Timing of waterfowl breeding on the Krunnit Islands, Gulf of Bothnia

Risto A. Väisänen

Väisänen, R. A. [Dept. of Genetics, Univ. of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki 10, Finland] 1974. — *Timing of waterfowl breeding on the Krunnit Islands, Gulf of Bothnia.* Ornis Fenn. 51:61—84.

Timing of egg-laying in 12 waterfowl species was studied on the Krunnit Islands and in the surrounding archipelago in the Gulf of Bothnia in the northern Baltic. The date of the first egg is known from the following numbers of clutches from three periods: 1883—91 N = 79, 1904—13 N = 89 and 1970—73 N = 197. The water test for determining the age of laid eggs was employed in the latest period.

Waterfowl species lay their first egg in the following order (means for populations): *Anser anser* May 11, *Anas platyrhynchos* May 15, *A. acuta* May 22, *A. crecca* May 24, *A. clypeata* May 28, *Mergus merganser* June 1, *Anas penelope* June 1, *Somateria mollissima* June 2 (now extinct), *Aythya fuligula* June 3, *Mergus serrator* June 3, *Melanitta fusca* June 7 and *Aythya marila* June 8. Within species dispersals are given.

In waterfowl one may distinguish between (1) early breeders, which breed considerably (22 days on average) earlier on the southern coast of Finland (May 3) than on Krunnit (May 25); a delay of 4 days/100 km, and (2) late breeders, which start laying rather simultaneously, June 5 on average, along the Finnish coasts. In the preceding list the first eight species are early breeders — most of them dabblers — whereas the last four species — all divers — are late breeders.

Anas acuta, Aythya fuligula and *Mergus serrator* now nest noticeably earlier (differences as large as 15—20 days), and *Mergus merganser* later, than 65 years ago. This is probably because the waterfowl of the Krunnit islands have changed their habitat from central, forested islands to the larid colonies of outer open islets in the course of the last 20 years. This is due to increased protection following the establishment of a bird sanctuary.

The availability of food, which is connected with the melting of ice, and sociability towards larids are important proximate factors influencing the onset of egg-laying among waterfowl, whereas light and temperature are less important.

Introduction

Geographical data on the timing of breeding provides important basic information for population studies. Although the ecology of waterfowl is otherwise rather well-known, breeding time data are scanty. Handbooks (e.g. Bauer & Glutz 1968—69) give dates for earliest known clutches, whereas data concerning the main part of a population in a defined geographical area are lacking or inaccurate.

The aim of this paper is to give basic information on the timing of laying in 12 species of Anseriformes in a northern archipelago, the Krunnit Islands (65° 25'N, 25°E), off the NE coast of the Gulf of Bothnia in Finland, and to attempt to find proximate factors determining it.

In Belopolskii's studies (1957) on the ecology of sea colony birds in the Barents Sea, about 600 km NE from my study area, the effects of several factors were analysed at the beginning of the egg-laying period. Availability of food for the female was the main factor determining the time of laying. The melting of ice and snow (related to the food factor) were also of importance, whereas the effect of air temperature (contra several authors, e.g. DANE 1966) and light seemed negligible. His data included only one waterfowl species, *Somateria mollissima*. Significance of the food factor for waterfowl was stressed by LACK (1967), who suggested that the average clutch of each species has evolved in relation to the average availability of food for the female around the time of laying, modified by the relative size of the egg.

Recently PERRINS (1970) has discussed the hypothesis that the date of laying in some species of birds is determined by the date at which the female is able to find enough food to form eggs. He also reviewed 'maternal' factors affecting the date of laying, e.g. the age of the female and the fact that in several species individual females tend to lay at similar dates in successive breeding seasons. (For these and ultimate factors related to the timing of waterfowl breeding see e.g. BEZZEL & KROSIGK 1971, MICHELSONS et al. 1972, KRAPU 1974).

Study area and methods

The Krunnit islands cover an area of 10 × 10 km in the commune of Ii, on the Finnish coast in the northern part of the Gulf of Bothnia. The distance from the mainland is 11—21 km. The archipelago consists of three large wooded islands, Maakrunni, Ristikari and Ulkokrunni, a smaller wooded island, Kraasukka, and about 18 treeless islets with an elevation of 0.5—2.5 m (due to the strong land upheaval, 75 cm per century, and flat topography, the number of islets is changing). For a description of the archipelago and the history of ornithological research there see VÄISÄNEN (1973).

Habitats of the waterfowl species are similar to those at Valassaaret 275 km SW of Krunnit, where HILDÉN (1964) studied the ecology of duck populations. An exception is *Anas penelope,* which according to HILDÉN (1964, p. 174) is a species favouring wooded central islands, but which at Krunnit also breeds all over the larid colonies on the open, outer islets. *Anser anser* does not breed on Valassaaret. On Krunnit some pairs probably breed in the deciduous forests of the central islands, but nowadays nests have only been found on the outer islets. In the following, estimates of the numbers of breeding waterfowl pairs in 1963 and 1972 are presented (data for 1963 in GRENQUIST 1965, census by myself; in 1972 census by myself and Eero Helle). A + sign indicates that the actual number of pairs exceeded that given in the list. This is relevant for species, which breed in the forests of the central islands.

	1963	1972
Anas platyrhynchos	22	3+
A. crecca	16	5+
A. penelope	21	12+
A. acuta	9	5+
A. clypeata	2	4
Aythya marila	7	6
A. fuligula	39	40
Melanitta fusca	7	9
Mergus serrator	41	21
M. merganser	16	13
Anser anser	5+	5+

HILDÉN (1964) and BEZZEL & KROSIGK (1971) have in their comparative studies of several anatids approximated the date of laying of the first egg of a clutch on the basis of the size of the young, roughly estimated using binoculars. In several monographs the same method has also been used (literature in BEZZEL & KROSIGK 1971). This method, however, gives rise to several errors. The incubation time decreases progressively towards the end of the breeding season (the change is three days in *Anas platyrhynchos* between March and June; HESS 1972), brood size is not identical with the original number of eggs, and the size of the young is a relatively inaccurate age indicator.

The onset of incubation of the clutch may be determined on the basis of the water test of eggs, but this method has been used very seldom during the 20 years it has been known (PAGE & CASSEL 1971, WELLER 1971). This seems to be due to practical difficulties: a bucket of water must be taken along, because there is in general not enough time to carry eggs from each clutch to the nearest shore for floating. In addition, practical advice on how to use the water test is lacking. (For an additional age determination method — candling of eggs — see WELLER 1956).

Materials for this study were collected in the following way: Larid nests were sought on open islets by criss-crossing their area once yearly. In 1970—73 also all waterfowl nests found were studied, the number of eggs was noted and three eggs per clutch were subjected to the water-test, if the eggs were not already cracking. Almost all materials originated from open islets; only three clutches came from central islands (one clutch each of

Anas crecca, A. penelope and *Mergus serrator*).

If the number of eggs in a clutch exceeded the species-specific normal range given in v. HAARTMAN et al. (1963—72), the clutch was taken to be from two females and was indicated as two clutches in the data. In the data of 197 clutches there are 22 such cases (= 11 double clutches). The number of eggs was divided by two when estimating the day on which the first egg was laid. Three *Anas platyrhynchos* clutches found in the years 1963—65 were included in the data, because of the shortage of materials for this species, so that the whole Krunnit materials constituted 200 clutches.

The water test was performed in the following way. Three eggs from a clutch were immersed in a plastic bucket filled with water in an ordinary colander, the handle of which had been bent upwards so that the colander could sink to the bottom of the bucket and the eggs could be taken up without wetting one's hands. If the egg sank to the bottom, its angle to the bottom was judged approximately with an accuracy of 15° (scale was 15°, 30°. . . , 90°). If the egg floated, the diameter of the part protruding above the water was measured using a sliding caliper with a clock scale with an accuracy of 0.1 cm. On the basis of these measurements I have calculated how many days, on average, the eggs of the clutch had been incubated. In the calculations the method of WESTERSKOV (1950) and formulae developed for gull and tern species were used (to be published). Species-specific values for the duration of incubation and the laying interval between eggs of the clutch were taken from v. HAARTMAN et al. (1963—72). Finally, the date of laying of the first egg of the clutch was calculated retroactively from the date of investigation, taking it as a serial number from May 1.

The most inaccurate part of this age determination is from the time the egg rises to the surface of water until the first signs of hatching appear as cracks in the egg. A small part only of my clutch data represent this phase: 32 % of clutches were fresh (incubation not started or proceeded 1—2 days), 49 % with eggs forming an angle of 30°—90° to the bottom, 13 % with eggs rising to the surface and 7 % were hatching.

The data from Krunnit have been compared with two older materials from nearby areas. I have estimated the laying dates of 88 waterfowl clutches from MERIKALLIO (1930), collected mainly in 1904—13, and 79 clutches from SANDMAN (1892), collected in 1883—91. It is important to evaluate the methods of these studies compared with mine (see also discussion).

At the beginning of this century the late Professor Einari Merikallio studied the breeding bird fauna at Krunnit and in the nearby archipelago of Haukipudas and Oulu (MERIKALLIO 1930). He performed the water test on some of the waterfowl clutches he found (partly for oological purposes) applying a cruder scale of seven phases: (1) the egg lying on its side on the bottom, (2) the egg standing straight up in water, the pointed end touching the bottom, (3) specific gravities of the egg and water equal, (4) a small part of the egg protruding above water, (5) a fairly large part of the egg protruding above water, (6) a large part of the egg protruding above water and (7) the chick hatching. I have included 88 clutches (⅓ from Krunnit) from MERIKALLIO's data (1930) in mine, applying my water test formulae — less exactly than in my own data, of course — on these. This may be done, since a large proportion of his clutches were fresh (66 %) or hatching (6 %). Only 27 % floated on the surface of water. These clutches were measured in 1884—1929 (a few of the earliest from oological collections), mainly, however, within a ten year period 1904—13 (85 %), most of them in 1907—10 (65 % of 88 clutches).

J. Albin Sandman was an eager oologist, who studied the avifauna of Hailuoto, a large island 35 km south of Krunnit, from 1883—91. On the basis of the dates of his clutch data he seems to have travelled around the island in most years from the beginning of the breeding season to the last third of June (SANDMAN 1892). Because clutches in an advanced state of incubation are difficult to blow, he was specially interested in fresh eggs. Of the 79 clutches that I have taken from his data, the percentage of incubated clutches is only eight (classified: slightly incubated, incubated, much incubated), 29 % of the clutches were unincubated on the basis of their very early date or small number of eggs (below six in *Anas* and *Aythya* species: such clutches are not full or eggs have been lost, cf. HILDÉN 1964, p. 204), the remaining 63 % were clutches marked fresh.

The length of yearly observation periods in 1970—73, monthly average temperatures compared with long-term values from 1931—60, and data on ice conditions of the preceding spring and winter are given in the lower part of Table 1. Temperatures were approximated in the following way: the Monthly Bulletin of the Central Meteorological Institute of Helsinki (Ilmatieteen laitoksen Kuukausikatsaus Suomen Ilmastoon) includes a map with isophenes of the deviations of average temperatures from the local mean values of 1931—60. The temperature for Krunnit was estimated from this map with an accuracy of 0.25°C.

