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## Geographical Variations in the Clutch-size of the Pied Flycatcher

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In European Passerine birds the average clutch-size is usually thought to increase from SW to NE (e.g. GROTE, LACK 1954). In the following text this trend is referred to as the SW—NE trend. The change in clutch-size from south to north is much stronger if tropical regions are compared with Europe (MOREAU) than within the temperate regions of Europe. Nevertheless, according to LACK (e.g. 1954, p. 38) a species like the Robin (*Erithacus rubecula*) shows the SW—NE trend in an almost perfect way within temperate Europe. More recent studies have revealed data which to some extent contradict this simple picture. Thus in Finland the Robin has an average clutch-size of only 6.0 (v. Haartman, unpublished) rather than 6.3 as stated by LACK, and in Switzerland the average was found to be 5.9 rather than 5.8 (GLUTZ VON BLOTZHEIM). Small as such differences may seem, they mar an otherwise consistent picture. A re-analysis of the SW—NE gradient in Central and Northern Europe would be

very desirable, although it would probably substantiate earlier assumptions.

The causes of the SW—NE trend are still insufficiently known. Feeding parent birds certainly enjoy a longer working day in Northern than in Central Europe, but this is in many cases connected with much earlier nesting in Central Europe, which causes the young to hatch long before the longest day at midsummer (v. HAARTMAN 1954, p. 68). As to the change from west to east, LACK (1954) suggests that the continental climate is more favourable for insect life, and so allows the parents to feed more young, but so far this explanation has not been tested.

In an earlier paper (v. HAARTMAN 1951, p. 34—35) I arrived at the conclusion that the Pied Flycatcher (*Ficedula hypoleuca*) is an exception to the rule that the clutch-size increases towards the north and east. A similar statement can be found in LACK (1954, p. 37), whereas CURIO (1959, p. 216), although denying a S—N trend, believes

Table 1. Clutch-size of the Pied Flycatcher in different areas.  
*Taulukko 1. Kirjosiepon munamäärä eri alueilla.*

	N	E		1	2	3	4	5	6	7	8	9	10	n	M
Ammarnäs <sup>1</sup>	64°30'	19°	HANSON <i>et al.</i>	—	2	2	6	19	56	17	2	—	—	104	5.76
*Lappfjärd	62°15'	21°30'	Rosengren unpub.	—	—	3	12	61	165	97	16	1	—	355	6.11
*S. Finland	c. 61°	24°	v. HAARTMAN	—	—	2	15	49	190	159	33	11	1	460	6.38
*Lemsjöholm	60°30'	22°	v. Haartman unpub.	2	6	13	34	123	490	464	73	5	—	1210	6.30
Rogaland <sup>1</sup>	59°30'	7°	MEIDELL	—	—	1	2	12	54	15	1	—	—	85	5.95
Kumla	59°	15°	ENEMAR	—	—	2	1	8	22	26	5	—	—	64	6.31
*Tranås	58°	14°30'	JANSSON	—	—	1	3	11	39	30	3	1	—	88	6.22
Near Moscow	55°	41°	STEPHAN	3	3	5	10	28	45	57	9	—	—	160	5.91
Near Moscow	54°30'	38°	LICHATSHEV	—	—	—	3	7	45	72	20	2	—	149	6.70
Oldenburg	53°	8°	Löhrl. unpubl.	—	—	—	3	4	39	29	1	—	—	76	6.28
*Berlin	52°30'	13°	CURIO	—	—	2	7	21	60	72	6	1	—	169	6.29
*Brunswick	52°	10°30'	BERNDT <i>et al.</i>	—	1	8	28	192	686	529	94	6	—	1544	6.30
*Forest of Dean	51°45'	2°30' <sup>6</sup>	CAMPBELL	—	1	3	12	30	102	233	117	16	1	515	7.12
*Dresden	51°	14°	CREUTZ	—	—	6	17	67	233	238	26	3	—	590	6.31
*Baden (deciduous) <sup>3</sup>	48°	8°	Löhrl. unpubl.	—	—	1	15	46	209	179	34	2	—	486	6.36
* „ (pine) <sup>4</sup>	49°	8°30'	Löhrl. unpubl.	—	—	1	11	61	207	54	3	—	—	337	5.92
*Switzerland <sup>5</sup>	c. 47°	8°	GLUTZ	—	—	4	27	119	253	44	1	1	—	454	5.70

\* Long-term studies. <sup>1</sup> Mountain area. <sup>2</sup> Average of 546 clutches = 5.95 (long-term study).

