourth hypothesis focuses on optimization of reproductive effort—the relative amount of resources allocated to reproduction. Because the residual reproductive value decreases with age, individuals are expected to increase their reproductive effort at the end of life, and consequently, relative reproductive performance improves in old birds ("Restraint hypothesis," Curio 1983; or "Residual reproductive value hypothesis," Nol and Smith 1987). A demonstration that reproductive effort increases with age "face formidable obstacles" (Clutton-Brock 1984), but a testable assumption of that hypothesis is that survival probability should decrease with age (Curio 1983).

Various degrees of support have been presented for the above hypotheses (review in Forslund and Pärt 1995). However, it is likely that several of the mechanisms act simultaneously in any species, but that their relative importance differs in relation to differences in life histories, mating systems, food preferences, etc. (Forslund and Pärt 1995).

An issue closely related to effects of individual age on reproduction is effects of pair-bond duration. A positive relation between pair-bond duration and reproduction is shown in a number of species (Rowley 1983, Black 1996). Individual age and pair-bond duration tend to be correlated, however, and their effects may be confounded (Fowler 1995, Cézilly and Nager 1996). Hence, students of age effects on reproduction should also consider possible pair-bond effects, and vice versa (Cézilly and Nager 1996, Pärt and Forslund 1996). Fowler (1995) suggested a protocol to separate their effects by using young and old birds to compare the performance of pairs of different duration and composition. If individual age matters, then newly formed pairs of old individuals should perform as good as old pairs with previous breeding experience. If pair-bond duration matters, then old pairs should perform better than new pairs of old birds. Cézilly and Nager (1996) suggested statistically controling for pair-bond duration when analyzing effects of individual age, whereas Pärt and Forslund (1996) emphasized the use of experiments to disentangle the relative importance of different factors, because there may be additional confounding factors, such as individual quality, which may be difficult to control for statistically.

In this study, we examine the effects of indivdual age and pair-bond duration, and also attempt to disentangle their relative effects on reproductive performance in the Lesser Spotted Woodpecker (*Dendrocopos minor*). The data comes from a long-term observational study of the species, which confines us to using statistical procedures to control for different factors.

STUDY SPECIES AND METHODS

The Lesser Spotted Woodpecker is a small (body mass 24 g) inhabitant of woodlands of the Palearctic region (Cramp 1985). Our study population show a strong seasonal trend in reproduction; clutch size declines steeply (1.1 egg/week) with progression of the season, and both number of fledglings produced and prospects for juvenile recruitment into the breeding population show a significant negative relation to clutch initiation date (Wiktander et al. 2001a). Hence, the start of egg-laying is an important component of reproductive success. In 9% of the 124 breeding attempts we followed during the study, pairs defended a territory and excavated a complete nest but laid no eggs, and 20% of the attempts failed after egg-laying (Wiktander et al. 2001a). The parents participate equally in parental care during incubation and as long as the nestlings require brooding, and biparental care at these stages appear to be necessary for successful breeding (Wiktander et al. 2001b). At the late stages of nestling feeding, however, the share taken by the male is often larger than that of the female (Wiktander et al. 2001b). Courtship feeding is never documented (Cramp 1985, Wiktander 1998). Only one brood is reared per season (Cramp 1985, Wiktander 1998). For a bird of this size, breeding territories are unusually large; 50 to 100 ha (Wiktander et al. in press), which is linked to its specialized foraging for insect larvae in dead wood and tree bark (Olsson 1998). It is a year-round resident with part-time partnerships (sensu Ens et al. 1996); outside the breeding season, individuals are solitary in a home-range surrounding the breeding territory, with territorial behavior and pair formation starting in late March (Wiktander et al. in press). In general, established adults remained in the same breeding territory for consecutive years, and territory shifts were very rare (out of 97 birds, 94% remained in the same territory, 5% moved to a neighboring territory between years, and 1% moved beyond a neighboring territory; Wiktander 1998). A likely reason for this apparent site-fidelity is the strong intrasexual competition and territoriality of established adults and a possible advantage of prior residency in territorial conflicts, leading to high costs for attempts to take over occupied territories, hence constraining the possibilties for territory shifts (Wiktander 1998). In support of this view, all territory shifts occurred to a territory where there was a vacancy (Wiktander 1998). Mate fidelity is very strong, with a divorce rate (sensu Rowley 1983) of only 3.4% in our study population (Wiktander 1998). The majority (89%) of the recruits of known age to the study area were yearlings, that is born the previous year, and only in one year (1991) was there an immigration of old birds (half of the recruits in that year; Wiktander 1998). Because of this dominance of yearlings among the recruits and the strong site-fidelity of established adults, we concluded that the birds in general remained for life in the territory where they first settled. Thus, for all years except 1990, we considered a bird that disappeared between two breeding seasons to have died rather than emigrated (Wiktander 1998). Birds that disappeared between 1990 and 1991 may have dispersed and are not included in figures on survival rates. During our study, the average annual mortality rate of adults was 0.36, and 48 individuals followed from their first year as adults were present on average 2.0 ± SD of 1.44 breeding seasons, with a maximum of seven seasons ($n = 3$) (U. Wiktander and O. Olsson unpubl. data).

From 1989 to 1998, we studied Lesser Spotted Woodpeckers in a 125 km^2 study area in the boreonemoral region in southern Sweden (56°40′N, 14°10′E). Most of the study area was covered by coniferous woodlands, but interspersed were 50 to 150 ha patches dominated by deciduous woods. In the deciduous woods, 10 to 17 Lesser Spotted Woodpecker breeding territories were established annually. For a more detailed description of the study area, see Olsson (1998) and Wiktander (1998).

