Reproductive success of Guillemots *Uria aalge* on the island of Stora Karlsö

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The reproductive success of Guillemots breeding on the island of Stora Karlsö (57°17′N, 17°58′E), situated in the Baltic Sea, was studied during 1974—77. The mean number of chicks fledged by a breeding pair averaged 0.80 and did not vary significantly between years. The high value indicates that reproductive success was not adversely affected by the high levels of chemical pollutants found in birds and eggs. Losses during fledging were small (1.3 %) and thus 0.79 chicks/pair reached the sea safely. In all years, pairs that started to breed late in the season were less successful than early and mid-season pairs. This was mainly because a large proportion of the late breeders consisted of inexperienced birds; pairs breeding for their first time were found to have a significantly lower breeding success than pairs with previous breeding experience. With experienced breeders, late pairs were not significantly less successful than earlier pairs, but replacement eggs and chicks hatched from replacements suffered from a considerably higher mortality than first eggs and chicks hatched from first eggs, respectively. Pairs that succeeded in raising a chick in one year were more likely to return the next year to the same nest-site than pairs that failed.

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Introduction

The Guillemot *Uria aalge* is one of the most numerous seabirds in the Northern Hemisphere (Tuck 1960) with over one million pairs breeding merely along the Atlantic coast of north-western Europe (Brun 1969, Cramp et al. 1974, Dyck & Meltofte 1975). During recent decades, however, the species has decreased markedly in several parts of its European breeding range (Birkhead & Ashcroft 1975, Tschanz 1978, Tschanz & Barth 1978), and the reasons for this decline have not been satisfactorily clarified.

In the Baltic Sea, the Guillemot is an uncommon breeding bird. The total population in 1974 was estimated at about 8800 breeding pairs, including 6400 pairs on the island of Stora Karlsö and 1200 pairs on the island of Lilla Karlsö off the west coast of Gotland (Hedgren 1975). Whether the Baltic population has decreased, increased, or remained stable during the last 20—30 years is unknown, reliable data on the size of the population being lacking for that period.

During 1972—77, I studied the breeding biology of the Guillemot on Stora Karlsö (57°17′N, 17°58′E). This paper presents data on the reproductive success and compares them

with results from the island of Skomer, Wales (Birkhead 1977a, b, Birkhead & Hudson 1977).

Descriptions of the study area are found in Hedgren (1975) and Hedgren & Linnman (1979).

Methods

During 1972—73, I made tests to measure the survival of eggs and chicks by marking them individually and then checking the presence or absence of the marked eggs and chicks at regular visits to the nest-sites. However, I gradually discovered that this method could not be used. The visits to the breeding ledges seriously disturbed the breeding Guillemots and caused too great losses of eggs and chicks. Therefore, data from these two years could not be used in calculating reproductive success.

Instead, from 1974, I used a method that did not involve any disturbance of the breeding birds. A number of breeding ledges were photographed at a time of the year when the Guillemots were not present, and from the photographs, large "photographic maps" of the ledges were made. When the Guillemots started to lay, the positions of the eggs were plotted on the maps as they were laid. The fate of the eggs, and subsequently, the chicks could then be recorded by observing the nest-sites through binoculars and a telescope from observation points situated 10—70 m from the breeding ledges. Observations were made between late April/early May and late July, and individual ledges were checked at intervals of a few days; at the beginning and at the end of the breeding season they were usually checked daily. Birkhead (1977a) used a similar method to measure reproductive success.

At an age of about 20 days, the chick leaves the nest-site to go out to sea accompanied by one of its parents (Hedgren & Linnman 1979). In the pairs in which the reproductive success was studied, only a few chicks were actually seen fledging. Therefore, in the calculations, chicks are assumed to have fledged successfully if they reached an age of at least 15 days before they were found to have disappeared from the breeding ledge. (The youngest chick seen fledging was 16 days old.)

In 1974, the study involved 287 pairs breeding on 10 ledges; during 1975—77 between 372 and 427 pairs breeding on 13 ledges. All the studied ledges were situated on the west side of the island, where about 90 % of the Guillemots breed. In 1975, the breeding was experimentally prolonged on one of the ledges by removing most of the first eggs (see Hedgren & Linnman 1979). This ledge was not included when calculating the reproductive success in 1975.