<sup>3</sup> 4 different areas. <sup>4</sup> 2 different areas. <sup>5</sup> Below 700 m. <sup>6</sup> W. long.

in the existence of a W—E trend. In a recent paper, BERNDT *et al.* (1967, p. 104) have challenged my conclusion. They believe that the clutch-size of this species "very clearly" increases both from S to N and from W to E.

When I wrote my earlier paper (1951) few exact data were available about the clutch-size of the Pied Flycatcher; from Germany, for example, the only data available (BERNDT *et al.* 1939) were obviously biased. Since then, the amount of information has increased so considerably that renewed treatment of the problem seems appropriate. I will restrict myself to those

parts of Europe from which statistical data are available. Possible trends in the clutch-size of the Pied Flycatcher in more southerly parts of its breeding range are outside the scope of this study, but may well exist.

If the clutch-size of the species very clearly tends to increase from SW to NE, one would expect it to be strikingly smaller in BERNDT's own study area in Brunswick (ca. 52° N, 10° 30' E) than in my area at Lemsjöholm (60° 30' N, 22° E). The reasonably large amount of data from both areas fails to reveal any such clear difference:

Clutch-size	1	2	3	4	5	6	7	8	9	n	M
Brunswick	—	1	8	28	192	686	529	94	6	1544	6.297
Lemsjöholm	2	6	13	34	123	490	464	73	5	1210	6.298

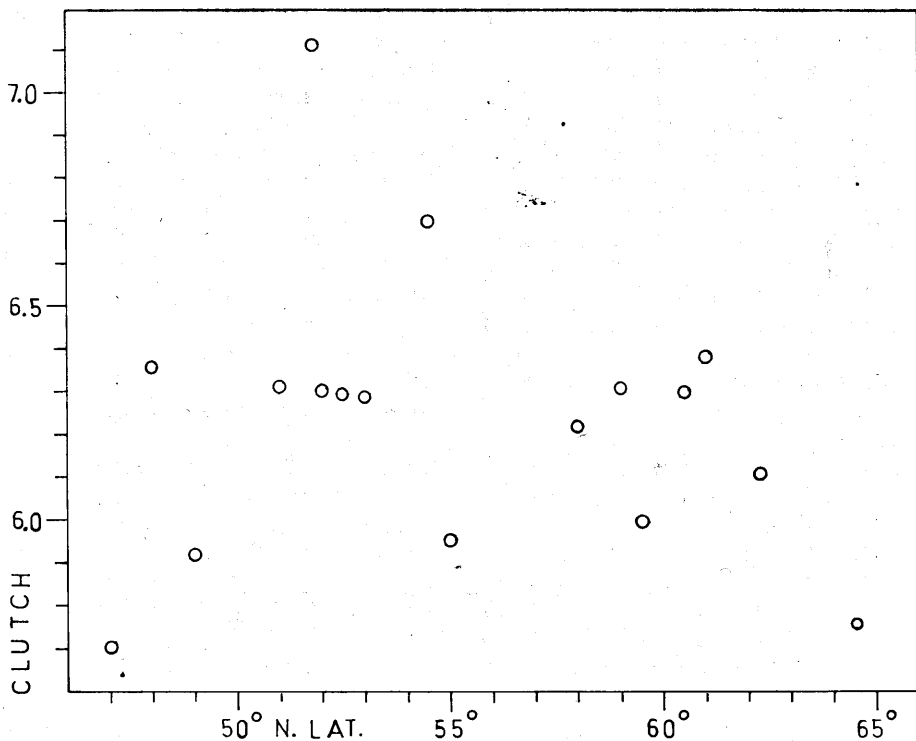


Fig. 1. Pied Flycatcher. Relation between average clutch-size and geographical latitude within Europe from Switzerland northwards. Every circle represents the average of a restricted study area, a group of areas within the same region, or a larger area. For details see Table 1.

Kuva 1. Kirjosiepon munamäärän suhde maantieteelliseen leveyteen Euroopassa Sveitsistä pohjoiseen. Kukin ympyrä edustaa keskiarvoa joko rajoitetulla tutkimus-alueella, ryhmässä saman vyöhykkeen alueita tai suuremmalla alueella. Käytetty aineisto taulukossa 1.

From the introductory remarks of BERNDT *et al.* it appears that they did not check their nest-boxes continuously. Since inevitably some eggs disappear during incubation, their data, in order to be fully comparable with mine, ought to be corrected upwards, although admittedly to a hardly appreciable extent. In view of this, there is clearly no need to speculate about an allegedly smaller clutch-size in the more southerly and westerly of these two study areas.

