

EFFECTS OF INCREASED POPULATION SIZE IN HERRING GULLS ON BREEDING SUCCESS AND OTHER PARAMETERS

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ABSTRACT.—Nest density, clutch initiation, egg volume, reproductive success, and chick growth of Herring Gulls (*Larus argentatus*) were studied in a 6-ha study plot on Terschelling Island, Netherlands, just before and after a dramatic increase in the numbers of breeding pairs on the island (1966–1969: 6000–8000 pairs, 1983–1984: 21,000–21,500 pairs). During the same time interval, Lesser Black-backed Gulls (*L. fuscus*), which form mixed colonies with Herring Gulls, also increased in numbers.

In 1983–1984, almost 100 pairs of large gulls bred per hectare, a 3-fold increase of the nest density compared to 1967–1969. In 1983–1984, Herring Gulls bred, on average, 5–9 days earlier than in 1967–1969 (1967–1969: 18.5–19.4 May, 1983–1984: 10.2–14.0 May). In 1983–1984 reproductive success was 0.34–0.44 fledged young per pair, compared to 1.25–1.50 young per pair in 1967–1969. The lower reproductive success resulted largely from increased predation by conspecifics. Breeding success was highest for early breeders, decreasing in 1983–1984 to almost zero for late breeders. As a consequence, early breeders are at present almost the only ones which contribute genetic material to subsequent generations. We suggest that this situation may have contributed to the shift in clutch initiation that has taken place since the late 1960s. In 1983, the volumes of all eggs in clutches of 3 were smaller than in 1969. In 1984, only b- and c-eggs had smaller volumes. In 1983–1984, chicks gained weight more slowly than in 1966–1968, resulting in a lower fledging weight than earlier. Wing length, however, grew as fast as in 1967–1968, suggesting that chicks were of the same size as in the 1960s but less well-fed than earlier ones.

The results of the study confirm the hypothesis of Coulson et al. (1982) that intraspecific competition is a main factor in the regulation of breeding success and other variables in the population dynamics of the species.

Gulls of the genus *Larus* are highly sociable birds. They breed in colonies and feed mainly in flocks. Such a behavioral pattern implies regular direct confrontations with conspecifics and other seabirds during breeding and feeding. Several studies have shown that gulls interfere with each other on the breeding grounds (e.g., Tinbergen 1960, Brown 1967, Parsons 1971, Hunt and Hunt 1975, Davis and Dunn 1976, Burger 1979, 1984) and in the feeding areas (e.g., Carrick and Murray 1964, Greig et al. 1983, Jones 1985).

Recently, Coulson et al. (1982) hypothesized that for Herring Gulls (*L. argentatus*) several factors associated with the population dynamics of the species—such as nest density, age of recruitment, proportion of young returning to the colony to breed, size of breeding birds and eggs, and reproductive success—are affected by the size of the local population. From 1972 to 1981, Herring Gulls on the Isle of May (Scotland) decreased considerably in numbers as a result of an intense cull program. During the same time, both the density of breeding birds and the age of recruitment decreased, but the proportion of young returning to the colony to breed, body weight and wing length of breeding gulls, and the volume of eggs increased. Coulson et al. (1982) ascribed the changes to reduced intraspecific

competition, either on the breeding colony or in the feeding areas, resulting from the decreased population level. If Coulson et al.'s (1982) hypothesis is correct, opposite changes in these parameters may be expected in an increased population. In this paper, we present the results of such a study.

In 1966–1969, just before Herring Gulls started to increase in numbers in The Netherlands, a study of the breeding biology of the species was made in the Boschplaat nature reserve, located on the eastern part of Terschelling, Dutch Frisian Islands (Fig. 1; Spaans and Spaans 1975). Since then the number of Herring Gulls on the island has tripled—from 6000–8000 pairs in 1966–1969 to 21,000–21,500 pairs in 1983–1984 (Fig. 2). During the same time interval, the numbers of Lesser Black-backed Gulls (*L. fuscus*), which form mixed colonies with Herring Gulls, increased from less than 1000 pairs to 13,000 pairs. For the Lesser Black-backed Gull, numbers have been stable since 1982; for the Herring Gull, numbers have decreased since 1985. The considerable increase in gull numbers during the 1970s started 3–4 years after the Herring Gull control program, initiated on the island in the late 1930s (Drost 1939), had been terminated.

