Breeding success of the Black-headed Gull *Larus ridibundus* in relation to the nesting time

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The breeding success was studied in 1974—78 on the heavily overgrown lake Engure on the coast of the Gulf of Riga, Latvian SSR, using the method of fenced experimental areas. The total number of areas was 42, their average size 80 m² and the mean number of nests 40. In these areas the fate of the chicks was followed until fledging. During the five years of the investigation the average numbers of chicks fledged per clutch were 1.55, 1.35, 1.28, 1.06 and 1.30.

The parameters used to evaluate breeding success were the mean numbers of eggs laid and chicks hatched and surviving per clutch, and the percentages of hatching, survival and overall breeding success (percentage of eggs producing chicks that fledged). These indices were highest in the early clutches and decreased during the season. The laying dates were more scattered in the late nesting areas. The average hatching date showed significant negative correlations with those parameters of success which mainly do not depend directly upon the chick-feeding conditions (clutch size, chicks hatched and surviving per clutch, hatching percentage). In contrast, the *SD* of the average hatching date (= degree of synchronization of nesting) showed a negative correlation with the survival percentage, which depends almost completely upon the chick-feeding conditions. One of the possible causes of the decrease in breeding success during the season is considered to be a reduction in the amount of information obtained from other members of the colony on the location of food.

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Introduction

In spite of numerous investigations on the biology of the Black-headed Gull, little is known about its breeding success. Data on the number of chicks surviving till fledging are particularly scarce (Bergman 1953, Ling 1965, Patterson 1965, Greenhalgh 1975). This problem appears, however, to be of considerable importance, as precisely the changes in breeding success have been supposed to be the cause of the recent population growth and expansion of breeding range of the species observed in large parts of Europe (see Kalela 1946, Kumari 1958, 1978, Viksne 1968a, Isenmann 1976—77).

The authors studied the breeding success of the Black-headed Gull in Latvia in 1974—78; the first results have been published elsewhere (Viksne 1976, 1979, 1980). The aim of the present article is to consider the breeding success in relation to nesting time.

Study area and methods

The study was carried out on the heavily overgrown coastal fresh-water lake Engure (35.4 km²), situated on the western coast of the Gulf of Riga. A detailed description of this lake is given elsewhere (Mihelsons et al. 1968). The population of the Black-headed Gull on Engure increased from 170—230 pairs in 1949 to about 26 000 pairs in 1972 (Viksne 1978); in recent years the number seems to have remained stable. The population growth coincided with a change in the diet of the Black-headed Gull, which began to include a greater proportion of food provided by human activity (food scraps, fish obtained on fishing vessels and in harbours, etc.). Nowadays this forms the main part of the chicks' food (Viksne 1975). The nesting colonies of the Black-headed Gull are situated on sloughs, formed mainly by *Typha angustifolia*, *Solanum dulcamare*, *Rumex hydrolapathum*, *Scirpus lacustris* and *Phragmites communis*, more seldom on islands covered by meadow vegetation.

The field work was done in selected experimental areas (average size about 80 m², the number of nests about 40), fenced in shortly before hatching with a wire net rising 40—60 cm above the water level. The chicks could not pass this fence until about 25 days old. In these experimental areas all the nests were marked, the incubation stage of the eggs was determined by a water test, and the chicks were ringed not later than two days after hatching. The chicks, including newly hatched ones, were ringed on the tibiotarsus, as rings placed on the tarsometatarsus may slip off. With this method neither ring losses nor leg injuries were observed. The chicks were checked at 3—5-day intervals until fledging. Those reaching the age of 25 days were considered to have survived; those found dead or disappearing before this age were not.

To minimize the disturbance in the colony, regular checks of the chicks in the experimental areas were not started until the oldest had reached about two weeks. Before then, only the dead chicks were counted at the ringing of newly hatched chicks, which took place almost daily. Checks of small young ringed earlier were carried out only under favourable conditions. The experimental areas were so selected that they included parts of the colony differing in density of nests, vegetation, time of nesting, etc. If the fenced area was located on particulary wet slough, a wooden frame was built at the level of the slough, on which we could walk without damaging the nests. This detail seemed to be particularly important, as precisely the difficulty of walking on the slough has prevented ornithologists from investigating the breeding success of the Black-headed Gull under conditions similar to ours.