Nor does the SW—NE trend become

more evident if we consider all the 17 available studies on the clutch-size of the species in different parts of Western, Central, Eastern, and Northern Europe, which are summarized in Table 1. What this table gives is a bewildering picture, a mosaic of local differences rather than a clear general trend. Take, for instance, the average clutch-size in two areas near Moscow. LICHATSHEV gives an average of no less than 6.7, whereas STEPHAN, on the basis of an even larger body of data, finds only

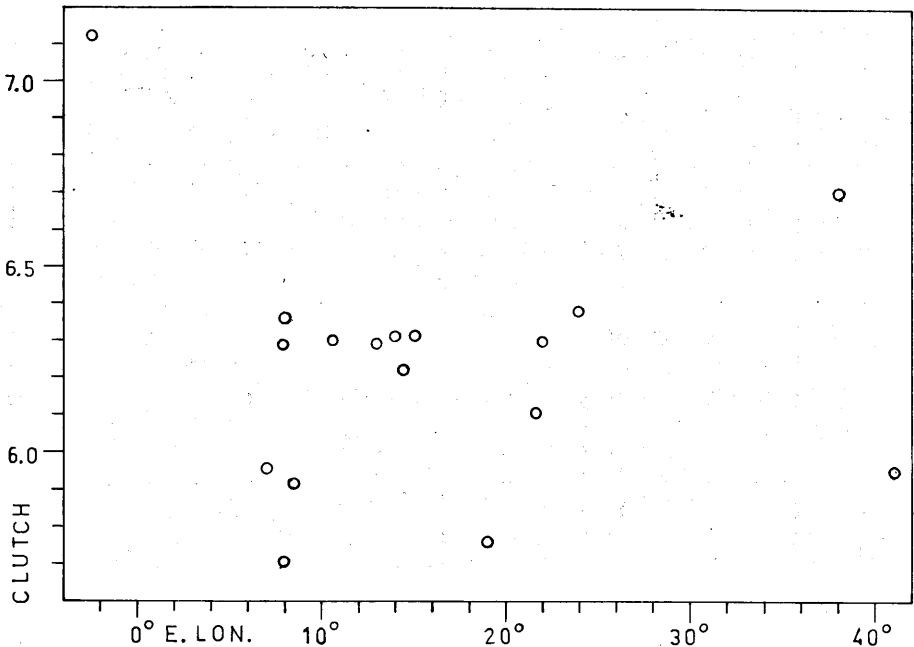


Fig. 2. Pied Flycatcher. Relation between average clutch-size and geographical longitude within Europe from Switzerland northwards. Explanations as in Fig. 1.

Kuva 2. Kirjosiepon munamäärän suhde maantieteelliseen pituuteen Euroopassa Sveitsistä pohjoiseen. Selitykset kuten kuvassa 1.

5.95. There goes the W—E trend of BERNDT *et al.*, which was founded on knowledge of only the first-mentioned of these studies.

In Figs. 1—2 the clutch-size is plotted against the latitude and longitude of the study areas. This test confirms the general impression gained from Table 1 that within the area in question the clutch-size does not show any clear geographical trend.

The causes of the local differences are still mainly obscure, but I wish to comment on a few points:

1. Mere chance plays a role even in fairly large series of data.

2. As there are considerable annual variations in the clutch-size of the Pied Flycatcher (cf. e.g. CAMPBELL's data in LACK 1966, and v. HAARTMAN 1967), a local average which is based on only

one or two years of study may well be quite misleading. For example, in the years 1963—65 the averages at Lemsjöholm were only 6.11, 6.28, and 5.73 respectively, i.e. constantly below the long-term average of 6.30. If my study had been restricted to these three years, I might easily have arrived at the conclusion that the clutch-size of the Pied Flycatcher in SW Finland is fairly small. For this reason, in Table 1 I have marked with an asterisk those studies that were prolonged over a greater number of years.

3. For some reason the number of extremely small and, one is tempted to say, unsuccessful clutches varies from study area to study area. It is far from certain whether this really has any implications with respect to the productivity of the females. On the other hand,

it would hardly be justified to exclude these small clutches when calculating the averages, at least before more is known of the circumstances under which they are produced. With extremely large clutches the same difficulty is not manifest; they are very few anyway, and some of them could safely be discarded as laid by two females (cf. v. HAARTMAN 1967).