STUDY AREA AND METHODS

The 4400-ha Boschplaat Nature Reserve (approximately 53°25'N, 05°28'E) comprises 5 low, undulating dune complexes (Eerste, Tweede, Derde and Vierde

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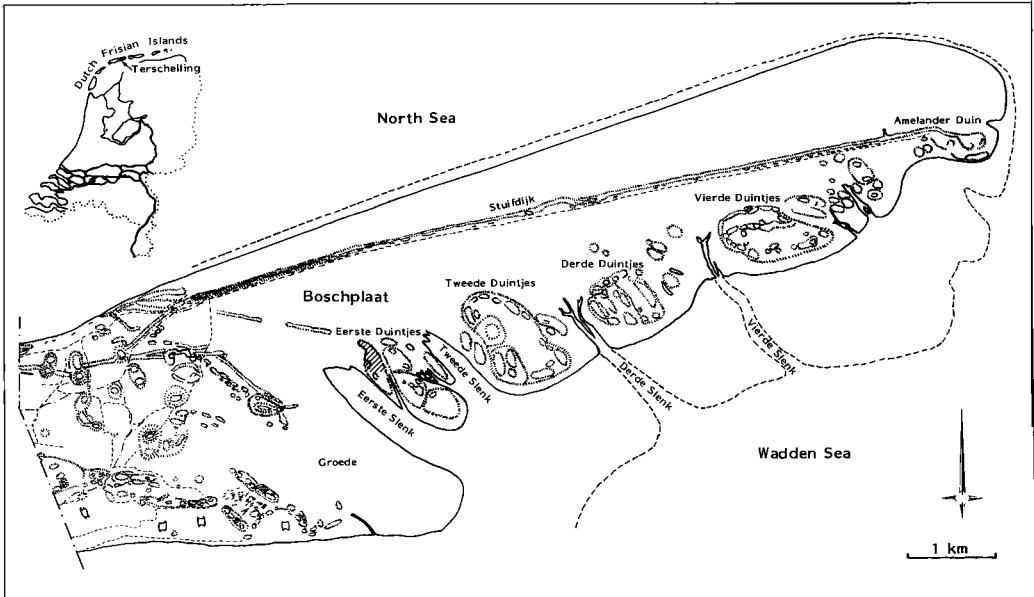


FIGURE 1. The eastern part of Terschelling, showing the Boschplaat Nature Reserve with the study plot (hatched) and the geographic names mentioned in the text.

Duintjes, and Amelander Duin); they are abutted by wide salt marshes and tidal mudflats, which are incised by 4 large tidal creeks (Eerste, Tweede, Derde, and Vierde Slenk) and a number of smaller ones (Fig. 1). The area is protected to the north by a semi-natural sand dam (Stuijdijk) covered by marram grass (*Amphiphila arenaria*). The western half of the reserve, up to the Derde Slenk, is closed to the public during the breeding season. The Groede, and the Eerste and Tweede Duintjes are the sites of large and long-established colonies of Herring Gulls and, since 1926, of Lesser Black-backed Gulls also. Only small numbers of gulls breed outside these areas. In 1983–1984, almost 25% of the Dutch Herring Gulls, and more than 60% of the Lesser Black-backed Gulls, bred in the reserve. Between the late 1930s and the middle of the 1960s, Herring Gulls were vigorously controlled by the poisoning of breeding birds and by the collection, oiling, and shaking of eggs. As a result, in the 1960s, the breeding population may have been younger than in the 1980s (cf. Duncan 1978, Coulson et al. 1982).

In 1966, a 6.06-ha study plot was selected on the northwestern part of the Eerste Duintjes (Fig. 1). In choosing a study site, we attempted to select a plot that comprised a large area of the typical breeding habitat of the Herring Gull, was free of disturbance by man and livestock, and could easily be reached without disturbing other breeding birds in the reserve. In both decades, the study plot included parts of the center and edges of the colony. The dunes in the study plot were covered predominantly with marram grass and buckthorn (*Hippophaë rhamnoides*), with local patches of lyme grass (*Leymus arenarius*), woody nightshade (*Solanum dulcamare*), and elder (*Sambucus nigra*). The dunes were interspersed with small grassy valleys dominated by sea couch (*Elymus pycnanthus*). Herring Gulls

bred mainly in the dunes, Lesser Black-backed Gulls predominantly in the valleys. The microhabitat of the plot was typical of the whole colony. In the 1980s, the dune complexes were covered with more vegetation than in the 1960s. However, there were fewer burrows of rabbits (*Oryctolagus cuniculus*) than in the 1960s, so that the possibilities for chicks to hide themselves against bad weather and predators did not differ much in the two periods.

In 1966, 150 nests randomly chosen within the study plot at the peak of egg laying were studied until late July. In 1967–1969 and 1983–1984 the study plot was searched, from late April through late June, daily for new clutches in such a way that the entire area was covered at least once every 2 days. In 1967–1969, all clutches found in the study plot were followed up to fledging of the young or to failure. In 1983, all clutches were followed up to hatching or failure, but only one out of every three found was further followed. In 1984, one of every three clutches found was further studied. Incomplete clutches and nests with eggs at hatching were checked once or twice a day to establish the dates of egg laying and hatching as accurately as possible.

Each nest was marked with a small numbered stick as soon as eggs were found. Each egg was marked a, b, or c, according to its laying order. In 1969 and in 1983–1984, maximum length and breadth of the eggs were measured to 0.01 mm using vernier calipers. Egg volume was calculated from: $\text{Volume} = 0.5035 \times \text{Length} \times \text{Breadth}^2$ (Spaans and Spaans 1975). In the 1960s data on clutch size and egg volume also included those from a small number of clutches from a small area adjacent to the study plot.