The method applied by us is useful for studying the breeding success only in places where there is no mammalian predation, as the enclosures can largely prevent it. But they do not prevent predation by birds, such as the Marsh Harrier *Circus aeruginosus* and Goshawk *Accipiter gentilis*. It is even possible that in some enclosures the chicks are more exposed to avian predation than usual, due to lack of hiding places. Also, predatory birds may like to sit on the wooden poles to which the wire net is fixed. However, it seems to us that the total picture of predation obtained in this study is more or less correct, although the breeding success probably was somewhat lowered due to the disturbance caused by us. Moreover, our ex-

TABLE 1. Breeding success of the Black-headed Gull on Lake Engure in 1974—78.

Year	No. of fenced areas	No. of clutches	Mean clutch size	No. of chicks hatched		No. of chicks surviving			Mean hatching date ± *SD*
				mean per clutch	percentage	mean per clutch	% of hatched chicks	% of eggs	
1974	7	261	2.72	2.34	86.0	1.55	66.4	57.1	31.V ± 6.5
1975	11	377	2.84	2.34	82.6	1.35	57.6	47.6	30.V ± 5.9
1976	9	328	2.70	2.27	84.2	1.28	56.2	47.3	9.VI ± 7.2
1977	8	415	2.47	1.75	70.7	1.06	60.7	42.9	7.VI ± 8.1
1978	7	296	2.51	2.00	79.7	1.30	65.1	51.9	5.VI ± 7.3

perimental areas did not represent a random sample of the total population in the area, as they comprised fewer nests in very large and very early colonies than in small and late colonies. However, the distribution of enclosures according to the various types of colonies remained similar every year, ensuring that the results obtained were comparable.

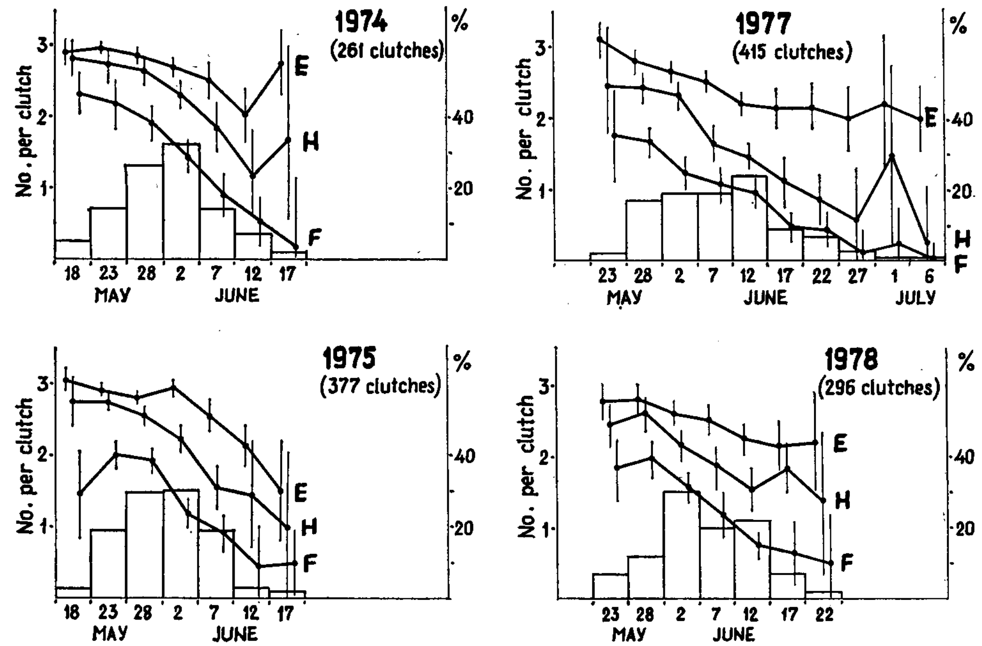
The following parameters are used to characterize breeding success: (1) average number of eggs per clutch (= clutch size), (2) average number of chicks hatched per clutch, (3) average number of chicks surviving per clutch, (4) hatching percentage, (5) survival percentage, i.e. percentage of hatched chicks reaching their 25th day of life, (6) overall breeding success, i.e. percentage of eggs that produced chicks reaching their 25th day of life.

To characterize the timing of breeding we used the hatching date of the first chick in the nests. In the case of clutches that failed, the expected hatching date was calculated from the laying date or the incubation stage of the eggs. The hatching date was chosen instead of the laying date of the first egg, because the former usually could be determined more precisely. The standard pentads proposed by Berthold (1973) were used.