4. The small clutch-sizes in the mountain areas of Scandinavia (Am-marnäs, Rogaland) stem from short-term studies, and should perhaps not be given too much weight. If, in the future, they are supported by more data, it will be safe to assume them to be the result of an "altitudinal trend". In Switzerland the average clutch-size in the lowlands (up to 700 m.) is larger than at higher levels (GLUTZ VON BLOTZHEIM). Whether the small average clutch-size in the Swiss lowland area can be explained by its, in fact, high absolute altitude (to 700 m.) or whether perhaps it marks a region where the clutch-size of the Pied Flycatcher begins to decrease, is still obscure.

5. Much has been written about the influence of habitat upon the clutch-size of the Pied Flycatcher (CREUTZ, LÖHRL 1965, MIHKELSON, BERNDT *et al.* 1967). Through the valuable studies of INOSEMTSEV we know that the feeding intensity remains unchanged in different forest types, but that the quality of the food (winged imagines versus larvae) differs, being greatly superior in oak and microphyll forests, and inferior in pine forests. (Cf. also the similar observations made by LÖHRL concerning early and late broods in the Collared Flycatcher.) Calculating the percentages of nestlings returning in later years to my study area at Lemsjöholm, I could not detect any differences in mortality between different forest types, but I do not consider this result generally valid

(unpublished). Now, of course, deciduous forests are scarce in Northern Europe. This is a "geographical trend", and if we wish to compare the clutch-size in Southern Finland and England, it is legitimate to compare an area with mainly needle-forest with one with deciduous forest. When we analyse the results, however, we have to remember that we not only compared different localities, but also different habitats. For this reason comparisons within the same habitat in different geographical areas would be desirable, but they are hardly possible; the same habitat just does not exist in Finland and England. It seems evident that the mosaic-like local variation of the clutch-size of the Pied Flycatcher is partly connected with the predominating habitats of the areas studied. Thus, in Baden, LÖHRL (1965, and *in litt.*) found a smaller clutch-size in pine areas than in areas of deciduous woodland.

Under these circumstances one cannot expect anything but a rather ill-defined picture of the geographical variation in the clutch-size of the Pied Flycatcher. Only an overwhelmingly strong general factor outweighing the influences of the various local ones could give the clutch-size a marked geographical trend. On the whole, it is perhaps more remarkable that such a factor exists in some Passerine birds than that it does not exist in the Pied Flycatcher.

A strange peak in the clutch-size of the Pied Flycatcher is exhibited by the population in the Forest of Dean, England (CAMPBELL). In Radnorshire, not far from the Forest of Dean, LLEWELYN found an average varying from season to season between only 5 and 6.3, but as he does not give any details, it is impossible to know how much importance to attach to these data.