Chicks were individually color-ringed on the day of hatching (day 0). Fledging success was calculated from sightings of fledged young in the immediate vicinity of

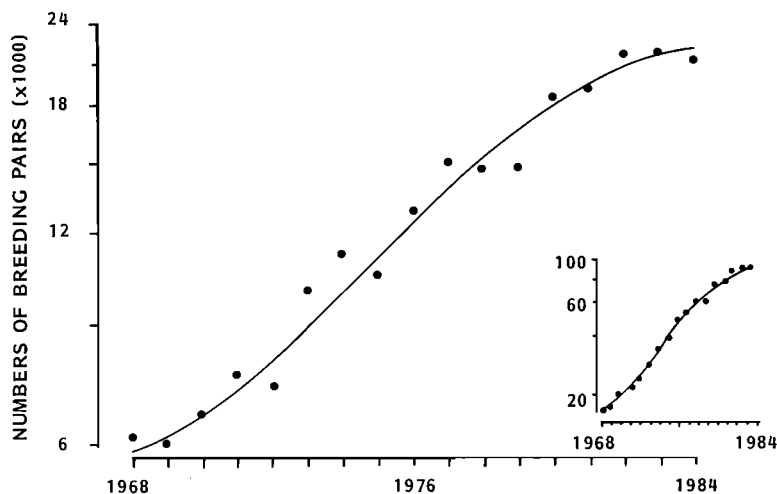


FIGURE 2. The numbers (logarithmic scale) of breeding pairs of Herring Gulls on Terschelling since 1968; the inset shows the population trend for the species in the entire country (curves fitted by eye). The data are taken from the annual Herring Gull censuses organized by the Research Institute for Nature Management and the State Forest Service.

the gullery between early July and late August. These data were supplemented with those of chicks seen alive in the fifth or sixth week of life and not found dead in the colony afterwards nor seen alive just after fledging, and of young that fledged unnoticed (as appeared from sightings or recoveries elsewhere later). The reports of gulls color-ringed at hatching in 1983–1984, when coverage outside the colony area was most intense, indicate that only a very few birds escaped notice just after fledging (Table 1).

Chicks were weighed to the nearest 1.0 g, using a spring balance, on each day they were found alive and healthy. In 1967–1968 and 1984, maximum wing chord was measured by ruler, from day 18, to the nearest 1.0 mm. Between days 4 and 30, the weight of chicks increased approximately linearly. From day 30, it remained approximately the same until fledging (Spaans 1971). Wing length increased linearly from day 18 at least until day 40, which is quite near the average day of fledging. The mean daily weight increases between days 4 and 30, and the mean daily increases in wing length between days 18 and 40 are used here as measures of chick growth. Data are presented according to original brood size and hatching date. Increase in weight and in wing length of cohorts of chicks were estimated by linear regression of weight and wing length on age, allowing for increasing variance with age. Although most chicks were weighed and measured more than once, only one randomly chosen datum per chick was used in order to minimize dependences between observations.

Although the field work was not conducted by the same people in the 1960s as in the 1980s, all worked in a very standardized manner and with about the same levels of contact with the gulls, so that a direct comparison of the results between the two decades seems valid.

Analyses of variance with Poisson-error distribution (McCullagh and Nelder 1983) were used to compare

the dates of clutch initiation and the clutch sizes between years and decades. The χ^2 -test for two independent samples and the Fisher test were used to test differences in the annual mean hatching/fledging success and in the annual mean percentages of the causes of egg/chick loss between the two decades. The volumes of a-, b-, and c-eggs within the same clutches were compared by means of paired t-tests. Differences in egg volume between years were tested by fitting parallel curves of volume against date of clutch initiation, and comparing intercepts of different years by the t-test. There was some, but not conclusive, evidence of divergence between the curves, but this was mainly a result of the small sample size for clutches initiated between 21 and 26 May 1984. Differences in mean daily increase of weight and wing length between years also were tested with t-tests. All tests are two-tailed.

RESULTS

NEST DENSITY

Between 172 and 201 (mean 185) clutches of Herring Gulls were found in the study plot in 1967–1969, and 526–549 (mean 538) clutches were found in the same area in 1983–1984, ex-

TABLE 1
THE NUMBERS OF HERRING GULLS RECORDED
OUTSIDE THE COLONY AREA TO 1 JANUARY 1986
ACCORDING TO THEIR FATE AFTER HATCHING

Fate of chicks	1983	1984
Fledged	23 (78) ²	20 (60)
Unknown ¹	1 (110)	1 (182)

¹ Chicks which were neither seen alive just after fledging nor found dead during the chick stage.

² Numbers in brackets indicate initial numbers of chicks.

