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# THE EVOLUTION OF RESIDENT VERSUS MIGRATORY HABIT IN BIRDS. SOME CONSIDERATIONS

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It has long been accepted (MAYR and MEISE, 1930) that migration in birds is the outcome of natural selection. How selection acts is another question. LACK (1954, p. 244) probably expressed a fairly generally held view when he stated that "the resident habit has been evolved in those species in which, on the average, migration involves greater losses than winter residence". In northern latitudes lack of food, low temperature, and short day-length will together make the breeding areas unsuitable during the winter for all but a few species.

Natural selection means differential reproductive rates, individuals carrying a certain gene or genes producing more descendants than individuals carrying alternative genes. Of course, the offspring of individuals bound to die prematurely is likely to be reduced. Stressing the early death of the individual (instead of its final result, the reduced number of offspring) we may refer to this mode of selection as *selection through differential mortality.*

The death rate, however, need not be involved. Phenotypes having a normal or even superior life expectancy may be selected against if they leave fewer offspring. This we may call *selection through differential rates of reproduction.*

Whereas I do not question the general validity of LACK's assumption that a resident or migratory habit mainly evolves through differential mortality, I think that the rate of reproduction will usually be higher among the resident stock, in some cases perhaps to the extent that the trend caused by mortality is reversed. Birds remaining in their nesting areas over the winter will clearly be in a better position with respect to choice of territory and nest-site. In addition, they will obviously have an increased chance of obtaining a mate. Recently, BERTHOLD has shown that migratory populations of the Starling (*Sturnus vulgaris*) show delayed breeding and retarded sexual maturity as compared to resident populations. ARMSTRONG (p. 52) remarks: "Wrens maintaining territory throughout the year are able to begin nest-building earlier, make more nests and *ceteris paribus* secure more mates and leave more progeny than late arrivals".

In studying the evolution of migration versus non-migration the partially migratory species are of special interest. In these species the resident males obviously start singing (and maintaining territories) long before the migrant stock has returned. The resident male Song Sparrows (*Melospiza melodia*) at Columbus, Ohio, started to sing from Jan. 7 on, and sang in earnest from Jan. 21 on, whereas no migrant males returned until late February (NICE, 1937). A Goldcrest (*Regulus regulus*) sang at Lemsjöholm in Southwestern Finland on March 16, 1966 (a very late spring), probably a couple of weeks or more before the arrival of the first migrants. The Crow (*Corvus corone cornix*) is often seen carrying nest-material in Southern Finland before the arrival of any appreciable contingent of the migratory stock. According to WALLGREN, in an area in S. Finland the Yellowhammer (*Emberiza citrinella*) started to sing on March 7, 1953. HILDÉN and LINKOLA give the return of the migratory individuals as late March — mid-May. In the spring of 1968, the Greenfinch (*Carduelis chloris*) has been heard singing in Helsinki from mid-February on; the migratory stock only returns in late March and April (HILDÉN and LINKOLA).

The migrants will undoubtedly in many cases have to settle in less favourable environments, especially when there is a high population density. In the Yellowhammer, territories occupied in March were superior to those taken up in April by birds which may have been migrants (WALLGREN). (The fact that many birds stick strictly to the same territory year after year only shows that it is more favourable to have a familiar territory than to choose a new territory of superior food productivity.)

According to NICE (1937) and LACK (1944), in species with partial migration fewer males migrate than females, and fewer adult males than young ones. This is quite in accordance with territorialism. Young males would not be able to compete with the old ones, anyway, and so it may be better for them to migrate. The females, again, do not settle until the males have done so, and in many species are fewer in numbers than these, so that there must be less competition among them. With the Song Sparrows on an island in British Columbia, TOMPA found that returning young females, because of the shortage of this sex, were able to settle successfully, whereas young males were seldom successful in obtaining a territory or, at any rate, a mate. Accordingly, young females could better afford to emigrate than young males, and there was a considerable difference between the sexes with respect to their autumn migration.