Like the Pied Flycatchers of the Forest of Dean, the English Great Tits

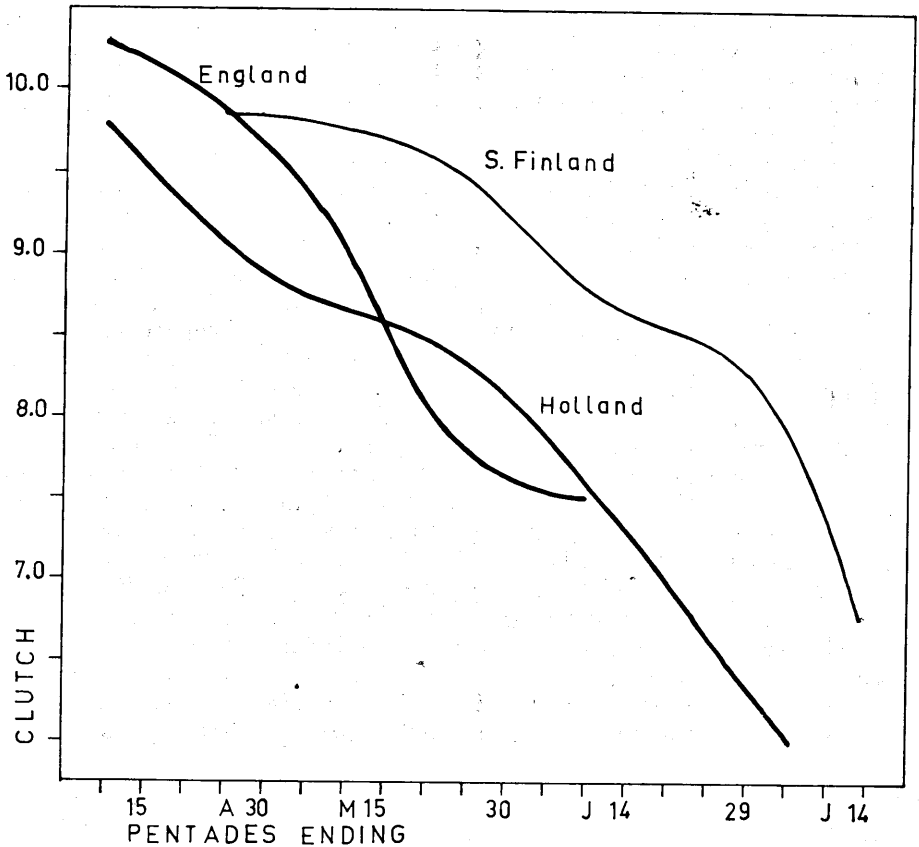


Fig. 3. Great Tit. Correlation between clutch-size and date of laying the first egg in the clutch. Smoothed curves. England according to LACK (1966), Holland according to KLUIJVER, and S. Finland according to v. HAARTMAN (1967).

Kuva 3. Talitiaisen munamäärän suhde pesueen ensimmäisen munan muninta-aikaan. Tasoitetut käyrät. Englanti LACKIN (1966) mukaan, Hollanti KLUIJVERIN mukaan ja Etelä-Suomi v. HAARTMANIN (1967) mukaan

(*Parus major*) have a larger clutch than those on the Continent (Fig. 3—4). The English Pied Flycatchers belong to the same subspecies as the Finnish ones, whereas the British Great Tits form a separate subspecies. The Rjasan Pied Flycatchers produce a smaller clutch than the Finnish ones, although Rjasan is further south than Finland, and both probably belong to the same subspecies. Against the belief of BERNDT *et al.*, the subspecies does not

seem to have much to do with the problem of average clutch-size.

In the Chaffinch (*Fringilla coelebs*), the Song-thrush (*Turdus philomelos*), and the Spotted Flycatcher (*Muscicapa striata*), the English populations have a markedly smaller clutch than their Finnish counterparts (Fig. 5—7). This is independent of whether these populations belong to the same or different subspecies.

