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Onset of Moult among breeding Pied Flycatchers *(Ficedula hypoleuca)* in Northern Finland

By Mikko Ojanen and Markku Orell

1. Introduction

Birds breeding in high latitudes are faced with the problem of how to arrange the yearly events of migration, breeding and moulting within the short space of time available. These phases have a high energy requirement, and it is thought that birds have evolved strategies for confronting these sequentially. Some migratory birds breeding in high latitudes, however, may start moulting while breeding, and the moult may still be in progress when they start their autumn migration (Haukioja 1971). Stationary birds seem to have plenty of time for breeding and moulting in high latitudes, but also breeding and moulting may still overlap to some extent in some such species (Haukioja 1971, Orell & Ojanen 1980).

The Pied Flycatcher, *Ficedula hypoleuca*, migrates mainly to Central Africa for the winter (e. g. Moreau 1972). It has insectivorous feeding habits (v. Haartman 1954), arrives in Finland comparatively late in spring (Hildén et al. 1979) and leaves quite early in autumn (Hyytiä & Vikberg 1973). Its time schedule in Finland is thus a short one.

We report the start of postnuptial moulting in the Pied Flycatcher in northern Finland, concentrating especially on the relationship between breeding and moulting. The adaptive significance of the overlap of these phenomenons is discussed.

2. Materials and Methods

The data were collected in the Oulu area (65°N, 25°E) of northern Finland in 1971—1980. The stage of the moult in breeding birds was checked almost every time they were captured from the nest boxes. A total of 891 Pied Flycatchers were studied. The method for recording the moult was that of Newton (1966). Old feathers are given the score 0, each fully grown new one the score 5, and those in the process of growth an intermediate value according to their length. The primary moult rate was calculated from the increase in the moult scores of individuals examined twice during moulting.

The speed of feather growth was measured in 1980 from a sample of actively moulting birds. Some birds were captured and the length of their growing feathers measured by inserting the jaw of a caliper gently at the root of the feather. The birds were recaptured after 3—10 d and the measurements repeated.

The numbering of the primaries (abbreviated in the text to P1, P2, etc.) is ascendant, and that of the secondaries (S) descendant. The innermost three feathers are named tertials (T).

The end of nesting was calculated as being the date when the nestlings reached the age of 12 d.

3. Results and discussion

3.1. Feather growth rate

The growth rate of individual feathers was measured from 5 females and 12 males which were captured at least twice at an interval of three days or more, and which had new feathers growing when first examined. The rate averaged about 3 mm per day in both sexes (Tab. 1). As P1 and P2 were about 50 mm in length in both sexes, their growth to full length would require about 17 d. This is perhaps a minimum figure, however, and a few additional days may be needed since growth is slow at the beginning (own observations) and may also be retarded at the end of growth in each feather.

3.2. Rate and Timing of Postnuptial Moult

The moult rate of the Pied Flycatcher, according to the recaptures in Oulu, was 0.84 points per day for the females and 0.90 for the males (Tab. 2). As the rate was obtained from breeding birds, it may be slightly lower than it would be for non-breeders. The start of the

Tab. 1: Growth rate of first and second primaries in the Pied Flycatcher (mean and standard deviation).

	Male	Female	t-test
Growth rate of P1 mm/d	2.6	3.2	NS[1])
S.D.	0.5	0.6	
n	12	5	
Growth rate of P2 mm/d	3.2	3.5	NS
S.D.	0.3	0.8	
n	6	3	

[1]) NS = not significant.

Tab. 2: Onset, duration and rate of the postnuptial moult in the Pied Flycatcher in the Oulu area.

	Males	Females
Sample size total	295	596
Sample size moulting	105	55
First breeding bird examined	15 June	28 May
First bird in moult examined	27 June	30 June
Daily increase in moult score, from recaptures	0.90	0.84
S.D.	0.11	0.23
n	3	4
Onset of moult (calculated back) of first bird in season		
1971	—	(14 July)
1972	20 June	30 June
1973	27 June	29 June
1974	4 July	4 July
1975	23 June	—
1977	24 June	6 July
1978	25 June	6 July
1979	27 June	—
1980	19 June	25 June
Average onset of moult of first birds	25 June/8y	2 July/6y
S.D. (d)	4.7	4.4
Average onset for all birds	1 July	5 July
S.D.	5.0	4.1
Duration of moult, from recaptures	50	54