To study nest-site tenacity, 68 adult Guillemots were individually marked with colour rings in 1972. An additional 7 of the Guillemots studied during 1974—77 carried a numbered metallic ring.

In all years, the number of fledging chicks were counted every evening during the whole fledging period at Västerberget, a steep cliff on the northwest side of the island. Almost 5000 pairs breed here (see Hedgren 1979).

In the following, means are given ± 1 standard error *(SE)*.

Results

Nest-site tenacity. Guillemots usually exhibit a high degree of nest-site tenacity and breed on the same square foot of ledge year after year. Birkhead (1977b) found that on Skomer over 95 % of the birds that returned in one year returned to the same nest-site as they had occupied the year before. Of the 75 individually marked Guillemots on Stora Karlsö, none were recorded to have changed nest-site from one year to the next. Undoubtedly, however, changes occur, and pairs that have failed in one year — due to disturbance or some other reason — probably are more likely to try a new nest-site next year. This is indicated by the fact that, during 1974 —77, 20.9 % of the pairs that failed to produce a fledging chick in one year did not return to the same nest-site next year, whereas only 4.3 % ($\chi^2 = 63.8$, $P < 0.001$) of the successful pairs disappeared (presumably because one or both birds in the pair had died). That successful breeders are more faithful to their nest-site than unsuccessful ones has been documented in studies of several other bird species (e.g. Ollason & Dunnet 1978, Harvey et al. 1979a).

TABLE 1. Summary of data on reproductive success of Guillemots breeding on the island of Stora Karlsö during 1974—77.

Year	Breeding pairs	Eggs[1] laid	Eggs[1]/ pair	Egg survival[2]	Hatching success[3]	Chick survival[4]	Breeding success[5]
1974	287	316	1.10	0.72	0.79	0.96	0.77
1975	372	387	1.04	0.82	0.85	0.94	0.80
1976	389	411	1.06	0.82	0.87	0.94	0.82
1977	427	455	1.07	0.79	0.85	0.97	0.82
Total	1475	1569	1.064 ±0.006	0.793 ±0.010	0.843 ±0.009	0.953 ±0.006	0.803 ±0.010

[1] Include replacement eggs. [2] Eggs hatched/eggs laid. [3] Eggs hatched/breeding pair. [4]Chicks fledged/eggs hatched. [5] Chicks fledged/breeding pair.

Time of breeding. During 1972—77, egg laying on Stora Karlsö usually started in the beginning of May (in 1972, one egg was found as early as 29 April) and reached a peak in mid-May. The median date of egg laying on the island, as calculated from the observed median dates of fledging (see Fig. 1 and Hedgren 1979), during 1972—77 varied between 9 May (in 1973 and 1974) and 19 May (in 1977). Laying in years with a cool spring (1976—77) occurred later than in years with a mild spring (1972—75) (Hedgren 1979). In all years, egg laying was highly synchronized and about half the pairs laid within a period of five days.

Hatching usually starts in the beginning of June and culminates in mid-June.

As already mentioned, the chick stays about 20 days on the breeding ledge before going out to sea, and consequently, the first chicks usually fledge at the end of June (earliest date: 19 June in 1973 and 1974). The median date of fledging varied from 30 June (in 1973 and 1974) to 10 (in 1977) (see Fig. 1).

About one third (34.4 %) of the pairs that lost their egg laid a replacement about 15 days after the loss. Lost eggs are more likely to be replaced if the loss occurs early in the season (Birkhead & Hudson 1977).

Productivity. The reproductive success of the Guillemots breeding on Stora Karlsö during 1974—77 is summarized in Table 1. The overall breeding success (= the mean number of chicks that attained fledging age per breeding pair) for these four years was 0.803 ± 0.010. The egg survival was 0.793 ± 0.010 and the chick survival 0.953 ± 0.006, which means that, on average, a higher percentage of eggs (0.71 %) than of chicks (0.24 %) was lost each day ($\chi^2 = 58.0$, $P < 0.001$). Breeding success did not vary significantly on different ledges ($\chi^2 = 7.2$, $P = 0.85$) (cf. Birkhead 1977b) or in different years ($\chi^2 = 0.41$, $P = 0.93$). The following analyses combine data from all four years.