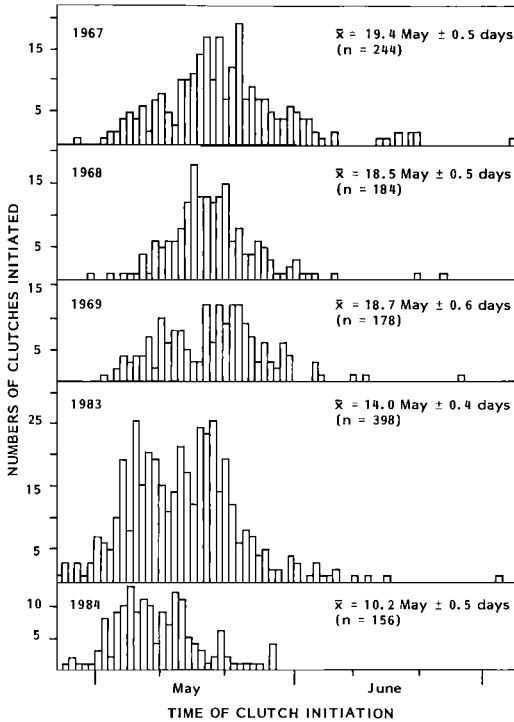


FIGURE 3. Frequency histograms of clutch initiations for 1967–1969 and 1983–1984. Mean dates \pm SE for clutches initiated before 11 June (1967–1969) or 6 June (1983–1984) are also given (see the text for reason of choice of different dates).

cluding a very few certain replacements in each year. In addition, between 46 and 50 (mean 48) clutches of Lesser Black-backed Gulls were found in 1983–1984, compared to only one clutch in 1967 (none in 1968–1969). The low numbers of Lesser Black-backed Gulls in the study plot resulted mainly from the very small area of the typical breeding habitat of the species in the plot.

The mean density for the two species of gulls together was 30.5 (28.4–33.2) nests \cdot ha⁻¹ in the late 1960s and 96.7 (94.4–98.9) nests \cdot ha⁻¹ in the early 1980s. The percentage increase in nest density of the Herring Gull in the study plot was almost as great as that in the total number of the species on Terschelling. This indicates that the

growth of the population here has resulted predominantly in a decrease of the internest distances rather than in an extension of the area occupied by the gulls. This was corroborated by our field observations.

MEAN DATE OF CLUTCH INITIATION

In the years for which we have data from the entire egg-laying season, the distribution of the dates of clutch initiation was not always unimodal (Fig. 3). Discrepancies from unimodality could be ascribed to delays in clutch initiation during periods of cold and wet weather. Besides, the distribution was in all years skewed toward the end of the season as a result of late replacements. Based on the distribution pattern over the season, we identified the end of the laying season for first clutches to be 10 June (1967–1969) and 5 June (1983–1984), respectively. For calculation of the mean dates of clutch initiation we used only clutches started at or before these dates.

There is a significant difference between the annual mean dates of clutch initiation (analysis of variance, $\chi^2 = 158.3$, $df = 4$, $P < 0.001$). In 1967–1969, the mean date of clutch initiation was 18.9 May and in 1983–1984 12.1 May, and were significantly different from one another (analysis of variance, $\chi^2 = 111.9$, $df = 1$, $P < 0.001$).

EGG VOLUME

In two of the three years for which we have data on egg volumes, we found a small but significant difference between the mean volumes of a- and b-eggs within the same clutch (Table 3, 1969: $t = 0.72$, $df = 71$, $P > 0.20$; 1983: $t = 2.98$, $df = 186$, $P < 0.01$; 1984: $t = 5.35$, $df = 188$, $P < 0.001$). In all three years, both a- and b-eggs were, on average, much larger than c-eggs (1969, a-c: $t = 10.29$, $df = 71$, $P < 0.001$; b-c: $t = 11.90$, $df = 71$, $P < 0.001$; 1983, a-c: $t = 18.16$, $df = 186$, $P < 0.001$; b-c: $t = 18.17$, $df = 186$, $P < 0.001$; 1984, a-c: $t = 20.90$, $df = 188$, $P < 0.001$; b-c: $t = 20.96$, $df = 188$, $P < 0.001$).

In 1983, all eggs in clutches of three with at least one egg of which the laying order was known were significantly smaller than their counterparts in 1969, the difference being most pronounced

TABLE 2
MEAN VOLUME (ML) \pm S.E. OF FIRST (A), SECOND (B), AND THIRD (C) LAID EGGS OF HERRING GULLS ON TERSCHELLING IN 1969 AND 1983–1984

Year	No. of clutches	a-egg	b-egg	c-egg
1969	73	89.3 \pm 0.71	89.0 \pm 0.70	83.5 \pm 0.71
1983	188	87.1 \pm 0.51	86.1 \pm 0.47	80.2 \pm 0.47
1984	190	90.1 \pm 0.51	88.3 \pm 0.43	81.9 \pm 0.41

