Flightlessness in some moulting passerines in Northern Europe

ERKKI HAUKIOJA

Department of Zoology, University of Turku

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The effects of wing and tail moult on flying ability have been evaluated for four passerine species (*Luscinia svecica, Phylloscopus trochilus, Motacilla flava, M. alba*) in Finnish Lapland and *Sylvia communis* in southern Finland. All species have a short postnuptial moult (between 35 and 50 days) and in *Luscinia svecica, Phylloscopus trochilus* and *Sylvia communis* some moulting specimens unable and/or unwilling to fly have been caught. The stage of the moult affects the probability of a bird being caught so that birds which are at the peak of their moult are more difficult to catch with nets. The phenomenon of flightlessness is therefore obviously more common than can be evaluated from moult card data.

Flightlessness depends on the fact that not only are many wingfeathers lost simultaneously but also that in *Luscinia svecica,* and to a lesser extent in *Phylloscopus trochilus,* tail feathers are lost simultaneously. The tail moult is most intense during a phase when there are not very large gaps in the wings: this helps in part to maintain as high a degree as possible of flying ability. Wagtails (open field species) can avoid flightlessness, in spite of a short moult, by a prolonged tail moult.

Introduction

The phenomenon that flight feathers are simultaneously shed in waterfowl, thus causing temporary flightlessness, is well known. The same tendency has also been verified in certain other groups of waterbirds (SALOMONSEN 1968). There are scattered data in literature showing that some passerines may be completely or nearly flightless during the most intense shedding of flight feathers. BALÁT (1960) and SULLIVAN (1965) have found that Dippers (*Cinclus cinclus* and *C. mexicanus*) were unable to fly during the wing moult. STRESEMANN & STRESEMANN (1966) cited two cases from Arctic regions concerning the Snow Bunting *Plectrophenax nivalis* and the Lapland Bunting *Calcarius lapponicus.* BERGER (1967) mentions that at least some Thrush Nightingales *Luscinia luscinia* lose their ability to fly during moult. HAUKIOJA & KALINAINEN (1968, 1972) added the following species: the Willow Warbler *Phylloscopus trochilus* and the Whitethroat *Sylvia communis.* HAUKIOJA (1971a) mentions that perhaps also the Bluethroat *Luscinia svecica* and the Redwing *Turdus iliacus* belong to those species which lose or may lose their ability to fly during the moult. Reduced numbers of caught birds during the postnuptial moult eg. the Bullfinch *Pyrrhula pyrrhula* (NEWTON 1966) and the Chaffinch *Fringilla coelebs* (DOLNIK & BLUYMENTAL 1967) are a possible indicator of reluctance to fly. In these species, however, the ability to fly is probably not threatened.

The aim of the present paper is to investigate the occurrence of flightlessness in some passerines and to try to find out what events in renewal of the feathers cause this phenomenon, and how it can be overcome by some species.

Materials and methods

There is a general tendency for small, insect-eating passerines to moult faster than larger, seed-eating species. In those species that moult after breeding the farther north (in the northern hemisphere) they live, the faster their moult tends to be. Therefore, the most intense moult and, accordingly, the most probable loss of the ability to fly during the moult, probably occurs in small insect-eating passerines at the northern limits of their distribution. Materials analysed in this paper refer therefore to four species from the Kevo area (ca 69.5°N, 27°E), Finnish Lapland. In addition, the Whitethroat, which on the basis of earlier results (HAUKIOJA & KALINAINEN 1972) would to be one of the southern Finnish species most likely to be unable to fly when moulting, has been taken into account.

The materials from Lapland have been collected largely in studying the late summer ecology of subarctic passerines in 1970 and 1971. The periods of field work at Kevo Subarctic Research Station were 16 July—18 August, 1970 and 3 July—27 August, and 15—19 September, 1971. Materials from southern Finland have been collected in connection with other studies and as a result of a moult inquiry (HAUKIOJA 1971b).

The normal sequence of the moult in the passerines dealt with here is the same as given by DWIGHT (1900). The moult starts with the shedding of the innermost primary and ends with the growth of the outermost primary or the innermost secondary.

For each species dealt with here, data are provided for the duration and time of the

TABLE 1. Rate, duration and time of the postnuptial moult in the Willow Warbler *Phylloscopus trochilus* in the Kevo area, Finnish Lapland.

AGE	ADULTS
SEX	BOTH
YEAR	1971
LOCALITY	
LATIT.	68 - 70 N
LONG.	26 - 28 E
FIRST BIRD EXAMINED (DATE)	2. 7.
FIRST BIRD IN MOULT EXAMINED (DATE)	4. 7.
LAST BIRD IN MOULT EXAMINED (DATE)	27. 8.
LAST BIRD EXAMINED (DATE)	27. 8.
SAMPLE SIZE (TOTAL)	131
SAMPLE SIZE (MOULTING)	90
REGRESSION EQUATION	X = 8.2+0.97Y
(EQUATION COMPUTED AS REGRESSION X ON Y)	
LINEARITY TEST	
F 1	32
F 2	56
F	3.12
DAILY INCREASE OF MOULT SCORE	
FROM REGRESSION EQUATION	1.04
SE	0.044
N	90
FROM RECAPTURES	1.14
SE	0.046
N	6
START OF MOULT	9. 7.
95 PER CENT SPREAD (DAYS)	22
END OF MOULT	21. 8.
DURATION OF MOULT (DAYS)	
FROM REGRESSION EQUATION	43
FROM RECAPTURES	39

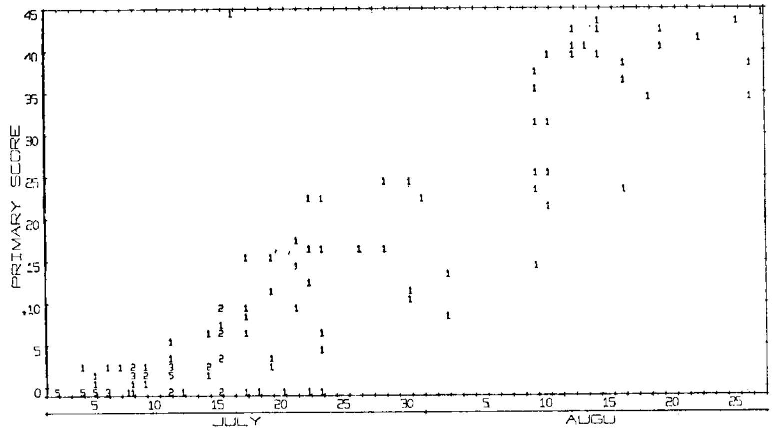

FIG. 1. Primary scores of adult Willow Warblers *Phylloscopus trochilus* at Kevo, Finnish Lapland in 1971.

postnuptial moult, which, as is common practice, has been calculated from primary scores (0 for an old wing and 45 for a new wing; for discussion of the method see Evans (1966). Other details of the moult, which are needed especially when discussing reduced flying ability, are the secondary score (from 0 to 30), raggedness of wing (rising from 0 and then falling back to 0), tail score (from 0 to 30) and raggedness of tail (rising from 0 and then falling to 0). Information on calculating raggedness values is given in Haukioja (1971b) and others eg. in Evans (1966).

The data have been processed using programmes devised for treating moult-inquiry data (Haukioja 1971b).

