

Polymorphic variability in clutch size and laying date of the velvet scoter, *Melanitta fusca* (L.).

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Introduction.

The evolution and biological significance of reproductive rates in animals has been a subject of lively interest in modern population ecology. A theory formulated by LACK (1947, 1948, 1954 a, b) postulates that each species (or population) has a fixed hereditary reproductive rate. This rate is thought to be adapted to the environmental conditions so as to result in the highest possible number of surviving descendants. All animals are thus assumed to reproduce as rapidly as they can. According to this theory the most effective reproductive rate is, however, not the highest number of offspring the parents are physiologically able to produce, as their ability to raise the young to independence limits the optimal clutch or litter well below this physiological reproductive potential.

Although LACK's ideas that »birds reproduce as rapidly as they can» (1951, p. 424) and that »natural selection cannot favour the evolution of a smaller egg-number as such» (1954 a, p. 149) have been criticized by authors (e. g. WYNNE-EDWARDS 1951, KOSKIMIES 1955) emphasizing the selective value of *low* reproductive rates in preventing excessive population growth under certain conditions, it is generally agreed that reproductive rates are adaptive, and hereditarily fixed. WAGNER (1957), it is true, emphasized the obvious fact that living conditions at the time the eggs are laid also play an important role in governing the clutch size of birds, more so perhaps than has been acknowledged by LACK. Similar evidence concerning the European tetraonids, the partridge and the European hare has been presented by SIIVONEN (1956, 1957).

It is probable that non-adaptive phenotypic variations occur in clutch and litter sizes. Such variations obviously tend to be parallel in homogeneous local populations. This should not, however, invalidate the fact the average reproductive rates of such local populations are probably genetically fixed and adaptive to environmental conditions.

The notions of adaptiveness and hereditary control of reproduc-

tive rates have, however, been primarily based on circumstantial evidence and logical reasoning only, in spite of the basic importance of these assumptions in LACK's theories, for instance. There is little proof of the hereditary character of clutch or litter sizes in animals (eg. LACK 1951, 1954 a, b).

It has usually not been possible to observe wild animals for periods long enough to demonstrate the patterns of heredity in clutch or litter size. Recently, LÖHRL (1957), however, gives evidence to suggest that the tendency to lay clutches of a given size is probably hereditary in *Muscicapa albicollis*. The laying rate of poultry is known to be sensitive to selection and thus genetically determined (e. g. HUTT 1949).

There is another possible way to test the mutual roles of genetic and environmental influences in the determination of clutch size. If the reproductive rate of each individual tends to remain constant from year to year and if these rates consistently differ between individuals within an environmentally homogeneous population, it is probable that these consistent differences are due to hereditary factors.

Obviously, evidence of this kind too is scanty. Distinct differences in individual clutch sizes may be expected only of species which lay relatively large clutches. On the other hand, a large clutch and high reproductive rate are usually combined with high adult mortality and a short life span. Therefore, it has not generally been possible to observe such species for periods long enough to demonstrate the intra-individual constancy and interindividual variability in clutch sizes. In the few cases where this has been possible (e. g. *Apus apus*, WEITNAUER 1947, LACK & LACK 1951; *A. melba*, LACK & ARN 1947; *Sturnus vulgaris*, LACK 1948; *Parus major*, KLUIJVER 1951; *Muscicapa albicollis*, LÖHRL 1957) the variability in the size of the successive clutches of a given individual has been smaller than the overall variability in the local population in question. With *Melospiza melodia*, too, individual constancy in clutch size has been considered probable (NICE 1937).

KLUIJVER (op. c., p. 74), however, considered it improbable that the slight individual constancy established in the great tit is genetically determined. He inclined rather to the idea that these constant differences arise because each individual is permanently exposed to certain constant environmental influences which modify the clutch size.

No corresponding data concerning nidifugous birds are known to the present author.

