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High nest predation rate in the Chaffinch

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The breeding biology of an individually marked Chaffinch *Fringilla coelebs* population was studied in coniferous forest in Lammi, in southern Finland, in 1990–91. In addition, the nesting success was analysed in the Finnish nest-card data from the years 1986–1991. Nest predation, calculated from the nests found during the building stage, was high both in Lammi (87.5%) and in the nest-card data (70.1%). Nest height or nest-tree species in the nest-card data had no effect on nest survival.

Nest predation seems to be a major factor affecting breeding success and probably lifetime reproductive success in the Chaffinch. It seems that the nest predation in this species is a probabilistic process which the parent birds are hardly able to influence. We discuss the implications of the high nest predation rate for the breeding behaviour of the Chaffinch.

1. Introduction

Nest predation has been found to be a major factor affecting breeding success in several bird species (e.g. Nolan 1963, Ricklefs 1969, Martin 1992a, b, 1993). Recently, nest predation has been considered to be an important factor affecting the evolution of clutch size, nest site selection and community structure (e.g. Slagsvold 1982, Hötker 1988, Martin 1988a, b). However, the vast majority of population studies and studies on the lifetime reproductive success of passerine birds have been focused on hole-nesting birds (e.g. Newton 1989, Blondel et al. 1990, Clobert & Lebreton 1991, McCleery & Perrins 1991, but see Best & Stauffer 1980, Hötker 1988, Orians & Beletsky 1989, Martin 1992a). Compared to the predation on open nests, predation is much smaller in nest boxes (Nilsson 1984, Møller 1989, 1992), and therefore the effect of predation has been underestimated or ignored in many cases. Among species breeding in natural cavities (non-excavators), the nest failure rate is higher and may equal the failure rates of open-nesters (Nilsson 1986, Martin & Li 1992). Studies on species which build open nests in trees are scarce (but see Longcore & Jones 1969, Best & Stauffer 1980), apparently due to the difficulty of finding and inspecting nests.

We gathered data on the breeding biology of the Chaffinch *Fringilla coelebs* during our radio-tracking study of a local breeding population. The Chaffinch nest is an open cup built at various heights in trees and bushes (Marler 1956, von Haartman 1969, Krägenow 1986). We investigated the nest predation rate in our own data and in addition, in the nest-card data collected by amateur ornithologists in Finland.

2. Material and methods

We observed the behaviour of male Chaffinches by radio tracking near Lammi Biological Station (61°N, 25°E) in southern Finland in 1990–1991 (for the method, see Hanski & Haila 1988, Hanski et al. 1992). The study area was in a spruce-dominated forest with an admixture of deciduous trees. The habitats were described in detail by Tiainen et al. (1983). Nearly all the nests of the radio-tagged males were found. The total number of nests found was 50; this includes 12 nests of birds that were colour-ringed, but not radio-tagged.

In addition, we analysed the Finnish nest-card data from the years 1986–1991 (Tiainen & Väisänen 1991). The total number of nests for which the final outcome was known in this data set was 291. When comparing the predation rate in the nest card data with our own field data, we used only records on nests found during the nest-building stage (67 nests), in forest habitats and in southern Finland (south of 7000 N, national uniform grid coordinate, roughly equalling 63°N).

We assumed that the nest had been preyed upon if the eggs or nestlings had disappeared (often also nest material had been moved from the nest) before the time of fledging or, in the nests which we were not able to visit (9 nests), if the female stopped incubation or the parents stopped feeding the nestlings. In most cases the pair made a new nesting attempt immediately after the predation.

3. Results

The 50 nests found in Lammi belonged to 29 pairs, including replacement nests of the same pairs. The nesting failure rate was high (Table 1).

Table 1. Predation on Chaffinch nests in Lammi and in the nest-card data. Only nests found during building stage and in southern Finland are included.

