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EFFECTS OF FEMALE AGE ON REPRODUCTIVE SUCCESS IN EUROPEAN NUTHATCHES BREEDING IN NATURAL CAVITIES

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ABSTRACT.—Breeding of individually color-banded European Nuthatches (*Sitta europaea*) was studied in central Sweden during 11 years. The birds bred in natural cavities. Timing of breeding varied between years and was negatively correlated with spring temperature. First-year females bred significantly later than older females and raised fewer young. The latter was not an effect of their later breeding as the difference did not disappear when hatching day was accounted for statistically. First-year females were no more likely than older females to experience total breeding failure. Although participation of the male may be important during breeding, his age had no effect on the variables studied. Thus, experience in breeding may be less important in males than in females. *Received 3 October 1991, accepted 28 May 1992.*

BREEDING SUCCESS is a factor of fundamental importance in ecology. The probability that an individual bird will breed successfully depends on many factors, some associated with the environment and others dependent on the parents themselves and their "competence" (see Newton 1989). Factors associated with an individual can either be fixed, like many components of size, or may change with time, like body condition. Some factors are associated with the age of an individual, as individuals often gain in both experience and social dominance with age. Age-related differences in breeding performance have been documented in several studies (Ficken and Ficken 1967, Pugesek and Diem 1983, Stutchbury and Robertson 1988, Gauthier 1989; review *in* Saether 1990).

The effect of age on breeding may vary among species. In species with a long expected life span, individuals may forgo early breeding although they are sexually mature (e.g. Ashmole 1963, MacLean 1986), while this would be a heavy penalty for an individual of a short-lived species with a low probability of surviving until the next breeding season. In such species there is a high premium for individuals to reach quickly a competence comparable to that of older individuals. Furthermore, not only the competence of an individual itself may influence breeding, but also that of its partner. If experience is important, a young individual could do better by pairing with an older, experienced mate than with one as inexperienced as itself (e.g. Loman 1984).

A shortcoming in studies of hole-nesting birds is the nearly universal reliance on nest boxes causing a general lack of studies in natural cavities (Karlsson and Nilsson 1977, van Balen et al. 1982, Nilsson 1987, East and Perrins 1988). As a consequence, many studies have been performed with a superabundance of nest sites of equal and high quality and, thus, the use of nest boxes may obfuscate factors associated with choosing a good nest site and competing for it. Results obtained from such studies may, but need not, apply to natural situations (e.g. East and Perrins 1988, Gauthier 1989).

In this paper I examine timing of breeding, number of young produced, and overall success rate in the European Nuthatch (*Sitta europaea*) and give special attention to age differences. This fairly short-lived passerine breeds in natural holes in trees and, at least in my study sites, avoids nest boxes.

METHODS

Study areas.—I studied nuthatches from 1981 to 1991 in areas of deciduous woodland in the vicinity of Uppsala, central Sweden (59°51'N, 17°38'E). The dominant tree species were oak (*Quercus robur*) and birch (*Betula* spp.), while the bush-layer mainly consisted of hazel (*Corylus avellana*). The study areas are described in detail by Enoksson (1987, 1990).

Nuthatch breeding behavior.—European Nuthatches are paired and use the same territory throughout the year (Enoksson 1987, Matthysen 1988). The nest is

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placed in a hole in a tree; nuthatches seldom use nest boxes if natural cavities are available. In the Uppsala area, nest building, which is performed by the female only, is initiated in late March to early April. She starts by plastering mud inside the entrance hole until she can only just enter the nest. This probably reduces the risk that European Starlings (*Sturnus vulgaris*), a larger competitor, will take over the hole. Usurpation of holes by starlings has been found to seriously influence breeding density in other species (Kerpez and Smith 1990). However, for my study sites, starlings are migratory and do not arrive until nuthatch breeding has commenced. The only other secondary hole nesters that are resident in the area are tits (*Parus* spp.). However, nuthatches are larger than tits and dominant over them (Enoksson 1988a).

Incubation takes about 15 days with only the female incubating. During this period, as during egg laying, she is fed by her mate, both in the nest and when foraging away from the nest. Both parents feed the nestlings, which remain in the nest for about 24 days. The female broods the nestlings when they are small. Both parents remove fecal sacs and also soiled nest material.

Field procedure.—The nuthatches in this study were caught in mist nets or in a trap, and color banded for individual identification. Most of the banding was done in summer and early autumn (i.e. when juveniles settle into territories; see Enoksson 1990). Nuthatches that immigrated into the study areas during other times of the year (mainly late winter and early spring; cf. Enoksson 1987) were banded as soon as possible after settling down in a territory.