All potential territories were visited at least weekly from March until the young fledged in late June. We inspected all found nests with an interval of three to five days, using a dentist's mirror and a lamp, to establish the date of laying of the first egg and the size of the full clutch. These inspections were continued through the season until a clutch was laid, allowing us to identify nonbreeding pairs (Wiktander et al. 1994). Most nests were found before or during egg-laying. For nests found with a full clutch, we used hatching date and assumed an incubation time of 11 days to calculate the laying date (Wiktander et al. 1994). To calculate the laying date of the first egg, we assumed the female laid one egg per day (Wiktander 1998). When the young were 17 days old, we cut a hole into the nest chamber, the young were counted and individually color-banded, and then put back in the nest and the hole closed again. To make sure this did not affect breeding, nests were observed from a distance for 1–2 days afterwards, and in all cases, the parents brought food normally. After the young had fledged, we sieved the nests contents to look for unfledged young.

We captured adults at the roosting or nesting hole with a bag net or a mist net for individual color-banding and aging. In 1989, 50% of the parent birds were color-banded and of known age, 75% in 1990, 90 to 100% in 1991 to 1997, and 80% in 1998. The birds were classed as yearling (born the previous year) or old (two years old or older), according to molt of the greater upper wing coverts (unmolted in yearlings) and secondaries (birds with more than one generation of feathers being old) (Baker 1993, Wiktander 1998). Most birds could be readily aged according to these criteria, but a few doubtful individuals have been excluded from analyses.

In this study, we consider the influence of female age, male age, and pair-bond duration (the number of years the same male and female bred together) on three measures of reproductive success: laying date (the date of laying of the first egg in the clutch), clutch size (number of eggs in the full clutch), and fledgling production (number of young fledged, including failed breedings and nonbreeding pairs). To control for the large annual differences in laying date (Wiktander et al. 1994, Wiktander 2001a), we set the median date of the population each year to zero and individual dates as a deviation from this. Thus, laying dates before the median got a negative value and laying dates after the median got a positive value. We consider first clutches only, that is, renestings following failure are excluded. We only discriminate between yearling birds and old birds, and between pairs of birds that bred together for the first time (new pairs) and pair bonds that lasted beyond the first year (old pairs). A reason for pooling all old birds in one class is that n-values decrease rapidly after age two years. Another reason is that we do not know the exact age of the individuals that were present at the start of the study, only if they were yearling or older. In the group with old birds, we have sought to avoid pseudoreplication due to the repeated occurrence of individuals and pairs that lived beyond the second year. (All individuals and pairs also occur as a separate value in the first-year group, because part of what is examined is the possible influence of the development of individuals as they age, see above.) On the basis of pairs, cases were selected randomly such that individual pairs occurred only once. With that selection, seven males and four females appeared twice, but we regard that as a reasonable compromise in order to maintain reliable n-values. Moreover, for none of the reproductive variables did those individuals differ significantly from individuals appearing only once (ANOVA, $P > 0.15$ in all cases). Hence, we feel confident that the repeated occurrence of some individuals does not affect the results.

Use of two age classes results in five possible constellations of pairs: four different new pairs, composed of two yearlings; young female and old male; old female and young male and two old birds, respectively; and finally old pairs, by definition, composed of two old birds. These classifications were made to separate effects of individual age and pair-bond duration, and to investigate mechanisms behind possible benefits of pair-bond effects. For those analyses we were not interested in comparing all categories against each other, but only between certain groups that were specified in advance (i.e. pairs with two yearlings vs. pairs with one old and one young bird, pairs with at least one yearling vs. new pairs with two old birds, new pairs with two old birds vs. old pairs, and new pairs vs. old pairs). Those analyses were made by means of planned comparisons following an overall one-way ANOVA (Sokal and Rohlf 1995).

RESULTS

Overall trends.—Old females started egg-laying significantly earlier than yearling females, and old pairs started significantly earlier than new pairs, whereas there was no significant difference between old and yearling males (Females: ANOVA, $F = 6.63$, df = 1 and 66, $P = 0.01$. Males: $F = 2.53$, df = 1 and 66, $P = 0.12$. Pairs: $F = 11.77$, df = 1 and 67, $P = 0.001$; Fig. 1A). Clutch size was not significantly different between age-classes in any case (Females: $F = 0.86$, df = 1 and 50, $P = 0.36$. Males: $F = 0.98$, df = 1 and 51, $P = 0.33$. Pairs: $F = 2.36$, df = 1 and 50, $P = 0.13$; Fig. 1B). Old males and old pairs, but not old females, raised significantly more young (Females: $F = 0.06$, df = 1 and 70, $P = 0.82$. Males: $F = 5.73$, df = 1 and 70, $P = 0.02$. Pairs: $F = 9.78$, df = 1 and 70, $P = 0.003$; Fig. 1C).