If the selective advantage of being the first to choose a territory is high enough, it should be possible for a population or part of it to endure a higher mortality in the resident area rather than to migrate. This has been claimed for the Goldcrest in Finland. Several different censuses of wintering birds indicate that the resident part of the population decreases from November to March in the proportion 10:1 (PALMGREN), 8.8:1 (KLOCKARS), 5.1:1 (LEHTONEN) or 4.9:1 (BERGROTH and BRUUN); in the tits the corresponding losses are much smaller. A perilous decrease of the Goldcrest population takes place even in comparatively mild winters (KLOCKARS). No corresponding estimate has been possible for losses among the migratory part ot the population, but they have been supposed to be of lesser magnitude (PALMGREN). ÖSTERLÖF is undoubtedly right in maintaining that the Goldcrest is a poor flyer and anything but well adapted for long migratory flights, but it seems unlikely that the death rate among the migrants could arise to 80—90 % of the population. This conclusion is incompatible with Lack's view that the migratory status is caused by differential mortality, and Lack (1954, p. 114—115) has promptly claimed the results of the censuses to be unreliable. Another alternative is that the mortality is correctly indicated by the censuses, and that the life expectancy is higher among the migrant individuals, but that non-migrants achieve more numerous offspring. Further studies in a marked population will be needed to solve the problem.

Probably in no other birds will the competition for breeding places be so severe as in the hole-nesting birds. This is evident even on theoretical grounds: (1) hole-nesting birds have a much higher nesting success than birds nesting in the open, (2) in spite of this, in the Palearctic and Nearctic faunas only a minority of the Passerine species nests in holes (v. Haartman), (3) the reason why not all species have adopted the more favourable hole-nesting habit must be that this ecological niche is completely saturated (Nice, 1957), the competition for the nest-hole making it impossible for a new species to utilize them. Excavating a nest-hole takes too much time and is practised by few Passerine species.

In contrast to so much of the struggle for existence, the fight for nest-holes is easy to observe in nature. The two main competitors for nest-boxes in Finland, the Great Tit (*Parus major*) and the Pied Flycatcher (*Ficedula hypoleuca*) often fight savagely, the stronger tit not infrequently killing the weaker flycatcher (v. Haartman). The nesting times of these species are fairly distinct, which probably to some extent reduces the amount of fighting between them.

Some ten years ago (v. Haartman, 1957) I observed a phenomenon which I could not, at the time, fully explain, i.e. that the number of hole-nesting species is proportionally higher among resident than among migratory Passerines. This holds true of both the Palearctic and the Nearctic fauna. In the Table below, I have tried to analyse the migratory status of the birds of Ontario (according to Godfrey, supplemented with data kindly placed at my disposal by Dr. and Mrs. Murray Speirs) and the southern half of Finland. Of course, the different categories used in the table merge into each other, and in many species the true status is uncertain. Although I am sure that other students would allot a number of species differently, I am convinced that the trend would remain unchanged.

| | S. Finland | | Ontario | |
|---|---|---|---|---|
| | Hole-nesting | Other | Hole-nesting | Other |
| Resident* | 9 = 50 % | 11 = 15 % | 9 = 50 % | 11 = 9 % |
| Partial migrant | 1 = 6 % | 6 = 8 % | 1 = 6 % | 3 = 3 % |
| Mainly migrant | 1 = 6 % | 3 = 4 % | — | 17 = 15 % |
| Migrant | 7 = 39 % | 53 = 73 % | 8 = 42 % | 83 = 73 % |

* Irruptive species have been included among the residents, as in many cases they are likely to arrive early or breed early.

If we consider the nesting times of Finnish Passerines* (see Figure), it is apparent that there is a trend towards earlier breeding among the hole-nesting species. Not a single hole-nester has a very late breeding season (starting to lay after the end of May), whereas among the other species no less than a third breed late. Again, nearly half of

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* It should be stressed that a number of species had to be omitted from the figure, owing to scanty information about their breeding time.