During 1972—77, a total of 22,078 chicks were observed fledging and of these only 294 (1.3 %) failed to survive (Table 2). All deaths were caused when chicks hit a rock when landing on the beach below the breeding ledges (Hedgren 1979). No fledglings were killed by gulls either on the beach or in the water (cf. Greenwood 1964, Williams 1975). Thus the mean number of chicks that left the island safely was 0.793 per pair.

TABLE 2. Mortality of fledging Guillemot chicks at Västerberget, the island of Stora Karlsö, during 1972—77.

Year	No. fledged	No. dead	% dead
1972	2427	31	1.3
1973	3507	46	1.3
1974	3684	53	1.4
1975	4166	48	1.2
1976	4113	64	1.6
1977	4181	52	1.2
Total	22078	294	1.3 ± 0.1

TABLE 3. Survival of first eggs and replacement eggs and survival of chicks hatched from first and replacement eggs, respectively.

	First eggs	Replacement eggs
Eggs laid	1475	94
Eggs hatched	1202	42
Egg survival	0.81 ± 0.01	0.45 ± 0.02
	$\chi^2 = 72.2$,	$P < 0.001$
Chicks fledged	1157	28
Chick survival	0.96 ± 0.01	0.67 ± 0.07
	$\chi^2 = 70.7$,	$P < 0.001$

Replacement eggs. As already mentioned, 34.4 % of the pairs that lost their first egg laid a replacement some 15 days after the loss. However, during 1974—77, only 29.8 % of the replacements resulted in a fledging chick compared with 78.4 % of the first eggs (Table 3). Thus only 2.4 % of the fledging chicks originated from a replacement egg (Fig. 2).

In 1975, 9 of 19 pairs (not included in the above calculations) that laid a replacement after their first egg had been removed hatched a chick — an egg survival of 0.47, which is significantly lower than the survival of first eggs in 1975 (0.83; $\chi^2 = 12.9$, $P < 0.001$). Of the 19 pairs, 18 had bred on the same ledge in 1974.

Pairs with previous breeding experience (see below) were more likely to re-lay if they lost their first egg than inexperienced pairs; of 55 pairs that bred for their first time and lost their egg, only 10 (18.2 %) replaced it.

Effects of breeding time and previous breeding experience on reproductive success. To study whether reproductive success varies with the season, I divided the pairs into three categories according to when they laid in relation to all studied pairs in a specific year: early (the first 10 per cent

to lay), late (the last 10 per cent), and mid-season. Early and mid-season pairs had the same breeding success (0.83), but late pairs had a breeding success (0.55) significantly lower than pairs in the other two categories (Table 4).

To assess how the reproductive success is affected by a previous breeding experience, I assumed that if a nest-site was occupied for two or more years in succession, it was occupied by the same individual pair and also when a new nest-site was occupied,

TABLE 4. Breeding success of early[1] and late[2] pairs compared with that of mid-season pairs.

Category	No. of pairs	Breeding success
Early pairs	152	0.83 ± 0.03
		$\chi^2 = 0.00, P > 0.9$
Mid-season pairs	1171	0.83 ± 0.01
		$\chi^2 = 64.3, P < 0.001$
Late pairs	152	0.55 ± 0.04