Time and duration of the post-nuptial moult

In the following, data of the moult of common, insectivorous passerines in the Kevo area are presented; however, the Redstart *Phoenicurus phoenicurus* and the Pied Flycatcher *Ficedula hypoleuca,* of which too few have been examined, are excluded. As a background to these data it may be mentioned that a moulting period shorter than 35—40 days is uncommon in passerines.

Luscinia svecica

Haukioja (1971a) gave the duration of the postnuptial moult in the Bluethroat as 38—40 days in 1970. More material gathered at Kevo in 1971 indicated a somewhat longer moult (42—45 days). The mean date for the start of the moult is the middle of July and for the completion of the moult the latter half of August.

Phylloscopus trochilus

Although the Willow Warbler has ten visible primaries, the computations have been carried out using only the nine innermost ones. This is reasonable because the ninth, long primary completes growing after the tenth, short primary, although they are shed in the normal order.

Haukioja & Kalinainen (1968) give 37 days (or an even shorter time according to a few recaptures) for the duration of the wing moult in the Willow Warbler in southern Finland. Haukioja (1971a) states that Willow Warblers in the Kevo area probably have as long a moult as in southern Finland. In 1971 rather reliable material was gathered at Kevo and, according to this (Fig. 1, Table 1), the duration of the moult was about 40 days.

Motacilla alba

The primary scores of White Wagtails caught at Kevo in 1970 and 1971 are presented in Fig. 2 and the summary of the moult in Table 2. The duration of the moult, 45—50 days, is considerably shorter than that recorded in a sedentary population of Pied Wagtails *Motacilla alba yarrellii* in England (76 days, Baggott 1970). This is probably the only clear-cut case where a difference between populations of the same species has been verified.

Motacilla flava

Haukioja & Kalinainen (1971) give the duration of the Yellow Wagtail's moult in southern Finland as roughly 40 days. Only 22 moulting specimens were studied in the Kevo area and all that can be said of them is that

Table 2. Rate, duration and time of the postnuptial moult in the White Wagtail *Motacilla alba* in the Kevo area, Finnish Lapland in 1970—1971.

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AGE                                               ADULTS
SEX                                                 BOTH
YEAR                                                 ALL
LOCALITY
  LATIT.                                        68 - 70 N
  LONG.                                         26 - 28 E
FIRST BIRD EXAMINED (DATE)                         4. 7.
FIRST BIRD IN MOULT EXAMINED (DATE)                4. 7.
LAST BIRD IN MOULT EXAMINED (DATE)                17. 8.
LAST BIRD EXAMINED (DATE)                         17. 8.
SAMPLE SIZE (TOTAL)                                   39
SAMPLE SIZE (MOULTING)                                35
REGRESSION EQUATION                       Y= -4.9+0.94X
(PERIOD USED IN COMPUTATION  12. 7.-17. 8.)
LINEARITY TEST
  F 1                                                 19
  F 2                                                 10
  F                                                 0.64
DAILY INCREASE OF MOULT SCORE
  FROM REGRESSION EQUATION                          0.94
   SE                                              0.115
   N                                                  31
  FROM RECAPTURES                                   0.98
   SE                                              0.059
   N                                                   3
START OF MOULT                                     8. 7.
  95 PER CENT SPREAD (DAYS)                           26
END OF MOULT                                      25. 8.
DURATION OF MOULT (DAYS)
  FROM REGRESSION EQUATION                            48
  FROM RECAPTURES                                     46
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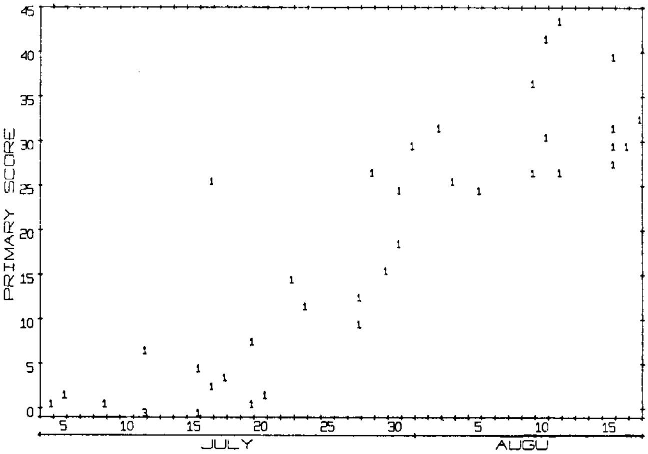


FIG 2. Primary scores of adult White Wagtails *Motacilla alba* at Kevo, Finnish Lapland in 1970—1971.

they moult from the June—July to the middle of August. Thus they complete their moult before the White Wagtail in the same area.

Sylvia communis

HAUKIOJA & KALINAINEN (1968) give 40 days as a rough estimate of the duration of the moult in the Whitethroat. A larger number of cards (including the above data) gathered in 1968—1970 (Fig. 3, Table 3) give the same estimate as regards to the length of the moult. As has been explained elsewhere (HAUKIOJA & KALINAINEN 1972), the Whitethroat is rather erratic in the manner in which it begins and passes through its secondary moult. Secondary moult often begins earlier in relation to the primary moult than in other passerines. It may start, besides from the first (outermost) secondary also from another point, usually from the sixth (innermost) secondary.

These species all have a rather short and intense moult and they live in an environment where time is rather short for completing the summer schedule. This includes at least the following phases: breeding, moult, pre-migratory fatdeposition and migration. The above phases are such that there is evidently only small possibility of reducing their length although a population lives at the limits of the distribution area of the species. The way in which it is possible to complete the whole summer cycle during the short summer is probably a compromise between all phases. This results in a solution where breeding and moulting overlap to a much greater extent than in more southern populations (HAUKIOJA 1971a). Because the moult

TABLE 3. Rate, duration and time of the postnuptial moult in the Whitethroat *Sylvia communis* in southern Finland in 1968—1970.

AGE	ADULTS
SEX	BOTH
YEAR	ALL
LOCALITY	ALL
FIRST BIRD EXAMINED (DATE)	1. 7.
FIRST BIRD IN MOULT EXAMINED (DATE)	8. 7.
LAST BIRD IN MOULT EXAMINED (DATE)	29. 8.
LAST BIRD EXAMINED (DATE)	29. 8.
SAMPLE SIZE (TOTAL)	89
SAMPLE SIZE (MOULTING)	79
REGRESSION EQUATION	X =16.0+0.81Y
(EQUATION COMPUTED AS REGRESSION X ON Y)	
LINEARITY TEST	
F 1	29
F 2	48
F	1.27
DAILY INCREASE OF MOULT SCORE	
FROM REGRESSION EQUATION	0.92
SE	0.082
N	79
FROM RECAPTURES	1.04
SE	0.154
N	14
START OF MOULT	15. 7.
95 PER CENT SPREAD (DAYS)	28
END OF MOULT	21. 8.
DURATION OF MOULT (DAYS)	
FROM REGRESSION EQUATION	37
FROM RECAPTURES	43