Nuthatches were observed throughout the year (cf. Enoksson 1987, 1988b, 1990). Thus, I knew the history of the birds prior to breeding. Studies of breeding began in 1981, but during the first two seasons, fewer nuthatches were banded and aged than in later years. Therefore, I only examined age effects from 1983 to 1991. In 1991, breeding was studied less closely, and I was not able to include 1991 in all analyses.

As nuthatches nest in natural cavities and reduce the entrance hole (to a diameter of 2.5–3.0 cm), I used a dentist's mirror fitted with a small lamp bulb to inspect nest contents (Nilsson 1986). When the female leaves the nest during incubation, she covers the eggs. This makes it difficult to count the eggs with certainty. However, I was able to count the nestlings in most nests. All but one nest required a ladder to be reached, and some nests were too high to be reached safely. Most nests were inspected twice, once soon after hatching and a second time when nestlings were at least two weeks old.

Timing of breeding.—I determined when incubation started and when hatching occurred by watching the behavior of the birds. When possible, I climbed to the nest and inspected the contents, but it was not always possible to see newly hatched young as they often bury themselves in the bark in the nest.

Nests, where the start of breeding possibly could have been delayed due to interference from European Starlings, or by one member of the pair being replaced by a new bird shortly before breeding, were excluded from this analysis. In the few cases, where incubation had started in a normal way but the eggs did not hatch (e.g. due to predation), and where I had a reliable estimate of the first day of incubation, I calculated the expected day of hatching and used this in the analysis. As hatching day was accurately determined for part of the population only in 1991, data from this year are not included.

Overall breeding success.—Although I could not count the number of fledglings for all pairs, it was almost always possible to determine if a pair fledged at least one young. Newly fledged nuthatches are quite noisy and remain with their parents for some time after fledging, while the parents continue to feed them. Also, it is easy to determine whether there are large nestlings in a nest, without climbing to it. Parents make frequent visits to feed the nestlings, which beg loudly and, at times, may even be seen in the nest entrance from the ground.

As an indication of success versus total failure, I used observations of fledged young or presence of large nestlings in the nest. This may have resulted in a slight, but unbiased (with regards to age), overestimate of the success rate. Failed breeding attempts were defined as those nests that had no young at this stage. I only included pairs that I had observed since nest building in this analysis. Inclusion of nests found at a later stage would overestimate breeding success, as failed nests are harder to find.

RESULTS

Hatching date varied among years (Table 1), and mean hatching date was negatively correlated with April temperature ($r = -0.78$, $P = 0.006$, 1981–1990; Fig. 1). First-year females bred significantly later than older females (Fig. 1a, Table 1). Male age had no effect (Fig. 1b, Table 1).

On average a nuthatch nest contained 4.0 young ($n = 141$ nests) during the late nestling stage (day 15 or later). However, some nests had already failed at that stage, and a more relevant analysis may be to discount nests with no young at this stage. Successful nests contained on average 5.3 nestlings ($n = 106$).

Successful first-year females had fewer young than successful older females (Tables 1 and 2). As with timing of breeding, there was no significant effect of male age.

There were no effects of age of the female or the male on the probability of total breeding

TABLE 1. Analysis of variance in hatching date and number of nestlings.

Source	Hatching date			No. nestlings[a]		
	F	*P*	df	*F*	*P*	df
Year[b]	13.68	0.000	7,88	1.75	0.103	8,76
Female age[c]	12.62	0.001	1,88	6.68	0.012	1,76
Male age[c]	0.88	0.351	1,88	0.41	0.523	1,76

[a] After day 15 in nest. Nests without nestlings at this stage excluded from analysis.

[b] Data for hatching date from 1983–1990 and for number of nestlings from 1983–1991.

[c] Comparison of first-year vs. older birds.

failure (Table 3). Most nuthatch pairs that commenced breeding managed to fledge at least some young. Only 35 of 177 cases (1981–1991) suffered a total failure. In 14 cases incubation was never initiated. In one case, this was due to the female disappearing during egg laying, while European Starlings took over the nest in four other cases. In the remaining nine cases, I do not know why the female failed to incubate. In 10 of the 21 nests that failed after the female had started incubation, the eggs did not hatch.