[1] The first 10 % of the pairs to lay their first egg.
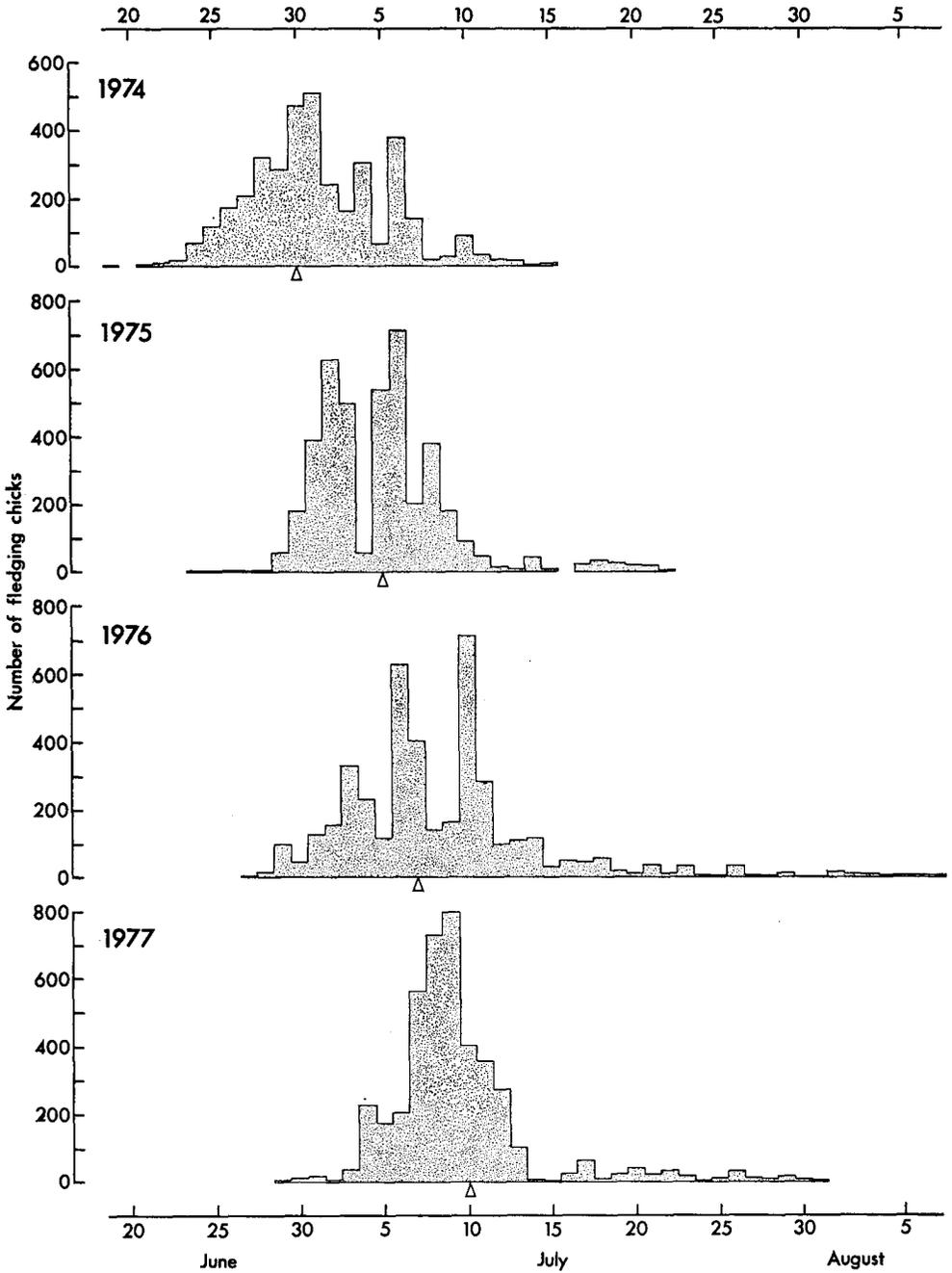[2] The last 10 % of the pairs to lay their first egg.

FIG. 1. Seasonal variation in numbers of Guillemot chicks fledging at Västerberget, the island of Stora Karlsö, during 1974—77. Arrows show median fledging dates.

TABLE 5. Breeding success in relation to previous breeding experience.

Years of previous breeding experience	No. of pairs	Breeding success
0	102	0.51 ± 0.05
		$\chi^2 = 7.7$, $P < 0.01$
1	44	0.77 ± 0.06
		$\chi^2 = 0.76$, $P > 0.3$
≧2	591	0.84 ± 0.02

TABLE 6. Breeding success in relation to onset of breeding in pairs with at least two years' previous breeding experience (cf. Table 4).

Category	No. of pairs	Breeding success
Early pairs	64	0.86 ± 0.04
		$\chi^2 = 0.05$, $P > 0.8$
Mid-season pairs	486	0.84 ± 0.02
		$\chi^2 = 1.3$, $P > 0.2$
Late pairs	41	0.76 ± 0.07

it was occupied by a newly-formed pair of young and inexperienced birds that bred for their first time. (Most Guillemots do not breed for their first time until at least five years old (Birkhead & Hudson 1977 and personal observations).) The observations of the marked birds indicated that these presumptions, in this case, were at least approximately true. Pairs presumably breeding for their first time had a significantly lower breeding success (0.51) than pairs with one year of previous breeding experience (0.77), but after the second year breeding success did not increase significantly with experience (Table 5).