Data set	Successful	Failed	Total	Failure %
Lammi	5	35	40	87.5
Nest cards	20	47	67	70.1
	$\chi^2 = 3.30$, df = 1, P = 0.07			

Of the 40 nests found during the building stage, 35 (87.5%) failed. In 29 cases (82.9%) the nest was preyed upon (eggs or nestlings disappeared), in one case the nestlings died (apparently after the female had died) and in the remaining five cases the nest was deserted for an unknown reason. In addition, we apparently caused desertion of three nests by visiting them during building or before egg laying, but these were not included in the failure analyses. There was no difference in failure rates between the nests of radio-tagged and only colour-ringed males (Fisher's exact probability test, P = 1.000).

In the nest-card data set, 47 of the total 67 (70.1%) nests found during the building stage failed. Of these, 44 (93.6%) were preyed upon and the rest were categorized as deserted (Table 1). In both Lammi and the nest-card data set, predation seemed to be the most important cause of losses, and consequently we shall consider nest losses as predation. The predation rate was slightly higher in Lammi than in the nest-card data, but the difference was not significant (Table 1).

We also tried to estimate the effect of the age of the parents on the nest predation rate in Lammi. The data were scanty and included replacement clutches of the same pairs. Thus, we did not make any statistical tests (Table 2), but it seemed to us that there was no difference in predation rate between young and old parents.

To get a rough estimate of the predation pressure in different habitat classes, we divided the nest-card data into three groups: forest, saplings and human settlement. The forest class comprises the areas classified as forests, bearing both conifers, mixed woods and deciduous trees; the sapling class comprises areas with early suc-

Table 2. Ages of parent Chaffinches and nesting success in Lammi. Juv = born in previous summer, old = born earlier. Note that the same nests occur for male and female parents.

Age and sex	Successful	Failed	Total
Juv male	2	15	17
Old male	3	22	25
Juv female	1	5	6
Old female	3	10	13

cessional woodland and bushes. The human settlement consists of rural and urban settlement and all kinds of parks. The analysis was applied to 291 nests for which the final outcome was known (Table 3). There were no differences in the nest predation rate among these breeding habitats.

We modelled the nest-card data with log-linear models to find out the possible effects of nest height and tree species on the predation rate (Table 4). We used four height classes (less than 2 m, 2–3 m, 3–4 m and over 4 m) and three tree species classes (spruce, pine and deciduous trees). The number of nests used in this analysis was 153. Only nests in forest were included and the juniper was omitted because it did not achive the higher height classes. In the best model, the nest predation rate was totally independent of either height or tree species (Table 4). Thus, neither nest height nor nest tree species had an effect on the predation rate, but height and tree species had a significant interaction, indicating, for example, that nests were situated higher in some tree species than in others.

Table 3. Predation on Chaffinch nests in three habitats in the nest-card data: forest, saplings and human settlement. Note that this analysis also contains nests found in the incubation and fledgling stages, which has lowered the failure rates.

Habitat	Successful	Failed	Total	Failure %
Forest	81	93	174	46.6
Saplings	31	43	74	41.9
Settlement	21	22	43	48.8
	$\chi^2 = 0.65$, df = 2, P = 0.721			

4. Discussion

Nest predation (including a small proportion of deserted nests) was high in the Chaffinch both in Lammi and in the nest-card data. The failure rates were very high compared with those reported in other studies of open-nesting species in the temperate zone (Nice 1957, mean 51%; Ricklefs 1969, mean 44.7%, calculated from Table 3a, on pages 9–11; Martin 1992b, mean 56%, but high in some species). However, Nolan (1963), Martin & Roper (1988) and Suárez & Manrique (1992) reported similar (67–90%, 80–93% and 70–80%, respectively) nest mortality rates for several shrub-habitat bird species, the Hermit Thrush and Iberian shrub-steppe bird communities. Bergman (1956), Newton (1964) and Payevsky & Vinogradova (1974) have also reported similarly high failure rates in the Chaffinch.