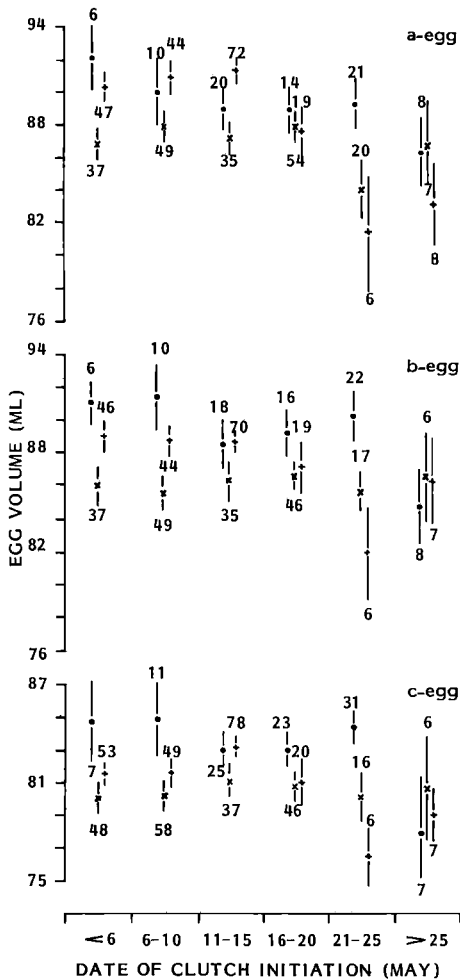


FIGURE 4. Annual mean egg volume (ml) \pm SE of first (a), second (b), and third (c) laid eggs of Herring Gulls on Terschelling before (1969, dots) and after (1983–1984, crosses, plus signs, respectively) the numerical increase in breeding pairs according to the date of clutch initiation. Numbers given are sample sizes.

in the b- and c-eggs (Fig. 4, a-eggs: $t = -2.75$, $df = 472$, $P < 0.01$; b-eggs: $t = -4.50$, $df = 457$, $P < 0.001$; c-eggs: $t = -4.60$, $df = 523$, $P < 0.001$). In 1984, the difference was significant only in the c-eggs, but nearly so in the b-eggs (a-eggs: $t = 0.07$, $df = 472$, $P > 0.20$; b-eggs: $t = -1.91$, $df = 457$, $P < 0.10$; c-eggs: $t = -2.62$, $df = 523$, $P < 0.01$). As can be seen from Figure 4, the smaller egg volumes hold for both early and late breeders.

REPRODUCTIVE SUCCESS

The mean clutch sizes for 1967–1969 and 1983–1984 are shown in Table 3. Two of the

TABLE 3
CLUTCH SIZE OF HERRING GULLS ON TERSCHELLING BEFORE (1967–1969) AND AFTER (1983–1984) THE NUMERICAL INCREASE IN BREEDING PAIRS

Year	Clutch size				Mean
	4	3	2	1	
1967	0	180	47	14	2.69
1968	0	147	30	5	2.78
1969	0	138	33	5	2.76
1983	1	331	155	62	2.49
1984	1	133	25	15	2.69

1322 clutches had 4 eggs. In 1983, 2 females were involved. The same may have been the case for the c/4 in 1984. For this reason, the 2 c/4 are further left out of consideration. Mean clutch sizes differed significantly between the five years (analysis of variance, $\chi^2 = 56.9$, $df = 8$, $P < 0.001$). In 1967–1969, the mean clutch size was 2.74 and in 1983–1984 2.54. These were significantly different from one another (analysis of variance, $\chi^2 = 35.0$, $df = 2$, $P < 0.001$). The difference between the two periods may be an artefact. Not all eggs were found immediately after laying. As a result of the larger predation pressure in the 1980s compared to the 1960s (Tables 4, 5), relatively more eggs may have been robbed unnoticed in the 1980s than earlier.

Hatching and fledging success were quite different in the two periods. In the 1980s, mean hatching success was 61.5%, which was much lower than that in the 1960s (76.5%, Table 4). The difference was due largely to an increase in the percentages of eggs eaten by conspecifics (Table 4). The percentages of added eggs and other causes of egg loss did not change. There was also a large reduction in the percentage of hatched chicks that fledged (Table 5). In the 1960s, mean fledging success was 58.2%, in the 1980s 23.2%. Predation by conspecifics, which may include some scavenging, was again the main cause of the losses (Table 5). The distribution of regurgitated color-rings over the colony suggested that predation was mainly by non-neighbors rather than by gulls from adjacent territories.

The reduction in hatching and fledging success held for all gulls, regardless of the date of clutch initiation (Figs. 5, 6). As a result of the large numbers of eggs and chicks lost in the 1980s, the number of fledged young per pair decreased from 1.25–1.50 (mean 1.35) in 1967–1969 to 0.34–0.44 (mean 0.39) in 1983–1984, a reduction of more than 70%, on average. At present, predation increases so much during the course of the breeding season, that even birds laying around the mean date of clutch initiation produce hardly any young to the age of fledging.