Data on the end of permanent ice cover and on the melting of ice on Krunnit were obtained from the Institute of Marine Research, Helsinki. Yearly data for the melting of ice on Krunnit are not, however, quite exact, for they have been obtained by interpolation on the basis of observations made at Ajos, Kemi, to the north and Virpiniemi, Haukipudas, to the south of Krunnit, but they seem to coincide with observations made by Mr. E. Reinilä on Krunnit (seven years compared). In 1941—70 the ice melted on average in the following days of May:

	end of permanent ice cover	disappearance of ice
	Mean±Sd.	Mean±Sd.
Ulkokrunni	21.4±6.7	23.8±7.3
Ulkokrunni, off side	20.2±9.6	25.4±8.4

Large standard deviations indicate strong yearly variations; factors affecting this are the severity of the winter and occurrence of stormy winds during the melting stage.

Results

Differences between years in the date of laying of the first egg were small within species (Table 1). Only one statistically significant difference was observed: *Aythya fuligula* bred in 1971 5—6 days earlier than in 1972 ($t = 3.61$, $P < 0.001$, df. 41). HILDÉN (1964) has observed considerable variation between years in the time of breeding of this species on Valassaaret. On Krunnit, however, no one year was especially early or late for several species simultaneously. (Yearly species samples comprising less than five clutches were not included in Table 1.)

Because the majority of duck and goose females start breeding in May on Krunnit, it may be noted that the May temperatures of the study years were near normal (Table 1). Three of the four months of June in 1970—73 were very warm, but this probably had little influence on my materials. The ice melted late in 1971 (cf. the low mean temperature in April that year). In 1972 the permanent ice cover disappeared about 20 days earlier than in 1971, but this did not result in any special difference in the timing of breeding of *Mergus merganser,* which, according to HILDÉN (1964), is easily influenced by ice conditions. Because no marked differences seem to be found between my years of study, I have in the following combined their data.

TABLE 1. Date of laying of the first egg of the clutch (mean±Sd.) of duck populations on Krunnit in 1970—73 from May 1; annual data for observation periods, temperatures and ice conditions.

		1970	1971	1972	1973
Anas penelope		31.6±5.28 (9)	32.4±4.83 (13)	34.0±3.99 (6)	30.8±4.65 (5)
A. acuta		20.7±5.16 (9)	23.3±5.61 (7)	—	—
Aythya fuligula		35.0±7.53 (15)	31.5±3.58 (20)	37.0±5.99 (23)	—
Mergus serrator		32.4±5.41 (5)	34.6±1.62 (7)	35.6±5.73 (5)	—
M. merganser		28.7±3.64 (7)	32.2±4.18 (9)	32.1±8.31 (9)	—
Observation period		June 6—18	June 7—16	June 13—20	June 7—13
Monthy deviation	April	—1.0°	—1.75°	0.75°	1.0°
from average temperature	May	0.0°	—0.75°	0.25°	0.5°
(1931—60)	June	2.0°	0.25°	2.75°	2.0°
End of permanent ice cover (Ulkokrunni)		May 23	June 3	May 14	May 14
Disappearance of ice		May 25	June 4	May 20	May 18
Max. ice area in the Baltic (1000 sq. km)		370	157	180	99

Because the populations studied were not marked, the proportion of young birds breeding for the first time is unknown. They generally breed later than more experienced adults. It is assumed that young birds are distributed evenly over species and years in the data.

Laying time of different species

In several species occasional late clutches are much delayed compared with the main distribution of the data (Figs. 1 and 2). Because they most probably represent replacement clutches, I have discarded the eight clearest cases from my calculations; this practice was also followed in Table 1 (clutches are indicated by arrows in Figs. 1 and 2). This could not be done for those species for which the material proved to be inadequate. In some species a part of the population started laying in the latter part of June, after I had left the archipelago (*Aythya marila, A. fuligula, Mergus serrator,* probably also *Melanitta fusca*; yearly observation periods in Table 1). In *Aythya fuligula* and *Mergus serrator* the peaks in the data for the years 1970—73 are located much earlier than the middle of June (Fig. 2), so the general result is little influenced by the exclusion of the latest breeders.

The data for *Anas platyrhynchos, A. crecca, Melanitta fusca* and *Anser anser* from separate areas have been combined, because the differences between samples were not statistically significant, and because the clutch numbers were small (Table 2). In the following list the 12 species are ranked according to the average date of laying of the first egg on Krunnit, mainly in the 1970's.

1. *Anser anser* May 11
2. *Anas platyrhynchos* May 15
3. *A. acuta* May 22
4. *A. crecca* May 24 (N = 3 only)
5. *A. clypeata* May 28
6. *Mergus merganser* May 31
7. *Anas penelope* June 1
8. *Somateria mollissima* June 2 (N = 4 from 1906—07, not breeding at present)
9. *Aythya fuligula* June 3
10. *Mergus serrator* June 3
11. *Melanitta fusca* June 7
12. *Aythya marila* June 8

TABLE 2. Date of laying of the first egg of the clutch in waterfowl species in three areas and periods from the northern Gulf of Bothnia. Means (from May 1)± standard deviations, the number of cluches, and results of t-tests between samples are given.

•	Hailuoto 1883—91	t-test	Oulu—Ii 1904—13	t-test	Krunnit 1970—73	t-test
Anas platyrhynchos	—	—	14.3± 5.32 (6)	0.61	16.3±5.01 (6)	—
A. crecca	—	—	(29.0) (1)	—	(21.0) (2)	—
A. penelope	28.5± 5.47 (6)	—	(27.5) (2)	—	32.2±4.69 (33)	1.74°
A. acuta	32.1± 8.08 (11)	1.39	27.0± 9.57 (13)	1.92°	21.8±6.20 (21)	4.01***
A. clypeata	19.3±12.47 (4)	—	—	—	28.5±5.24 (6)	1.65
Aythya marila	26.0± 6.16 (6)	—	—	—	38.8±2.71 (6)	4.67***
A. fuligula	39.2± 9.24 (17)	2.90**	51.9±13.62 (10)	6.86***	34.3±6.13 (62)	2.58*(*)
Melanitta fusca	37.7± 5.28 (6)	—	—	—	38.3±7.91 (11)	0.17
Somateria moll.	—	—	32.5± 9.11 (4)	—	—	—
Mergus serrator	34.1± 5.25 (8)	5.87***	52.5± 7.98 (16)	8.74***	34.4±4.27 (20)	0.12
M. merganser	17.0±11.61 (9)	1.33	21.8± 7.70 (21)	4.48***	30.6±6.17 (28)	4.59***
Anser anser	10.6± 3.78 (10)	0.43	12.0± 9.57 (9)	0.40	9.7±3.06 (3)	0.39

• = $P < 0.10$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

In the following the timing of breeding of different species is studied separately (cf. Table 2) and compared with data from other parts of Finland.

1. *Anser anser.* Laying from Hailuoto to Krunnit starts May 1—25 (a range of 25 days). On the coast of the Gulf of Finland this species is also the earliest breeder among waterfowl. E.g. in the western archipelago of Hanko laying begins about April 18 (FABRICIUS 1962); the difference from the mean value for Krunnit is about 20 days. (In Central Europe laying starts even earlier, from the beginning of March onwards; the main period according to the data of HUDEC & ROOTH (1970) is March 10 —April 10.) Contrary to earlier assumptions (e.g. v. HAARTMAN et al. 1963—72), the melting of the ice is not decisive for the onset of breeding in the Grey-lag Goose, for on Krunnit it lays on icebound outer islets.

2. *Anas platyrhynchos.* The mean start of laying in 1904—73 was 15.42±5.02 (Sd., N = 12) in May, ranging May 7—22 (16 days) — noticeably later than in southern Finland. South of 62°N the main laying season is about April 21—May 20 (v. Haartman, MS, 1969) or April 21—May 10 (v. HAARTMAN et al. 1963—72). Also on Valassaaret the Mallard breeds earlier than on Krunnit. Mallard broods are the firs to hatch among the ducks of Valassaaret, often as early as late May (HILDÉN 1964, p. 227).

3. *Anas acuta.* The laying time of the Pintail has become progressively earlier, if we compare only the means and disregard the irregular distributions in data from the three periods in Fig. 1. The shift was five days between 1883—91 and 1904—13, and between 1904—13 and 1970—73. Neither of changes is statistically significant, but the shift of 10 days between 1883—91 and 1970—73 is highly significant (Table 2). Nowadays most of the Pintail population begins laying about May 13—28 (range 16 days) on Krunnit.

The first broods on Valassaaret hatch around June 4—5 (mean of seven years, data from HILDÉN 1964, p. 230), about 7—10 days earlier than on Krunnit. In southern and central Finland the main population of the Pintail starts laying at the beginning of May (v. HAARTMAN et al. 1963—72); both in southern Finland and about 65°N most clutches have been found in the period May 11—June 20, in Lapland June 1—30 (v. Haartman, MS, 1969).

4. *Anas crecca.* Laying begins around May 13—28 (N=3, mean 23.67±8.39, Sd.). Possibly these clutches give a mean value some days too late for the date of laying of the first egg in this species, because the two hatching date observations of RAUTKARI (1952) from Haukipudas and the four of SIIRA (1959) from Liminganlahti indicate a mean start of laying about May 15—20.

On Valassaaret the onset of laying seems to be about May 15 (on the basis of brood observations over four years from HILDÉN 1964, p. 228), but it continues to June. In the southern part of Finland the Teal probably lays in the middle of May and in Lapland during the latter part of May (v. HAARTMAN et al. 1963—72). South of 64°N the earliest clutches have been recorded in the last days of April; between 62—64° laying starts from the beginning of May onwards; at 65°N laying may begin as early as the first week in May (Hailuoto June 9, 1948, small young); the earliest record from Lapland indicates laying from May 20 on (v. Haartman, MS, 1969).

5. *Anas clypeata.* Excluding an early clutch from the early spring of 1890 (Fig. 1), the laying of the Shoveler has begun about May 16—31 (range 16 days). On Krunnit five of the six observations were made, however, between May 28—31 (a range of four days). On Valassaaret the earliest broods hatch around June 15 (data over six years from HILDÉN 1964, p. 230), so the first eggs were laid around May 12. In

southernmost Finland laying reaches a peak in the beginning of May (v. Haartman, MS, 1969). The breeding of the Shoveler population on Krunnit clearly occurs later than in the more southern parts of Finland, perhaps also earlier than in adjacent coastal areas, because near Oulu the earliest females start laying in the first days of May (according to v. HAARTMAN et al. 1963—72). However, the mean onset of laying of the four clutches recorded by SIIRA (1959) from Liminka is as late as about May 22.