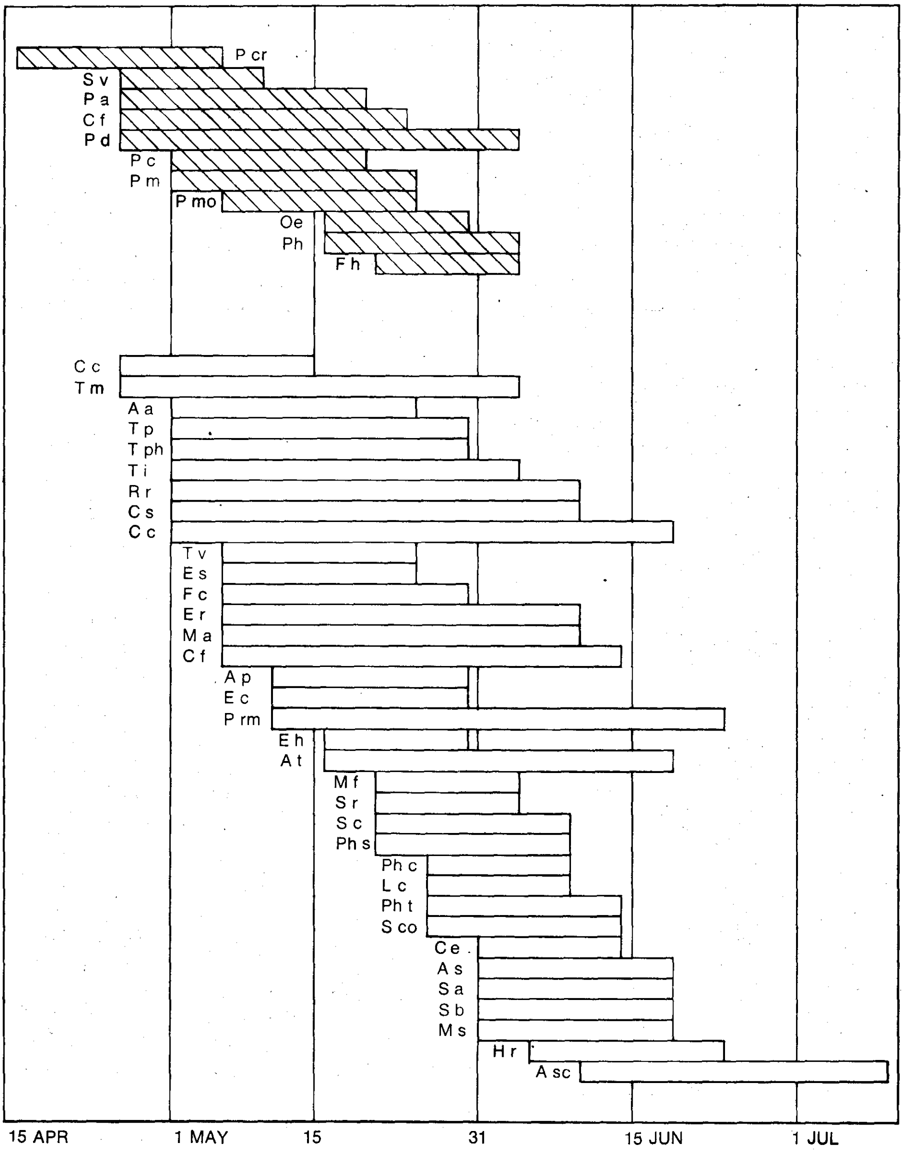

FIG. 1. The laying periods of Passerine species (excluding the family CORVIDAE) in Southern Finland, mainly based on data from nest-cards. Laying periods are taken as the periods within which ca. 75 % of the population starts to lay. Only species in which the season could be reasonably well determined were considered. The numbers refer to:

(A) Species nesting in holes (oblique hatching): P c = *Parus cristatus,* S v = *Sturnus vulgaris,* P a = *Parus ater,* C f = *Certhia familiaris,* P d = *Passer domesticus,* P c = *Parus caeruleus,* P m = *P. major,* P mo = *P. montanus,* Oe = *Oe. oenanthe,* Ph = *Ph. phoenicurus,* F h = *Ficedula hypoleuca.*

(B) Other species, including species nesting in niches (no hatching): C c = *Carduelis chloris,* T m = *Turdus merula,* A a = *Alauda arvensis,* T p = *Turdus pilaris,* T ph = *T. philomelos,* the hole-nesters are very early (starting within April), whereas among the other species only about 6 % can be placed in this category. It also deserves mention that among the 8 species of diving ducks (subfamilies AYTHYINI and MERGINI) which regularly breed in Southern Finland, 3 species nest early, i.e. *Somateria mollissima, Bucephala clangula,* and *Mergus merganser,* of which the two latter are hole-nesters, whereas none of the remaining five late-breeding ducks nests in holes (v. HAARTMAN *et al.*).

According to an old Swedish proverb, he who arrives first at the mill may grind. This holds true, *mutatis mutandis,* of the birds competing for a nest-hole. In the Pied Flycatcher, I found that the females nesting in defective nest-boxes were, on the average, later than other females. For species starting to lay in June, very few nest-holes will be available in nature. The most reliable way to secure a nest-hole is undoubtedly to be resident.

In a discussion Prof. Günther Niethammer pointed out to me another factor that may be important in explaining the correlation between hole-nesting and resident habits. Many hole-nesting species also spend the cold nights in holes. The microclimate in the roosting cavity has been studied by KENDEIGH and found to be more favourable than the open air, as the temperature inside the hole is higher than outside (e.g. at —8°C no less than 6.2° higher), and the protection against wind is complete. When clearing the nest-boxes after the winter, one is struck by the very few dead tits found in them (Dr. Olavi Hildén, orally, and own observations). For these birds death probably comes in the daytime rather than at night. KENDEIGH concludes (pp. 145—146) that ”the amount of energy thus conserved may make the difference between survival and death during periods of extreme weather during the winter. Likewise, roosting in cavities may enable a species to occur farther north during the winter than it otherwise would”. Or, in other words, roosting in cavities may make it possible for a bird to acquire a resident instead of a migratory status.