To investigate which factor or factors had a significant influence on the breeding parameters, we used multiway ANOVA or ANCOVA and excluded insignificant factors ($P > 0.1$) with stepwise backward elimination while controlling for possible associations between the factors. In all analyses, female age, male age, pair-bond duration, year, and the interaction

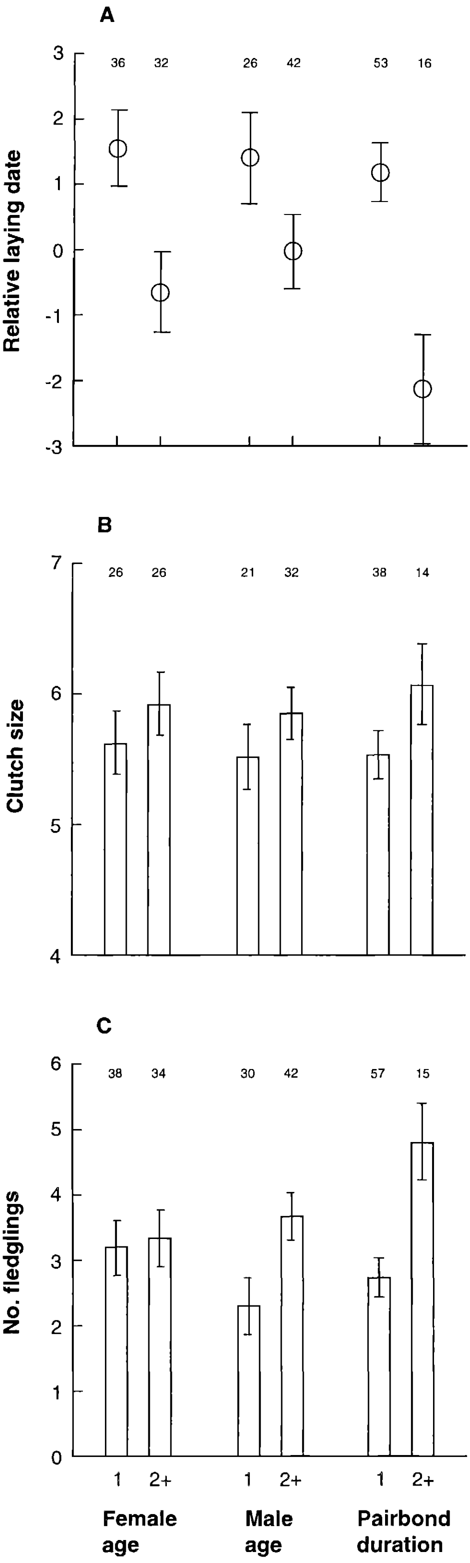

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FIG. 1. Reproductive performance in relation to female age, male age, and pair-bond duration in the Lesser Spotted Woodpecker, where 1 represents yearling birds or new pairs, and 2+ old birds or pairs. Vertical lines show one standard error. N-values are shown above each group. (A) Relative laying date of the first egg. (B) Clutch size. (C) Number of young fledged.

between female age and male age were factors in the original model. For relative laying date, pair-bond duration was the only remaining significant factor (result as above, Fig. 1A). The last factor to be eliminated was female age. The effect of female age at this level was ($F = 0.94$, df = 1 and 61, $P = 0.33$), and pair-bond duration was ($F = 3.77$, df = 1 and 61, $P = 0.06$). Hence, there was a nearly significant effect of pair-bond duration also when female age was controlled for, indicating an independent effect of pair-bond duration on start of egg-laying.

For clutch size, no significant factor remained, the final factor being pair-bond duration (result as above, Fig. 1B). With relative laying date included as a covariate in the model, only this variable remained, showing a highly significant negative relation with clutch size ($F = 21.64$, df = 1 and 55, $P < 0.0001$).

For fledgling production, remaining factors were pair-bond duration, with a significant effect ($F = 5.36$, df = 1 and 62, $P = 0.02$), and year, whose effect approached significance ($F = 1.88$, df = 8 and 62, $P = 0.08$). The effect of year depended on a single year, 1991, when only 33% of the breeding attempts resulted in fledged young (Wiktander et al. 1994). The last factor to be eliminated was male age. The effect of male age at this level was ($F = 0.32$, df = 1 and 57, $P = 0.57$), and pair-bond duration was ($F = 3.77$, df = 1 and 57, $P = 0.06$). Hence, pair-bond duration also had a nearly significant effect when male age was controlled for, also indicating an independent effect of pair-bond duration on fledgling production. With relative laying date included in the model, both that variable and year remained with significant effects of both (relative laying date: $F = 7.69$, df = 1 and 60, $P = 0.007$; year: $F = 3.37$, df = 8 and 60, $P = 0.003$).

Survival in relation to reproduction.—By means of logistic regression, we analysed the relationship between the reproductive performance of yearling birds and their survival until 20 March the following spring. For relative laying date, there was a significant negative relationship in females ($G = -6.12$, df = 1, $P = 0.01$), whereas the survival of males was unaffected by laying date ($G = 1.56$, df = 1, $P = 0.21$). Neither female nor male survival was affected by clutch size (females: $G = 1.32$, df = 1, $P = 0.25$; males: $G = 0.23$, df = 1, $P = 0.63$). There was no significant relation between fledgling production and female survival ($G = 1.97$, df = 1, $P = 0.16$), but a positive significant relation in males ($G = 5.02$, df = 1, $P = 0.03$).

This differential survival among yearlings could be a mechanism causing the difference in start of egg-laying between yearling and old females (Fig. 1A) and the difference in fledgling production between yearling and old males (Fig. 1C). The start of egg-laying by surviving yearling females did not differ from old females ($F = 0.013$, df = 1 and 45, $P = 0.91$), whereas nonsurviving yearling females started egg-laying significantly later than old females ($F = 7.13$, df = 1 and 48, $P = 0.01$; Fig. 2A). The number of young produced by surviving yearling males was not different from old males ($F = 1.27$, df = 1 and 56, $P = 0.27$), whereas nonsurviving males produced significantly less young than old males ($F = 11.00$, df = 1 and 51, $P = 0.002$; Fig. 2B).