6. *Mergus merganser.* Contrary to the changes observed in *Anas acuta,* laying in this species has become progressively later, about 14 days between 1883—91 (Hailuoto) and 1970—73 (Krunnit). The change is statistically highly significant (Table 2). In the beginning of the 20th century the start of laying near Krunnit took place about May 10—31 (range 22 days), but nowadays it occurs about May 22—June 12 (range 22 days), about nine days later than 65 years ago. The difference is highly significant. Both the older (1883—1914) and the later (1970—73) distributions are bimodal (Fig. 2), first a low peak, and about 10—15 days later a major peak.

On Valassaaret broods hatch around mid-June or in the latter half of the month (HILDÉN 1964, p. 261). The start of laying of these clutches can be inferred to have occurred around May 2. The laying season of the majority of the population on the southern coast of Finland is difficult to establish (v. Haartman, MS, 1969). According to BERGMAN (1939) most clutches in Espoo—Kirkkonummi hatch in mid-June; also PAAVOLAINEN (1957) states that the broods appear in large numbers after June 10. So the breeding of the Goosander is rather simultaneous on Valassaaret and the southern coast of Finland, whereas my recent data from Krunnit are extremely late when compared with these areas. In the beginning of this century the difference was much less obvious. v. HAARTMAN et al. (1963—72) consider the Goosander, together with *Anas platyrhynchos,* as the earliest breeder among duck species, but this does not hold true at Krunnit.

7. *Anas penelope.* If the scant older data are combined, the laying of the Wigeon in 1883—1913 started about May 22—June 6 (range 16 days). The mean value for that period (28.25±5.80 (Sd.), N = 8) differs fairly significantly (t = 2.05*, df. = 39) from the present mean for Krunnit. Nowadays laying starts about four days later, mainly between May 25—June 9 (range 16 days). On Valassaaret the earliest Wigeon broods hatch about June 21 (data over eight years from HILDÉN 1964, p. 228), about five days earlier than nowadays at Krunnit. In southernmost Finland the earliest eggs are laid at the end of April and probably the onset of most clutches is in mid-May (v. Haartman, MS, 1969).

8. *Somateria mollissima.* Along the coast of the Gulf of Finland at Espoo and Kirkkonummi, half of the females had complete clutches by about May 8 (BERGMAN 1939); in the early spring of 1957 at Tvärminne most females started laying April 26—30 (v. Haartman, MS, 1969). On Valassaaret the mean date for the start of laying of the first females is May 1 (from data over six years in HILDÉN 1964, p. 249). There was considerable annual variation, due primarily to the time of the melting of the ice. The last clutches, which are generally replacement clutches, hatch there at the beginning of July (HILDÉN 1964), so they are started at about the same time as the four clutches of the years 1906—07 from Selkäletto, south of Krunnit. These clutches were begun around May 22—June 12 (range 22 days; on the coast of the Barents Sea the Eider lays at about the same time, BELOPOLSKII 1957, Fig. 83). They may, however, include renestings because

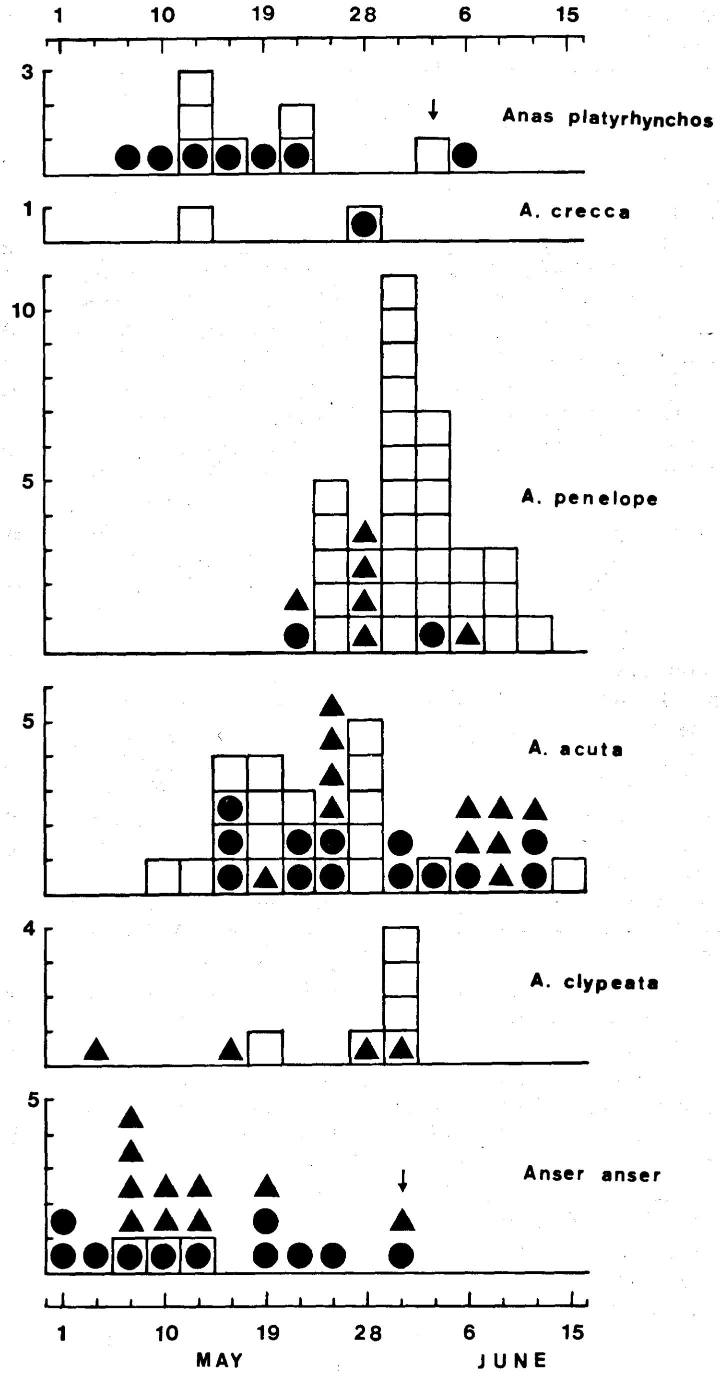

FIG. 1. Distribution of the date of laying of the first egg at Hailuoto in 1883—91 (triangles), near Krunnit in 1904—13 (circles) and on Krunnit in 1970—73 (open squares) in six dabbler species. Arrows indicate probable replacement clutches.

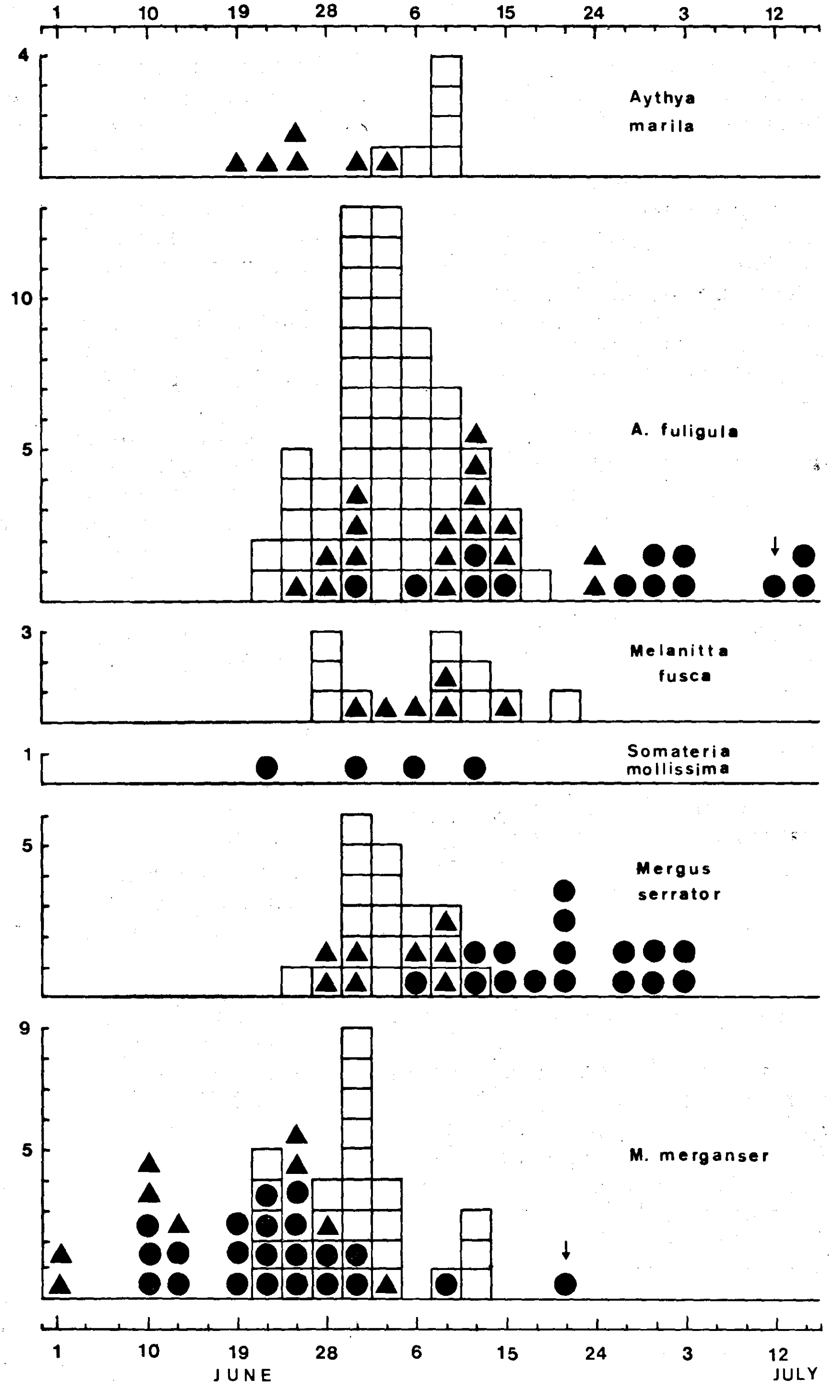

FIG. 2. Distribution of the date of laying of the first egg at Hailuoto in 1883—91 (triangles), near Krunnit in 1904—13 (circles) and on Krunnit in 1970—73 (open squares) in six diving duck species. Arrows indicate probable replacement clutches.

MERIKALLIO (1930) never observed hatched broods: clutches were plundered by fishermen and Hooded Crows *Corvus corone*. The Eider bred for the last time on Selkäletto possibly in 1910 (MERIKALLIO 1958).

9. *Aythya fuligula.* At Hailuoto in 1883—91 laying started about May 28—June 24 (range 28 days). In the beginning of the 20th century in Oulu—Ii it occurred about June 6—July 2 (range 26 days) and nowadays on Krunnit the main period is about May 22—June 15 (range 25 days). The Tufted Duck therefore now breeds highly significantly about 18 days earlier on Krunnit than 65 years ago, but (significantly) only about five days earlier than at Hailuoto about 85 years ago. The clutches for the period 1904—13 from the archipelago around Krunnit were extremely late.

On the basis of Fig. 32 in HILDÉN (1964), the bulk of young hatch about June 27—July 8 on Valassaaret. This gives the same period for the onset of laying as nowadays on Krunnit. (The yearly variations mentioned in the preceding section should, however, be observed.) In southernmost Finland laying is less unusual from May 11 onwards; the main laying season starts about May 21 and more clutches are started in June than in May (v. Haartman, MS, 1969). According to BERGMAN (1939), slightly less than a half of all clutches in Espoo and Kirkkonummi were started by June 5.