It seems that the velvet scoter, *Melanitta fusca*, breeding in the archipelago areas of the Baltic Sea offers unusually good opportunities for a study of the control of the reproductive rates. This species has a relatively large clutch (7—10), which probably evolved from conditions in the original breeding environment of this species, i. e. the small lakes in the coniferous zone of northern Eurasia (e.g. KOSKIMIES 1957). Originally, a reproductive rate as high as this was obviously concomitant with a relatively high adult mortality. As the species has established itself secondarily in the archipelagos of the gulfs of the Baltic, many of the mortality factors effective in the original breeding environment have probably lost their significance entirely or to a large extent. Hence adult mortality (at least in females) in the archipelago is extremely low. In a population of about 30 pairs in a bird sanctuary off the Finnish south coast the annual mortality of breeding females during a period of 9 years averaged 5 % (KOSKIMIES op. c.). This obviously means a considerable increase in the average age as compared with the original conditions. As scoter females, in addition, are extremely site-tenacious and easy to capture at the nest, the conditions for a long-term study of the nesting behaviour of individually marked females are unusually good.

As a result of systematic marking since 1948 the clutch sizes and laying dates of individually marked females are now known for consecutive layings for a period of 10 years. The purpose of this study is to test the idea of constant interindividual differences in clutch size (and laying date) in this species on the basis of the data obtained.

The study area, the bird sanctuary of Aspskär, has been described in earlier papers (e.g. KOSKIMIES 1949, 1957, and especially KOSKIMIES & ROUTAMO 1953). It consists of four small islets (9.2, 3.8, 2.8 and 2.5 ha.) which are separated by channels no wider than 10—15 metres. The full clutch of 25—30 breeding velvet scoter females has been controlled in this area every year since 1948. Where possible, the date of laying of the first egg of the clutch has also been recorded. During the years 1948—1956 a total of 37 females was captured and marked. All but two of them were recaptured in 1—6 later years, and information on their breeding recorded. The

total material from the period 1948—1957 consists of records of 128 clutches and of 104 laying dates.

Conventional methods have been used in the statistical treatment of the data (e.g. SNEDECOR 1946). Value pairs of the structure 9.6 ± 0.3 indicate the arithmetic mean \pm the standard error of the mean. P indicates the probability that the established difference could be caused by mere chance.

Clutch size.

The clutch size of 17 females is known for at least four years (Table 1). The average clutch size of the individual females varies from 7.5 ± 0.3 to 9.6 ± 0.2 . The analysis of variance of all these data establishes highly significant differences between the clutch sizes of individual females ($F = 5.30$; $P < 0.001$). This indirectly permits the conclusion that the clutch size of each female has been significantly constant from year to year.

This result does not as such prove that the individual differences in the clutch size were genetically determined. They may also be thought to be due to differences of age of the laying individuals. The effect of age on the clutch size has been established in *Parus major*

Table 1. The clutch sizes of marked velvet scoter females in 1948—1957.

$M \pm \delta$ = mean \pm standard error of the mean.

♀	1948	49	50	51	52	53	54	55	56	57	$M \pm \delta$
4990	10	10	9	9	10	—	9	10	—	—	9.6 ± 0.2
8804	—	—	—	—	10	10	—	8	10	—	9.5 ± 0.5
4984	—	10	—	9	—	9	9	9	—	9	9.2 ± 0.2
8802	—	—	—	—	8	10	—	9	10	9	9.2 ± 0.4
4954	9	—	—	8	—	9	9	9	9	—	8.8 ± 0.2
5741	—	—	—	—	—	9	—	9	8	9	8.8 ± 0.2
4987	—	8	—	9	—	9	9	8	8	—	8.5 ± 0.2
5746	—	—	—	—	8	8	9	—	9	—	8.5 ± 0.3
10062	—	—	—	—	—	9	8	—	8	9	8.5 ± 0.3
8815	—	—	—	—	7	—	9	—	9	9	8.5 ± 0.5
8803	—	—	—	—	7	9	7	9	8	9	8.2 ± 0.4
5747	—	—	—	8	8	8	9	8	8	8	8.1 ± 0.1
10052	—	—	—	—	—	8	8	8	8	—	8.0 ± 0.0
10067	—	—	—	—	—	8	8	8	8	8	8.0 ± 0.0
8811	—	—	—	—	7	8	8	—	8	—	7.8 ± 0.2
5748	—	—	—	—	8	8	8	7	—	8	7.8 ± 0.2
8857	—	—	—	—	—	—	7	8	8	7	7.5 ± 0.3

(KLUIJVER 1951), *Phoenicurus phoenicurus* (RUITER 1941), *Apus apus* (WEITNAUER 1947), *A. melba* (ARN 1945) and *Megadyptes antiopodes* (RICHDALE 1949), for instance. Another possible explanation would be that suggested by KLUIJVER (1951) for *Parus major* viz. that each breeding female is continually exposed to certain particular environmental (e.g. habitat) conditions and these affect the clutch size.