Age of first breeding.—The vast majority of the yearling birds, that is, 37 out of 40 females (93%) and the mates to 29 out of 32 yearling males (91%), laid eggs in their first potential breeding season. Thus, there was almost no variation in age of first breeding. Of the three nonbreeding females, two bred the following year and performed, if anything, worse than the average (relative laying date +3 and clutch size 5 in both cases; number of young fledged 5 and 0, respectively). The third female did not reappear the following year. Of the three nonbreeding males, one bred the following year (relative laying date −3, clutch size 6, and 4 fledged young), whereas the other two did not reappear the following year.

Individual improvement.—To investigate if individual birds or pairs improved with age, we compared the reproduction of a yearling bird or a new pair with the performance of the same bird or pair when older with paired t-test. Pairs improved significantly in start of egg-laying ($t = 2.40$, df = 11, $P = 0.03$; Fig. 3) but not females ($t = 0.41$, df = 11, $P = 0.69$) or males ($t = 0.78$, df = 13, $P = 0.45$). Clutch size did not improve significantly in any category (females: $t = 0.61$, df = 7, $P = 0.57$; males: $t = 0.35$, df = 7, $P = 0.74$; pairs: $t = 0.82$, df = 6, $P = 0.44$) and the same was true for fledgling production (females: $t = 0.73$, df = 9, $P = 0.48$; males: $t = 0.80$, df = 11, $P = 0.44$; pairs: $t = 1.77$, df = 7, $P = 0.12$).

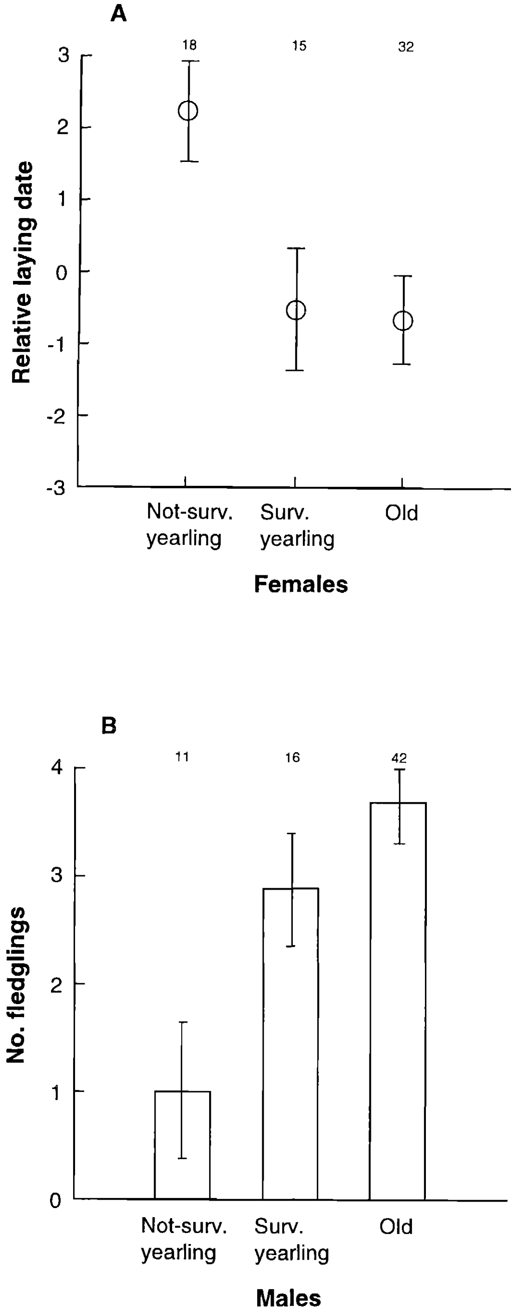

FIG. 2. Reproductive performance of yearling birds not surviving to the following year, surviving yearlings, and older birds, respectively. Vertical lines show one standard error. N-values are shown above each group. (A) Relative laying date of females. (B) Number of young fledged by males.

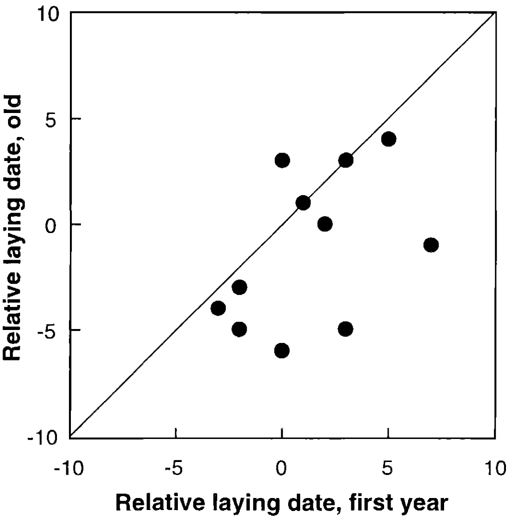

FIG. 3. Relative laying date of new pairs, compared with the performance of the same pairs when old.

Age-specific survival.—If anything, the probability of surviving until 20 March the following year appeared to increase rather than decrease up to at least age 5 years in both males and females (Fig. 4). Moreover, the survival rate of yearling females (45%) was significantly lower than for females in the older age-classes (69%) ($\chi^2 = 4.13$, df = 1, $P = 0.04$), but the survival rate of yearling males (63%) was not sig-

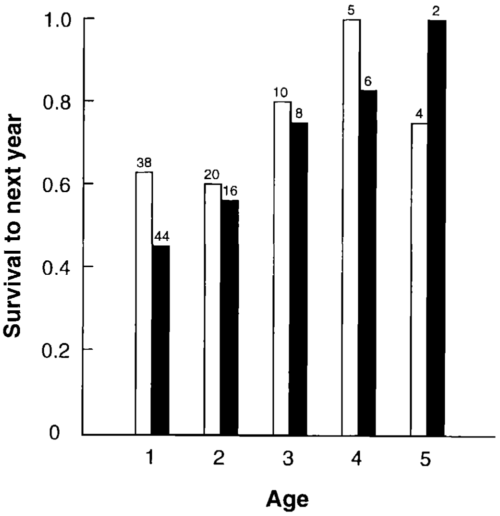

FIG. 4. Age-specific rates of survival until 20 March the following year. Open bars = males, filled bars = females. N-values shown above bars.

nificantly different from males in the older age-classes (72%) ($\chi^2 = 0.66$, df = 1, $P = 0.42$).