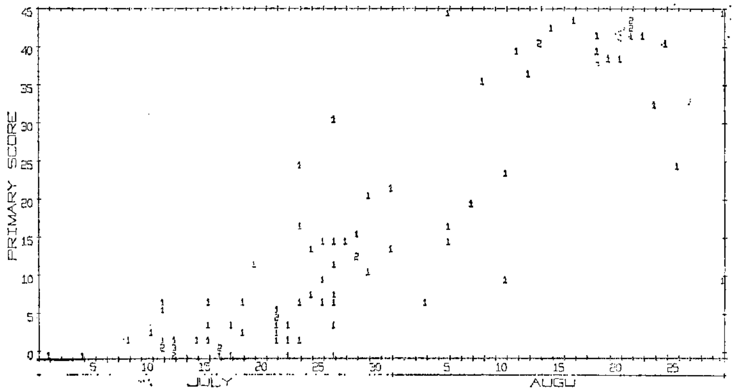


FIG. 3. Primary scores of adult Whitethroats *Sylvia communis* in southern Finland in 1968—1970.

is, at least in most cases, as long in Lapland as in southern Finland, I have also used materials originating from other parts of Finland for those species (the White and Yellow Wagtail) where the numbers caught at Kevo are rather small. Data for secondary and tail scores and raggedness values have been gathered from the following areas:

Bluethroat, years 1970—1971, Finnish Lapland. Willow Warbler, years 1970—1971, Finnish Lapland. White Wagtail, years 1970—1971, Finnish Lapland and years 1969—1970, different parts of Finland. Yellow Wagtail, years 1970—1971, Finnish Lapland and years 1969—1970, different parts of Finland. Whitethroat, years 1968—1970, southern parts (60°—64°N) of Finland.

Flying ability and moult

In order to test the reduction in the flying surface of wings, the raggedness values were plotted against the date (Figs. 4—8).

All these figures have the same basic form; two peaks with the intervening valley occurring between or near primary scores 15—20. The steep rise in raggedness values in the first stages of primary moult reflects the fact that in the species dealt with, the first primaries (five or fewer) fall in swift succession or, often, almost simultaneously. The shedding of secondaries does not usually start at this phase (Figs. 9—13). As those primaries which have fallen earlier grow and the following primaries are lost more slowly, the raggedness values fall until the beginning of secondary moult. At this phase birds have two moulting centres per wing at the same time. Raggedness values rise again and usually reach their peak between primary stages 25—40. Then raggedness values fall again as the moult nears its completion.

In order to compare the raggedness of wing in different species, and also to a certain degree, the ability to fly, I have calculated the mean raggedness values during primary scores 30—39 for each species (Table 4). This phase of the moult, also used by HAUKIOJA & KALINAINEN (1972), was chosen arbitrarily but it is useful because in most species it covers the phase when points

TABLE 4. Mean raggedness of wing during moult stages 30—39 in five passerines.

Species	Raggedness of wing		
	Mean	SE	N
Luscinia svecica	19.8	1.06	9
Phyllosc. troch.	17.6	1.38	11
Motacilla alba	13.7	1.00	12
M. flava	16.8	0.42	43
Sylvia communis	21.5	2.92	6