When I excluded all first- and second-year pairs and recalculated breeding success in relation to time of breeding, using only pairs with at least two years' breeding experience, there was no difference in the breeding output of early, mid-season, and late pairs (Table 6). Thus the low success of late laying was due to young birds rather than to the date of laying of the first egg.

Discussion

During 1974—77, a total of 325 eggs were lost or failed to hatch, and 59 chicks did not survive to fledging (cf. Table 1), but the causes of the egg and chick losses were mostly unknown — usually eggs and chicks just disappeared. However, casual observations suggest that the main cause of egg loss was that eggs rolled off the ledge or into a crack from where they could not be retrieved. A few eggs were broken during incubation (12 cases observed) or were deserted (6 cases), and two chicks died during hatching. About 300 pairs of Herring Gulls Larus argentatus and 650 pairs of Lesser Black-backed Gulls L. fuscus breed on the island but do not have much effect as long as the breeding Guillemots are not disturbed and forced to leave their eggs and chicks unattended. Of the 325 eggs lost, only one was actually seen to be taken by a Herring Gull. In contrast, predation by gulls and corvids was the main cause of egg and chick losses on Skomer (Birkhead & Hudson 1977). In most other instances when Herring Gulls were observed to take Guillemot eggs or small chicks on Stora Karlsö, the parents had left them unguarded after having been disturbed, directly or indirectly, by humans or human activities. Guillemots always reacted more strongly to the Herring
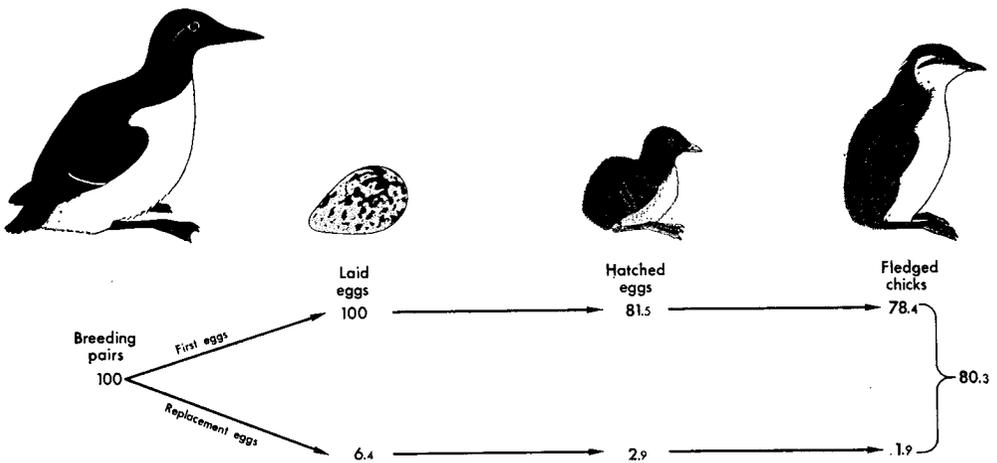
FIG. 2. The mean reproductive output of 100 Guillemot pairs on the island of Stora Karlsö during 1974—77.

Gulls' alarm calls than to the direct sight of a human approaching the breeding ledge. However, the gulls were never observed to use the calls merely to drive the Guillemots off their eggs and chicks.

The seasonal decline in breeding success was mainly a result of the later laying of young and inexperienced birds, which had a lower breeding success than pairs with previous breeding experience. Experienced pairs that began to breed late in the season were not significantly less successful than earlier pairs. Breeding experience has been shown to improve breeding success in several other bird species (e.g. Kluijver 1951, Coulson & White 1958, Nelson 1966, Harris 1969, Ollason & Dunnet 1978, Lloyd 1979, Harvey et al. 1979b).

Despite most replacement eggs being laid by birds with previous breeding experience, they were considerably less successful than the first eggs and contributed rather little to the reproductive output. The reasons for this are not known. However, on average,

the replacement eggs were laid 1—2 weeks later than the late first eggs. In 1977, the mean laying date of the late first eggs was 1 June $(N = 45, SD = 10.2$ days) and of the replacement eggs 12 June $(N = 28, SD = 7.1$ days). Thus the replacement eggs did not hatch until almost all chicks had fledged (see Fig. 1) and most of the adult birds had left the island. Possibly, social factors could play a role, and the remaining Guillemots become more nervous and spend less time brooding the egg and guarding the chick as the number of birds on the ledges decrease during the fledging season. If so, the eggs and chicks should become more exposed to attacks from gulls (Birkhead 1977b). The behaviour of the latest breeders was not studied systematically on Stora Karlsö, but casual observations indicate that they in fact left their egg and chick unattended more often than earlier breeders.