Effects of pair-bond constellations.—To examine further the relation between individual age and pair-bond duration, we compared the reproductive performance of pairs composed of the different combinations of yearling and old birds (Fig. 5). There were significant differences among the categories of pairs in start of egg-laying ($F = 3.15$, df = 4 and 57, $P = 0.02$; Fig. 5A) and fledgling production ($F = 3.97$, df = 4 and 59, $P = 0.006$; Fig. 5C), but not clutch size ($F = 0.64$, df = 4 and 42, $P = 0.63$; Fig. 5B). Three planned comparisons revealed that the laying date of pairs where an old male or female was paired to a yearling did not differ from pairs with two yearlings ($F = 0.01$, df = 1 and 57, $P = 0.93$), new pairs with two old birds did not differ from pairs with at least one yearling ($F = 0.29$, df = 1 and 57, $P = 0.59$), and new pairs with two old birds tended to start laying later than old pairs ($F = 2.63$, df = 1 and 57, $P = 0.11$). Old pairs started egg-laying earlier than new pairs, which is known from previous tests (Fig. 1A). Regarding fledgling production, the planned comparisons showed that mixed-age pairs were not different from pairs with two yearlings ($F = 1.12$, df = 1 and 59, $P = 0.29$), new pairs with two old birds did not differ from pairs with at least one yearling ($F = 0.001$, df = 1 and 59, $P = 0.97$), and new pairs with two old birds produced significantly less young than old pairs ($F = 5.97$, df = 1 and 59, $P = 0.02$). From previous tests (Fig. 1C), it is known that old pairs raised more young than new pairs.

Age and failure to produce fledged young.—We knew the age of both parents and the pair bond for seven nonbreeding pairs, that is, pairs that defended a territory and excavated a nest but laid no eggs, and for 16 breeding attempts that failed after egg-laying. All nonbreeding pairs were new pairs, but were composed of all four

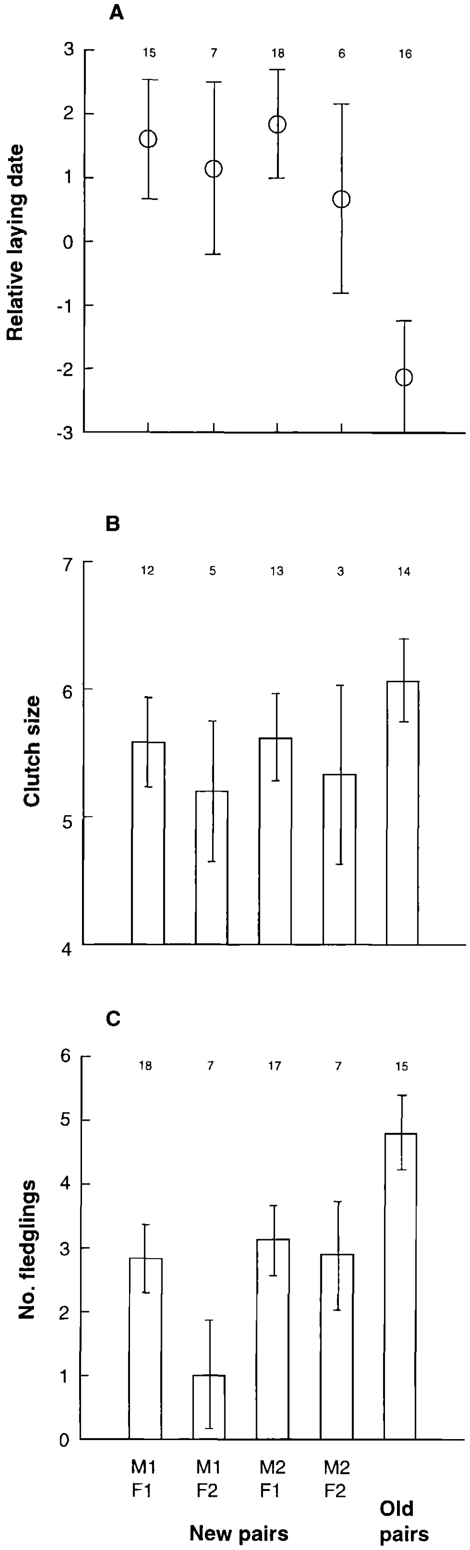

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FIG. 5. Reproductive performance of new and old pair constellations, with new pairs grouped according to the age of the included male (M) and female (F), where 1 represents yearling bird and 2 represents older bird. Vertcal lines show one standard error. *N*-values are shown above each group. (A) Relative laying date of the first egg. (B) Clutch size. (C) Number of young fledged.

TABLE 1. Distribution of Lesser Spotted Woodpecker pairs, categorized according to the age of the pair members, which laid no eggs, failed after egg-laying, or successfully raised young to fledging.