Our data lend no support to the idea that the individual differences in clutch size were caused by differences in the ages of the birds concerned. No consistent trend in the year-to-year variation of the clutch sizes can be established within a period of 8—9 years (Table 1). At the most, there is perhaps a slight indication to that the first clutch may be smaller than the subsequent ones, but this does not affect our conclusions.

To test the possible influence of constantly differing environmental conditions, a comparison was made between the clutch size of females nesting regularly on different islets (total 20 individuals). The mean of the two highest clutch sizes of each female was used for the comparison and only those individuals were considered whose clutch size was known for at least three years. The largest clutches were used to prevent the biasing effect of repeat clutches (which, as a rule, are smaller than the first ones; e.g. KOSKIMIES & ROUTAMO 1953) or otherwise incomplete sets of eggs. The smallest average thus computed was found for birds nesting on the islet Enskär (cf. also KOSKIMIES & ROUTAMO *op. c.*, p. 50). However, the analysis of variance of the data does not indicate any significant differences between this and the other islets, nor between the latter (F between all islets = 0.77). The close proximity of the islets makes such differences seem *a priori* rather implausible.

It thus seems evident that the interindividual differences in clutch size are not caused by differences of age nor by constantly differing environmental influences.

Our data suggest that each individual female has its own characteristic basic clutch size and that the considerable interindividual differences in this respect are due to hereditary factors.

There is nothing to indicate that the intraindividual variations in clutch size were adaptive. It seems more plausible that they are mere phenotypic modifications due to the effect of weather and other chance factors of the environment.

Table 3. The dates of laying of the first egg in marked velvet scoter females in 1949—1957. 26—31 = May dates; 1—16 = June dates.

♀	1949	50	51	52	53	54	55	56	57	M ± δ
5741	—	—	—	—	26	—	27	26	—	26.3 ± 0.3
4984	28	—	30	—	27	30	28	—	30	28.8 ± 0.5
8804	—	—	—	27	28	—	—	30	—	29.0 ± 1.5
8860	—	—	—	—	—	—	29	30	30	29.7 ± 0.3
8813	—	—	—	28	29	—	—	3	—	30.3 ± 1.9
5746	—	—	—	1	1	1	—	—	—	1.0 ± 0.0
8811	—	—	—	6	31	30	—	31	—	1.3 ± 1.6
8803	—	—	—	2	2	1	4	29	2	1.5 ± 0.8
5747	—	—	—	5	31	2	6	4	28	2.3 ± 1.4
4954	—	—	—	—	—	2	1	5	—	2.7 ± 1.2
4990	—	3	3	31	—	5	4	—	—	3.0 ± 0.8
4987	—	—	5	—	4	1	6	5	—	4.2 ± 0.8
5744	—	—	—	4	—	3	—	—	6	4.3 ± 0.9
5748	—	—	—	1	7	3	7	—	4	4.4 ± 1.2
8802	—	—	—	4	—	—	7	4	—	5.0 ± 1.0
10062	—	—	—	—	5	13	6	4	—	7.0 ± 2.0
10067	—	—	—	—	6	9	9	5	—	7.2 ± 1.1
8857	—	—	—	—	—	13	—	6	16	11.7 ± 3.0

ing the largest average clutches tend to start laying earlier on the average than those producing small clutches.

It is probable that these two tendencies are genetically linked. It may well be thought that only the tendency to lay on a given date is governed genetically whereas the size of the clutch is dependent phenotypically on the laying date. If this were the case, it would imply a correlation also between the laying dates and clutch size *within* each female. Our data do not support this idea. Out of 17 females in which the difference between the laying dates of the earliest and the latest clutch was at least 3 days, in 8 cases the earliest clutch was equal to, in 7 cases larger than and in 2 cases smaller than the last clutch. The difference of the means (0.27 ± 0.96 ; early > late) is statistically not significant ($t < 1.0$).

Discussion.