10. *Mergus serrator.* The timing of breeding resembles very much that of *Aythya fuligula,* because the mean date in Oulu—Ii in 1904—13 was very much later than that of the two other samples (Table 2). Laying started then about June 12—July 3 (range 23 days), but 20 years before and 65 years later about May 28—June 12 (range 15(+) days). The difference of 18 days between the means is highly significant (Table 2), but no doubt too large at least for the data of 1970—73, because my study period did not cover the end of June. At this time the latest females start laying; on the other hand, their clutches would not easily be separated from replacement clutches. The change is, howewer, not entirely due to methods, for the peak of laying is now in the beginning of June and only one clutch according to MERIKALLIO (1930) was initiated in the first ten days of this month.

The first clutches on Valassaaret were started about May 27 (four years, data from HILDÉN 1964, p. 262). Most clutches hatch around mid-July (HILDÉN 1964), so the peak of the onset of laying is about the first ten days of June, the same time as nowadays on Krunnit. In southernmost Finland (very few data) laying may start a few days earlier than on Krunnit. The earliest southern clutches recorded (v. HAARTMAN et al. 1963—72) were started about May 20. In Espoo—Kirkkonummi BERGMAN (1939), however, never found eggs before June 1.

11. *Melanitta fusca.* The first eggs of the Velvet Scoter on Krunnit are laid about May 28—June 17 (range 20 days), at about the same time as at Hailuoto about 85 years ago (Table 2) and on all other coasts of Finland (on Aspskär and Valassaaret May 28—June 10, according to KOSKIMIES & ROUTAMO 1953 and HILDÉN 1964; Espoo—Kirkkonummi June 1—20, according to BERGMAN 1939). The mean for my combined data from Hailuoto and Krunnit is 38.06 ± 6.92 (Sd., N = 17).

12. *Aythya marila.* Both the samples from Hailuoto (1883—91) and Krunnit (1970—73) are small. The date, 13 days later on average, for the start of laying on Krunnit, however, gives a statistically highly significant difference (most probably owing to methods; see discussion). The clutches from Hailuoto were started about May 19—June 3 (?) (range 16 days); those from Krunnit indicate an onset of laying between

June 3—9 (range 7(+) days). Apparently some Scaup clutches, the female of which was not seen, have been included in the data for the Tufted Duck on Krunnit.

On Valassaaret most Scaup clutches hatch in the first half of July (HILDÉN 1964, p. 244), at the same time as nowadays on Krunnit. If we compare the earliest clutches, the Tufted Duck starts laying about nine days earlier than the Scaup (data taken from HILDÉN 1964). If we compare the means of populations, the difference is only about 4—5 days (my data from Krunnit). Data on the start of laying of the Scaup are scant from southernmost Finland, but its breeding time seems to be correlated with that of the Tufted Duck also there (a few days later, v. HAARTMAN et al. 1963—72). We may conclude that the Scaup breeds in the same period on all Finnish coasts.

Discussion

Factors determining the time of laying in waterfowl

The possibilities of comparing the rather comprehensive data on the timing of breeding in waterfowl on Krunnit with data from other areas are limited. Times for the mean onset of laying may be calculated approximately, maybe with an accuracy of ± 5 days, only in the case of Valassaaret (HILDÉN 1964) and the southernmost coast of Finland (data collected and reviewed by v. HAARTMAN et al. 1963—72 and v. Haartman, MS, 1969). These data have been presented in the preceding section.

The twelve species included in the study may be divided into two groups (Fig. 3):

(1) Early breeders containing the six dabbler species studied and two diving duck species: *Anser anser, Somateria mollissima, Mergus merganser, Anas platyrhynchos, A. acuta, A. clypeata, A. crecca* and *A. penelope.*

(2) Late breeders are all diving ducks: *Aythya fuligula, Mergus serrator, Melanitta fusca,* and *Aythya marila.*

Nesting in the former group is progressively delayed towards the north. If we take as crude means for the date of laying of the first egg in these species on the south coast, Valassaaret and Krunnit May 3, 13 and 25, respectively, the delay towards the north is about 4 days/100 km (between 60°30′—65° 30′N). On the other hand, the late breeders start laying rather simultaneously, on average around June 5 on all Finnish coasts. The difference from the early breeders on the southern coast of Finland is about one month and on Krunnit about two weeks.

Spring isotherms of 0°, 5° and 10° (KOLKKA 1966) were compared with the areal timing of waterfowl breeding in Finland. Clearly 0° isotherms are too early, but 5° isotherms on the northern coast of the Gulf of Finland and Valassaaret coincide with the peak in the start of laying in several early breeding waterfowl species (Figs. 3 and 4). A delay in breeding time from Valassaaret to Krunnit is not, however, explained by the temperatures (and not, of course, in the differences in the amount of light along the Finnish coasts). In both areas the mean temperature of five degrees is reached about May 10. On Valassaaret, however, the early breeders start laying on average earlier and, on Krunnit later, than this. The ice melts, however, about 20 days later on Krunnit than on Valassaaret. This might better explain the difference in the breeding time of ducks between these areas.

However, the date of the melting of the ice in the sea is evidently not correlated with the timing of waterfowl breeding, because the ice in fastflowing sounds and bays around forest islands and in small ponds in the inner parts of the islands thaws several weeks earlier than in the sea. Dabblers feed in these small open waters, often in large flocks

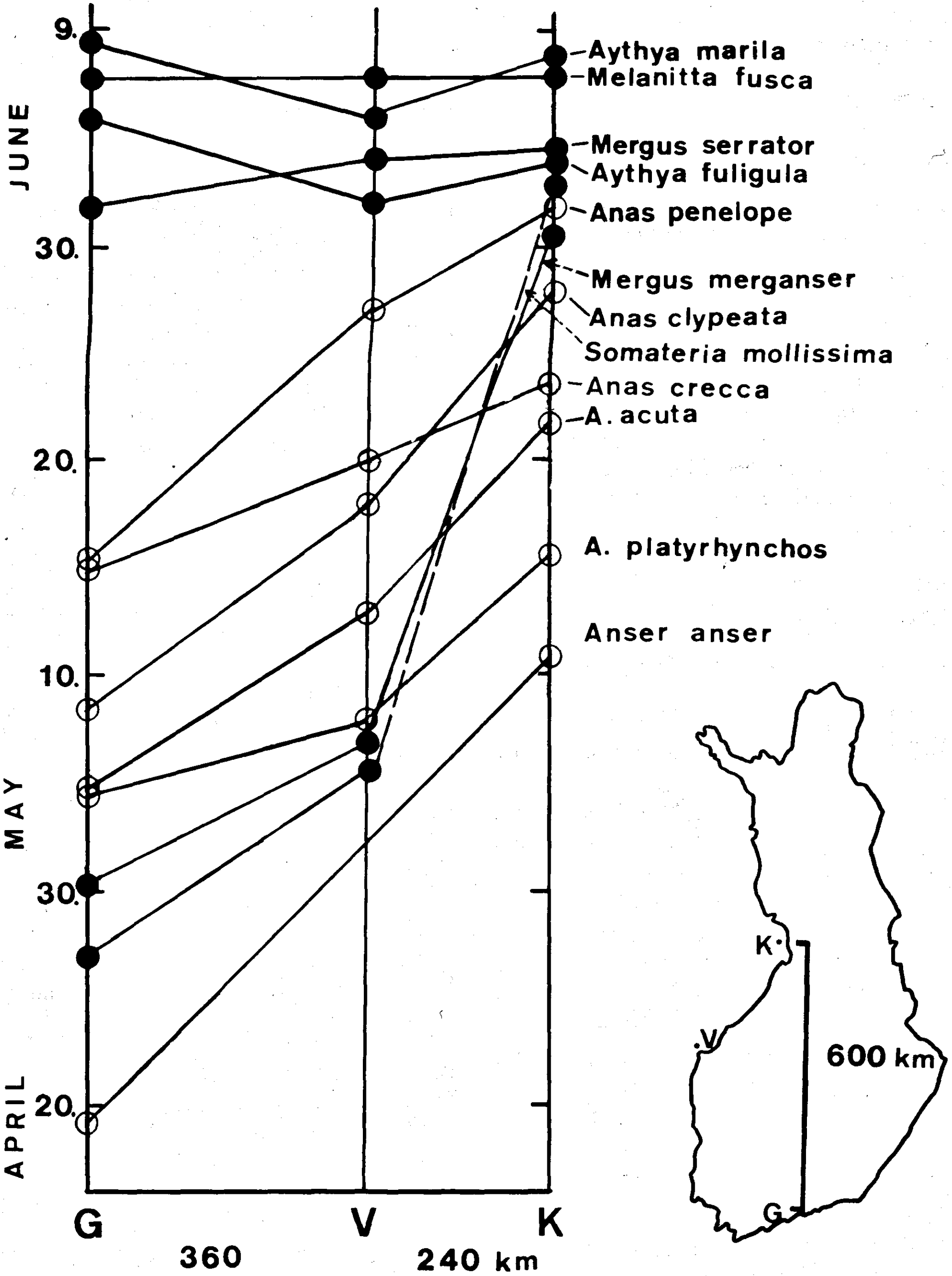

FIG. 3. Mean date of laying of the first egg of 12 waterfowl species on the northern coast of the Gulf of Finland (G), on Valassaaret (V) and Krunnit (K). Open circles indicate dabblers, black circles diving ducks.

that disappear after the ice has melted in the sea: on May 3, 1946, 120, and on May 3, 1949, 60 Mallards were observed on Ristikari (Salkio 1952). Presumably the most important reason for the difference in the timing of early breeding waterfowl species between Valassaaret and Krunnit is to be found in the opening of these small waters and in the development of food supply in them. There are no statistics on their phenology, but most probably the difference of 20 days in the opening of the sea between Valassaaret and Krunnit is directly related to the yearly build-up of the feeding areas of ducks.

The breeding of two early diving duck species seems to depend on the melting of sea ice and the opening of the feeding areas there.

(1) The breeding of *Mergus merganser* is remarkably delayed from Valassaaret to Krunnit (the difference is smaller, if we take the breeding time for the years 1904—13 for the Krunnit population, see Table 2). This may be directly correlated with the opening of the fishing waters for this species. The Goosander arrives in its breeding areas early in the spring, but does not start breeding until the ice has melted. Hildén (1964) has observed that the birds tend to settle on the islets adjacent to the earliest open waters.