	Nonbreeders	Failed breeders	Successful breeders	Total
	New pairs			
Two yearlings	3	5	10	18
Yearling male and old female	1	3	3	7
Old male and yearling female	1	4	12	17
Two old birds	2	3	2	7
Total	7	15	27	49
	Old pairs			
	0	1	14	15

possible combinations of yearling and old individuals (Table 1). All but one (94%) of the pairs that failed after egg-laying were new pairs, again composed of all four possible combinations of yearling and old individuals (Table 1). Thus, failure to produce fledged young appeared not to be related to the age of either the male or the female, but strongly so to the age of the pair-bond. A significantly larger proportion of the new pairs (45%) failed to produce fledged young, compared with old pairs (7%) ($\chi^2 = 7.29$, df = 1, $P = 0.007$; Table 1).

DISCUSSION

Breeding performance improved with age of individuals in the Lesser Spotted Woodpecker, in that old females started egg-laying earlier and old males produced more young than yearlings. However, several analyses suggest that there were also additional independent effects of pair-bond duration. First, the multiway analyses indicated effects of pair-bond duration also when individual age was controlled for. Second, in the comparison of different pair constellations, old pairs performed better than any group of new pairs, showing that a change of mate reduced reproductive performance irrespective of the age of the new mate. Hence, according to Fowler (1995), effects on reproduction may be attributed to pair-bond duration rather than individual age, in which case new pairs with two old birds should have performed as good as old pairs. Third, failure to produce fledged young was associated with the age of the pair-bond, in that 96% of all failures and nonbreeding pairs occurred in new pairs, irrespective of the age of the individual birds involved.

We found support for one of the proposed hypotheses for the improved breeding performance with age of individuals. Both the difference in laying date between yearling and old females, and the difference in fledgling production between yearling and old males could be explained by the differential survival of yearlings in relation to reproductive performance, supporting the bad-quality birds or selection hypotheses. With only surviving yearlings included, there was no difference between the age-classes. An explanation for the mechanism of that hypothesis is that individuals differ in quality; poor quality individuals are both poor reproductive performers and subject to high mortality, hence there is a selection for good quality individuals to enter the next age-class (Curio 1983). However, we suggest the possibility that differences in territory quality could generate the same result by selecting for individuals on good territories, given that territory quality affects both reproductive performance and survival probability, and that the variation in quality between individuals is minor compared to the variation in quality between territories. An additive effect of individual and territory quality is possible in species with frequent territory shifts, and where poor-quality birds may be subordinate and confined to poor territories (Newton 1986, Bensch and Hasselquist 1991). However, in a year-round resident with life-long territory fidelity like the Lesser Spotted Woodpecker, we anticipate there may be substantial influence of territory quality. That is because the possibilities for changing to a better territory may be limited, unless vacancies occur, owing to likely large costs in terms of time and energy for evicting an established bird from an occupied territory. Hence, an individual may largely be confined to the territory where it first managed to settle. Regarding reproduction, Olsson et al. (1999) found that food availability had a significant influence on both start of egg-laying and number of young fledged in this population. Moreover, there was little variation in foraging competence between individual birds, whereas there were marked differences in food availability between territories, suggesting that reproduction was influenced by territory quality rather than individual quality (Olsson et al. 1999). Regarding survival, our available data do not allow a direct test of survival in relation to territory quality. But Olsson et al. (2000) showed that the higher the food availability in their territory, individuals spent less time foraging and devoted more time to preening, perching, and predator scanning, which should have a positive influence on survival, hence indicating a positive relationship between territory quality and survival.

The examination of the performance of individual birds gave no support for the "constraint" or "maturation" hypotheses; neither individual females nor males improved in any of the measures of reproductive success. However, pairs of birds that bred together for consecutive years improved in start of egg-laying. Because neither new pairs with two old birds nor old birds mated to yearling partners performed any better than pairs with two yearlings, it is not surprising that we found no improvement in breeding with age in individual birds.

The "delayed breeding hypothesis" assumes that good and poor reproductive performers should differ in age of first breeding. However, the vast majority of Lesser Spotted Woodpeckers commenced breeding in their first potential breeding season, which renders that hypothesis unlikely to apply in this species. An implication of that result is that chronological age in general corresponds with breeding experience (e.g. Forslund and Pärt 1995).

A testable assumption of the "restraint hypothesis" is that survival probability should decrease with age, a pattern not found in the Lesser Spotted Woodpecker, where the survival probability for both females and males rather increased up to age five years. Although this is not a direct test of the hypothesis, the result shows that one important underlying assumption is not fulfilled. A decreasing life expectancy in old individuals is shown for a number of species, but the general pattern is that this decline occurs late in life, after an increase during the early years (Newton 1989).

Partners may reunite for consecutive breeding seasons, and hence long-term pair-bonds develop, either as the result of an active choice of mate, or as the consequence of a choice of nest-site and territory, in which case mate fidelity arises as a mere by-product of site fidelity (Ens et al. 1996). The latter mating pattern is associated with species where territoriality and competitve advantages of prior residency constrains possibilities for territory shifts by elevating the costs for attempts to evict established territory holders. Owing to the strong territoriality and apparent site-fidelity of Lesser Spotted Woodpeckers, that seems a likely mechanism generating long-term pair-bonds in this species, rather than a direct choice of partner.