Results

Our observations involved five seasons, and the results are presented in Table 1. Two of the seasons (1974, 1975) can be considered early, two (1976, 1977) late, while one (1978) takes an intermediate position. The delay of nesting in 1977 and 1978 was caused by high spring floods, which covered many traditional nesting places longer than usual (especially in 1977). In 1976, the delay obviously resulted from unusually cold weather in the first two-thirds of May, when laying normally reaches its peak in our conditions. Unfortunately, the period of five years is too short to permit any analysis of the influence of the average annual laying date upon breeding success. In 1977, the poor breeding success resulted from the small clutch size and low percentage of eggs hatching, caused by the high water level. Due to strong competition for the few dry nesting places, the eggs often rolled out of the nests before hatching or even before they had been recorded.

The average number of eggs, chicks hatched and juveniles reaching their 25th day of life in the different pentads of the breeding seasons are presented in Fig. 1. All these parameters decreased gradually in the course of the season, which means that the early clutches were the most successful ones.



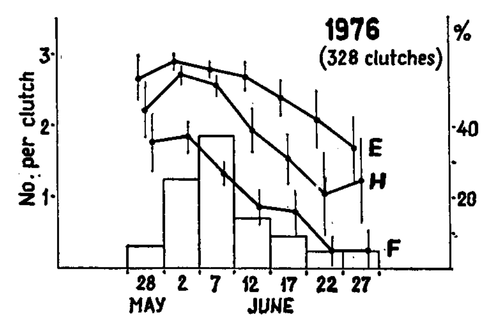


FIG. 1. Average numbers of eggs per clutch (E), chicks hatched per clutch (H) and chicks surviving (F) per clutch (± 2 standard errors) in pentads. The histogram shows the distribution of the clutches (%) according to the pentad in which the hatching (actual or calculated) of the first chick took place. Abscissa = mean dates of pentads.

In some years, however, the clutches of the first pentad formed an exception, being somewhat less productive than those of the second pentad. In some years these parameters showed a slight increase at the very end of the season, but mostly this concerned only the average number of eggs and chicks hatched.

Similar changes during the breeding season also took place with the relative parameters — the hatching percentage, survival percentage and overall breeding success (Fig. 2). The highest values of all these parameters were noted in the first or second pentad of the season, after which a gradual decline took place. In all years, the highest values of all the breeding success parameters occurred before the pentad in which the largest numbers of broods started to hatch.