(2) The melting of the ice also has a clear effect on the timing of the start of breeding of *Somateria mollissima* (e.g. Paavolainen 1957, Belopolskii 1961, Hildén 1964, Grenquist 1965). Nowadays the Eider occurs very

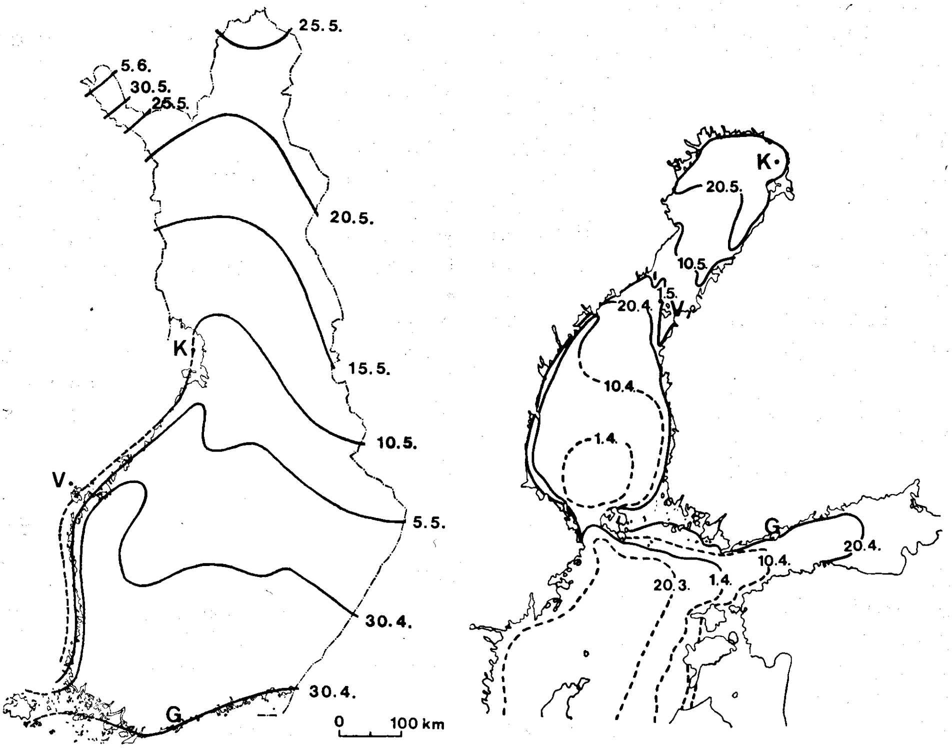

Fig. 4. The average dates of 5°C isotherm in Finland (Kolkki 1966) and of the disappearance of the ice in the Baltic (Palosuo 1966) in 1931—60. G = the northern coast of the Gulf of Finland, V = Valassaaret, K = Krunnit.

rarely in the Gulf of Bothnia north of Valassaaret; the northern limit of its regular breeding area is the northern margin of the Quark Straits. Like several authors before him, HILDÉN (1964, p. 199) suggested that food is most likely the factor determining the distribution pattern of the Eider along the Finnish coasts, since the abundance of its main food supply — marine molluscs, especially *Mytilus edulis* — decreases towards the heads of the gulfs of the Baltic along with the gradual decrease in salinity. The date of the melting of the ice is a further modifying factor reducing the breeding area of this early breeding species.

These hypotheses do not, however, accord with the former occurrence of the Eider along the whole Finnish coast of the Gulf of Bothnia (KRANK 1898, MERIKALLIO 1930, 1958) and the recent increase of the population at the eastern end of the Gulf of Finland (on Haapasaaret 20 pairs in 1951 (PAAVOLAINEN 1957), 71 pairs in 1967 (KANERVA 1970)). Also HILDÉN (1966, p. 253) has rejected food conditions as an explanation for the decline: "The disappearance of Eiders from the Bothnian Bay can apparently be attributed to plundering by man, motorboats having been in common use since the beginning of the century."

The Eider is a species with noticeable geographical differentiation. MILNE & ROBERTSON (1965) were able to distinguish two adjacent populations in Scotland, which differed from each other in their migratory behaviour: one was sedentary, the other migratory. Also differences in gene frequencies were observed in their study of egg white proteins. In Hudson Bay, the development of a resident race of the Eider is suggested to have resulted from local climate factors and larger body size among non-migrants in the original postglacial colonizing population of North Atlantic Eiders (FREEMAN 1970). For more data on the geographical differentiation of the Eider see PLOEGER (1968, p. 115—117).

It may be supposed that the Gulf of Bothnia was originally occupied by an indigenous Eider population, with a north-south cline of late breeding and adaptation to local food resources. Due to increased human interference in the outermost archipelago in the early spring, the population was destroyed during the period 1850—1910. Nowadays the species has difficulty in spreading from the Quark Straits to the north because (1) the spreading process is slow for the early breeding and *Mytilus*-eating population, and (2) if some pairs try to settle in the archipelago between the Quark and Krunnit, their clutches would most probably be destroyed, since only a few islets are protected along this 275 km of coast.

Other divers included in this study belong to the group of late breeders. They start breeding fairly simultaneously along all Finnish coasts. They arrive at their breeding areas noticeably early (see HILDÉN 1957), and wait rather long before they start breeding. The 10°C isophene follows the coasts of Finland on May 30, so the mean temperatures of the distant archipelago are everywhere about the same when the majorities of the populations of *Aythya marila, A. fuligula, Melanitta fusca* and *Mergus serrator* begin nesting. The ice has disappeared by this time. I suggest that the late breeding time of these species is genetically determined. This is, however, influenced by environmental factors to a different degree in different species. The average laying dates in *Melanitta fusca* tend to be individually constant in relation to the yearly mean of the populations, apparently as a result of hereditary factors (KOSKIMIES 1957; see also parallel observations of KLUIJVER 1951, RICHDALE 1957, SERVENTY 1963, DRENT 1965, and HARRIS 1966). *Aythya fuli-*

gula seems to be largely influenced by environmental factors. In an early spring laying may start two weeks earlier on Valassaaret than in a late spring (HILDÉN 1964, p. 233; even earlier observations have been made since 1964, O. Hildén, pers. comm.). Also age affects the time of breeding: year-old females tend to nest some 10 days later than two-year-olds do (MIHELSONS et al. 1972).

In the timing of breeding *Aythya fuligula* is clearly more opportunistic than *Melanitta fusca.* In the southern parts of its breeding range, the breeding time of *Aythya fuligula* does not, however, vary much. In Upper Bavaria it lays at the same time as on the Finnish coasts (see BEZZEL & KROSIGK 1971), as also in the whole of central Europe (BAUER & GLUTZ 1969, p. 132).

Changes in the timing of breeding

The shifts in the timing of breeding of six species, *Anas penelope, A. acuta, Aythya marila, A. fuligula, Mergus serrator* and *M. merganser,* during the last 85 years on Krunnit and nearby islands of the northern Gulf of Bothnia are striking. The most marked changes are that, among the early breeders, *Anas acuta* lays earlier and *Mergus merganser* later than before and, among the late breeders, both *Aythya fuligula* and *Mergus serrator* lay earlier than in the beginning of this century, though the difference is not as pronounced in comparison with their breeding time in Hailuoto in 1883—91.

As a basis for these changes I shall discuss the following possibilities:

(1) Methods used when collecting data in 1883—91, 1904—13 and 1970—73 have biased the materials.
(2) Ice conditions in the springs of 1904—13 were, on the average, exceptional.
(3) During the last 65 years, the decrease of severe winters has changed the genetical constitution of populations by affecting mortality in wintering areas.
(4) In the same period, an increase of mild springs and earlier melting of the ice have changed selection pressures affecting the breeding time of populations.
(5) The changes have resulted from immigration.
(6) A principal reason for the changes is the social attraction towards larids, for nowadays most ducks on Krunnit breed in larid colonies, which was not the case in the beginning of the century.

(1) *Methods.* If we compare the breeding times for separate species given by SANDMAN (1892) and laying periods calculated by me on the basis of his clutch data, these coincide for most species. Exceptions are found, however, and these have most probably resulted from Sandman's oological aims. Because he tried to find fresh clutches, he seems to have collected and/or marked in his notes disproportionally many clutches of the earliest breeding specimens of some species. In two cases this is of importance for the species which were listed in the beginning of this section. (a) He maintains that the laying times of *Anas acuta, Aythya fuligula* and *A. marila* are the same (first half and middle of June), but the six clutches of *Aythya marila* in Fig. 2 represent only the earliest females. (b) *Mergus serrator* would breed very late ("vanligen först omedelbart före midsommar, stundom mycket senare"), but the laying dates of the eight clutches are from the turn of May—June (Fig. 2).

In the beginning of the century Dr. Merikallio made observations within his study area throughout the breeding season over a period of several years, as can be seen from the timing of his clutch data in Figs. 1 and 2. As Sandman, he did not perform the water test for all duck clutches he found, and apparently he was oologically interested in very early and late clutches. To some extent this has increased the standard deviations of his data, although I have tried to exclude the most obvious replacement clutches from the calculations. In my opinion his samples are rather reliable, and so are mine from 1970—73 (see the methods section), except for those few clutches laid late in the end of June and in the beginning of July. The magnitude of changes that have taken place in breeding times would exclude the possibility that biased age distribution of females in my data (a deficiency of young, late birds breeding for the first time) could have had any considerable effect.

(2) *Ice conditions in 1904—13.* Because the statistics on ice conditions on the Finnish side of the Gulf of Bothnia are inadequate before the year 1914, I have calculated the averages for the dates at which ice melted from those for the Swedish harbour towns of Kalix and Luleå (primary data from ÖSTMAN 1937, Table 12) to arrive at values for Krunnit. The ice disappeared in 1931—60 around May 20 at these three places (PALOSUO 1966). This is seen also in the melting dates (May) of the period 1914—36:

	Mean ± Sd.
Kalix—Luleå	24.4 ± 6.8
Ulkokrunni	23.4 ± 6.7

Correlation between these variables is r = 0.717, which gives ($R = 100 \times r^2$) 51.4 % for the proportion of explainable variance. The melting dates of the ice off Kalix—Luleå from the winters 1880—1936 are correlated with the most extensive annual freezing of the Baltic (r = 0.511, R = 26.1 %).

In the years 1904—13 ice conditions varied considerably (Table 3). Melting dates were on the average near normal, although these winters in the whole Baltic area were very mild.

If the years 1906, 1910 and 1913 are considered to be early and the others late, *Mergus merganser* materials from the beginning of this century contained nine clutches from the early years and 11 from the late ones. There is no significant difference in the dates of laying of the first egg between these years (t = 0.66, df. 18):

	date in May Mean ± Sd.
early years	19.78 ± 6.94
late years	21.82 ± 6.84

So the change in the breeding time of this species during the last 65 years seems real.

(3) *Ice conditions in winters 1830—1973.* Using maximal ice area in the Baltic as an index for the severity of the winter (JURVA 1952), PALOSUO (1953) has divided the winters 1720—1950 (= 1719/20 — 1949/50) into three classes:

Winter	Maximum extent of the ice cover	Frequency
mild	60 000—180 000 sq km	38.0 %
normal	180 000—300 000 sq km	21.7 %
severe	300 000—420 000 sq km	30.3 %

The upper limit, 420 000 sq km, means ice cover throughout the Baltic. This index correlates highly with the average temperature of the winter months December—March (r = 0.91, temperatures from Mariehamn, PALOSUO 1965). (For the peculiar frequency distribution with mild and severe winters predominating, see PALOSUO 1953).