CODY has recently developed a

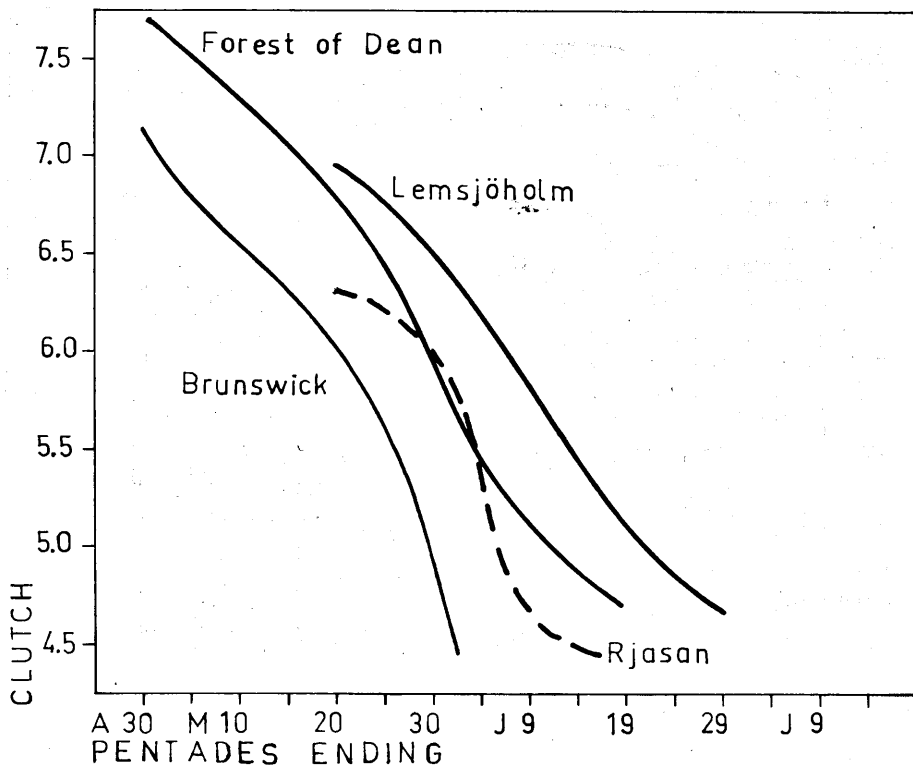


Fig. 4. Pied Flycatcher. Explanations as in Fig. 3. Forest of Dean according to CAMPBELL (cited by LACK 1966), Brunswick according to BERNDT *et al.* (1967), rearranged by me in order to change the time-scale from hatching dates to laying dates, Rjasan according to STEPHAN, and Lemsjöholm according to my own data. *Kuva 4. Kirjosiepon munamäärä. Selitykset kuten kuvassa 3. Forest of Dean CAMPBELLin (Ref. LACK 1966) mukaan, Brunswick BERNDTin et al. mukaan aika muutettuna vastaamaan kuoriutumisen sijasta munintaa, Rjasan STEPHANin mukaan ja Lemsjöholm (Lempisaari) oman aineistoni mukaan.*

theory of clutch-size based, among other things, upon the assumption that the clutch-size in hole-nesters, i.e. birds with safe nests, rises proportionally less from the tropics northwards than the clutch-size in birds with less safe nests. It may be of some interest to note that in two well studied hole-nesting species the English population has a higher clutch-size than the Finnish one, whereas in three well-studied species nesting in the open or semi-open the trend is reversed (the Spotted Fly-

catcher nests in niches, but its nests are, in fact, very unsafe). Whether this difference is more generally valid is not known, so far.

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BERNDT *et al.* (1967, p. 112) extend their polemics to include other aspects of clutch-size besides its geographical variation. They claim that, in contradiction to me (v. HAARTMAN 1951, p. 28), they have "for the first time strikingly shown" that the clutch-size of the Pied

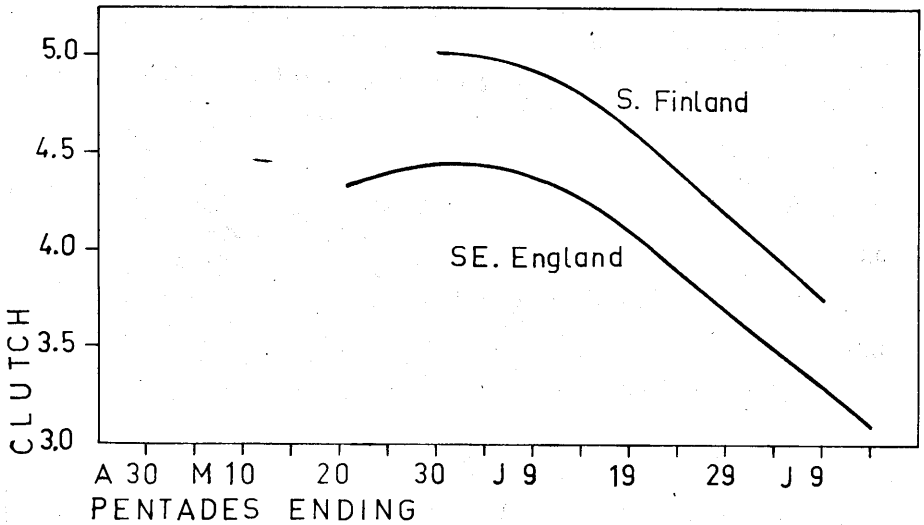


Fig. 5. Spotted Flycatcher. Explanations as in Fig. 3. England according to SUMMERS-SMITH, S. Finland according to v. HAARTMAN (1967).

Kuva 5. Harmaasiepon munamäärä. Selitykset kuten kuvassa 3. Englanti SUMMERS-SMITHin mukaan ja Etelä-Suomi v. HAARTMANin (1967) mukaan.

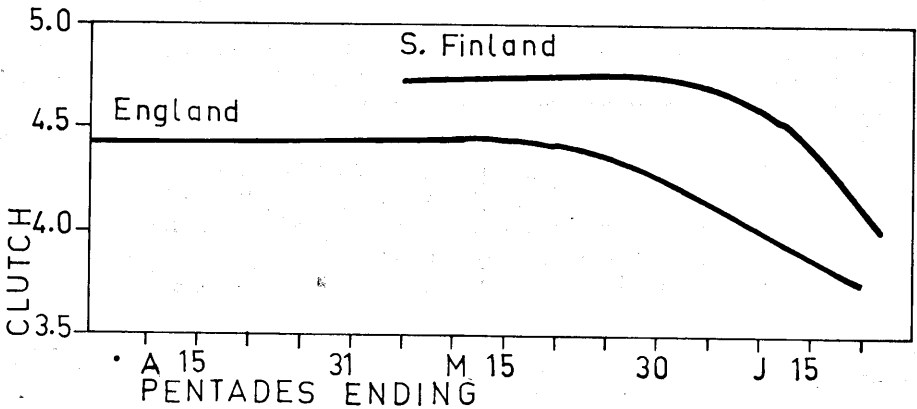


Fig. 6. Chaffinch. Explanations as in Fig. 3. England according to NEWTON, S. Finland according to v. HAARTMAN (1967).