The results of the present study suggest that in the velvet scoter both the clutch size and the laying date tend to be individually constant and, although there is no direct proof of it, the interindividual differences in these characteristics are due to hereditary factors.

As the individual differences occur within one and the same breeding colony, reasonably homogeneous in its environmental influences, they must be considered as expressions of balanced polymorphism (LACK 1954, HUXLEY 1955). Clutch size in particular is a characteristic in which it is biologically desirable for the population to possess more than just one exactly fixed genetic type. The clutch size producing the most descendants is certainly variable in different periods and different areas depending on more or less random and »unexpected» variations in the environmental conditions (e.g. LACK 1948, HUXLEY 1951). Similarly, it is obviously favourable for a population tending to disperse to new environments or living under regularly changing environmental conditions to be able to »offer» natural selection several genetic alternatives of clutch size.

It seems not unnatural that variation in laying dates should be adaptively linked with polymorphism in clutch size. In a species with quite a long laying interval (about 40 hours in the velvet scoter; cf. KOSKIMIES & ROUTAMO 1953) the hatching dates of clutches of different sizes would be rather variable unless the laying of the larger clutches were started earlier. It should be borne in mind that natural selection is thought to operate on breeding seasons by adjusting the *rearing* period to suit the most favourable season of the year (e.g. LACK 1950). This should obviously coincide for clutches of all sizes, whence it is to be expected that within a population natural selection tends towards uniform hatching times regardless of clutch size.

In fact, the rate of change in the laying date with changing clutch size seems to correspond to the time that should be »taken into account» to adjust the starting date of laying so as to result in roughly simultaneous hatching of clutches of different sizes. The change in laying date occasioned by a change of one egg in the clutch size is fairly accurately equal to the average laying interval in regular egg-laying (Fig. 1). Thus, for instance, a female laying average clutches one egg larger than »normal» would start laying about one egg-interval (40 hours) earlier than a female laying »normal-size» clutches. In this way the clutch in both cases is complete at about the same date and (as incubation starts from the last egg only) hatching tends to occur at the same date regardless of the size of the clutch (cf. also KOSKIMIES & ROUTAMO *op. c.*, p. 89).

It is probable that while this kind of variability in laying dates is

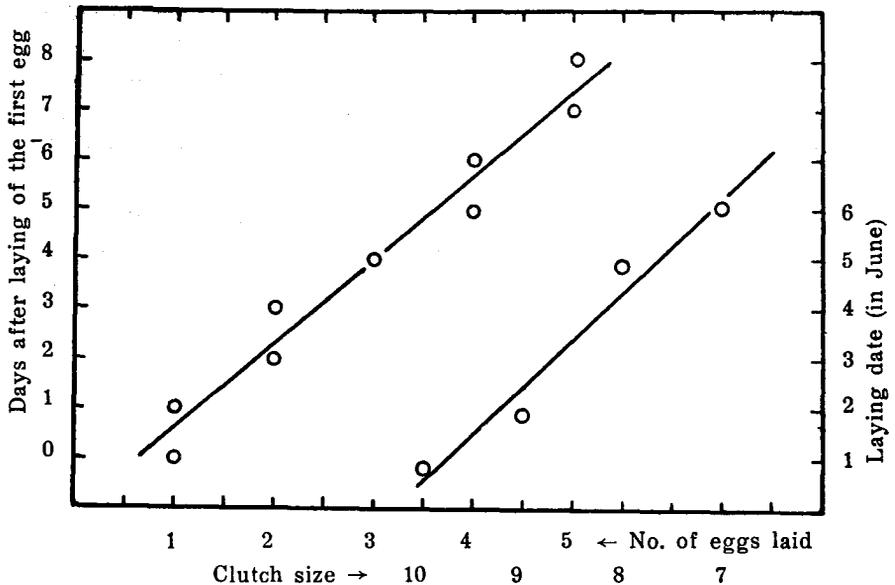


Fig. 1. Average course of egg-laying (from KOSKIMIES & ROUTAMO 1953, p. 54) and relation of date of laying of the first egg to clutch size in the velvet scoter. The lines computed by the method of least squares.

adaptively correlated with differences in clutch size, other kinds of interindividual variability (independent of clutch sizes) in the laying dates offer the material for the adaptive evolution of breeding (hatching) season (cf. e.g. LACK 1950).