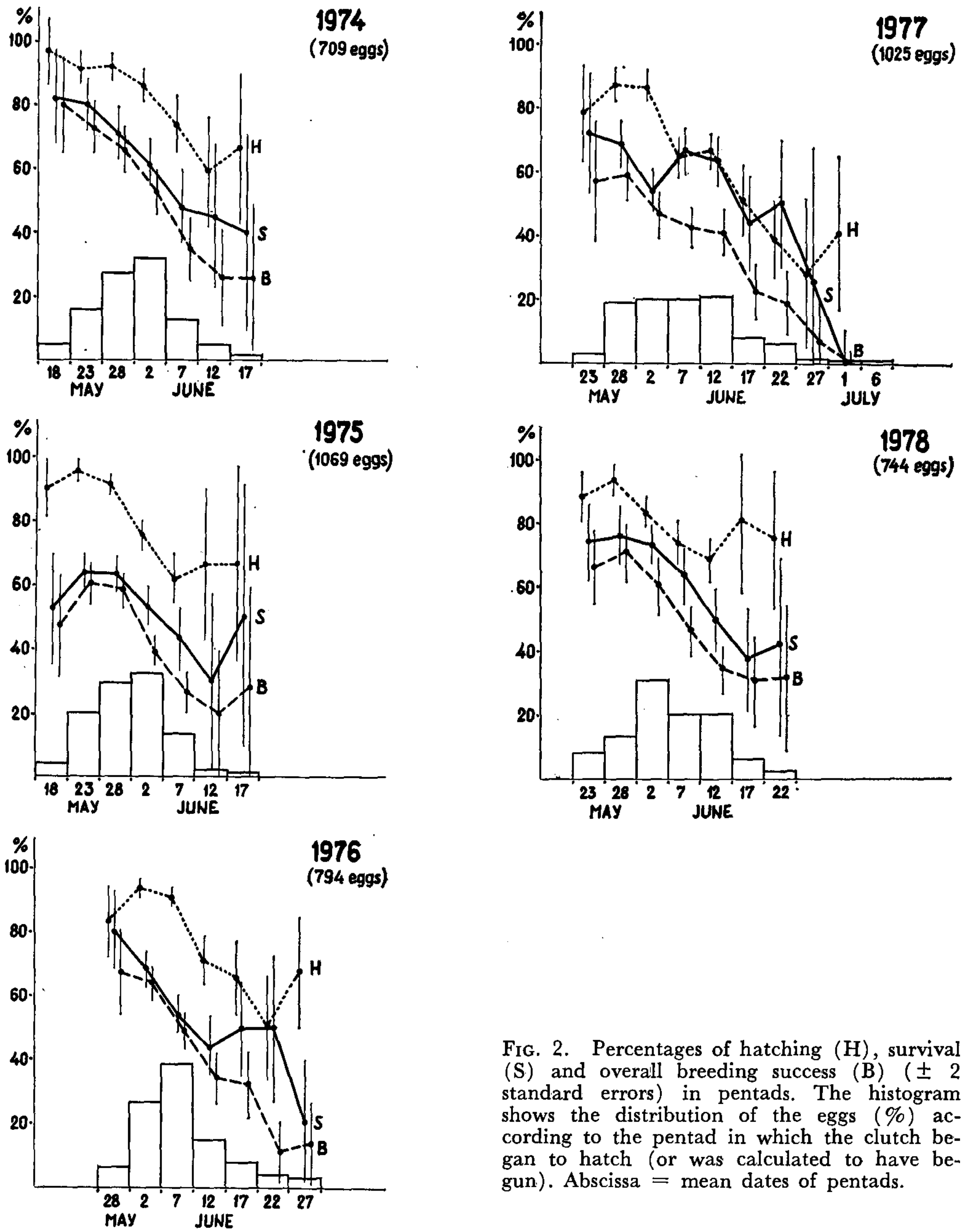


FIG. 2. Percentages of hatching (H), survival (S) and overall breeding success (B) (± 2 standard errors) in pentads. The histogram shows the distribution of the eggs (%) according to the pentad in which the clutch began to hatch (or was calculated to have begun). Abscissa = mean dates of pentads.

Similar results were also obtained in the separate experimental areas. Due to the small amount of data for the single areas, the decreasing trend

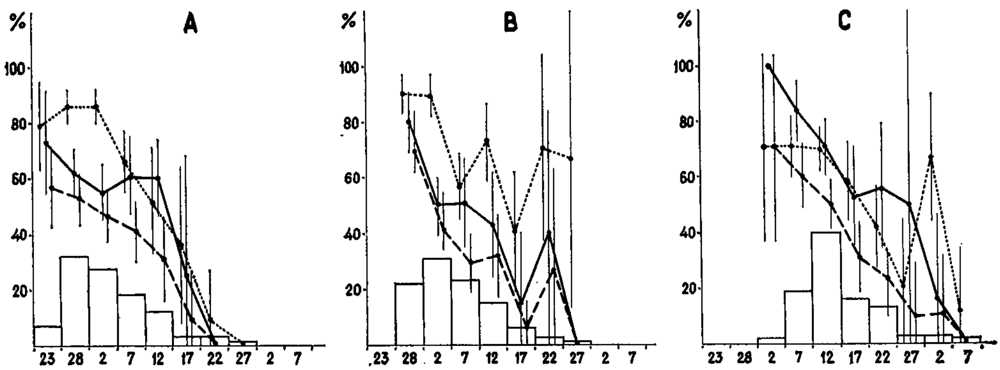


FIG. 3. Percentages of hatching (dotted line), survival (continuous line) and overall breeding success (dashed line) (± 2 standard errors) in pentads in the experimental fenced areas with early (A), medium (B) and late (C) hatching. Abscissa = mean dates of pentads.

shown by breeding success in the course of the season was less pronounced, yet it still existed in areas of both early and late hatching. It can be seen particularly well from the data of 1977, the year in which the differences in breeding date between the colonies were especially marked after high and prolonged spring floods. In Fig. 3, the experimental areas in this year have been divided into three groups according to the date of hatching. In each diagram breeding success can be observed to decrease throughout the season, the highest values occurring before the peak of hatching.

Comparison of the average productivity within these three groups of experimental areas in 1977 shows that the areas of early hatching were superior to the areas of medium and late hatching with respect to clutch size, number of chicks hatched and number of young surviving (Table 2). On the other hand, the hatching percentage, survival percentage and overall breeding success did not show any significant trends.