Kuva 6. Peipon munamäärä. Selitykset kuten kuvassa 3. Englanti NEWTONin mukaan ja Etelä-Suomi v. HAARTMANin (1967) mukaan.



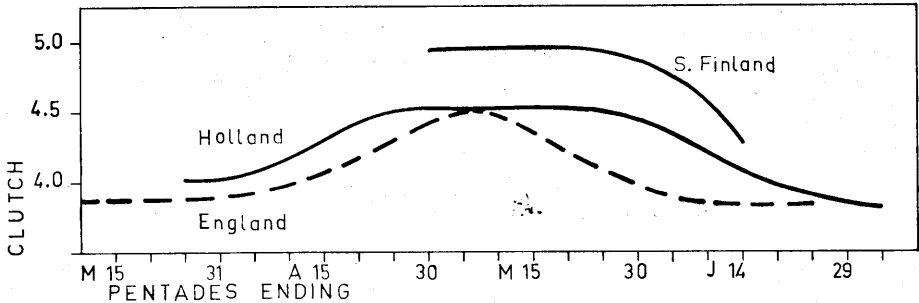


Fig. 7. Song-thrush. Explanations as in Fig. 3. England according to SNOW, Holland according to LACK (1949), S. Finland according to v. HAARTMAN (1967).

Kuva 7. Laulurastaan munamäärä. Selitykset kuten kuvassa 3. Englanti SNOW'n mukaan, Hollanti LACKin (1949) mukaan ja Etelä-Suomi v. HAARTMANIN (1967) mukaan.

Flycatcher is larger in years when nesting is early. Unfortunately, their quotation from my 1951 paper is incorrect. There I stated that the problem was not definitely solved. Further, I have since, but long before BERNDT *et al.*, shown that "in years with early egg-laying, the mean clutch-size is higher, and the percentage of large clutches (c/8—9) is much higher than in years with late egg-laying" (v. HAARTMAN 1956, p. 19—21). Figures pointing in the same direction had, besides, already been published the year before by CREUTZ (1955, p. 275).

### Summary

In Europe north of Switzerland and between England in the west and Moscow in the east, no increase in the clutch-size of the Pied Flycatcher could be shown to take place from SW to NE. Local variations occur in a rather irregular way. Mere chance, and variations due to habitat and, perhaps, altitude, may explain many of these local differences.

An English population of Pied Flycatchers and the English Great Tits have larger clutches than the corresponding Continental and Finnish populations. In the Chaffinch, Song-thrush, and Spotted Flycatcher, the clutch-size is smaller in England than in Finland.

### Selostus: Kirjosiepon munamäärän maantieteellisestä vaihtelusta.

Euroopassa Sveitsin pohjoispuolella, Englannin ja Moskovan välillä ei ole osoitettavissa kirjosiepon munamäärän kasvua siirryttäessä lounaasta koilliseen (kuvat 1 ja 2). Paikallisia vaihteluja esiintyy melko epäsäännöllisesti. Monet niistä selittynevät pelkän satuman, biotooppierojen ja ehkä myös korkeuserojen avulla (ks. taulukko 1).

Eräässä englantilaisessa kirjosieppo-populaatiossa ja englantilaisilla talitiaisilla munamäärä on suurempi kuin Euroopan mantereella ja Suomessa (kuvat 3 ja 4). Peipon, laulurastaan ja harmaasiepon munamäärä on Englannissa pienempi kuin Suomessa (kuvat 5, 6 ja 7).

### References

- BERNDT, R. & F. FRIELING 1939. Siedlungs- und brutbiologische Studien an Höhlenbrütern in einem nordwestsächsischem Park. Journ. f. Ornith. 87:593—638.
- BERNDT, R. & W. WINKEL 1967. Die Gelegegrösse des Trauerschnäppers (*Ficedula hypoleuca*) in Beziehung zu Ort, Zeit, Biotop und Alter. Vogelwelt 88:87—136.
- CAMPBELL, B. 1955. A Population of Pied Flycatchers (*Muscicapa hypoleuca*). Acta. XI Congr. Internat. Ornith. Basel 1954, p. 428—434.
- CODY, M. L. 1966. A general theory of clutch size. Evolution 20:174—184.