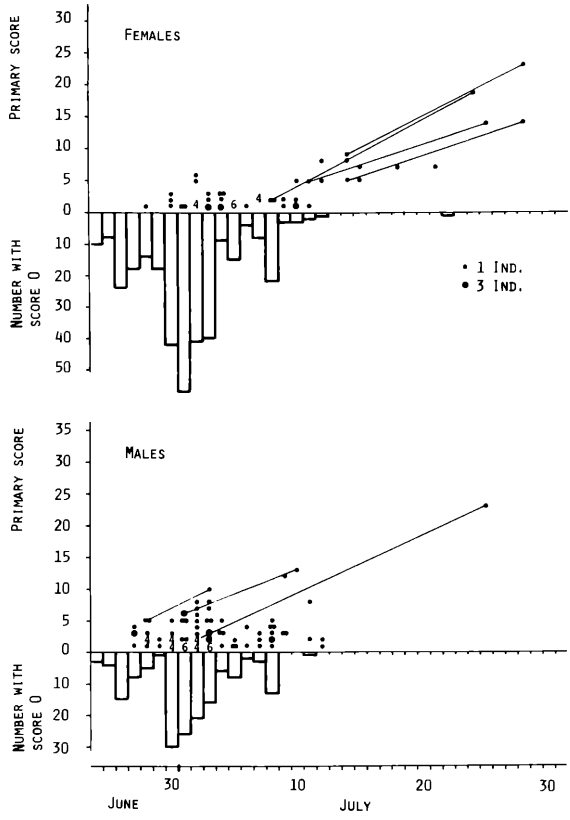

Fig. 1. Primary scores for male and female Pied Flycatchers in Oulu. Records of same individuals in active moult connected with line. More than 3 moulting birds captured on the same day and having same moult score are marked with numbers instead of dots. Only latest record accepted from those with score 0.

moult was estimated using the rates above by counting back from the moult stage of first capture. First male started on 19 and first female on 25 June (Fig. 1).

The moult usually started with the dropping of P1, but some individuals also dropped P2 simultaneously. In 14 out of 50 males these feathers had dropped at the same time, or had grown to about the same length, while the respective figures for the females were 4 out of 30. This difference between sexes was not significant, however.

The average onset of the moult, calculated from all moulting individuals, occurred on 1 and 5 July in the males and females respectively (Tab. 2). DHONDT (1973), however, pointed that this method gives too early an estimate, as a substantial proportion of the birds will not have begun their moult during the period when the data is collected. Irrespective of the moult stage, more moulting than non-moulting Pied Flycatcher males were captured on 6 July, whereas the corresponding date for the females was 12 July (this analysis is based on very limited data, however). The latter figures may be more realistic estimates for the onset of the moult than the earlier averages.

There was a clear annual variation in the onset of the moult among the females, as moulting individuals were rare of absent in years other than 1972, 1973 and 1980, when 11, 9 and 30 moulting individuals were captured respectively (very few birds altogether were captured in 1976). Moulting males were more evenly distributed between the years, although, a total of 51 were captured in 1980 alone. The last non-moulting male was captured on 11 July and last two females on 12 and 22 July.

HYYTIÄ & VIKBERG (1973) mentioned, without giving detailed data, that in Kilpisjärvi (69°N, 20°40'E) Pied Flycatchers started to moult during the period 25 June—25 July, whereas in southern Finland they did so between the end of June and the end of July. The onset of the moult in the Oulu population thus took place at about the same time as in Finland as a whole. The last individuals in the populations mentioned by HYYTIÄ & VIKBERG may have started to moult late in the season, but this evidently does not concern the Oulu population.

The moult was estimated to last 50—54 d according to the rate from recaptures (Tab. 2). This gives a slightly longer period than that estimated by HAUKIOJA for this species (45 d) from Finnish moult-card data (in HYYTIÄ & VIKBERG 1973). Our material is restricted to the early period of moulting, which partly explains the slow rate, as the rate is often slow at first (e. g. HAUKIOJA & REPONEN 1968, DHONDT 1973). A slightly higher rate than that obtained here might be expected for the Pied Flycatcher, since long-distance migrants (e. g. the Willow Warbler, *Phylloscopus trochilus*, LEHIKOINEN & NIEMELÄ 1977) usually have short moulting periods.

As the last non-moulting birds were captured on 12 July (and one female 22 July), the moult was estimated to have ended by 5 Sep. The length of the moulting period for the majority of the Pied Flycatcher population in the Oulu area was thus about 70 d (25 June—5 Sep).

Tab. 3: Breeding Pied Flycatchers moulting also feathers other than primaries.

Date of capture	Sex and number of individuals		Development stage of feather[1])										Age of young
			P1	P2	P3	P4	P5	P6	S1	T1	T2	T3	(d)
28. 7.—73	♀	49	5	5	5	4	3	0	0	3		0	9
24. 7.—80	♀	142	5	5	5	3	1				3		6
30. 7.—80	♀	102	5	5	4	1					0		12
25. 7.—80	♂	102	5	5	4	4	3	2	2		4	2	7
25. 7.—80	♂	142	5	5	4	3	3	2	2		4	2	7

Notes: [1]see p. 445; 0 = feather just dropped; = old feather.