In Table 3 the significant correlation between the *SD* of the mean hatching date, which represents the degree of nesting synchronization, and the mean hatching date shows that nesting synchronization depends upon the nesting time. The mean hatching date has significant negative correlations with the first four parameters of breeding success. Three of these (average clutch size, average number of chicks hatched per clutch, hatching percentage) do not depend directly on the chick-feeding conditions, while the fourth (average number of chicks surviving per clutch) is determined mainly by clutch size. On the other hand, the *SD* of the mean hatching date has significant negative correlations with the percentage of chicks surviving and overall breeding success, both parameters depending mainly upon the chick-feeding conditions. In other words, the less synchronized the hatching in a given area, the lower is the survival of the chicks and overall breeding success. This relationship shows that the chick-feeding conditions are in some way connected with nesting synchronization, the former most probably being determined by the latter.

TABLE 2. Breeding success of the Black-headed Gull in 1977 in fenced areas divided according to hatching date.

Parameters	Hatching early (1)	Hatching medium (2)	Hatching late (3)	Significance of difference (Student's *t*-test)	
Average clutch size	2.69	2.46	2.22	1—3 1—2 2—3	$P<0.01$ n.s. n.s.
Average number of chicks hatched	2.00	1.88	1.36	1—3 2—3	$P<0.01$ n.s.
Average number of chicks surviving	1.20	1.04	0.93	1—3	$P<0.02$
Hatching percentage	72.2	76.8	61.9	—	—
Survival percentage	59.7	55.2	68.6	—	—
Overall breeding success (percentage)	45.0	42.6	42.5	—	—

Discussion

One of the main reasons for the lower overall breeding success in late clutches is the decrease of clutch size during the course of the season. This decrease is partly due to the fact that the young birds nest later and lay fewer eggs than the older, experienced birds. Later nesting of young birds has been reported earlier in the Black-headed Gull (Svärdson 1958, Viksne 1968b, Greenhalgh 1975) and in other larids as well (e.g. Coulson & White 1960, 1961, Onno 1967, 1972, Vermeer 1970, Parsons 1975). There is some evidence that the clutch size may decrease as the season progresses even in birds of the same age, but this has not yet been clearly demonstrated for the Black-headed Gull.

It seems possible that a decrease in clutch size during the season has adaptive value and is connected with the possibility of feeding the chicks. It is widely accepted that the timing

TABLE 3. Correlations between mean hatching date, *SD* of mean hatching date and indices of breeding success (1974—78, 42 fenced areas).

	Mean hatching date	*SD* of mean hatching date
Mean hatching date	—	0.48*
SD of mean hatching date	0.48*	—
Average no. of eggs per clutch	—0.67**	—0.43*
Average no. of chicks hatched per clutch	—0.57**	—0.25
Average no. of chicks surviving per clutch	—0.41*	—0.08
Hatching percentage	—0.45*	—0.09
Percentage of hatched chicks reaching 25th day of life	—0.12	—0.44*
Overall breeding success	—0.30	—0.42*

* $P<0.01$ ** $P<0.001$

of the breeding seasons of birds is closely connected with the period of the richest food supply for the chicks (e.g. Lack 1968, Perrins 1970). Therefore, it can be supposed that a decrease in the clutch size of birds of the same age reflects poorer feeding conditions later in the season, food becoming scarcer or more difficult to obtain.

We do not have exact data on the fluctuations in the total amount of food within the feeding region of the Engure gulls. However, several facts suggest that the amount of natural food (insects, worms, etc.) and also the food supplied by human activity (fish scraps at canneries, fish at harbours, waste food from settlements, etc.) increases rather than decreases during the feeding season (late May — early July). However, the food resources are rather unevenly distributed and sometimes located far away, up to 40 km from the colony. The occurrence of food in the traditional feeding places is unpredictable, depending on the hour, day, weather conditions, etc.

Thus, though the absolute amount of food in the vicinity does not decrease during the season, the probability of its being obtained by individual birds definitely becomes poorer. If one of the functions of colonial nesting is the supply of information about the location of unevenly distributed food resources (e.g. Ward & Zahavi 1973, Erwin 1978), then the possibility of obtaining this information will vary with the nesting time. In general, birds nesting close to the modal pentad ought to be in the best position. Birds nesting at the beginning of the season appear to be in a somewhat less favourable situation, but this drawback is compensated by the superior experience and knowledge of the locality in old birds. Therefore, the survival percentage is usually highest at the beginning of the season (Fig. 2). Birds nesting in the middle and later part of the season have to feed their chicks at a time when the number of birds in the colony is gradually declining and the amount of information is consequently decreasing. In addition, their chance of successfully feeding the chicks is reduced by their lack of experience (mainly birds nesting for the first time).