- CREUTZ, G. 1955. Der Trauerschnäpper (*Muscicapa hypoleuca* (Pallas)). Eine Populationsstudie. Journ. f. Ornith. 96: 241—326.
- CURIO, E. 1959. Beiträge zur Populationsökologie des Trauerschnäppers (*Ficedula h. hypoleuca* PALLAS). Zool. Jahrb. 87: 185—230.
- ENEMAR, A. 1948. Några erfarenheter från fem års holkfågelstudier. Vår Fågelvärld 7:105—117.
- GLUTZ VON BLOTZHEIM, U. 1962. Die Brutvögel der Schweiz. — Aarau.
- GROTE, H. 1939. Klimatisch bedingte Schwankungen der Gelegegröße innerhalb derselben Vogelrasse. Ornith. Monatsber. 47:52—54.
- V. HAARTMAN, L. 1951. Der Trauerfliegenschnäpper. II. Populationsprobleme. Acta Zool. Fenn. 67:1—60.
- 1954. Der Trauerfliegenschnäpper. III. Die Nahrungsbiologie. Ibid. 83:1—96.
- 1956. Finska Vetenskaps-Societetens fenologiska undersökningar. Några synpunkter och nya arbetsuppgifter. Soc. Scient. Fenn. Årsbok 23 B:1—23.
- 1967. Clutch-size in the Pied Flycatcher. Proc. XIV Internat. Ornith. Congr. Oxford 1966, p. 155—164.
- HANSON, S. Å., I. LENNERSTEDT, H. MYHRBERG & E. NYHOLM 1966. Holkstudier vid Ammarnäs 1965. Fauna o. Flora 1966:225—254.
- INOSEMTSEV, A. A. 1963. The Selectivity of Avian Feeding and some Reasons for its Variation. (In Russian.) Ornithologiya 6:424—450.
- JANSSON, K. E. 1960. Några siffror och rön från sju års studier av småfåglar häckande i holk. Vår Fågelvärld 19:127—136.
- KLUIJVER, H. N. 1951. The Population Ecology of the Great Tit, *Parus m. major* L. Ardea 39:1—135.
- LACK, D. 1949. Family size in certain thrushes (*Turdidae*). Evolution 3:57—66.
- 1954. The Natural Regulation of Animal Numbers. — Oxford.
- 1966. Population Studies of Birds. — Oxford.
- LLEWELYN, C. V. 1933—34. On some breeding habits of the Pied Flycatcher. Brit. Birds 27:251—255.
- LICHATSHEV, G. N. 1955. The Pied Flycatcher (*Muscicapa hypoleuca* Pall.) and its connection with the breeding area. (In Russian). Pap. Ringing Bureau Moscow 8:123—156.
- LÖHRL, H. 1957. Populationsökologische Untersuchungen beim Halsbandschnäpper (*Ficedula albicollis*) in Südwestdeutschland. Bonner Zool. Beitr. 8:130—177.
- 1965. Zwei regional und ökologisch getrennte Formen des Trauerschnäppers (*Ficedula hypoleuca*) in Südwestdeutschland. Ibid. 16:268—283.
- MEIDELL, O. 1961. Life history of the Pied Flycatcher and the Redstart in a Norwegian mountain area. (Rewritten by LARS V. HAARTMAN.) Nytt Magasin f. Zool. 19:5—58.
- MIHKELSON, S. 1964. Tehispesade kasutamise tulemusi Pärnu metsamajandis. Eesti Loodus 7:46—47.
- MOREAU, R. E. 1944. Clutch-size: a comparative study, with special reference to African birds. Ibis 86:286—347.
- NEWTON, I. 1964. The breeding biology of the Chaffinch. Bird Study 11:47—68.
- SNOW, D. W. 1955. The breeding of the Blackbird, Song Thrush, and Mistle Thrush in Great Britain. Ibid. 2:72—83, 169—178.
- STEPHAN, B. 1961. Beitrag zur Biologie einiger Höhlenbrüterarten aus dem Naturschutzgebiet an der Oka (Rjasan, UdSSR). Wissenschaftl. Zeitschr. d. Humboldt-Univ. zu Berlin, Mathem. — Naturw. Reihe 10:147—175.
- SUMMERS-SMITH, D. 1952. Breeding biology of the Spotted Flycatcher. Brit. Birds 45:153—167.

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