TABLE 4
COMPARISON OF ANNUAL MEAN HATCHING SUCCESS AND CAUSES OF EGG LOSS BY PERCENTAGES (MEANS, RANGES) OF EGGS LAID BY HERRING GULLS ON TERSCHELLING BEFORE (1967-1969) AND AFTER (1983-1984) THE NUMERICAL INCREASE IN BREEDING PAIRS

Fate of eggs	1967-1969	1983-1984	Tests of significance of differences
Hatched	76.5 (75.5-77.9)	61.5 (54.8-68.1)	$\chi^2 = 78.9, P < 0.001$
Predation ¹	8.2 (6.8-9.9)	22.4 (15.0-29.8)	$\chi^2 = 114.0, P < 0.001$
Infertility/embryonic death	13.2 (11.7-15.1)	14.4 (14.0-14.8)	$\chi^2 = 0.9, n.s.^2$
Died during hatching	1.2 (1.0-1.5)	1.6 (0.4-2.8)	$\chi^2 = 0.9, n.s.$
Rolled out of nest	0.8 (0.4-1.3)	0.0 (0.0)	Fisher test, n.s.
Destroyed by observer	0.1 (0.0-0.2)	0.1 (0.0-0.1)	Fisher test, n.s.
No. of eggs studied	1374	1697	

¹ Largely by conspecifics.

² n.s. = not significant.

SIZE OF FLEDGLINGS

In 1983-1984 chicks gained weight slower than in 1966-1968, in 17 of the 22 possible pairwise comparisons between the two periods (Fig. 7). In two cases, the difference was significant (b/3, 12-19 May, 1966-1983: $t = 2.41, df = 33, P < 0.05$; b/3, <6 May, 1967-1984: $t = 2.74, df = 37, P < 0.01$). The slower weight increase resulted in a lower weight of the chicks at day 30 than in the 1960s, as calculated from the regression equations. In five cases, the difference was significant (b/3, <6 May, 1967-1984: $t = 4.10, df = 37, P < 0.001$; b/3, 6-11 May, 1968-1983: $t = 2.65, df = 13, P = 0.02$; b/3, 12-19 May, 1966-1983: $t = 2.90, df = 33, P < 0.01$; b/3, 12-19 May, 1967-1983: $t = 2.59, df = 46, P < 0.02$; b/2, 6-11 May, 1967-1984: $t = 2.81, df = 6, P < 0.05$), and in two cases nearly so (b/3, 6-11 May, 1967-1983: $t = 1.91, df = 14, P < 0.10$; b/2, 12-19 May, 1967-1983: $t = 3.09, df = 3, P < 0.10$). In both decades, weight varied around the 30th day level at least until fledging, so that the differences in weight at day 30 must have been reflected in the weight of the birds at fledging.

We have fewer data on wing length than on weight. However the few data we have suggest that in the 1980s, wing length between days 18 and 40 increased as fast as in the late 1960s (Table 6, b/3, <6 May, 1967-1984: $t = -0.82, df = 19, P > 0.20$; b/3, <6 May, 1968-1984: $t = -0.05, df = 14, P > 0.20$; b/3, 6-11 May, 1967-1984: $t = -1.43, df = 15, P > 0.20$; b/3, 6-11 May, 1968-1984: $t = -1.62, df = 15, P > 0.10$; b/3, 12-19 May, 1967-1984: $t = 0.46, df = 26, P > 0.20$; b/3, 12-19 May, 1968-1984: $t = 0.72, df = 3, P > 0.20$). In none of the cases did wing length on day 40 differ significantly ($P > 0.20$). These results suggest that in the 1980s young were of the same size as in the 1960s but less well-fed than earlier.

DISCUSSION

The total number of large gulls on Terschelling has shown a 5-fold increase over the last 15 years. The larger population has resulted in a 3-fold increase of the nest density within our study plot, where in 1983-1984 almost 100 pairs of large gulls bred per hectare.

TABLE 5
COMPARISON OF ANNUAL MEAN FLEDGING SUCCESS AND CAUSES OF CHICK LOSS BY PERCENTAGES (MEANS, RANGES) OF HERRING GULL CHICKS ON TERSCHELLING BEFORE (1967-1969) AND AFTER (1983-1984) THE NUMERICAL INCREASE IN BREEDING PAIRS

Fate of chicks	1967-1969	1983-1984	Tests of significance of differences
Fledged	58.2 (56.4-60.4)	23.2 (19.1-27.2)	$\chi^2 = 175.8, P < 0.001$
Predation/scavenging	9.8 (5.8-13.6) ¹	23.0 (21.3-24.7)	$\chi^2 = 162.9, P < 0.001$
Other causes of death		14.7 (13.2-16.2)	
Fate unknown ²	32.0 (28.2-33.8)	39.2 (38.3-40.0)	$\chi^2 = 7.8, P < 0.01$
No. of chicks studied	865	596	

¹ No distinction made between predation/scavenging and other causes of death, because only a very few chicks fell in the former category in those years.

² Almost all these chicks died unnoticed before fledging (see Table 1).