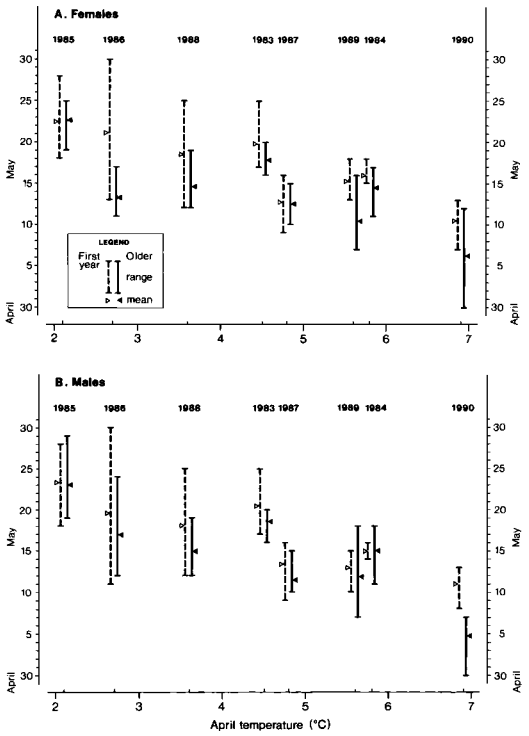

Fig. 1. Hatching date in different years in relation to mean temperature during April. Clutches of first-year versus older (A) females and (B) males.

TABLE 2. Number of nestlings in successful nests of first-year and older females and males.[a]

Year	Females		Males	
	First year	Older	First year	Older
1983	6.00 (2)	3.50 (2)	5.00 (4)	4.00 (2)
1984	4.67 (6)	5.33 (6)	5.17 (6)	5.00 (5)
1985	4.60 (5)	4.75 (4)	4.25 (4)	4.43 (7)
1986	5.33 (6)	6.00 (1)	5.20 (5)	6.00 (2)
1987	4.75 (4)	6.00 (8)	5.00 (5)	6.17 (6)
1988	4.80 (5)	5.83 (6)	5.17 (6)	5.60 (5)
1989	5.00 (1)	5.75 (4)	5.00 (1)	5.75 (4)
1990	5.43 (7)	6.50 (6)	6.00 (8)	5.83 (6)
1991	5.33 (6)	7.67 (3)	7.00 (2)	5.67 (6)
Total	5.07 (42)	5.80 (40)	5.29 (41)	5.42 (43)

[a] After day 15 in nest. Nests without nestlings at this stage were excluded. *n* given in parentheses.

In one case, the female had died, while the eggs in three nests were predated. Further, one nest was invaded by ants (*Formica* spp.), apparently making the nest uninhabitable for the incubating female. The cause was unknown for the other cases. One nest failed (for unknown reasons) around hatching time, and I do not know whether the eggs had hatched or not. There were six cases of predation on hatched young and four where the nestlings were found dead (probably starved) in the nest. The most probable predators were weasels (*Mustela nivalis*) or Great Spotted Woodpeckers (*Dendrocopus major*).

DISCUSSION

Age differences in female breeding performance.— First-year females bred later in the season than did older females and raised fewer young, while the age of the male was unimportant. The most commonly suggested factors affecting timing of breeding, as well as clutch size, are food abundance and food quality. Food, either during the prelaying period and/or the laying period, when the female has to acquire energy and nutrients for egg formation, or during the period when the nestlings are to be fed, can be crucial (e.g. Lack 1954, Perrins 1965, 1970). For example, high insect abundance was associated with early breeding in both House Martins (*Delichon urbica*; Bryant 1975) and Western Kingbirds (*Tyrannus verticalis*; Blancher and Robertson 1987). Density of food in turn is influenced by environmental conditions, especially in areas with strong seasonal variation in climate. In my study,

TABLE 3. Percent successful breeding attempts[a] in first-year and older females and males.

	Females				Males			
Year	First year	Older	*G*	*P*	First year	Older	*G*	*P*
1983	85.7 (7)	100.0 (4)	0.96	0.327	85.7 (7)	100.0 (7)	1.46	0.226
1984	85.7 (7)	81.8 (11)	0.05	0.827	100.0 (5)	72.7 (11)	2.55	0.110
1985	100.0 (5)	100.0 (4)	0.00	1.000	100.0 (5)	100.0 (7)	0.00	1.000
1986	80.0 (10)	33.3 (6)	3.52	0.060	85.9 (9)	28.6 (7)	6.52	0.011
1987	83.3 (6)	100.0 (9)	1.94	0.164	100.0 (6)	100.0 (6)	0.00	1.000
1988	66.7 (12)	83.3 (6)	0.59	0.443	75.0 (12)	80.0 (5)	0.05	0.823
1989	57.1 (7)	100.0 (9)	5.88	0.015	75.0 (4)	80.0 (10)	0.04	0.839
1990	87.5 (8)	87.5 (8)	0.00	1.000	80.0 (10)	100.0 (6)	2.05	0.152
1991	80.0 (10)	25.0 (4)	3.74	0.053	50.0 (8)	71.4 (7)	0.72	0.395
Total	79.2 (72)	82.0 (61)	0.17	0.684	81.8 (66)	80.3 (66)	0.05	0.824