Summary.

37 female velvet scoters were captured and marked in 1948—1956 in a bird sancturay in the outermost archipelago off the Finnish south coast. 35 of them were recaptured in 1 to 6 later years, and information about their clutch size and date of laying recorded. The total material from the years 1948—1957 consists of records of 128 clutches and of 104 laying dates.

There are highly significant differences between the clutch size of individual females (Table 1), the average individual clutches varying from 7.5 ± 0.3 to 9.6 ± 0.2 . These differences are probably not caused by differences of age of the laying females nor by constantly

differing environmental influences. It seems probable that they are due to hereditary factors.

There is a correlation between clutch size and laying date the earliest clutches being the largest (Table 2). The average laying dates tend to be individually constant (Table 3). The individuals with the earliest average laying dates lay the largest average clutches.

It is suggested that the individual clutch size and the individual laying date are genetically linked. It is shown that the correlation of clutch size and laying date results in roughly simultaneous hatching of all clutches regardless of their size. This should also theoretically be expected, if natural selection is thought to operate on breeding seasons by adjusting the rearing period to suit the most favourable season of the year, as has been suggested.

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nricurus ph. phoenicurus (L.). *Ardea* 30. — SIIVONEN, L., 1956, The correlation between the fluctuations of partridge and European hare populations and the climatic conditions of winters in South-West Finland during the last thirty years. *Pap. Game Research* 17: 1—30. — 1957, The problem of the short-term fluctuations in numbers of tetraonids in Europe. *Ibid.* 19: 1—14. — SNEDECOR, G. W., 1946, *Statistical methods*. Ames. — WAGNER, H. O., 1957, Variation in clutch size at different latitudes. *Auk* 74: 243—250. — WEITNAUER, E., 1947, Am Neste des Mauerseglers, *Apus apus apus* (L.). *Orn. Beob.* 44: 133—182. — WYNNE-EDWARDS, V. C., 1955, Low reproductive rates in birds, especially sea-birds. *Acta XI Congr. Int. Ornith. (Basel) 1954*, pp. 540—547.

Selostus: Pesyekoon ja munimisajan yksilöiden välisestä vaihtelusta pilkkasiivellä. Vv. 1948—1956 on Aspskärin lintusuojelualueella Suomenlahden uloimmassa saaristossa pyydystetty ja merkitty 37 pesivää pilkkasiipinaarasta. Niistä 35 on tavattu 1—6 myöhempänä vuonna pesivinä samalta saariryhmältä. Mainittuja yksilöitä koskeva kokonaisaineisto vuosilta 1948—1957 käsittää tiedot 128 pesyeen koosta sekä 104 pesyeen munimisajasta.

Kullakin naaraalla on taipumus munia vuosittain saman kokoisia pesyeitä (taul. 1). Käytettävissä olevan aineiston mukaan yksilöiden keskimääraisten pesyekokojen erilaisuus ei voine johtua niiden ikäeroista eikä pysyvästi erilaisista ulkoisista vaikutuksista. On todennäköistä, että kullekin yksilölle ominainen pesyekoko on perinnöllisesti määräytynyt.

Pesyekoon ja munimisajan kesken vallitsee selvä korrelaatiosuhte siten, että aikaisemmat pesyeet ovat keskimäärin suurimpia (taul. 2). Myös eri yksilöiden munimisajat pysyttelevät vuodesta toiseen kutakuinkin vakioina (taul. 3). Yksilöt, jotka aloittavat munimisen keskimäärin aikaisemmin, munivat keskimäärin suurimpia pesyeitä.

On todennäköistä, että yksilöllinen pesyekoko ja yksilöllinen munimisaika ovat perinnöllisesti toisiinsa kytkeytyneet. Pesyekoon ja munimisajan havaittu korrelaatiosuhte johtaa kaikkien pesyeiden suunnilleen samanaikaiseen kuoriutumiseen pesyeen koosta riippumatta. Tämä on teoreettisestikin odotettavissa, jos hyväksytään ajatus, että pesimisajat ovat luonnon valinnan tuloksena kehittyneet sellaisiksi, että poikasten hoidon kausi sattuu ulkoisilta olosuhteiltaan edullisimmaksi vuodenajaksi.