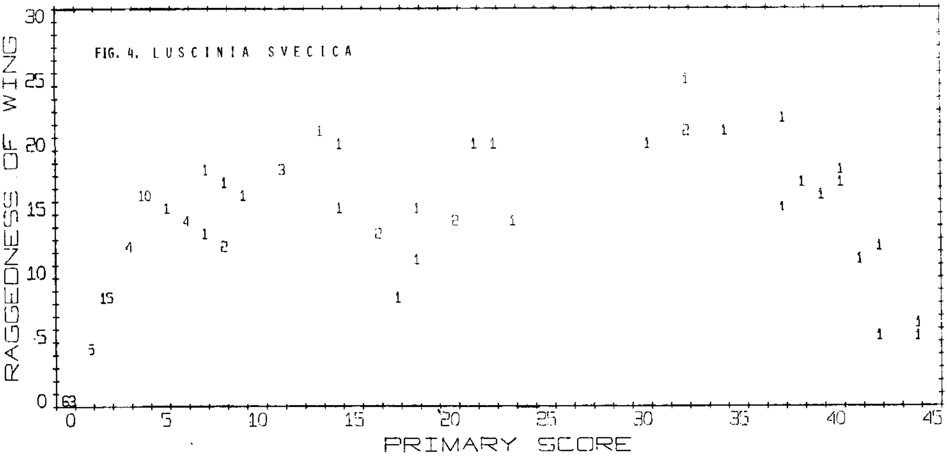


FIG. 4. LUSCINIA SVECICA

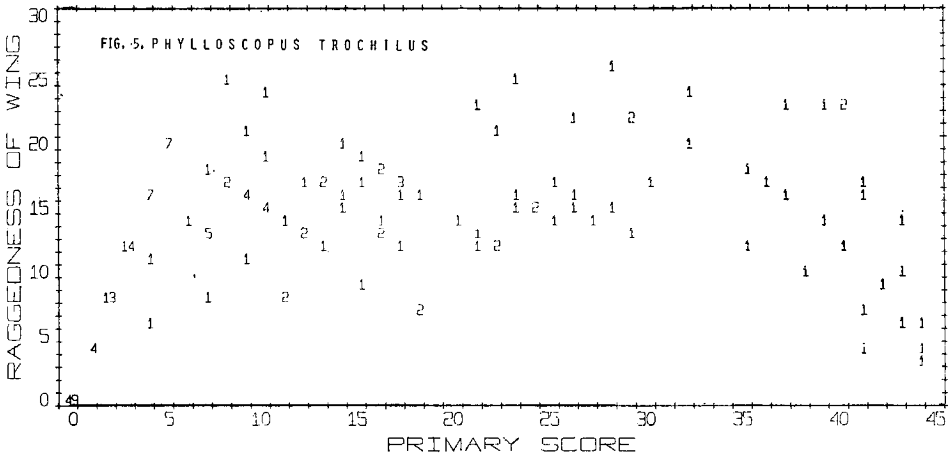


FIG. 5. PHYLLOSCOPUS TROCHILUS

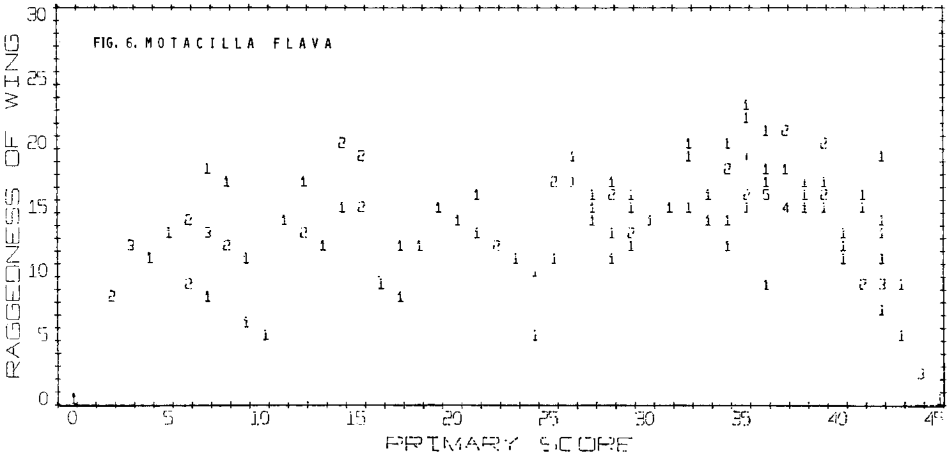
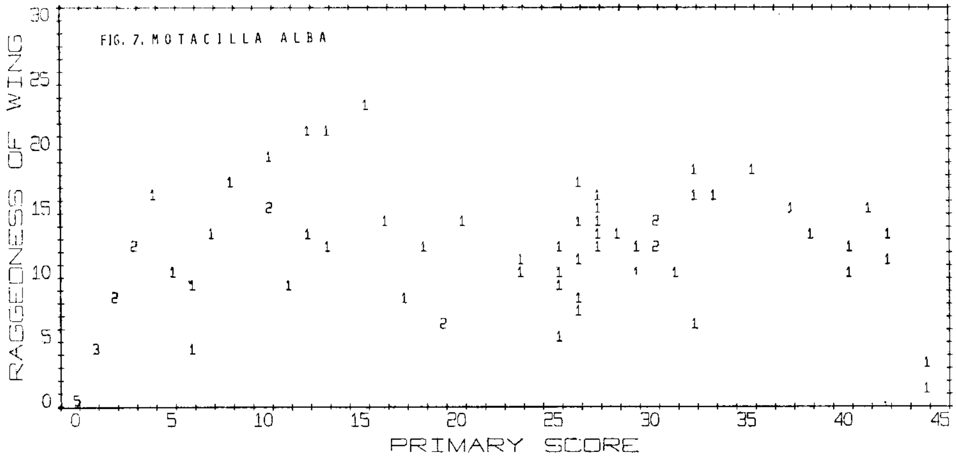
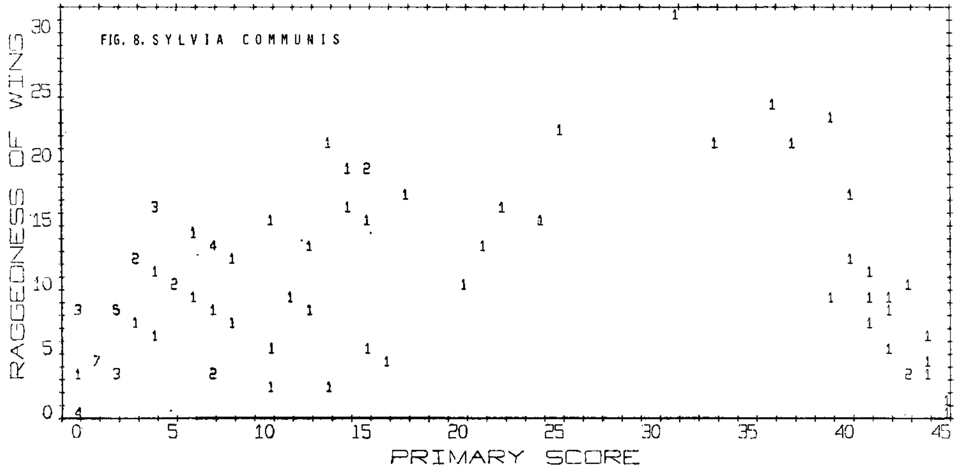


FIG. 6. MOTACILLA FLAVA





Figs. 4—8. Raggedness of wing in relation to primary scores in five passerines.

on the raggedness curve are at a high level for the second time, and ends before the final decline. In most cases the secondary moult is also in good progress but has not come to an end (Figs. 9—13). According to Table 4 the wings of species dealt with can be put to the following order from the most ragged to the least ragged: Whitethroat, Bluethroat, Willow Warbler, Yellow Wagtail, and White Wagtail.

There are field observations of the first three species showing that, while evidently not injured in any way, the birds did not start to fly when released in an open field but escaped by running. Unfortunately these cases have not been recorded systematically, but there are more than ten such cases among the materials presented here. Raggedness values of these birds were in most cases near 25.