[a] *n* given in parentheses. Probability given for *G*-test.

nuthatches bred earlier when the spring was warmer, which is in accordance with the food hypotheses. The fact that female, but not male, age affected timing, as well as clutch size, suggests that factors acting only, or mainly, on the female are responsible. Both parents feed nestlings, while only the female builds the nest, lays the eggs, and incubates. Thus, the cause should lie in the period prior to laying or incubation, rather than during the nestling period.

In the nuthatch, first-year birds suffer higher winter mortality than older birds (Enoksson 1988b). Possibly, also among survivors, older birds are in better condition than first-year birds and, thus, could be able to initiate breeding earlier. Moreover, age-related differences in foraging have been documented in several species (e.g. Orians 1969, Gochfeld and Burger 1984, Breitwisch et al. 1987, Jansen 1990). If first-year females are less efficient in foraging, it may take them longer to acquire enough energy and/or nutrients for egg formation and, thus, cause them to breed later than older females and lay a smaller clutch. Although juvenile nuthatches are as efficient as adults in handling seeds by their first autumn (Enoksson 1988a), older birds may still be better at finding food (cf. Brandt 1984). Furthermore, in spring, nuthatches eat more insects and first-year birds may be less adept in handling such food.

Breeding involves not only egg laying, but also choice of an appropriate nest site, building the nest, etc. Perhaps previous experience of breeding is valuable and may shorten the length of time prior to incubation. Breeding experience per se was found to improve breeding success in Western Gulls (*Larus occidentalis*; Pyle et al. 1991). In my study five females did not raise a clutch in their first year, but survived and bred successfully in their second year. In their second year, all were late breeders (hatching on day 16, 15, 19, 16 and 34, while the mean hatching dates for adult females that year were 10.3, 10.9, 13.2, 14.5 and 16.7, respectively). Three of the females had also paired with new mates just prior to breeding, which might have caused or contributed to the delay. While supporting data certainly are limited, this may suggest that previous breeding experience enhances an individual's probability of breeding earlier.

There also may be physiological reasons for age-related differences in breeding. For example, Westin (1989) found a tendency for first-year Willow Tit (*Parus montanus*) females to have both lighter ovaries and smaller follicles in spring when compared to older females. Such factors may cause or contribute to later breeding and/or smaller clutches in first-year birds.

In many bird species, clutch size decreases with season (e.g. Bryant 1975, Alatalo et al. 1981), which might explain why individuals that breed later raise fewer young. Taking hatching day (as deviation from mean hatching day for "undisturbed nests" for each year 1983–1990) into account, the effect of female age on number of young is still significant, while male age is not (ANCOVA; female age, $P = 0.05$; male age, $P = 0.92$, df = 1, 63). Thus, first-year nuthatch females produced fewer young also when hatching date was controlled for, and, therefore, the lower number of young in the nests of first-year females must have another basis.

One possibility is that, because first-year females breed later than older females, they may partly compensate for this by reducing clutch

size. Laying a full clutch would delay the young female even further. This assumes that a female first determines when to start laying, and that clutch size then depends on when she stops, and begins to incubate the eggs. If so, a female that lays a smaller clutch can start incubation earlier. Her young will hatch earlier than those of a female that initiates laying on the same day, but lays a full clutch. Another possibility is that first-year females suffer higher within-nest loss of eggs and/or young. However, they were no more likely to suffer total breeding failure than older females.

The nest site itself also influences many aspects of breeding, including timing of breeding, clutch size and risk of failure (Gofman 1977, Karlsson and Nilsson 1977, O'Connor 1978, Nilsson 1984, van Balen 1984). Among hole nesters, nest choice is likely to exert a stronger influence when birds use natural cavities than in nest-box studies when, typically, a surplus of nest sites of high and equal quality are provided. Even so, insulation properties of nest boxes influenced timing of laying in a nest-box study of the Great Tit (*Parus major*; O'Connor 1978), and nest-box size was found to influence clutch size in several species (Karlsson and Nilsson 1977). Variation in such factors will be higher and much more important in populations that breed in natural holes.