We are then faced by the question why more species do not utilize cavities for roosting. Here, again, the limited number of holes available may play a role. Fighting for a roosting-place just before nightfall, when it may be too late to find another suitable place, may be extremely dangerous.

It is, for the present, impossible to judge the respective selective effects of roosting in holes and being the first to acquire a nesting-hole in spring. Both factors may well play a role in making hole-nesting species apt to be resident and open-nesting species apt to migrate.

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T i = *T. iliacus,* R r = *R. regulus,* C s = *Carduelis spinus,* C c = *C. cannabina,* T v = *Turdus viscivorus,* E s = *Emberiza schoeniclus,* F c = *Fringilla coelebs,* E r = *Erithacus rubecula,* M a = *Motacilla alba,* C f = *Carduelis flammea,* A p = *Anthus pratensis,* E c = *Emberiza citrinella,* Pr m = *Prunella modularis,* E h = *Emberiza hortulana,* A t = *Anthus trivialis,* M f = *Motacilla flava,* S r = *Saxicola rubetra,* S c = *Sylvia curruca,* Ph s = *Phylloscopus sibilatrix,* Ph c = *Ph. collybita,* L c = *Lanius collurio,* Ph t = *Phylloscopus trochilus,* S co = *Sylvia communis,* C e = *Carpodacus erythrinus,* A s = *Acrocephalus schoenobaenus,* S a = *Sylvia atricapilla,* S b = *S. borin,* M s = *Muscicapa striata,* H r = *Hirundo rustica,* A sc = *Acrocephalus scirpaceus.*

KUVA 1. *Varpuslintujen (paitsi varislinnut) munintakaudet Etelä-Suomessa, pääasiassa pesäkorttien mukaan. Munintakaudeksi on katsottu aika, jona n. 75 % populaatiosta alkaa munia. Huomioon on otettu vain lajit, joiden munintakausi on voitu hyvin määritellä. Vinoviivoitus = koloissa pesivät lajit (lyhennysten selitykset yllä; A). Avoimet sauvat = muut lajit (selitykset yllä; B).*

## Summary

(1) The idea is accepted that usually the resident habit has been evolved in species in which migration involves greater losses than non-migration.

(2) The resident habit will be favoured by the opportunity of the resident individuals to choose their territories and nesting-places before the migratory stock, and by their increased chance to obtain a mate. Also, sexual maturity may be delayed in migrants.

(3) It is possible that selection through differential reproductive rates (point 2 above) will reverse the trend caused by selection through differential mortality (point 1 above). It has been claimed that the death rate among Goldcrests overwintering in Finland is considerably higher than among the migrating individuals. Still, the resident stock has not been eradicated by natural selection.

(4) In hole-nesting species there is severe competition for holes. Therefore there will be a high premium on choosing the nest-hole as early as possible. Thus it is not surprising to find that there is a correlation between hole-nesting and residence (Table, p. 3), and between hole-nesting and early breeding (Figure, p. 4).

(5) The death rate among resident hole-nesting birds may be reduced by their habit of roosting in protected cavities. The factors mentioned under points (4) and (5) probably together explain the correlation between hole-nesting and the resident habit.

Selostus: **Paikkalintu/muuttolintu-elintavan kehityksestä linnuilla.**

Tekijä tarkastelee eräitä näkökohtia, jotka voivat tulla kysymykseen toisaalta muuttolintujen, toisaalta paikkalintujen elintavan evoluutiossa.

1. Kirjoittaja hyväksyy käsityksen, että tavallisesti ne lajit kehittyvät paikkalinnuiksi, joilla muutto aiheuttaa enemmän menetyksiä kuin paikallaan pysytteleminen.

2. Paikkalintujen mahdollisuus varhaiseen reviirin ja pesäpaikan valintaan ennen muuttavia lintuja sekä parinmuodostuksen varmistuminen suosivat paikkalintu-elintapaa. Myös sukukypsyys voi muuttajilla viivästyä.

3. Erilaisilla lisääntymistuloksilla operoiva valinta (yllä kohta 2) voi mahdollisesti kumota erilaisten kuolevuuksien aiheuttaman valinnan vaikutuksen (yllä kohta 1). On väitetty, että Suomessa talvehtivien hippiäisten kuolevuus olisi huomattavasti korkeampi kuin muuttavien. Tästä huolimatta luonnon valinta ei ole vielä hävittänyt talvehtivaa kantaa.