Because the oldest of the annual ice data are rather uncertain, I have in the following table considered only the last

TABLE 3. Data for ice conditions in the years 1904—13.

Year	Melting of the ice off Kalix—Luleå (May 1 = 1.0)	Max. ice area in the Baltic (1000 sq. km)
1904	25	178
1905	23.5	135
1906	16	90
1907	30.5	140
1908	25	240
1909	38.5	185
1910	19	80
1911	29	110
1912	23.5	160
1913	13.5	120
Mean ± Sd.	24.4 ± 7.3	144.8 ± 48.5

144 winters, from the year 1830 on (data from the Institute of Marine Research, Helsinki):

Winter	1830—1903 N = 74	1904—73 N = 70
mild	32 (43 %)	42 (60 %)
normal	13 (18 %)	15 (21 %)
severe	29 (39 %)	13 (19 %)

Before 1904 severe ice winters were much more common than after that time. About 20 % of the winters have changed from *severe* to *mild* in the last 70 years.

High mortality is observed in hard winters in several duck species especially in the western Baltic, when wintering birds are packed into progressively smaller areas of open water, where hunters easily reach them (GRENQUIST 1965). Greatest losses occur in *Aythya fuligula,* which winters rather far north, (see e.g. LAMPIO 1946, v. HAARTMAN 1957, HILDÉN 1965). The population fluctuations of the two *Mergus* species, however, do not seem to be clearly correlated with the severity of the winter. It is difficult to believe that winter mortality would change the constitution of populations in relation to their genetical basis for the determination of the breeding time. The possibility that the early breeders of a population might winter farther north than late breeders, and so suffer proportionally lighter losses in severe winters, seems improbable.

(4) *Increase of early springs in the 20th century.* A more realistic connection between the severity of the winter and changes in breeding times might be found in the fact that, on average, after a severe winter the spring is late and the melting of the ice is delayed. If early springs have become more common, have the breeding results of early breeding birds in populations of e.g. *Aythya fuligula* and *Mergus serrator* been superior to those of late breeding females? If so, hereditary factors affecting early breeding have become more common. An analogous evolution has been described in the Ringed Plover *Charadrius hiaticula* by VÄISÄNEN (1969). From the beginning of this century, especially during the last 50 years, the breeding time of this species has become earlier in extensive northern areas. The populations have changed especially strongly in the Gulf of Bothnia, where breeding nowadays takes place perhaps 20 days earlier than before (VÄISÄNEN 1969, p. 50—52, Fig. 11).

If this explanation is applicable to ducks, then after hard winters adverse weather conditions would be more common at hatching time than after milder winters — bad weather is the most important factor influencing juvenile mortality (HILDÉN 1964, see also KOSKIMIES & LAHTI 1964). Variables measuring this would be difficult to construct, and I have not attempted it, even though changes in *Anas acuta, Aythya fuligula* and *Mergus serrator* would seem to support this theory. Changes in *M. merganser,* however, — the breeding time of an early diver has become later — certainly cannot be explained in the same way.

(5) *Immigration.* Have more northern and later breeding populations of *Mergus merganser* shortened their migration and changed the constitution of the population of the Gulf of Bothnia? Have the earliest breeding specimens of more southern populations in *Aythya fuligula* and *Mergus serrator* prolonged their migration to this area?

Ringing statistics on ducks are meagre and it is difficult to estimate the nest site tenacity of northern duck populations. Females of almost all species included in this study may even nest for several years in the same spot (e.g. KOSKIMIES & ROUTAMO 1953, GRENQUIST 1965). However, the dispersal of the young from their place of birth is not known. In one large *Aythya fuli-*

gula population in Latvia a very high nest site tenacity has, however, been observed. If conditions were favourable, old females returned year after year. Most of the young females returned to the lake and, in favourable conditions, nested in the vicinity of the nest site where they were hatched (MIHELSONS et al. 1972). On the other hand, birds born in the Netherlands have been found in Dalarna, the Åland Islands and Estonia (data reviewed by BAUER & GLUTZ 1969, p. 128).

Some duck populations may change their breeding areas. *Anas penelope* was, at the end of the 19th century, the commonest duck species around the town of Oulu and abundant in wide areas as late as 1906, in the same numbers as *A. platyrhynchos* and *A. acuta* (MERIKALLIO 1930). In the summer of 1909 it was already almost absent in this area and the same trend was observed in the following years (MERIKALLIO 1930). A new vigorous increase in the population did not begin until the end of 1950's (GRENQUIST 1965, Fig. 18). — It is of interest that the new Wigeon population nests about five days earlier than that at the end of the last century. This might indicate an immigration of a population genetically different from the previous one (the change is, however, so small that it could also be explained on the basis of biased collecting of the clutches of the earliest breeding specimens in earlier times).

Strong yearly fluctuations also occur in the Finnish populations of *Anas querquedula* and *A. clypeata* (v. HAARTMAN et al. 1963—72), and in the *Mergus merganser* population of Krunnit (1970 22 ♂♀, 1972 13 ♂♀; see GRENQUIST 1965 Fig. 23 for earlier data). The distribution ranges of several waterfowl species have changed markedly in this century in Finland. Southern species have extended their breeding area northwards (*Podiceps cristatus, Aythya ferina, Tadorna tadorna, Cygnus olor*) and the distribution area of some northern species has declined (*Gavia stellata, Melanitta nigra*) (v. HAARTMAN et al. 1963—72). — Seen against this background immigration may, to some extent, have played a part in changing the populations and their breeding times in my study area.

(6) *Social attraction towards larids.* According to SANDMAN (1892), the most common larids on Hailuoto in 1883—91 were *Larus fuscus* on the outer islets (tens of clutches on even very small islets) and *L. canus* of which there was an abundant population along the coasts of Hailuoto and on small lakes in the inner parts of the island. *Sterna hirundo* and *S. paradisaea* were also very common on the coasts.

In the beginning of this century larid colonies on Krunnit and in the archipelago of Haukipudas were very small. Most gull species bred in solitary pairs; only *Larus fuscus* formed colonies of some 20 pairs on the islets of Hietakraasukka and Tyni (MERIKALLIO 1930). Some 5—10 pairs of *Hydroprogne caspia* bred on Tasasenletto. *Sterna hirundo* and *S. paradisaea* colonies were larger but these were not exactly censused.

On the basis of some pair values given in MERIKALLIO (1930) it seems that the tern population at that time was perhaps 1/4—1/3 of the numbers of the early 1970's. Larid numbers reached their minimum in the 1930's and 1940's and it was not until the 1950's that their numbers began to rise sharply due to intensified protection (VÄISÄNEN 1972).

According to MERIKALLIO (1930) *Anas platyrhynchos, A. crecca, A. acuta, A. penelope, Aythya fuligula, Mergus serrator* and *Anser anser* nested in 1904—13 on the central islands, in deciduous forests and on shore meadows; only extremely seldom did some pairs breed on open, outer islets. *Soma-*

teria mollissima occurred only on open islets, where most *Mergus merganser* pairs were also observed. *Anas clypeata* was found on Krunnit very occasionally, and *Aythya marila* and *Melanitta fusca* were probably absent from this area.

Censuses made in the years 1939 (MERIKALLIO 1950) and 1948—55 (SALKIO 1952, GRENQUIST 1965) on Krunnit do not reveal the distribution of waterfowl pairs within the archipelago. MERIKALLIO (1950) was not able to distinguish between breeding and non-breeding individuals. The figures given by SALKIO (1952) were most probably too high for most species (cf. the same criticism by HILDÉN 1966, p. 251) and estimates in 1950—55 were made too late in July, so that many waterfowl broods had already moved from the outer islets to the feeding areas around the forest islands. In 1956 the census took place early enough, June 16—22 and July 1—15 (GRENQUIST 1965) to be compared with the figures for 1972:

	Changes in pair numbers 1956—72	
	Forest islands	Open islets
Larids	26 → 14	385 → 1252
Waterfowl	55 → 32—45	41 → 86

The numbers of waterfowl have increased on the open outer islets, as the ducks and geese have shifted their breeding habitat into continuously expanding larid colonies. Nowadays the majority of pairs of all waterfowl species (except *Anas crecca* and perhaps *Mergus serrator*) breed on outer open islets.

The possible intraspecific differences in breeding time on forest islands and open islets cannot be compared on the basis of my clutch data from the years 1970—73, because the data were collected from the open islets, inhabited by continuous dense gull and tern colonies (density in 1971—72 23—120 pairs/ha). An additional factor is that I did not have time to seek scattered clutches on the forest islands. Satisfactory samples of *Anas penelope* and *Mergus serrator* might perhaps be obtainable there.

Although *Larus argentatus* colonies on Krunnit start laying in the beginning of May, the main period for other larids culminates about May 20—June 4 (Fig. 5). The mean onset of laying in duck species has in the last 65 years moved to coincide with this period — in *Aythya fuligula* and *Mergus serrator* laying begins earlier and in *M. merganser* later than before. The changes in *Anas acuta* and *A. penelope* have taken place within the period May 20—June 4.

HILDÉN (1964, p. 202) has classified these species on the basis of their sociability towards larids as follows:

Sociability very strong:	*Aythya fuligula*
Sociability moderate:	*Anas acuta* *Mergus serrator*
Sociability ± nil:	*M. merganser*

In my opinion, the social attraction towards larids is the most important reason for the changes in the breeding time of the first three species.

In the last 20 years foxes *Vulpes vulpes* have many summers frequented Maakrunni and Ulkokrunni, attracted by local hare *Lepus timidus* populations. Foxes may be taken as an important negative factor in the habitat selection of waterfowl (BERGMAN 1957). This has certainly accelerated the observed change of breeding habitats to outer islets, where birds are safe from this predator.