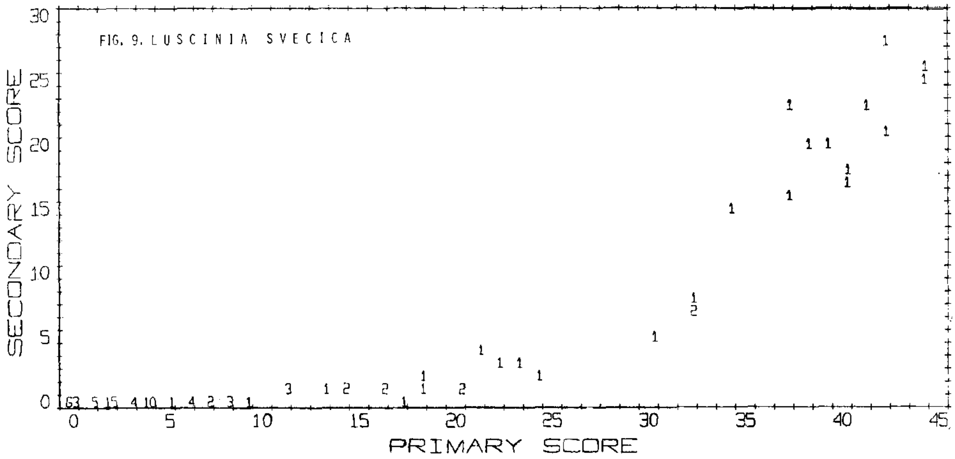


FIG. 9. LUSCINIA SVECICA

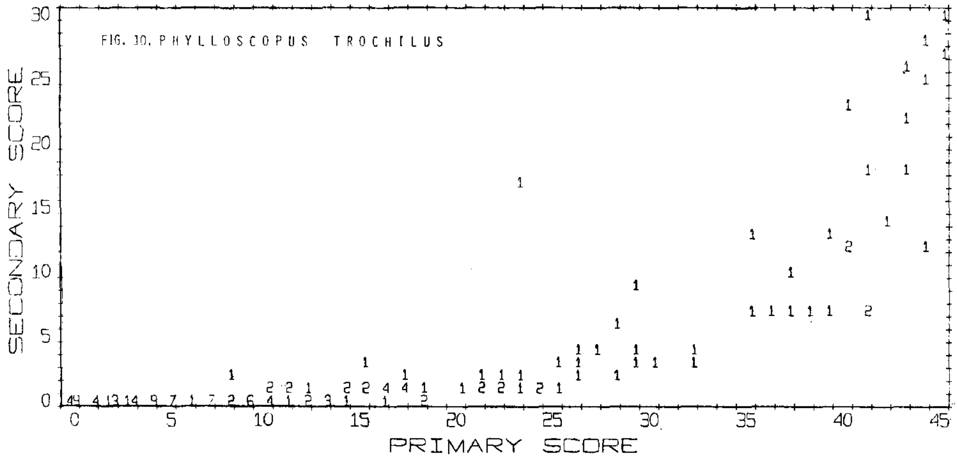


FIG. 10. PHYLLOSCOPUS TROCHILUS

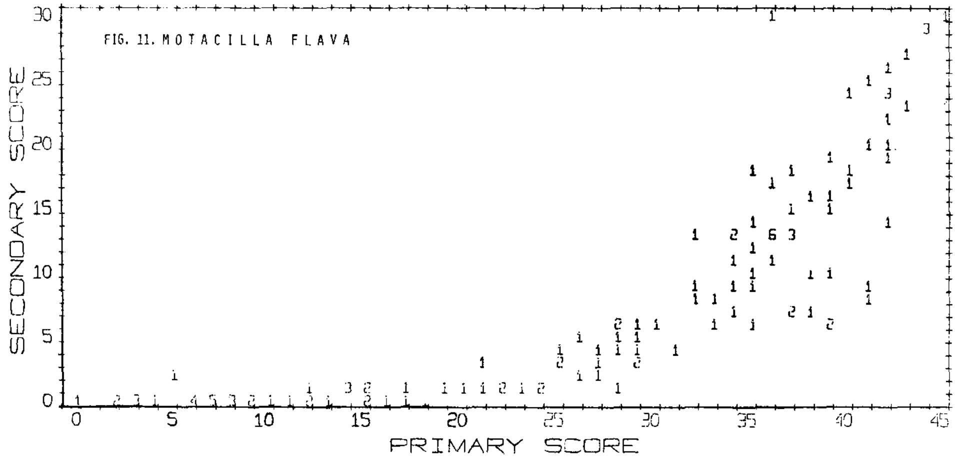
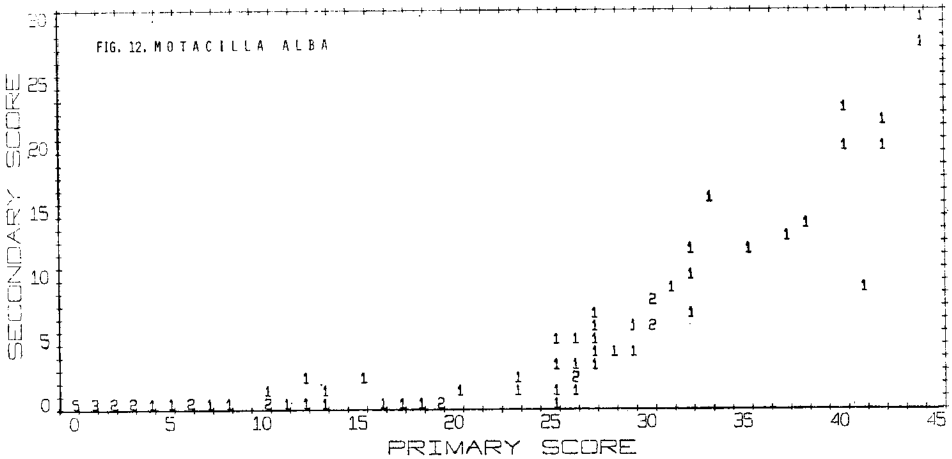
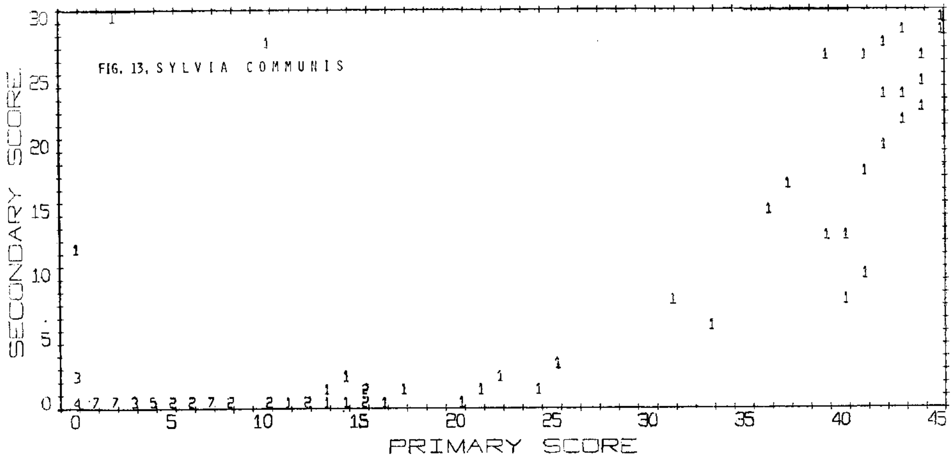


FIG. 11. MOTACILLA FLAVA





FIGS. 9—13. Secondary scores in relation to primary scores in five passerines.

From the above data it seems evident that rather few birds actually lose their ability to fly when moulting even among those species selected here. However, great bias may exist in the fact that all birds caught for moult examinations were caught using mist-nets and it is obvious that those individuals that lose their ability to fly totally, are rather difficult to get into nets which are constructed primarily in order to catch flying individuals.

In order to determine whether and to what degree moulting affects the probability of a bird's being caught, I constructed Fig. 14 where mean catches of adult Bluethroats and Willow Warblers in 1971 at Kevo have been plotted against the date (and against primary scores of the population).

Both species are caught rather effectively in relation to catching effort on the first half of July (the peak in catches probably indicates the phase

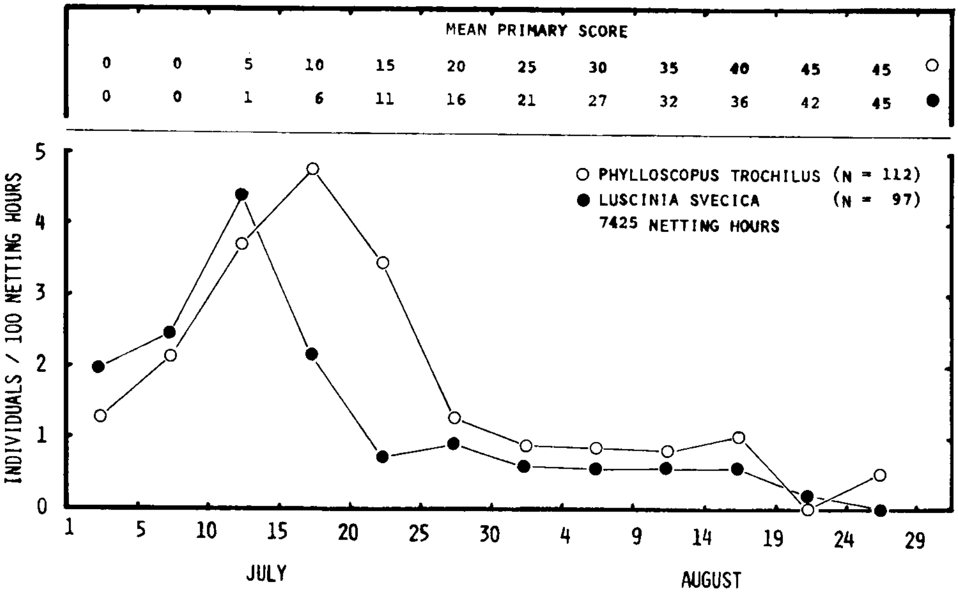


FIG. 14. Numbers of adult Bluethroats and Willow Warblers caught/100 netting hours at Kevo, Finnish Lapland in July—August 1971.

when birds relax from breeding activities and begin to stray more). In the latter half of July catches in relation to the catching efficiency suddenly drop for both species and remain at a low and rather stable level up to the phase when birds complete their moult and leave the area evidently just after completion the moult.