Five individuals dropped feathers other than the primaries (Tab. 3). The dropping of S1 took place when the primary score was 23 in one female and about 20 in two males. All five individuals had dropped tertials. The median tertial (T2) seems to be dropped first, but as observed commonly in other birds (e. g. the Great Tit, *Parus major*, DHONDT 1973, and Song Sparrow, *Melospiza melodia*, DHONDT & SMITH 1980), a certain amount of variation is often seen in the dropping order.

We can compare the moult of the Pied Flycatcher, a migratory bird, with that of a stationary one, the Great Tit. The males of the latter species started moulting about at the same time as did the male Pied Flycatchers, but the females about a week later than the female Pied Flycatchers. The length of the moulting period was 72 d for individual Great Tit males and 70 d for females, and it took approximately 105 d for the whole Oulu population of this species to moult (ORELL & OJANEN 1980).

3.3. Breeding and Moulting

The summer schedule of this species is a rapid one. The first Pied Flycatchers laid their eggs in this area on 20 May in the years 1969—80 (own observations), and the most intensive laying occurred during the first ten days of June. After that the number of new clutches decreased rapidly. By 10 July about 95% of the nestlings had left the nest boxes and breeding was practically over (Fig. 2).

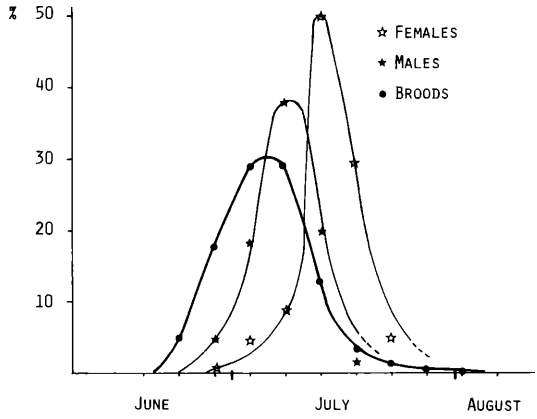

Fig. 2. Percentage of Pied Flycatcher broods with fledglings near leaving the nest (= age 12 days) and estimated percentage of males and females beginning the moult during each five-day period.

The early-breeding individuals did not start moulting when feeding their young, whereas breeding and moulting overlapped to some extent in those among the latest to breed (Fig. 2., Tab. 4). The females did not start to moult during nesting as frequently as did the males (Tab. 4). The onset of the moult nevertheless took place equally as often during the various nesting stages (laying, incubation, feeding the young) in both sexes. In this respect the species differed from the Great Tit, in which the males often started to moult at an earlier nesting stages than did the females (ORELL & OJANEN).

HAUKIOJA & KALINAINEN (1972) stated that moulting while breeding is exceptional in passerines in Southern Finland, but such a strategy is presumably much more common among birds breeding at higher latitudes (see HAUKIOJA 1971, HUSSELL 1972, DHONDT & SMITH 1980, ORELL & OJANEN 1980). In hole-nesting species, which have a longer breeding period than open nesters (see LACK 1968), the habit of overlapping breeding and moulting may be a common strategy.

The effect of local conditions, e. g. variation of food between years, in the timing of moult should be stressed in this respect. Pied Flycatchers, and especially the females, start their moult during breeding in a highly variable manner from one year to another, and it may be strongly suspected that the availability of food is the crucial factor. The moult schedule may be highly adaptable, as Red-billed Firefinches *Lagonosticta senegala* always completed their wing moult in c. 40 d when kept in captivity, whereas breeding individuals moulted over two or three months (PAYNE 1980).

Tab. 4: Onset of the moult in Pied Flycatchers at different nesting stages (I = beginning, II = middle, III = end of the incubation).

		Nesting stage																					
		Laying	Incubation			Feeding of nestlings (age in d)																	Total number moulting
			I	II	III	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14			
Males	1972—1979	2			7	5	2	1	2	6	5	2	2	7	2	4	2	2	2	2			55
	1980			1		3	1	4	5	6	4	4	5	5	5	2	3	2					50
Females	1971—1979		1	3		2			2	3		1		2	3		3	3		2			25
	1980	1			2				1			1	–	5	3	6	2	4	5				30

3.4. Adaptive value of moulting while breeding

Pied Flycatchers arrive into Finland relatively late, at the beginning of May (HILDÉN et al. 1979), and commence their breeding activities immediately (v. HAARTMAN 1949). They start moulting during, or commonly after breeding and once the moult is finished they are ready for the autumn migration, which takes place in August — first half of September (HYYTIÄ & VIKBERG 1973).