In 1883—91 the larid colonies of Hailuoto were of medium size compared with the small populations of the archipelago between Oulu—Ii about 20 years later and large numbers on Krunnit nowadays. I should associate the early breeding in *Aythya fuligula* and *Mergus serrator* on Hailuoto 85 years ago with the rather strong larid populations. *Aythya fuligula* nested on *Phragmites*-shores, but SANDMAN (1892) did not at that time pay any attention to

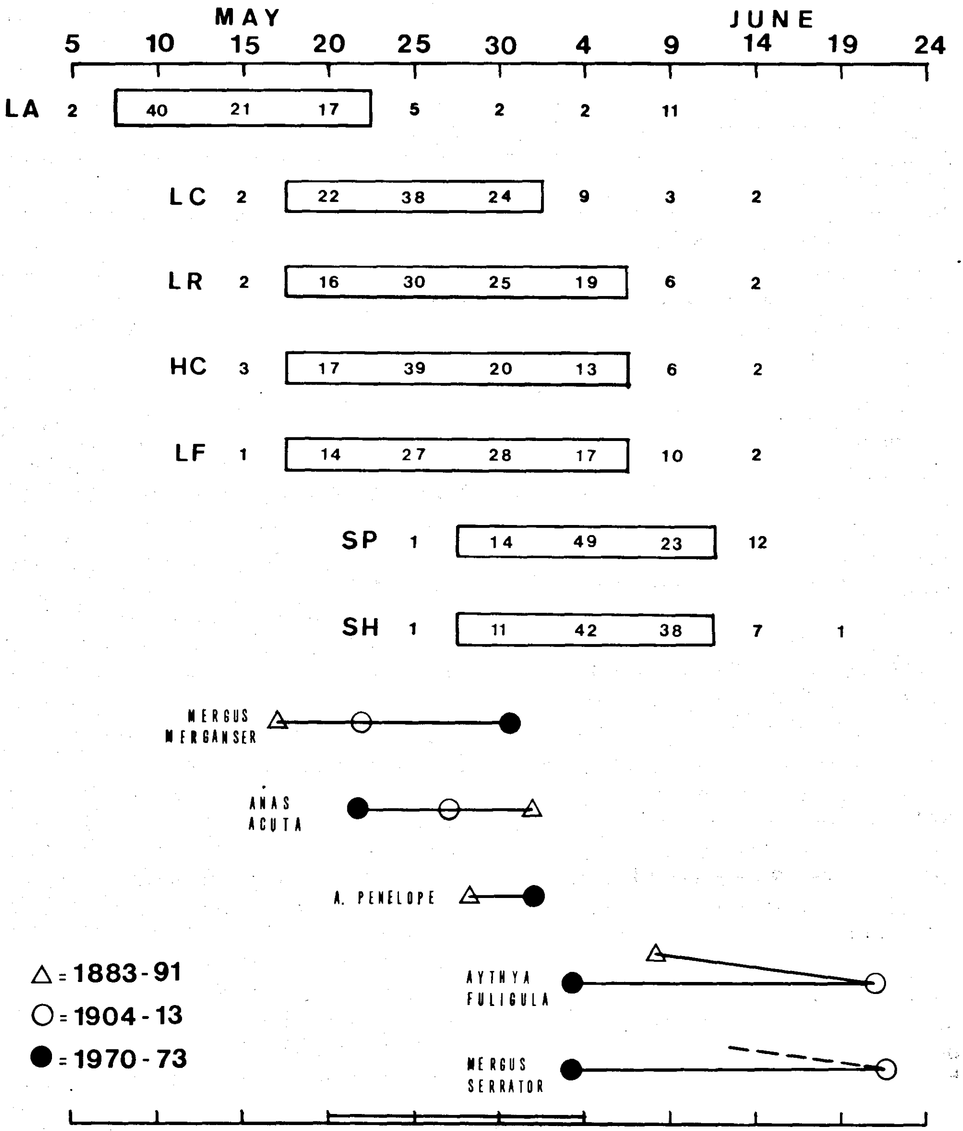

FIG. 5. Distribution of the date of laying of the first egg in seven larid species (percentages, with class interval of five days) in 1968—73 on Krunnit and the changes in the mean date of laying of the first egg in five duck species. Larids: LA = *Larus argentatus* (126 clutches), LC = *L. canus* (401), LR = *L. ridibundus* (252), HC = *Hydroprogne caspia* (761), LF = *Larus fuscus* (720), SP = *Sterna paradisaea* (744) and SH = *S. hirundo* (174).

relations between duck habitats and larid colonies. Nowadays the biotope is the same, and dense *Aythya fuligula* groups nest in *Larus canus* (+ *Sterna* and *L. ridibundus*) colonies; most probably the same tendency could have been observed also in 1883—91. In *Mergus serrator* the sample of the same time is biased towards early breeding birds, but in any case it shows that a part of population bred early, in my opinion due to sociability towards larids.

On the other hand, it may be concluded that *Mergus merganser* did not breed in larid colonies on Hailuoto 85 years ago, because it nested very early, compared with the breeding time on Krunnit nowadays.

The only reports suggesting social dependence of *M. merganser* on larids are, according to HILDÉN (1964, p. 192), those of BERGMAN (1941, 1957), who emphasised that in a tern colony even the Goosander may nest openly in grass. On Valassaaret HILDÉN (1964) concluded that it nests on islets regardless of whether there are many, few or no nesting larids. The location of the nest may be slightly dependent upon the abundance of larids; in dense larid colonies the Goosander may nest in less sheltered cavities than otherwise.

It is interesting to observe that *Somateria mollissima* is the other species with ± nil sociability towards larids according to HILDÉN's classification (1964). These two species are the earliest breeding duck species on the coasts of southern and central Finland (see Fig. 3). The phase releasing the habitat selection in these species may occur so early in spring that the most attractive larid colonies (e.g. *Larus canus, L. fuscus*) have not yet been established or the larids have not yet returned from migration (*Sterna*). This seems to be confirmed by the timing of my larid clutch data from the coast of the Gulf of Finland. I therefore believe that *Mergus merganser* is socially attracted towards larids in areas where its breeding is late enough to coincide with the laying period of smaller larid species.

What is the process by which the breeding time of the local Goosander population on Krunnit has been delayed enough to coincide with that of larids this century? One may suppose that such factors as heavy plundering of the eggs of this species (fishermen do this to some extent even nowadays on unprotected islands) and possible immigration of later breeding birds have been of importance.

Summary of the proximate factors determining the time of waterfowl breeding

The following proximate factors seem to exert considerable (+) or little (—) influence on the timing of waterfowl breeding:

1. (+) food
2. (+) melting of ice
3. (—) air temperature
4. (—) light
5. (+) sociability towards larids

This list is, except for the last point, similar to that presented by BELOPOLSKII (1957), pp. 241—257) for colonies of sea birds in the Barents Sea.

(1) *Food.* On Krunnit no direct data on the quantity of waterfowl food exist for periods preceding laying. The prime importance of the food factor was concluded on the basis of indirect geographical comparisons on the breeding phenology of separate species along the Finnish coasts. (For a more profound discussion, besides BELOPOLSKII 1957, p. 254—257, see PERRINS 1970, KRAPU 1974).

(2) *Melting of the ice.* On Krunnit the importance of this factor was treated in the formation of areas of open water on and near the central islands, and in the difference between the time the sea ice melted on Valassaaret and Krunnit.

(3) *Air temperature.* Several *early*-nesting waterfowl species start laying at different temperatures along the Finnish coasts, *late* species start at constant temperatures, however. In passerines the opposite trend has been observed in Finland (v. Haartman 1963): *early*-nesting species start at a relatively constant temperature, despite latitude, but *late*-nesting species start at lower temperatures in the north.

The effect of extremely cold temperatures on the laying process cannot be excluded, however. In several waterfowl species a correlation has been reported between clutch initiation and mean daily temperature (Sowls 1955, Hanson & Browning 1959, Dane 1966). In my opinion, however, extreme temperatures affect the start of laying only by a matter of a few days. They may also have some indirect influence upon females through the availability of food during a cold spell.

(4) *Light.* There are considerable differences between areas in the amount of light at the time of breeding of the duck populations along the Finnish coasts, but this does not seem to have any apparent influence on the timing of waterfowl breeding (northern populations do not breed earlier).

(5) *Sociability towards larids.* Where larid colonies are present, it may be assumed that these synchronize waterfowl breeding. The effect is strongest upon species otherwise breeding at about the same time or later than the larids. If a species breeds much earlier than larids, it is not affected, but if the difference is only moderate, a delay may possibly take place in its breeding time.

Acknowledgements

I am indebted to Dr. Göran Bergman and Mr. Olli Järvinen, for constructive criticism of the manuscript; to Prof. Erkki Palosuo for advice on the ice conditions of the Baltic and to Mr. Hannu Grönwall and Mr. Erkki Reinilä for ice phenological data; to my wife, Mrs. Kaarina Väisänen, for help in the field work at Krunnit; to Dr. Anssi Saura, who revised my English and to Mr. Christopher Grapes, who checked the final version of the manuscript.

Selostus: **Vesilintujen pesinnän ajoittuminen Iin Krunneilla.**

Tutkimuksessa pyrittiin määrittämään 12 vesilintulajin pesyeiden keskimääräinen 1. munan muninta-aika Iin Krunneilla ja tärkeimmät siihen vaikuttavat pesintää laukaisevat (proksimaattiset) tekijät.

Pesyeille suoritettiin vesikoe seuraavasti: Mukana kuljetettiin pientä vedellä täytettyä muovisankoa ja siihen sopivaa siivilää, jonka kahva oli taivutettu ylöspäin. Mikäli munissa ei vielä ollut kuoriutumissäröjä, pesyeestä uitettiin kolme munaa. Pohjaan painuvista munista arvioitiin kulma pohjaa vasten 15° tarkkuudella (asteikkona 15°, 30° ... 90°) ja pinnassa kelluvista mitattiin kellotyöntötulkilla pinnan yläpuolelle työntyvän kalotin halkaisija (tarkkuus 0,1 cm). Näiden mittausten sekä pesyeen munien lukumäärän ja lajikohtaisten munien munimavälien ja haudonta-aikojen pohjalta voitiin laskea pesyeen **1. munan** munimapäivä.

V. 1970—73 aineistossa on 197 pesyettä, lisäksi siihen liitettiin 79 J. Albin Sandmanin v. 1883—91 Hailuodosta ajoittamaa pesyettä ja 89 Einari Merikallion pääasiassa v. 1904—13 Krunneilta ja lähisaaristoista hieman karkeammalla vesikoemenetelmällä määrittämää pesyettä.

Krunnien populaation keskimääräisiksi pesyeen 1. munan munimapäiviksi saatiin eri lajeilla seuraavat (lajit nykyisessä varhaisuusjärjestyksessä): merihanhi 11.5., sinisorsa 15.5., jouhisorsa 22.5., tavi 24.5., lapasorsa 28.5., isokoskelo 31.5., haapana 1.6., haahka 2.6. (vuosisadan alun havaintojen perusteella), tukkasotka 3.6., pikkukoskelo 3.6., pilkkasiipi 7.6. ja lapasotka 8.6. Lajiensisäinen hajonta selviää kuvista 1 ja 2 ja taulukosta 2.

Vertaamalla eri sorsalintujen pesimäaikoja Krunneilla, Valassaarilla ja Suomen etelärannikolla lajit voitiin jakaa (1) varhaispesijöihin, joiden pesimäaika muuttuu keskimäärin 22 vrk myöhäisemmäksi siirryttäessä etelärannikolta Krunneille (n. 3.5. → 25.5., 4 vrk/100 km), ja (2) myöhäispesijöihin, joiden muninta alkaa samanaikaisesti, keskimäärin 5.6. kaikkialla Suomen rannikoilla. Luettelon 8 ensimmäistä lajia kuuluu varhaispesijöihin (pääosin puolisukeltajia) ja loput myöhäispesijöihin (kokosukeltajia).