Thus the phase of the moult affects to likelihood of the birds' being caught rather a lot. This indicates that birds are less active when moulting and are more often unable to fly than seems to be the case when the numbers found among netted birds are examined. The following possible sources of error have, however, to be taken into account:

1. Birds may have suffered from a high mortality during the moult; this would cause late summer numbers to be rather low. As this decrease in numbers also occurred in 1970, however, it is improbable that this 2/3 decrease was due to mortality. This kind of phenomenon occurs also in southern Finland; where there is some evidence that the numbers of eg. Willow Warblers rise again at the end of the moult, although the situation is a little complicated (HAUKIOJA & KALINAINEN 1972).
2. Birds may have started migration during the moult. This is, however, improbable (see HAUKIOJA 1971a).
3. Birds may have moved to a safer biotope, eg. to thickets. This also is an improbable explanation because netting was carried out in one of the most luxuriant parts in the whole Kevo area.

In the following I discuss factors other than raggedness of the wing which may affect to the ability to fly during the moult and compare the species treated in this paper.

The time when the numbers in catches decrease markedly (Fig. 14) falls near the primary score of 15 in the Willow Warbler and a little earlier in the Bluethroat. Raggedness values are not very high at this phase but Figs. 15 and 16 show that the tail moult for both species has entered its first stages. For Fig. 20 I calculated the mean numbers of growing tail feathers and raggedness of the tail in relation to the primary score for each species. In the Bluethroat and the Willow Warbler tail feathers are shed almost simultaneously and consequently their tail raggedness rises to a very high level. In the Bluethroat the tail moult is more intense and occurs a little earlier in relation to the primary moult than in the Willow Warbler. It therefore coincides well with the situation shown in Fig. 14. Decreased activity occurs at the time when the tail is lost. However, activity remains at a low level even during the phase when the tail has again reached nearly full length. As was shown earlier, the raggedness curve generally has two peaks, and in the Willow Warbler the tail moult is most intense between these peaks. This evidently means that the ability to fly is maintained at as high a level as possible the whole time. In the Bluethroat smaller materials indicate that the first peak of wing raggedness (if it can be distinguished at all) and the peak of tail raggedness coincide. It is not quite so simple to evaluate effects on the ability to fly as the Bluethroat has a slightly longer moult and does not seem to shed more than four primaries at a time while the Willow Warbler often sheds five. In the Bluethroat the tail is again in rather good condition (especially as regards width, see EVANS 1966, p. 199) when the raggedness values of the wing reach the second peak.

When compared with other species in Fig. 20, wagtails, which are open field species, begin their tail moult at the same phase as the two former species, but the tail moult continues longer than in these species and thus makes possible longer and more slow progress in the tail moult (see also BAGGOTT 1970). Because the tail moult is more asynchronous in wagtails than in passerines in general and is also rather prolonged (Figs. 17 and 18), rather good steering ability is probably maintained the whole time. The White Wagtail was earlier mentioned as having a more long moult than the Yellow Wagtail and, consequently, it has lower raggedness values for the tail than the Yellow Wagtail. This depends largely on the fact that the Yellow Wagtail has more tail feathers growing simultaneously, which is the usual way of achieving a quick moult (eg. BERTHOLD et al. 1970).

The fifth species, the Whitethroat, differs from the above species because the way in which it begins its moult varies (HAUKIOJA & KALINAINEN 1972). Because the tail moult may start early and end late (even before or after the moult of the primaries) a rather low course in the raggedness values of the tail is arrived at in spite of a rather fast moult. Consequently, flightlessness in the Whitethroat depends mainly on the high raggedness values for the wings.

Discussion

It is clear that in some northern passerines some individuals at least lose their ability to fly during the moult. In fact this possibility can be refuted only in rather few insectivorous passerines in northern Europe. Flightlessness is probably more common than can be estimated from the mere numbers of birds caught for moult examination and evidently much more common than can be argued from visual observations in the field. In most cases the first indication may be that moulting adults are difficult to find with or without nets, but this does not necessarily prove anything more than that the activity of moulting birds decreases or that they change their