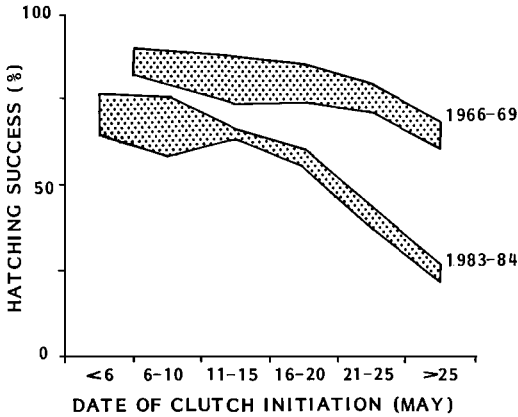


FIGURE 5. Annual mean hatching success (percentages, ranges) of Herring Gulls on Terschelling before (1966–1969) and after (1983–1984) the numerical increase in breeding pairs according to the date of clutch initiation.

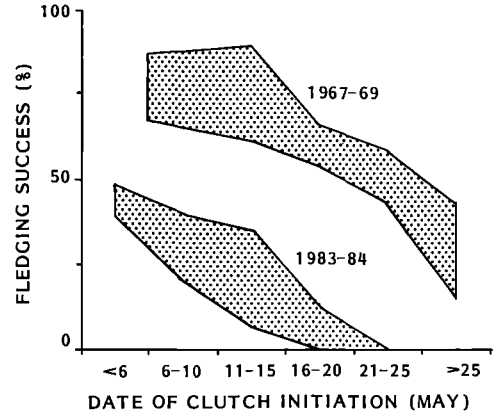


FIGURE 6. Annual mean fledging success (percentages, ranges) of Herring Gulls on Terschelling before (1967–1969) and after (1983–1984) the numerical increase in breeding pairs according to the date of clutch initiation.

We found marked changes in the breeding biology of the Herring Gull in the 1980s compared to the late 1960s. The number of fledged young per pair in the 1980s decreased by more than 70%, largely resulting from an increase in the percentages of eggs and chicks robbed by conspecifics. Moreover, eggs decreased in size, and chicks gained weight more slowly and fledged at lower weight. In fact, the differences in growth between the two decades must have been even larger than those shown, for two reasons. Firstly, in the 1980s, as a result of the higher chick mortality, many more original b/3 and b/2 decreased in size than in the 1960s. Most of the mortality

occurred in the first week after hatching. As a consequence, in the 1980s chicks met less competition for food after the first few days of life than in the 1960s and should therefore have grown better than earlier. Secondly, c-chicks are smaller than a- and b-chicks and hatch a few days after these, resulting in much higher post-hatching mortality of the c-chicks (Parsons 1970, Spaans and Spaans 1975). Therefore, in the 1980s, relatively more a- and b-chicks, which are not only larger but also grow faster than c-chicks, remained alive than in the 1960s. This factor should also have positively influenced mean weights in the 1980s. Yet, in these years, chicks

TABLE 6
MEAN DAILY INCREASE PER ANNUM IN WING LENGTH (MM) BETWEEN DAYS 18 AND 40 \pm S.E. OF HERRING GULL CHICKS ON TERSCHELLING BEFORE (1967–1968) AND AFTER (1984) THE NUMERICAL INCREASE IN BREEDING NUMBERS¹

Brood size	Date of clutch initiation (May)	1967	1968	1984
b/3	<6	7.0 \pm 3.8 (8)	9.0 \pm 0.6 (3)	10.1 \pm 0.8 (15)
b/3	6–11	8.6 \pm 0.6 (8)	8.1 \pm 0.5 (8)	10.4 \pm 1.1 (11)
b/3	12–19	9.0 \pm 0.5 (26)	9.1 \pm 0.5 (3)	8.2 \pm 0.5 (4)
b/3	20–26	6.8 \pm 1.3 (12)	9.4 \pm 0.9 (16)	
b/3	>26	12.4 \pm 2.7 (4)		
b/2	<6			6.3 \pm 2.9 (5)
b/2	6–11			8.9 \pm 1.5 (5)
b/2	12–19	9.3 \pm 2.2 (3)		
b/2	20–26	8.0 \pm 3.7 (3)		
b/1	6–11	7.4 \pm 0.9 (5)	8.1 \pm 0.1 (3)	
b/1	12–19	8.9 \pm 0.6 (10)		
b/1	20–26	7.6 \pm 0.8 (9)	10.9 \pm 2.0 (7)	
b/1	>26	9.7 \pm 1.2 (5)		

¹ Data are given according to the original brood size and the date of clutch initiation. Numbers of chicks measured indicated in brackets.