Neljän lajin pesimäaika on selvästi muuttunut Krunneilla viimeisten 65 vuoden aikana; jouhisorsalla, tukkasotkalla ja pikkukoskelolla varhaisemmaksi (kahdella jälkimmäisellä lajilla ehkä jopa 15—20 vrk) ja isokoskelolla myöhäisemmäksi. Todennäköisin syy näihin muutoksiin on sorsalintujen sosiaalisuudessa lokkilintuja kohtaan. Krunnien avosaarten lokkilintukoloniat ovat nimittäin kasvaneet todella suuriksi vasta viimeisten 20 vuoden aikana. Tähän on liittynyt sorsalintujen siirtyminen pesimään suurilta metsäisiltä pääsaarilta avosaarten lokkilintukolonioihin, ja habitaatin muutoksen yhteydessä lajien pesimäajat näyttävät liukuneen valkosiipisten munimakauden intensiivisintä vaihetta (20.5.—4.6.) kohti.

Tärkein sorsalintujen muninnan alkua ajoittava laukaiseva tekijä näyttää olevan ravinto (1); naaras nimittäin aloittaa muninnan vasta kun saa tarpeeksi vararavintoa munien muodostamiseen (niiden yhteispaino on usein 100 % tai yli sorsanaaraan painosta). Jäidenlähdöllä merestä ja ruokailusulien muodostumisella pääsaarille (2) on ravintotekijään kytkeytyneenä merkityksensä muninnan alkamiselle. Ilman lämpötilalla (3) ja valon määrällä (4) ei ole kovin suurta merkitystä muninnan alkamiselle, sensijaan sorsalintujen sosiaalisuus lokkilintuja kohtaan (5) vaikuttaa merkittävästi edellisten pesinnän laukeamisen ajankohtaan.

References

Bauer, K. M. & Glutz von Blotzheim, U. N. 1968—69. Handbuch der Vögel Mitteleuropas. Vol. 2—3. — Akademische Verlagsgesellschaft, Frankfurt am Main.

Belopolskii, L. O. 1957. Ekologiya morskikh kolonial'nykh ptits Baretsova Morya. — Izdatel'stvo Akademii Nauk SSSR, Moskva — Leningrad. (Ecology of sea colony birds of the Barents Sea. Translated (1961). — Israel Program for Scientific Translations, Jerusalem.)

Bergman, G. 1939. Untersuchungen über die Nistvogelfauna in einem Schärengebiet westlich von Helsingfors. — Acta Zool. Fenn. 23:1—134.

— 1941. Om simfåglars och vadares häckning i måsfågelkolonier. — Dansk Ornithol. Foren. Tidssk. 35:120—123.

— 1957. Das Porkalagebiet als biologisches Experimentalfeld. — Acta Soc. F. Fl. Fenn. 74(3):1—52.

Bezzel, E. & Krosigk, E. von. 1971. Zum Ablauf des Brutgeschäftes bei Enten. — J. Orn. 112:411—437.

Dane, C. W. 1966. Some aspects of breeding biology of the Blue-winged Teal. — Auk 83:389—402.

Drent, R. H. 1965. Breeding biology of the Pigeon Guillemot, Cepphus columba. — Ardea 53:99—160.

Fabricius, E. 1962: Grågås Anser anser. In G. Rudebeck (Ed.), Våra svenska fåglar i färg. — Stockholm.

Freeman, M. M. R. 1970. Observations on the seasonal behaviour of the Hudson Bay Eider (Somateria mollissima sedentaria). — Can. Fld. Nat. 84:145—153.

Grenquist, P. 1965. Changes in abundance of some duck and sea-bird populations off the coast of Finland. — Finnish Game Res. 27:1—114.

Haartman, L. von. 1957. Population changes in the Tufted Duck, Aythya fuligula (L.). — Comm. Biol. Soc. Scient. Fenn. 16(5):1—11.

— 1963. The nesting times of Finnish birds. — Proc. Int. Orn. Cong. 12:611—619.

— 1969. The nesting habits of Finnish birds II. Non-Passeriformes. — Unpublished manuscript, Helsinki.

Haartman, L. von, Hildén, O., Linkola, P., Suomalainen, P. & Tenovuo, R. 1963—72. Pohjolan linnut värikuvin. — Otava, Helsinki.

Hanson, W. C. & Browning, R. L. 1959. Nesting studies of Canada Geese on the Hanford Reservation. — J. Wildl. Mgmt. 23:129—137.

Harris, M. P. 1966. Age of return to the colony, age of breeding and adult survival of Manx Shearwaters. — Bird Study 13: 84—95.

Hess, E. H. 1972. "Imprinting" in a natural laboratory. — Scient. Amer. 227(2): 24—31.

Hildén, O. 1958. Über den Frühjahrszug der Vögel auf den Inseln Valassaaret im Bottnischen Meerbusen. — Arch. Soc. 'Vanamo' 12(2):156—185.

— 1964. Ecology of duck populations in the island group of Valassaaret, Gulf of Bothnia. — Ann. Zool. Fenn. 1:153—279.

— 1966. Changes in the bird fauna of Valassaaret, Gulf of Bothnia, during recent decades. — Ann. Zool. Fenn. 3:245—269.

Hudec, K. & Rooth, J. 1970. Die Graugans. — Die Neue Brehm-Bücherei 429. A. Ziemsen Verlag, Wittenberg Lutherstadt.

Jurva, R. 1952. On the variations and changes of freezing in the Baltic during the last 120 years. — Fennia 75:17—24.

Kanerva, J. 1970. Haapasaarten linnusto. — Kymenlaakson Luonto 11:1—26.

Kluijver, H. N. 1951. The population ecology of the Great Tit, Parus m. major L. — Ardea 39:1—135.

Kolkki, O. 1966. Tables and maps of temperature in Finland during 1931—1960. — Meteorological Yearbook of Finland 65 (Suppl. 1a):1—42.

Koskimies, J. 1957. Polymorphic variability in clutch size and laying date of the Velvet Scoter, Melanitta fusca (L.). — Ornis Fenn. 34:118—127.

Koskimies, J. & Lahti, L. 1964. Coldhardiness of the newly hatched young in relation to ecology and distribution in ten species of European ducks. — Auk 81:281—307.

KOSKIMIES, J. & ROUTAMO, E. 1953. Zur Fortpflanzungsbiologie der Samtente, Melanitta f. fusca (L.). I. Allgemeine Nistökologie. — Pap. Game Res. 10:1—105.

KRANK, H. 1898. Fågelfaunan uti Gamla Karleby, Larsmo och en del af Kronoby socknar. — Acta Soc. F. Fl. Fenn. 15(4): 1—67.

KRAPU, G. L. 1974. Feeding ecology of Pintail hens during reproduction. — Auk 91: 278—290.

LACK, D. 1967. The significance of clutch-size in waterfowl. — Wildfowl Trust. Ann. Rep. 18:125—128.

LAMPIO, T. 1946. Tvärminnen eläintieteellisen aseman ja sen lähiympäristön linnuston viimeaikaisesta kehityksestä (Summary: The effect of the last cold years and of modifications in the natural conditions on the avifauna of the Zoological Station at Tvärminne and adjacent districts.). — Ornis Fenn. 23:33—49.

MERIKALLIO, E. 1930. Oulun-, Haukiputaan ja Iin meriseudun linnusto. M. Sc. Thesis. — The Merikallio archives, Department of Zoology, University of Oulu, Oulu.

— 1950. Krunnien linnusto. Kvantitatiivinen tutkielma v. 1939 (with an English summary). — Oulun Luonnonyst. Yhd. julk. A I (4):3—11.

— 1958. Finnish birds. Their distribution and numbers. — Fauna Fenn. 5:1—181.

MIHELSONS, H., LEJINŠ, G. & MEDNIS, A. 1972. Connection between nesting territory and nesting density regulation of Aythya fuligula. — Proc. Int. Orn. Cong. 15:668 —669.

MILNE, H. & ROBERTSON, F. W. 1965. Polymorphisms in egg albumen protein and behaviour in the Eider Duck. — Nature, London 205:367—369.

PAAVOLAINEN, E.-P. 1957. Die Vogelfauna des äusseren Schärenhofes im östlichen Teil des Finnischen Meerbusens. I. Quantitative Übersicht. — Ann. Zool. Soc. 'Vanamo' 18(5):1—51.

PAGE, R. D. & CASSEL, J. F. 1971. Waterfowl nesting on a railroad right-of-way in North Dakota. — J. Wildl. Mgmt. 35: 544—549.

PALOSUO, E. 1953. A treatise on severe ice conditions in the central Baltic. — Fennia 77(1):1—130.

— 1965. Duration of the ice along the Finnish coast 1931—1960. — Merentutkimuslaitoksen Julkaisuja 219:1—49.

— 1966. Ice in the Baltic. — Oceanogr. Mar. Biol. Ann. Rev. 4:79—90.

PERRINS, C. M. 1970. The timing of birds' breeding seasons. — Ibis 112:242—255.

PLOEGER, P. L. 1968. Geographical differentiation in arctic Anatidae as a result of isolation during the last glacial. — Ardea 56:1—159.

RAUTAKARI, M. 1952. Kellon saariston linnusto (Summary: The avifauna in the archipelago of Kello in the northern Gulf of Bothnia.). — Ornis Fenn. 29:49—63.

RICHDALE, L. E. 1957. A population study of penguins. — Oxford Univ. Press, New York.

RICKLEFS, R. E. 1966. The temporal component of diversity among species of birds. — Evolution 20:235—242.

SALKIO, V. 1952. Lintuhavaintoja Maakrunnista (Summary: Observations on the avifauna of the archipelago of Maakrunni.). — Ornis Fenn. 29:108—116.

SANDMAN, J. A. 1892. Fågelfaunan på Karlö och kringliggande skär. — Medd. Soc. F. Fl. Fenn. 17:187—272.

SERVENTY, D. L. 1963. Egg-laying timetable of the Slender-billed Shearwater, Puffinus tenuirostris. — Proc. Int. Orn. Cong. 13:338—343.

SIIRA, J. 1959. Anas-lajien pesivän kannan arvioimisesta (Summary: Notes concerning the census of breeding populations of species of the genus Anas.). — Ornis Fenn. 36:98—107.

SOWLS, L. K. 1955. Prairie ducks. — Wild. Mgmt. Inst., Harrisburg, Stackpole Co., and Washington, D.C.

VÄISÄNEN, R. A. 1969. Evolution of the Ringed Plover (Charadrius hiaticula L.) during the last hundred years in Europe. A new computer method based on egg dimensions. — Ann. Acad. Sci. fenn. A IV 149:1—90.

— 1972. Krunnien linnuston suojelu 1939—1971 (with an English summary). — Suomen Luonto 31:134—137.

— 1973. Establishment of colonies of Caspian Tern Hydroprogne caspia by deserting flights in the northern Gulf of Bothnia. — Ornis Scand. 4:47—53.

WELLER, M. W. 1956. A simple field candler for waterfowl eggs. — J. Wildl. Mgmt. 20:111—113.

— 1971. Experimental parasitism of American Coot nests. — Auk 88:108—115.

WESTERSKOV, K. 1950. Methods for determining the age of game bird eggs. — J. Wildl. Mgmt. 14:56—67.

ÖSTMAN, C. J. 1937. Isförhållandena vid Sveriges kuster under vintrarna 1870/71—1934/35. — Meddelanden från Statens Meteorologisk-Hydrografiska anstalt 6(6): 1—63.

Received March 1, 1974.