It seems improbable that the observed high failure rates were caused by our visits to the nests. Nine of the nests were situated in sites which we could not reach and had to observe from a distance, but all of them were preyed upon. Furthermore, most of the nests failed more than one day after our visit. An investigator may disturb nesting birds and thus increase predation, but the effect has been found to be relatively small in passerines, compared with other taxa (Götmark 1992). Nest desertion, especially during the building stage, may also be caused by

Table 4. Successful and failed Chaffinch nests in different tree species and in different height (in metres) categories and the best log-linear model derived from the data.

		Height (H)				
Fate (F)	Tree species (T)	<2m	2–3m	3–4m	>4m	Total
Successful	Spruce	16	11	6	4	37
	Pine	3	5	1	4	13
	Deciduous	9	4	11	2	26
Failed	Spruce	10	13	4	8	35
	Pine	1	3	2	2	8
	Deciduous	5	9	11	9	34

Best model: F, HT $G^2 = 12.48$, df = 11, P = 0.329

predators. For a Chaffinch it may be profitable to desert an unfinished or empty nest after an observed predator visit: no investment has yet been made in the eggs and the probability that the same predator will visit the nest later is high.

Nest cards give no data on how well the nests were hidden. We did not try to quantify this factor either. Only six of the 50 nests yielded fledglings. Two of them were situated fairly openly in birch and pine, but the rest were well concealed in spruces. Among the failed nests, however, several were very carefully hidden under needled twigs in spruces. They were extremely difficult to see from the sides or above, even at a distance of some tens of centimetres. Concealment of the nest has been found to decrease the predation rate in several other species (e.g. Martin & Roper 1988, Møller 1988, Tuomenpuro 1991, Martin 1992b and references therein), but not in all cases (Caccamise 1977, Best & Stauffer 1980, Holway 1991, Martin 1992b and references therein).

It might be possible that the parents could improve nest survival until fledging by hiding their nest, though unable to achieve total security. This could be expected to happen with increasing experience and increasing age. However, our data do not show any tendency for nesting success to increase with age, and carefully hidden nests were also preyed upon. In any case our material is too scanty to allow any definite conclusions.

We can only speculate on the predator species which were causing the nest losses in our study area (see Andrén 1992, Suárez & Manrique 1992 and references therein). We have only once seen a corvid-sized bird fleeing from a Chaffinch nest and in another study area a Pygmy Owl *Glaucidium passerinum* and a Great Spotted Woodpecker *Dendrocopos major* were seen eating nestlings. However, several possible avian and mammalian predators were regularly observed in our study area. The most abundant species were the Jay *Garrulus glandarius*, Hooded Crow *Corvus corone*, red squirrel *Sciurus vulgaris* and pine marten *Martes martes*. We also observed the Great Spotted Woodpecker, Magpie *Pica pica*, least weasel *Mustela nivalis* and stoat *Mustela erminea* several times each.

Very little is known about the prey-searching tactics of different predator species. The movements of parent birds may lead a predator to the nest and predators may even make systematic searches of trees and branches, as has been noted in observing the activities of a radio-tagged stoat (J. Heikkilä, pers. comm.). On the other hand, formation of "searching image" (Croze 1970, Martin 1987) for Chaffinch nests seems less likely, due to their concealed placement and variable height and in trees, especially in coniferous forest, where there are probably no preferred nest-habitat patches in which a predator could concentrate its search (cf. Martin 1992b).

It seems that nest survival until fledging is a more or less stochastic event in the Chaffinch. This conclusion is supported by the fact that the nest predation rate was similar in all habitat classes in the nest card data, which have been gathered from an extensive area. If this is correct, the parents can have only a minor affect on their breeding success. Therefore, nest predation is probably the major factor together with longevity (not studied here) affecting lifetime reproductive success. This may also apply to other open-nesting birds, whose nests are more vulnerable to predation (Nilsson 1984, Møller 1989) than those of the more commonly studied hole nesters (e.g. Newton 1989, Blondel et al. 1990, McCleery & Perrins 1991).