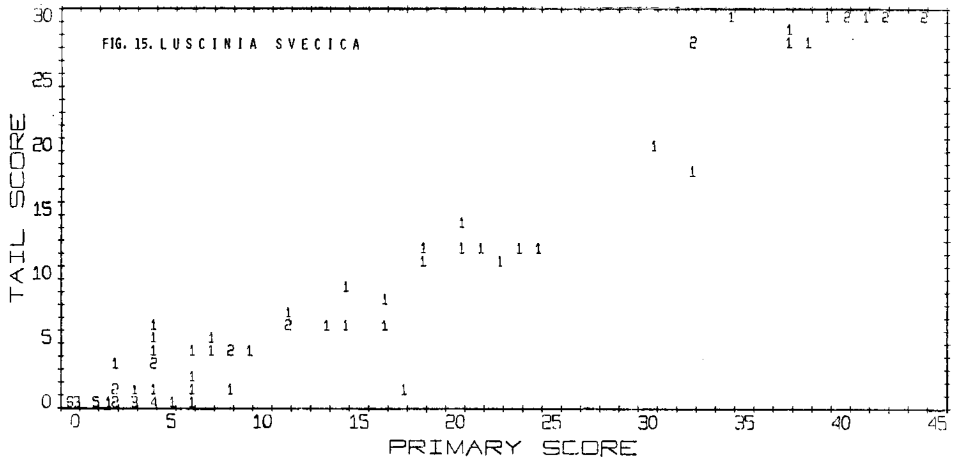


FIG. 15. LUSCINIA SVECICA

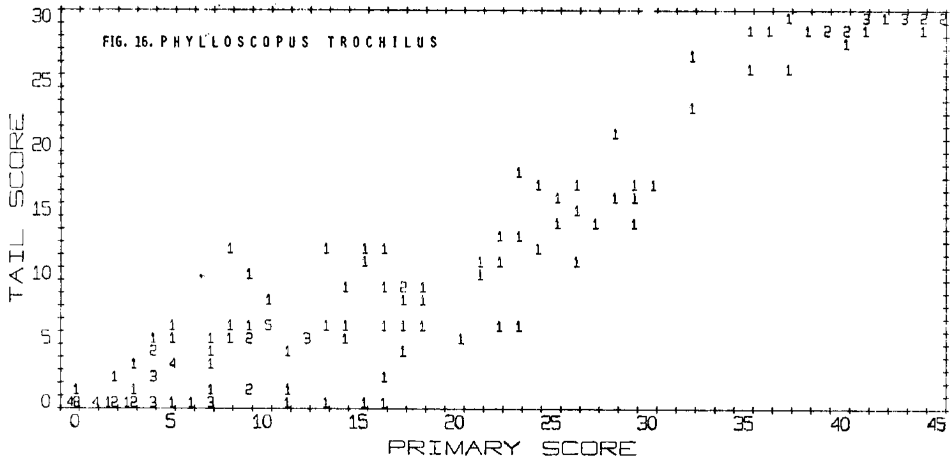


FIG. 16. PHYLLOSCOPUS TROCHILUS

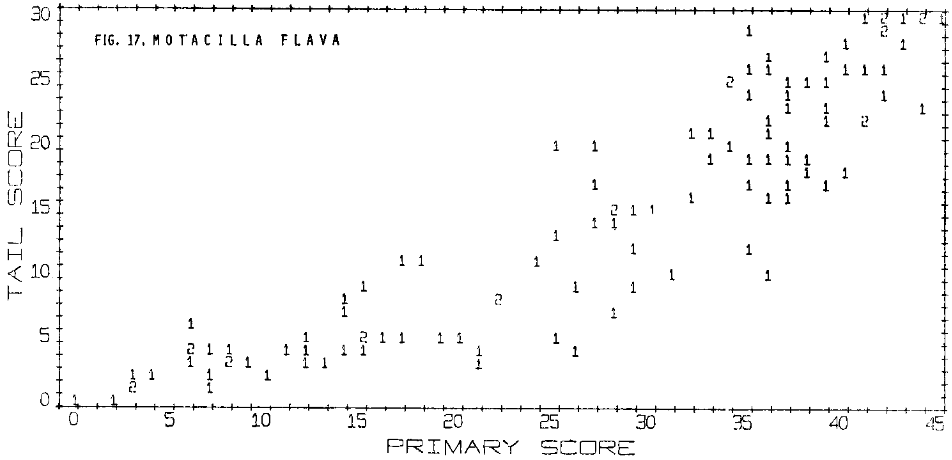
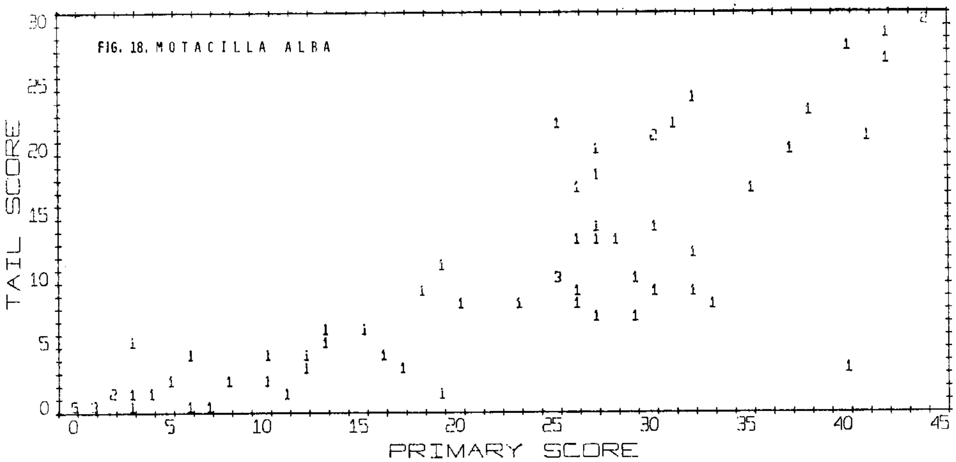
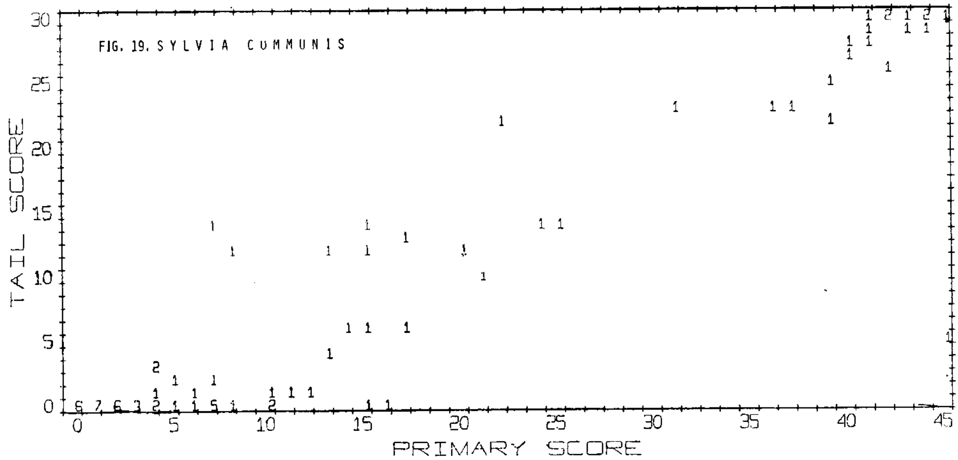


FIG. 17. MOTACILLA FLAVA

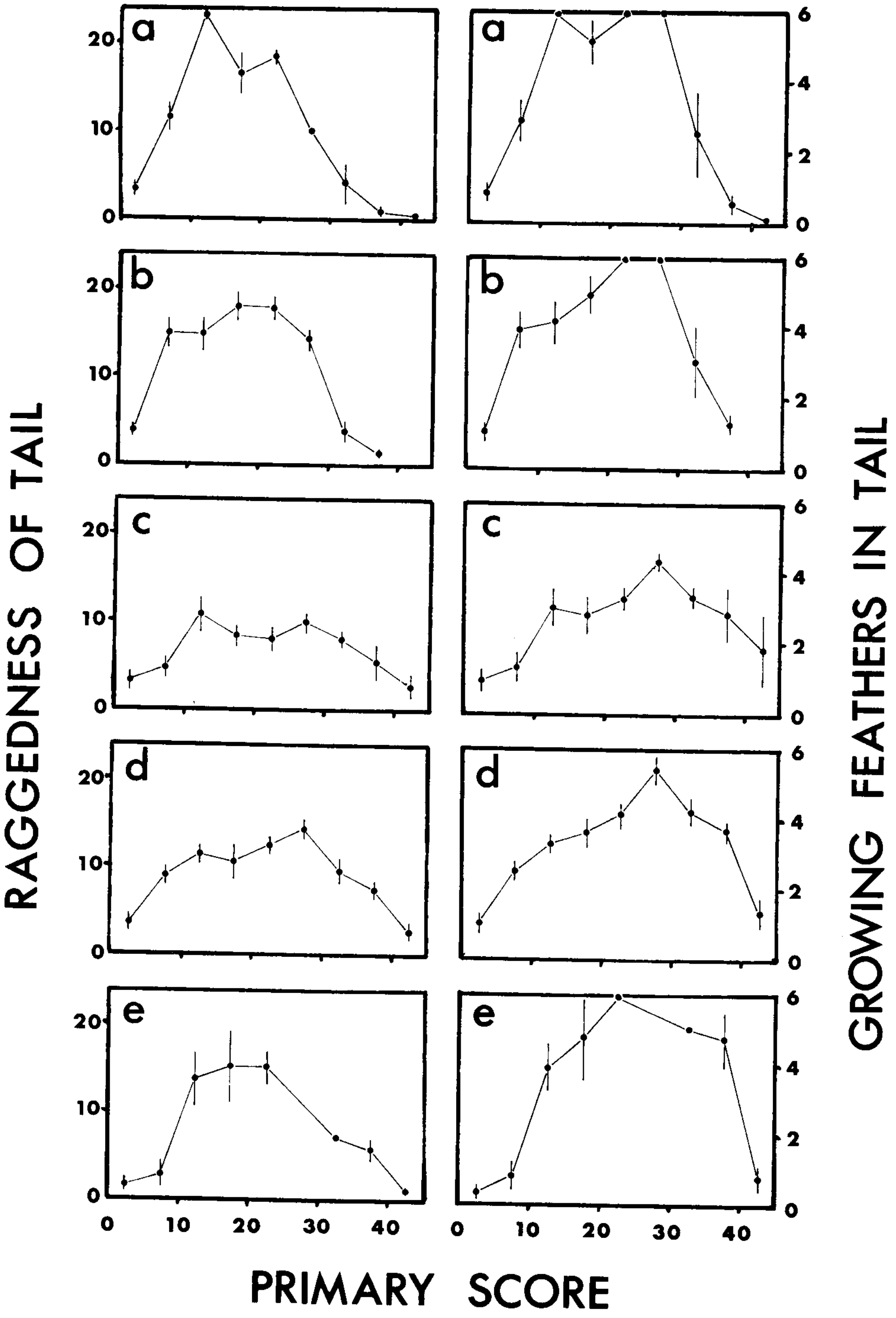




FIGS. 15—19. Tail scores in relation to primary scores in five passerines.