The records of HYYTIÄ & VIKBERB on migrating Pied Flycatchers at Signilskär, SW-Finland in 1971 show 11 out of 57 birds captured to have been moulting their secondaries during the period of 4 Aug.—17 Sep., whereas none of the 26 captured between 2 Aug.—2 Sep. 1972 were doing so. These observations are interesting, since several individuals moulting while breeding were recorded in Oulu in 1972, but only one late breeding female in 1971.

Thus it seems that either breeding and moulting or moulting and autumn migration can overlap in this species, but that an overlap is not seen twice during the same breeding season. It is not adaptive for birds to start autumn migration before the moult is completed, and several explanations have been proposed for this behaviour: a high energy loss due to poor insulation, high energy demands for growing feathers and reduced flying ability due to the raggedness of the wings (see PAYNE 1972, BERTHOLD 1975 for further discussions). Hence it is possible that in order to be able to breed at the level of Oulu, Pied Flycatchers required to face extra risks compared with those breeding in southern latitudes, where the summer phases are sequential.

However, the circannual events, as rhythms in body weight, moult and nocturnal restlessness are proved to be endogenous for a number of species (e. g. the Willow Warbler and Wood Warbler *Phylloscopus sibilatrix*, GWINNER 1968; Garden Warbler *Sylvia borin* and Blackcap *S. atricapilla* BERTHOLD et al. 1972), these being highly adaptive. Experimentally GWINNER et al. (1972) showed, that postjuvenile moult began and terminated at an earlier age in Willow Warblers from southern Finland than in conspecifics from southwestern Germany. Similarly, the moult started at about the same date in Red-backed Shrikes *Lanius collurio* from Finland and from France, but terminated earlier in Finnish birds (GWINNER & BIEBACH 1977). The results confirmed the adaptive value of endogenous start and duration of moult in both these experiments, where birds from different populations were held in the same environmental conditions. The results also were in accordance with several field observations, in which populations breeding in the North moulted faster than their Southern relatives (for further details see ORELL & OJANEN 1980). BERTHOLD (1977) suggested, that such differences in circannual events may have genetic basis.

According to CREUTZ (1955) some male Pied Flycatchers may start moulting while breeding as south as near Dresden. Although no additional moulting data from southern populations of this species is not available, similar adaptive differences in the start and duration of moult, as in other species, may exist between northern and southern populations. Pied Flycatchers are known to be philopatric (or loyal to certain geographical area, BERNDT & WINKEL 1975, 1979, own observations), and thus if the circannual events are genetically regulated (to a certain degree) the differences in these events, if such exists, between different populations may persist.

The habit of breeding and moulting can be also explained with the concepts of life-history strategies. Assumingly, adults increase their future reproductive efforts (see WILLIAMS 1966) by moulting and breeding simultaneously, and thus ensuring early start of autumn migration with little risk of encountering e. g. adverse autumn weathers. The return rates of those birds moulting while breeding and those not doing so would clarify the validity of this hypothesis. Such investments into future reproduction may involve risks for fledgelings due to decreased ability of adults to feed them. For clarifying this problem the feeding rate and also amount of food carried to youngs by moulting and nonmoulting individuals must be tested.

4. Summary

The onset of the moult was studied in 891 breeding Pied Flycatchers in Oulu, northern Finland, in 1971—1980. The average onset date was between 1—6 and 5—12 July in the males and females respectively, and the duration of the moult about 50—54 days. The moulting period of the Pied Flycatcher population as a whole covered approximately 70 days.

A substantial proportion of population began to moult while still breeding in some years, which is thought to be due to a shortage of time in the summer schedule of this species. This kind of behaviour may increase the future reproductive efforts of parents.

5. Zusammenfassung

Bei Oulu im nördlichen Finnland wurden von 1971—1980 insgesamt 891 Brutvögel des Trauerschnäppers *(Ficedula hypoleuca)* auf Mauser hin untersucht. Der mittlere Mauserbeginn lag bei ♂ zwischen dem 1. und 6. bei ♀ zwischen dem 5. und 12. Juli; die Mauserdauer betrug ungefähr 50—54 Tage. Bei der Trauerschnäpper-Population insgesamt umfaßte die Mauserperiode etwa 70 Tage.

In einigen Jahren begann in der untersuchten Population ein wesentlicher Teil der Individuen schon mit der Mauser, als sie noch mit der Brut befaßt waren, was mit der bei dieser Art nur knapp bemessene Zeit bis zum Wegzug zusammenhängen dürfte. Ein derartiges Verhalten kann die zukünftige Fortpflanzungsleistung der Elternvögel steigern.

6. Literature

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