Benefits of long-term pair-bonds in terms of increased reproductive success is demonstrated in a number of long-lived seabirds (for example Coulson 1966, Mills 1973, Bradley et al. 1990, Emslie et al. 1992) and waterfowl (Scott 1988, Forslund and Larsson 1991) and also in some shorter-lived passerines like Great Tit (*Parus major*; Perrins and McCleery 1985) and Marsh Tit (*Parus palustris*; Smith 1993) (also see Black 1996). The mechanisms behind the advantage of long term pair-bonds remain unclear, however (Ens et al. 1996, Pärt and Forslund 1996). One explanation focuses on the age of individuals, that there is a positive correlation between the age of the individuals in a pair and their reproduction (Rowley 1983). By retaining the partner, an individual benefits from breeding with an older and more experienced partner. A prediction that follows is that the performance of pairs where an old bird is mated to a new but old partner should be similar to that of old pairs, but better than that of pairs with at least one young bird (Forslund and Larsson 1991). Such a pattern was found in the Barnacle Goose (*Branta leucopsis*; Forslund and Larsson 1991) but appears not to be the case in the Lesser Spotted Woodpecker. Another explanation is that the benefit comes from repeated breeding with the same particular partner (Coulson 1972). Retaining the partner leads to an increased familiarity and coordination between pair members in breeding activities, which enhances reproduction. A prediction in this situation is that newly formed pairs with two old birds should perform worse than old pairs (Forslund and Larsson 1991). The woodpeckers in this study conform to this prediction, suggesting that the benefit of long-term pair bonds in the Lesser Spotted Woodpecker may be due to repeated breeding attempts with the same particular partner, rather than effects of age and experience of individuals.

The mechanisms of how repeated breeding with a particular partner could improve reproductive performance are poorly understood (Ens et al. 1996). Several behaviors that may be positively affected by an increased familiarity and coordination between pair-members and that may enhance reproduction have been suggested, but few if any studies have demonstrated such a causal relationship (Ens et al. 1996). Examples of suggested behaviors are courtship feeding, protection against nest predators, coordination of incubation, feeding, and other parental-care duties. For the Lesser Spotted Woodpecker, we can at present only discuss potential mechanisms. One factor could be the equal participation in parental care by both parents. Biparental care appears to be necessary during incubation and as long as the nestlings need brooding (Wiktander et al. 2001b), and associated with this are likely many behaviors that potentially could be improved from coordination with a particular partner. Another possible factor, which is not primarily associated with familiarity with the partner, is familiarity with the territory. For much of the year, the Lesser Spotted Woodpecker feeds on wood-living insect larvae, of which each species is associated with certain tree species (Olsson 1998). As the prey species vary in abundance between years, so do different tree species and forest stands vary in profitability between years (Olsson et al. 1999). Because territories are very large (~100 ha) and composed of a mosaic of stands of varying tree-species composition and, consequently, varying profitability (Olsson 1998, Wiktander et al. 2001b), familiarity with the territory may be important in order to exploit its resources efficiently. An additional factor where familiarity with the territory may be important is in finding suitable nest sites. Hence, perhaps it may be beneficial that both partners have experience of living in and exploring the same territory, leading to an improved reproductive performance for old pairs, compared to pairs where one or both members are new in the territory.

To conclude, it appears that much of the patterns of age effects on reproduction in the Lesser Spotted Woodpecker may be governed by the territorial system and effects of territory quality (although effects of individual quality can not be conclusively excluded). Strong territoriality constrains possibilities for territory shifts, which is a likely mechanism behind site fidelity, with mate fidelity arising as a by-product. No doubt there exists a direct positive effect of territory quality on reproduction (Olsson et al. 1999). However, there may also be an indirect positive effect of territory quality, acting through increased survival, hence generating long-term pair-bonds, which positively affects reproduction. A crucial issue for future study is to establish the influence of territory quality, and other possible factors, on survival. The pattern of territoriality and site fidelity may also explain the very low divorce rate in our study population. However, an additional factor explaining the low divorce rate may be the apparent benefit from repeated breeding with a particular partner, indicating a cost of divorce, even if a possibility to move to a new territory and a choice of a new mate should arise. A pattern found in several species is that divorce is preceeded by breeding failure in the previous season (e.g. Coulson 1966, Mills 1973, Newton 1986, Bradley et al. 1990, Ens et al. 1996). We could see no such pattern in the Lesser Spotted Woodpecker, where among the pairs that reunited were three nonbreeding pairs and four pairs who failed in the previous season, whereas the only divorce occurred in a pair that successfully raised young in the previous season (Wiktander 1998). A lack of correlation between divorce and previous breeding failure is also reported by Forslund and Larsson (1991) and Emslie et al. (1992).

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LITERATURE CITED

BAKER, K. 1993. Identification Guide to European Non-passerines: BTO Guide 24. British Trust for Ornithology, Thetford, United Kingdom.

BENSCH, S., AND D. HASSELQUIST. 1991. Territory infidelity in the polygynous Great Reed Warbler *Acrocephalus arundinaceus*: The effect of variation in territory attractiveness. Journal of Animal Ecology 60:857–871.

BLACK, J. M., ED. 1996. Partnerships in Birds. The Study of Monogamy. Oxford University Press, Oxford.

BRADLEY, J. S., R. D. WOOLLER, I. J. SKIRA, AND D. L. SERVENTY. 1990. The influence of mate retention and divorce upon reproductive success in Short-tailed Shearwaters *Puffinus tenuirostris.* Journal of Animal Ecology 59:487–496.

CÉZILLY, F., AND R. G. NAGER. 1996. Age and breeding performance in birds: The influence of pair stability. Trends in Ecology and Evolution 11:27.

CLUTTON-BROCK, T. H. 1984. Reproductive effort and terminal investment in iteroparous animals. American Naturalist 123:212–229.

CLUTTON-BROCK, T. H., Ed. 1988. Reproductive Success. University of Chicago Press, Chicago.

COULSON, J. C. 1966. The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull *Rissa tridactyla.* Journal of Animal Ecology 35:269–279.

COULSON, J. C. 1972. The significance of the pair-bond in the Kittiwake (*Rissa tridactyla*). Pages 424–433 *in* Proceedings XV International Ornithological Congress (K. H. Voous, Ed.). Brill, Leiden, The Netherlands.