Moreover, replacement eggs are somewhat smaller than first eggs (c. 6 %; Hedgren & Linnman 1979). In several bird species, a decrease in egg

size has been found to be associated with a reduced egg survival and an increased chick mortality (see O'Connor 1979 and references in that paper; also Lundberg & Väisänen 1979). It is thus possible that the smaller size of the Guillemots' replacement eggs in itself could have contributed to their lower success.

In the early 1970s, high levels of mercury and chlorinated hydrocarbons (DDT and PCB) were reported in Guillemots and their eggs from Stora Karlsö (Jensen et al. 1969, 1972, 1974). Also eggshell thickness was shown to have decreased by at least 10 % this century (Odsjö & Johnels 1972). However, the breeding success of the Guillemots on Stora Karlsö during 1974— 77 (0.80 chicks/pair) was even somewhat higher than that of the Guillemots on Skomer Island during 1973— 75 (0.72 chicks/pair; Birkhead 1977a, Birkhead & Hudson 1977). The good breeding result indicates that the high levels of chemical pollutants found in birds and eggs and the observed decrease in eggshell thickness did not adversely affect reproduction. (Concentrations of organochlorine residues in Guillemot eggs from Stora Karlsö are much higher than those reported from Irish Sea colonies, where also only a marginal thinning of the egg shells has been recorded (Bourne 1976).) Andersson et al. (1974), studying Razorbills *Alca torda* breeding on the east coast of Sweden, reached a similar conclusion.

Selostus: **Etelänkiislan pesimistulos Stora Karlsön saarella**

Etelänkiislan pesimistulosta tutkittiin Stora Karlsössä, Itämeren suurimmassa yhdyskunnassa, kesinä 1974—77. Aineisto käsitti vuosittain 287—427 paria, joiden pesinnän onnistuminen selvitettiin seuraamalla munien ja poikasten kohtaloa kaukoputkella läpi pesimäkauden. Muninta alkoi toukokuun alussa ja saavutti huippunsa kuun keskivaiheilla; n. puolet kannasta muni viiden päivän sisällä (vrt. kuoriutumista esittävään kuvaan 1). Munan tuhoutuessa naaras yleensä munii uuden n. 15 vrk myöhemmin.

Keskimäärin 84 % :sta munia kuoriutui poikanen ja näistä 95 % selviytyi n. 20 vrk:n ikään, jolloin poikanen hyppää mereen; täten kukin pari kasvatti keskimäärin 0.80 poikasta (taul. 1, kuva 2). Pesimistuloksessa ei ilmennyt merkitseviä vuosittaisia eroja. Hyvä pesimistulos osoittaa, ettei kiisloista ja niiden munista löydetyillä korkeilla myrkkypitoisuuksilla ole sanottavaa vaikutusta pesinnän onnistumiseen. Vain 1.3 % poikasista sai surmansa iskeytyessään kallioita vasten mereen siirtymisen yhteydessä (taul. 2). Lokeilla ei ollut merkitystä muna- tai poikastappioiden aiheuttajina.

Uusintamunien poikastuotto oli paljon heikompi kuin ensimmäisten munien (taul. 3), samoin myöhään pesintänsä aloittaneet parit onnistuivat pesinnässään joka vuosi huonommin kuin aikaisemmin aloittaneet (taul. 4). Tämä johtui pääasiassa siitä, että myöhään pesijät olivat suureksi osaksi ensi kertaa pesiviä kokemattomia lintuja, joiden pesimistulos oli huonompi kuin vanhempien yksilöiden (taul. 5). Vanhojen, kokeneiden lintujen parissa myöhäisempi pesintä ei sen sijaan heikentänyt merkitsevästi pesimistulosta (taul. 6). Pesinnässään epäonnistuneet parit saattoivat vaihtaa pesäpaikkaa seuraavana vuonna.

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