If experienced birds choose better nest sites, this would result in age-related differences in breeding. Even if there are no differences between age groups in nest-site quality, it could take inexperienced birds longer to decide on the most suitable site. Both of these explanations could apply to my study. Another possibility is that first-year birds have territories of lower quality, and that territory quality influences timing of breeding or clutch size, for example, through differences in food supply. However, as nuthatches very rarely leave a territory after breeding there (Enoksson 1987), difference in territory quality is unlikely to be an important factor.

In this way, many factors may influence breeding and also cause age-related differences. Further studies that include both the physiological basis for breeding and how females reach breeding condition, as well as behavioral studies on foraging and breeding activities of individuals of different age groups, are needed to disentangle the causes of variation in timing of breeding and number of young raised.

Importance of early breeding.—Timing of breeding may be an important factor affecting recruitment. Fledging date is a very important factor for territorial settlement of juvenile nuthatches. Of the vacant territories available, the best ones are occupied first (Matthysen 1989, 1990). Thus, early breeding should be important to nuthatches. Further support for this comes from the fact that nuthatches raise only one brood per year. Presumably, young from second clutches would have very low chances of establishing themselves, as all vacant territories would already have been claimed by young from first clutches. In fact, nuthatches do not even lay replacement clutches if, for example, the first clutch is predated. Thus, both the smaller clutch and the later breeding in young nuthatch females is likely to decrease their recruitment success.

How important is the male?—Why is the age of the male unimportant? In some species, a male's competence in establishing and defending a good territory may exert an important influence on breeding performance (e.g. Hill 1988), but this effect will be much less pronounced in pair-territorial species such as the European Nuthatch. If a female nuthatch is widowed but repairs before breeding, the nest may be placed either in her territory or in that of her new mate (Enoksson 1987, unpubl. data).

If timing of breeding mainly depends on the female's ability to acquire enough energy and nutrients for egg laying (e.g. Perrins 1970), there may be little the male can do to be of assistance. At the least, individual differences between males are likely to be less important than those between females. Also, all nest building is performed by the female. This does not, however, mean that the male does not contribute to the breeding effort at this stage. For example, courtship feeding has been shown to be important in Blue Tits (*Parus caeruleus*) and Marsh Tits (*P. palustris*; Nilsson and Smith 1988). The male could also improve foraging conditions for the female, when she has an increased need for food, by being vigilant and, thus, enabling her to spend more time actually feeding (Dahlgren 1990, Enoksson and Eriksson in prep.).

There is also some evidence that full participation of the male is important for successful breeding. At least five territorial females were single at the onset of the breeding season and, although each was regularly observed together with a neighboring (and paired) male in her territory, none of them bred. Thus, females may be reluctant to breed if the male is unlikely to

cooperate fully in the raising of the young. Still, three females that were widowed at the start of incubation continued the breeding attempt, although only one fledged young. The other two nests were predated. However, two parents may be needed to raise offspring that can successfully compete for territories. For example, Alatalo et al. (1988) showed that, although single parents (widowed during nestling stage) in the Pied Flycatcher (*Ficedula hypoleuca*) successfully fledged young, these weighed less than fledglings raised by pairs. Furthermore, single parents raised significantly fewer young than did pairs.

Thus, although the participation of the male may be important during breeding, there is evidently little difference between first-year and older males. Experience in breeding may be less important in males than in females.

Consequences for mate choice and breeding dispersal.—The age-related differences in breeding performance among European Nuthatch females should have consequences for dispersal and mate choice. An older female is likely to have higher breeding success than a first-year female, while male age does not matter in this respect. Therefore, a male can improve his fitness by pairing with an experienced female, while the age of the partner is unimportant for a female. This gives interesting predictions for mate choice and dispersal. Contrary to what is the case for many species of birds, the European Nuthatch should show male mate choice rather than female mate choice. This could in turn influence dispersal (Greenwood 1980, Enoksson 1987, in prep.); a female should only desert her territory if she faces the risk of remaining single, while a male could increase his fitness by pairing with an older female, even if this involves leaving his territory. This has indeed been observed (Matthysen and Dhondt 1983, Enoksson 1987, in prep.).

To conclude, I argue that year-around territoriality in the European Nuthatch places a premium on early breeding and that the young females' later breeding (and fewer young) then influences both mate choice and breeding dispersal. In this way, different aspects of a species' ecology tie together. To fully understand one aspect, we cannot ignore the others.

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