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Selostus: **Peipon suuret pesätuhot**

Tutkimme peipon pesimämenestystä Lammin biologisen aseman ympäristössä vuosina 1990–91. Lisäksi analysoimme Etelä-Suomessa vuosina 1986–91 kerätyn pesäkorttiaineiston. Rakennusvaiheessa löydetyistä pesistä laskettu tuhoutumisaste oli erittäin suuri sekä Lammilla (87.5%; Taulukko 1) että pesäkorttiaineistossa (70.1%). Pesiin kohdistuva saalistus oli ylivoimaisesti tärkein pesätuhojen syy molemmissa aineistoissa.

Elinympäristöllä ei ollut pesäkorttiaineiston perusteella vaikutusta pesätappioiden suuruuteen (Taulukko 3). Myöskään puulajilla tai pesän korkeudella puussa ei ollut vaikutusta pesän säilymistodennäköisyyteen (Taulukko 4).

Avopesijöiden pesiin kohdistuvan saalistuspaineen on todettu olevan suuren myös useissa muissa tutkimuksissa. Pesäpredaatio lienee tärkein peipon lisääntymismenestykseen sekä luultavasti myös sen elinikäiseen jälkeläistuottoon vaikuttava tekijä. Luonteeltaan predaatio näyttää olevan sattumanvaraista, ja emojen vaikutusmahdollisuudet sen välttämiseksi ovat vähäiset.

References

Andrén, H. 1992: Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. — Ecology 73:794–804.

Bergman, G. 1956: Zur Populationsdynamik des Buchfinken, Fringilla coelebs. — Ornis Fennica 33:61–71.

Best, L. B. & Stauffer, D. F. 1980: Factors affecting nesting success in riparian bird communities. — Condor 82:149–158.

Blondel, J., Gosler, A., Lebreton, J.-L. & McCleery, R. (eds.) 1990: Population biology of passerine birds. An integrated approach. — Springer-Verlag, Berlin, 496 pp.

Caccamise, D. F. 1977: Breeding success and nest site characteristics of the Red-winged Blackbird. — Wilson Bull. 89:396–403.

Clobert, J. & Lebreton, J.-D. 1991: Estimation of demographic parameters in bird populations. — In: Perrins, C. M., Lebreton, J.-D. & Hirons, G. J. M. (eds.), Bird population studies. Relevance to conservation and management: 75–104. Oxford Univ. Press, Oxford.

Croze, H. 1970: Searching image in Carrion Crows. — Z. Tierpsychol., Beih. 5:1–85.

Götmark, F. 1992: The effects of investigator disturbance on nesting birds. — Current Ornithol. 9:63–104.

von Haartman, L. 1969: The nesting habits of Finnish birds. I. Passeriformes. — Comm. Biol. Soc. Sci. Fennica 32:1–187.

Hanski, I. K. & Haila, Y. 1988: Singing territories and home ranges of breeding Chaffinches: visual observation vs. radio-tracking. — Ornis Fennica 65:97–103.

Hanski, I. K., Haila, Y. & Laurila, A. 1992: Variation in territorial behaviour and breeding fates among male Chaffinches. — Ornis Fennica 69:72–81.

Holway, D. A. 1991: Nest-site selection and the importance of nest concealment in the Black-throated Blue Warbler. — Condor 93:575–581.

Hötker, H. 1988: Lifetime reproductive output of male and female Meadow Pipits Anthus pratensis. — J. Anim. Ecol. 57:109–117.

Krägenow, P. 1986: Der Buchfink. — A. Ziemsen Verlag, Wittenberg, Lutherstadt, 100 pp.

Longcore, J. R. & Jones, R. E. 1969: Reproductive success of the Wood Thrush in a Delaware woodlot. — Wilson Bull. 81: 396–406.

Marler, P. 1956: Behaviour of the Chaffinch. — Behaviour, suppl. 5:1–184.

Martin, T. E. 1987: Artificial nest experiments: effects of nest appearance and type of predator. — Condor 89:925–928.