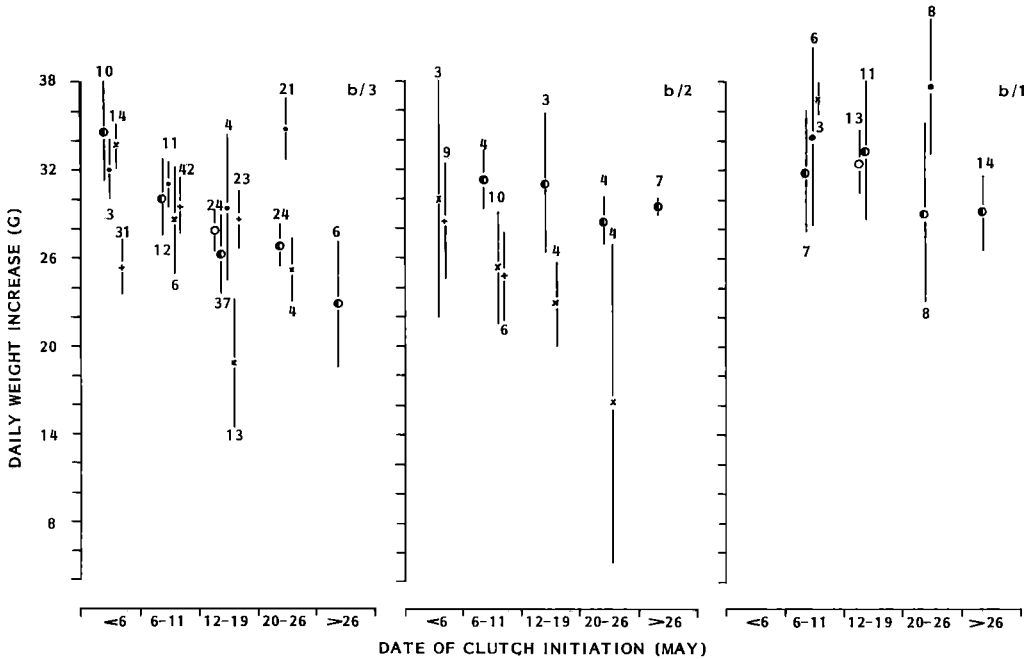


FIGURE 7. Mean daily weight increase per annum between days 4 and 30 (g) \pm SE of Herring Gull chicks on Terschelling before (1966–1968, open, half-open, and black dots, respectively) and after (1983–1984, crosses, plus signs, respectively) the numerical increase in breeding pairs according to the original brood size and the date of clutch initiation. Numbers given are sample sizes.

gained weight more slowly and reached lower fledging weights than did earlier ones.

Considering Figures 4–7, it can be argued that it would be more appropriate to compare egg volume, breeding success, and chick growth in relation to the peak of egg-laying rather than to the date of clutch initiation. We did this and found that the trends remain the same. Therefore, we conclude that the negative changes we found are due not only to a shift in the timing of breeding, but also to some other factor(s).

One may hypothesize that any increase in predation rates may have resulted from observer disturbance of pairs at higher densities. We reject this idea because the low breeding success was not limited to the study plot but was characteristic of the entire colony, as shown from the ratio adults/fledged young at the colony edge during low tide at the end of the breeding season (more young than adults in the late 1960s and the opposite in the 1980s). Several aspects of the breeding performance of Herring Gulls such as date of clutch initiation and egg size are known to vary with age, females laying progressively earlier up to at least 9 years old and laying eggs progressively increasing in volume up to 7 or 8 years of age and then declining (Davis 1975). As a result of the intense cull program conducted

on the island between the late 1930s and the middle of the 1960s, the Herring Gull population may have been younger at the beginning of the study period than at the end. The decrease in the volume of eggs on the island, however, held for all cohorts irrespective of the date of clutch initiation (Fig. 4). Such a pattern is unlikely if only an age effect were operative. An age effect, however, cannot be excluded as a reason for the shift that took place in the mean date of clutch initiation since the 1960s (cf. Davis 1975). Alternatively, the strong positive selection—resulting from the seasonal trend in egg and chick predation—in favor of gulls which lay their eggs early in the season may have played a role.

Coulson et al. (1982) showed that several factors of population dynamics changed in a colony that had been reduced to a quarter of its former level. Thus, an appreciable increase in egg size, wing length, and body weight of the breeding birds occurred, while there was also some evidence for an improvement of the breeding success. Moreover, there was an increase in the proportion of third- and fourth-year birds in the breeding population. We have no data on the age at which recruits enter the population at Terschelling, but in 1983–1984, breeding birds retaining feathers typical of immature gulls were

seen by us occasionally. The same pattern was observed by Coulson et al. (1982) prior to the starting of the cull program on the Isle of May; it is interesting to note that nest density at that time was approximately the same as was the density on Terschelling in 1983–1984.

The changes found by us in a population that had increased are, therefore, just opposite to those found by Coulson et al. (1982) in a population that had decreased, confirming the prediction put forward in the introduction. Herring Gulls clearly show marked changes in factors related to the population dynamics of the species when the number of breeding birds fluctuates; the direction of the changes is opposite to the direction of the population trend. However, the question still remains as to whether competition takes place primarily on the breeding grounds or in the feeding areas. The pattern of predation on Terschelling (by non-neighbors rather than by gulls from adjacent territories) suggests that the increase in predation is related there to food shortage rather than to stress on the breeding area (contra de Wit and Spaans 1984). The smaller eggs and the poorer condition of the chicks support the idea of a food shortage (cf. Verbeek 1986).

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