biotope (see HAUKIOJA & KALINAINEN 1972); they may, however, still be able to fly. Birds moulting slowly probably do not lose the ability to fly at all. What the critical limit in the duration of the moult is I do not know and, as shown in this paper, birds having a moult of about the same duration (eg. the Willow Warbler and the Yellow Wagtail) may well adapt to different situations.

NEWTON (1966) has mentioned that, in order to avoid avian predators, birds in active wing moult have adopted skulking behaviour. For species shedding wing and/or tail feathers faster than the Bullfinch, which NEWTON (1966) investigated, this is still more important. Eg. the Willow Warbler in heavy moult flies fluttering and is evidently unable to change direction quickly. It is my subjective opinion that it is easily caught by predators at this stage when flying. Another important point is that by decreasing their flying activity, skulking birds probably save energy for feather synthesis and thermogenesis, demands


RAGGEDNESS OF TAIL
GROWING FEATHERS IN TAIL
PRIMARY SCORE
a
b
c
d
e
0
10
20
30
40
0
2
4
6

for both of which increase considerably during the moult (Lustick 1970).

The phenomenon that, at the height of the moult, birds moulting quickly are caught less efficiently than at the beginning or at the end of the moult, means that in such species moult scores plotted against date probably are not normally distributed. This might cause difficulties in computing the duration of the moult and especially its confidence limits, but these difficulties may be overcome eg. by using mean dates for certain moult scores in computations (see Flegg & Cox 1969, Haukioja 1971b).

What inability or reluctance to fly affect the ecology of birds is practically unknown. It may however, have some importance for survival during heavy rain, etc., and requires more investigation than has been carried out hitherto. The same can be also said, however, for most other ecological aspects of moulting.

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Selostus: **Sulkasatokautisesta lentokyvyttömyydestä eräillä pohjoiseurooppalaisilla varpuslinnuilla.**

Siipi- ja pyrstösulkasadon vaikutusta lentokykyyn on selvitetty neljällä lappalaisella varpuslinnulla (sinirinta, pajulintu, keltavästäräkki ja västäräkki) sekä pensaskertulla eteläsuomalaisten aineistojen perusteella. Kaikilla näillä lajeilla on hyvin nopea sulkasato (35:n ja 50:n päivän välillä) ja eräitä rajusti sulkivia, lentokyvyttömiä tai lentohaluttomia yksilöitä on saatu verkkopyynnin yhteydessä. Koska linnun sulkasadon vaihe vaikuttaa selvästi pyydystetyksi tulemisen todennäköisyyteen (kuva 14) siten, että rajuimmassa sulkasadossa olevat linnut eivät juuri lennä verkkoihin, lentokyvyttömyys on todennäköisesti tavallisempaa kuin sulkasatokorttiaineistot osoittavat.

Lentämisen välttäminen riippuu, paitsi rajusta siipisulkasadosta, myös siitä, että erityisesti sinirinnalla ja vähemmässä määrin myös pajulinnulla, kaikki pyrstösulat vaihdetaan samanaikaisesti. Pyrstösulkasato on voimakkaimmillaan vaiheessa, jolloin siipien aukkoisuus ei ole kovin korkea. Tämä osoittaa pyrkimystä ylläpitää ainakin vähäinen lentokyky läpi sulkasadon. Avoimilla mailla elävät västäräkit pystyvät lyhyehköstä sulkasadostaan huolimatta ylläpitämään melko hyvän lentokyvyn sulkasadon aikana, mikä johtunee etupäässä pitkälle ajalle jakautuvasta pyrstösulkasadosta.

References

Baggott, G. K. 1970. The timing of the moults of the Pied Wagtail. Bird Study 17:45—46.

Balát, F. 1960. A study of moulting in the Dipper, Cinclus cinclus (L.). Zool. Listy 9:257—264.

Berger, W. 1967. Die Mauser des Sprossers (Luscinia luscinia L.). J. Orn. 108:320—327.

Berthold, P., E. Gwinner & H. Klein 1970. Vergleichende Untersuchung der Jugendentwicklung eines ausgeprägten Zugvogels, Sylvia borin, und eines weniger ausgeprägten Zugvogels, S. atricapilla. Die Vogelwarte 25:297—331.

Dolnik, V. R. & T. I. Bluymental 1967. Autumnal premigratory and migratory periods in the Chaffinch (Fringilla coelebs coelebs) and some other temperate zone passerine birds. Condor 69:435—468.

Dwight, K. L. 1900. The sequence of plumages and moults of the Passerine birds of New York. Ann. New York Acad. Sci. 13:73—360.

Evans, P. R. 1966. Autumn movements, moult and measurements of the Lesser Redpoll

Fig. 20. Raggedness of tail and numbers of growing tail feathers (in half a tail) in relation to primary scores in five passerines. a = *Luscinia suecica,* b = *Phylloscopus trochilus,* c = *Motacilla alba,* d = *M. flava,* and e = *Sylvia communis.*

Carduelis flammea cabaret. Ibis 108: 183—216.

FLEGG, J. J. M. & C. J. Cox 1969. The moult of British Blue Tit and Great Tit populations. Bird Study 16:147—157.

HAUKIOJA, E. 1971a. Summer schedule of some subarctic passerine birds with reference to postnuptial moult. Rep. Kevo Subarctic Res. Stat. 7:60—69.

— 1971b. Processing moult card data with reference to the Chaffinch Fringilla coelebs. Ornis Fenn. 48:25—32.

HAUKIOJA, E. & P. KALINAINEN 1968. Pajulinnun (Phylloscopus trochilus), pensaskertun (Sylvia communis) ja niittykirvisen (Anthus pratensis) postnuptiaalisesta sulkasadosta. Porin Lintutiet. Yhd. Vuosik. 2:75—78.

— 1972. Eräiden varpuslintujen sulkasatokauden ekologiaa. Porin Lintutiet. Yhd. Vuosik. 3:5—16.

LUSTICK, S. 1970. Energy requirements of molt in cowbirds. Auk 87:742—746.

NEWTON, I. 1966. The moult of the bullfinch Pyrrhula pyrrhula. Ibis 108:41—67.

SALOMONSEN, F. 1968. The moult migration. Wildfowl 19:5—24.

STRESEMANN, E. & V. STRESEMANN 1966. Die Mauser der Vögel. J. Orn. Sonderheft 107: 1—445.

SULLIVAN, J. O. 1965. "Flightlessness" in the Dipper. Condor 67:535—536.

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