4. Kolopesijöillä esiintyy kovaa kilpailua pesäpaikoista. Pesäkolon valinta mahdollisimman aikaisin on sen vuoksi edullista. Näin ollen ei ole yllättävää havaita, että toisaalta kolopesinnän ja paikkalintu-elintavan (taulukko sivulla 3) ja toisaalta kolopesinnän ja pesintäkauden varhaisuuden (kuva 1) välillä on korrelaatio.

5. Koloissa pesivien paikkalintujen talvikuolevuutta saattaa vähentää niiden tapa yöpyä suojaisissa koloissa. Edellisessä ja tässä kohdassa mainitut tekijät yhdessä selittänevät kolopesinnän ja paikkalintu-elintavan välisen korrelaation.

## References

ARMSTRONG, E. A. 1955. The Wren. — London, 312 pp.

BERGROTH, S. and H. BRUUN 1939. Bidrag till kännedomen om vinterfågelbeståndet i Åbo-traktens skogar. Ornis Fenn. 16: 41—45.

BERTHOLD, P. 1964. Über den Fortpflanzungszyklus südwestdeutscher Stare (Sturnus vulgaris L.) und über bedingende Faktoren der Brutreife beim Star. Vogelwarte 22:236—275.

GODFREY, W. E. 1966. The Birds of Canada. — Ottawa, 428 pp.

v. HAARTMAN, L. 1957. Adaptation in hole-nesting birds. Evolution 11:339—347.

v. Haartman, L., O. Hildén, P. Linkola, P. Suomalainen and R. Tenovuo 1963—67. Pohjolan linnut värikuvin. I. — Helsinki, 439+96 pp.

Hildén, O. and P. Linkola 1962. Suuri lintukirja. — Helsinki, 860 pp.

Kendeigh, S. Ch. 1961. Energy of birds conserved by roosting in cavities. Wilson Bull. 73:140—147.

Klockars, B. 1936. Försök till kvantitativ undersökning av vinterfågelbeståndet. Ornis Fenn. 13:139—147.

Lack, D. 1944. The problem of partial migration. British Birds 37:122—130, 143—150.

„ 1954. The Natural Regulation of Animal Numbers. — Oxford, 343 pp.

Lehtonen, L. 1948. Über die Wintervogelfauna von Gross-Helsinki. Ornis Fenn. 25:1—18.

Mayr, E. and W. Meise 1930. Theoretisches zur Geschichte des Vogelzuges. Vogelzug 1:149—172.

Nice, M. M. 1937. Studies in the life history of the Song Sparrow. I. A population study of the Song Sparrow. Trans. Linn. Soc. New York 4, 247 pp.

„ 1957. Nesting success in altricial birds. Auk 74:305—321.

Palmgren, P. 1936. Über den Massenwechsel bei Regulus r. regulus (L.). Ornis Fenn. 13:159—164.

Tompa, F. 1963. Behavioral responses of Song Sparrows to different environmental conditions. Proc. XIIIth Intern. Orn. Congr. pp. 729—739.

Wallgren, H. 1956. Zur Biologie der Goldammer, Emberiza citrinella L. Acta Soc. Fauna Flora Fenn. 71, 4:1—44.

Österlöf, S. 1966. Kungsfågelns (Regulus regulus) flyttning. Vår Fågelvärld 25: 49—56.

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# NOTES ON THE ROOSTING BEHAVIOUR OF THE GREAT SPOTTED WOODPECKER *(DENDROCOPOS MAJOR)* AND THE THREE-TOED WOODPECKER (*PICOIDES TRIDACTYLUS*)

Erik S. Nyholm

At dusk 15.58 hours on 17th Nov. 1961, I observed at Kivisuo, Utajärvi (64°47' N) a sparse mixed forest an aspen tree approx. 30 cm thick broken at a height of 9 metres. A male Three-Toed Woodpecker climbing the tree was being chased by a male Great Spotted Woodpecker. Both birds called and moved around the tree several times. Finally, the aggressive behaviour of the latter caused the former bird to fly to the base of a spruce some 50 metres away. The Great Spotted Woodpecker looked around for some time whilst calling softly and then entered hole No. 1.

After some time, another Great Spotted Woodpecker of unknown sex flew to the same aspen tree and entered hole No. 4. When I then moved close to the tree and knocked at it, the birds flew away from their holes, and a third bird of unknown sex from hole No. 3. Thus three birds of the same species were spending the night in different holes of the same aspen trunk.

I continued to watch from my hiding