Breeding success is also affected by predation and by territorial conflicts between the members of the colony. According to the model developed by Hunt & Hunt (1976), when predation pressure is strong, the young hatched in the middle of the season have the greatest chance of survival. If the chicks mainly suffer from aggressive neighbours, the young hatching at the beginning of the season have the greatest chance of survival. Our facts agree with this model: predation is insignificant on Lake Engure and the losses are mainly due to aggressive neighbours — consequently the early clutches are the most successful. However, it is not clear whether the losses caused by aggressive neighbours are greater than the influence of insufficient feeding due to the gradual decrease of information on the location of food.

As the breeding success of gulls is affected by a large number of factors (predation, mutual aggression and cannibalism, feeding, meteorological conditions, etc.), the results obtained may vary between different authors. In a number of studies on larids, the clutches laid in the middle of the season were most successful (e.g. *Larus ridibundus* — Patterson 1965, Greenhalgh 1975; *L. argentatus* — Kadlec & Drury 1968; *L. fuscus* — Brown 1967), but some cases are also known where the breeding success increased towards the end of the season (Harris 1969 in *L. argentatus*). However, cases in which the indices of success (similar to the parameters used by us) decrease gradually during the season, or fall sharply at the end of the season also appear to be fairly common (e.g. Vermeer 1970 on *L. californicus, L. delawarensis* and *L. glaucescens;* Parsons 1975 on *L. argentatus*). It seems that "lack of information" may, at least partly, explain these cases, too.

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Selostus: **Naurulokin pesintätuloksen riippuvuus pesimäajasta**

Naurulokin pesintätulosta tutkittiin vv. 1974—78 Enguren lintujärvellä Latviassa metalliverkolla aidatuilla näytealoilla. Aitauksia oli yhteensä 42, niiden keskikoko 80 m² ja pesien määrä n. 40 kussakin. Järven lokkikanta kasvoi n. 200 parista 1949 n. 26 000 pariin 1972 ja pysyi tutkimusvuosina suunnilleen tällä tasolla. Pesät merkittiin, poikaset rengastettiin ja niiden varttuminen lentokykyisiksi selvitettiin kullakin näytealalla.

Viitenä tutkimusvuotena munia oli 2.47—2.84, kuoriutuneita poikasia 1.75—2.34 ja lentopoikasia 1.06—1.55/pari (taul. 1). Kaikki nämä muuttujat osoittivat laskevaa suuntausta pesimäkauden kuluessa, eli aikaisimmat pesyeet olivat tuottoisimpia (kuva 1; E = pesyekoko, H = kuor. poikasia/pari, F = lentopoikasia/pari). Sama tulos ilmenee kuvasta 2, jossa muuttujina ovat kuoriutumis-% (H), poikasten eloonjäämis-% (S) ja lentopoikasten osuus alkuperäisestä munamäärästä (B); samoin kuvasta 3, joka esittää pesintätuloksen riippuvuutta pesimäajasta varhaisissa (A), keskimääräisissä (B) ja myöhäisissä (C) aitauksissa. Poikastuoton kannalta aikaisimmat yhdyskunnat olivat parhaita (taul. 2). Niissä aitauksissa, missä pesintä oli aikainen, se vaihteli parien välillä vähemmän kuin myöhäisissä aitauksissa; mitä eriaikaisempaa pesintä oli, sitä huonommaksi jäi pesintätulos (taul. 3).

Havaintojen mukaan ravinnon kokonaismäärä Enguren naurulokkien ruokailuympäristössä ei vähene pesimäkauden aikana. Ravinnon saanti on kuitenkin oikukasta ja tärkeä tekijä sen löytämisessä on lajikumppanien käyttäytymisellään välittämä tieto. Kun pesivien lokkien määrä kesän kuluessa vähenee, käy jäljellä oleville pareille yhä vaikeammaksi löytää ravintolähteitä, ja tämä otaksutaan yhdeksi tekijäksi pesimistuloksen huononemiseen kauden edistyessä. Toinen syy on se, että myöhään pesijöistä huomattava osa on kokemattomia nuoria lintuja, kolmas on myöhäisten pesyeiden pieni koko.

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