— 1988a: Habitat and area effects on forest bird assemblages: is nest predation an influence? — Ecology 69:74–84.

— 1988b: Processes organizing open-nesting bird assemblages: competition or nest predation? — Evol. Ecol. 2:37–50.

— 1992a: Interaction of nest predation and food limitation in reproductive strategies. — Current Ornithol. 9:163–197.

— 1992b: Breeding productivity considerations: what are the appropriate habitat features for management? — In: Hagan III, J. M. & Johnston, D. W. (eds.), Ecology and conservation of Neotropical migrant landbirds: 455–471. Smithonian Inst. Press.

— 1993: Nest predation among vegetation layers and habitat types: revising dogmas. — Am. Nat. In press.

Martin, T. E. & Li, P. 1992: Life history traits of open- vs. cavity-nesting birds. — Ecology 73:579–592.

Martin, T. E. & Roper, J. J. 1988: Nest predation and nest-site selection of a western population of the Hermit Thrush. — Condor 90:51–57.

McCleery, R. H. & Perrins, C. M. 1991: Effect of predation on the numbers of Great Tits Parus major. — In: Perrins, C. M., Lebreton, J.-L. & Hirons, G. J. M. (eds.), Bird population studies. Relevance to conservation and management: 129–147. Oxford Univ. Press, Oxford.

Møller, A. P. 1988: Nest predation and nest site choice in passerine birds in habitat patches of different size: a study of Magpies and Blackbirds. — Oikos 53:215–221.

— 1989: Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds? — Oikos 56:421–423.

— 1992: Nest boxes and the scientific rigour of experimental studies. — Oikos 63:309–311.

Newton, I. 1964: The breeding biology of the Chaffinch. — Bird Study 11:47–68.

— (ed.) 1989: Lifetime reproduction in birds. — Academic Press, London, 479 pp.

Nice, M. M. 1957: Nesting success in altricial birds. — Auk 74:305–321.

Nilsson, S. G. 1984: The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. — Ornis Scand. 15:167–175.

— 1986: Evolution of hole-nesting in birds: on balancing selection pressures. — Auk 103:432–435.

Nolan, V. Jr. 1963: Reproductive success of birds in a deciduous scrub habitat. — Ecology 44:305–313.

Orians, G. H. & Beletsky, L. D. 1989: Red-winged Blackbird. — In: Newton, I. (ed.), Lifetime reproduction in birds: 183–197. Academic Press, London.

Payevsky, V. A. & Vinogradova, N. V. 1974: Breeding biology and demography of Chaffinch at Kurische Nehrung according to ten-years data. — Trudy zool. inst. Ak. Nauk SSSR 55:186–206.

Ricklefs, R. E. 1969: An analysis of nestling mortality in birds. — Smithsonian Contr. Zool. 9:1–48.

Slagsvold, T. 1982: Clutch size variation in passerine birds: the nest predation hypothesis. — Oecologia (Berl.) 54:159–169.

Suárez, F. & Manrique, J. 1992: Low breeding success in Mediterranean shrubsteppe passerines: Thekla lark Galerida theklae, Lesser Short-toed Lark Calandrella rufescens, and Black-eared Wheatear Oenanthe hispanica. — Ornis Scand. 23:24–28.

Tiainen, J., Vickholm, M., Pakkala, T., Piiroinen, J. & Virolainen, E. 1983: The habitat and spatial relations of breeding Phylloscopus warblers and Goldcrest Regulus regulus in southern Finland. — Ann. Zool. Fennici 20:1–12.

Tiainen, J. & Väisänen, R. A. 1991: Nest record scheme — In: Koskimies, P. & Väisänen, R. A. (eds.), Monitoring bird populations: 75–86. Zoological Museum, Finnish Museum of Natural History.

Tuomenpuro, J. 1991: Effect of nest site on nest survival in the Dunnock Prunella modularis. — Ornis Fennica 68:49–56.