CRAMP, S., ED. 1985. The Birds of the Western Palearctic, vol. IV. Oxford University Press, Oxford.

CURIO, E. 1983. Why do young birds reproduce less well? Ibis 125:400–404.

DHONDT, A. A. 1989. The effect of old age on the reproduction of Great Tits *Parus major* and Blue Tits *Parus caeruleus.* Ibis 131:268–280.

EMSLIE, S. D., W. J. SYDEMAN, AND P. PYLE. 1992. The importance of mate retention and experience on breeding success in Cassin's Auklet (*Ptychoramphus aleuticus*). Behavioral Ecology 3:189–195.

ENS, B. J., S. CHOUDHURY, AND J. M. BLACK. 1996. Mate fidelity and divorce in monogamous birds. Pages 344–401 *in* Partnerships in Birds. The study of Monogamy (J. M. Black, Ed.). Oxford University Press, Oxford.

FORSLUND, P., AND K. LARSSON. 1991. The effect of mate change and new partner's age on reproductive success in the Barnacle Goose, *Branta leucopsis.* Behavioral Ecology 2:116–122.

FORSLUND, P., AND T. PÄRT. 1995. Age and reproduction in birds: Hypotheses and tests. Trends in Ecology and Evolution 10:374–378.

FOWLER, G. S. 1995. Stages of age-related reproductive success in birds: Simultaneous effects of age, pair-bond duration and reproductive experience. American Zoologist 35:318–328.

HAMANN, J., AND F. COOKE. 1987. Age effects on clutch size and laying dates of individual female Lesser Snow Geese, *Anser caerulescens.* Ibis 129: 527–532.

KLOMP, H. 1970. The determination of clutch size in birds. Ardea 58:1–124.

MILLS, J. A. 1973. The influence of age and pair-bond on the breeding biology of the Red-billed Gull *Larus novaehollandiae scopulinus.* Journal of Animal Ecology 42:147–162.

NEWTON, I. 1986. The Sparrowhawk. T. and A.D. Poyser, Calton, United Kingdom.

NEWTON, I., ED. 1989. Lifetime Reproduction in Birds. Academic Press, London.

NOL, E., AND J. N. M. SMITH. 1987. Effects of age and breeding experience on seasonal reproductive success in the Song Sparrow. Journal of Animal Ecology 56:301–313.

OLLASON, J. C., AND G. M. DUNNET. 1988. Variation in breeding success in Fulmars. Pages 263–278 *in* Reproductive Success (T. H. Clutton-Brock, Ed). University of Chicago Press, Chicago.

OLSSON, O. 1998. Through the eyes of a woodpecker: Understanding habitat selection, territory quality and reproductive decisions from individual behaviour. Ph.D. dissertation, Lund University, Lund, Sweden.

OLSSON, O., U. WIKTANDER, N. M. A. HOLMGREN, AND S. G. NILSSON. 1999. Gaining ecological information about Bayesian foragers through their behaviour. II. A field test with woodpeckers. Oikos 87:264–276.

OLSSON, O., U. WIKTANDER, AND S. G. NILSSON. 2000. Daily foraging routines and feeding effort of a small bird feeding on a predictable resource. Proceedings of the Royal Society of London, Series B 267:1457–1461.

PÄRT, T., AND P. FORSLUND. 1996. Age and breeding performance in monogamous birds: The influence of mate experience. Trends in Ecology and Evolution 11:220.

PERRINS, C. M., AND R. H. MCCLEERY. 1985. The effect of age and pair bond on the breeding success of Great Tits *Parus major.* Ibis 127:306–315.

ROWLEY, I. 1983. Re-mating in birds. Pages 331–360 *in* Mate Choice (P. Bateson, Ed.). Cambridge University Press, Cambridge, United Kingdom.

SÆTHER, B.-E. 1990. Age-specific variation in reproductive performance of birds. Current Ornithology 7:251–283.

SCOTT, D. K. 1988. Reproductive success in Bewick's Swans. Pages 220–236 *in* Reproductive Success (T. H. Clutton-Brock, Ed.). University of Chicago Press, Chicago.

SMITH, H. G. 1993. Parental age and reproduction in the Marsh Tit *Parus palustris.* Ibis 135:196–201.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry, 3rd ed. W. H. Freeman and Company, New York.

WIKTANDER, U. 1998. Reproduction and survival in the Lesser Spotted Woodpecker. Effects of life history, mating system and age. Ph.D. dissertation, Lund University, Lund, Sweden.

WIKTANDER, U., S. G. NILSSON, O. OLSSON, AND A. STAGEN. 1994. Breeding success of a Lesser Spotted Woodpecker *Dendrocopos minor* population. Ibis 136:318–322.

WIKTANDER, U., O. OLSSON, AND S. G. NILSSON. 2001a. Annual and seasonal reproductive trends in the Lesser Spotted Woodpecker *Dendrocopos minor.* Ibis 143:in press.

WIKTANDER, U., O. OLSSON, AND S. G. NILSSON. 2001b. Parental care and social mating system in the Lesser Spotted Woodpecker *Dendrocopos minor.* Journal of Avian Biology 32:in press.

WIKTANDER, U., O. OLSSON, AND S. G. NILSSON. 2001. Seasonal variation in home-range size, and habitat area requirement of the Lesser Spotted Woodpecker *Dendrocopos minor* in southern Sweden. Biological Conservation 46:in press.

WOOLLER, R. D., J. S. BRADLEY, I. J. SKIRA, AND D. L. SERVENTY. 1990. Reproductive success of Short-tailed Shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. Journal of Animal Ecology 59:161–170.

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