

Breeding behaviour and breeding success of a colony Little Gulls *Larus minutus* in the Netherlands

Broedgebied en broedsucces van een kolonie Dwergmeeuwen *Larus minutus* in Nederland

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The breeding distribution of the Little Gull *Larus minutus* ranges from Southern Finland and Russia to Central- and East-Siberia (figure 1). Sometimes breeding colonies appear far beyond the normal breeding range. Such settlements have been recorded from Sweden, Denmark, Germany and the Netherlands. Until recently, in the Netherlands breeding records of Little Gulls were only known from the SE of the province of Friesland, where a varying number of pairs (maximum 15) nested between 1942 and 1956. In 1972, after an absence of many years, breeding was recorded from Oostelijk Flevoland (Marra 1973) and Lauwerszee (Franke & Meijer 1974). In the Lauwerszee area Little Gulls have been recorded nesting ever since.

From 1975 onwards the Little Gulls of the Lauwerszee area have been subject of a study on communication behaviour. Since we could not find in the literature any study that could inform us about the general breeding behaviour and ecology of the species, some general data were collected as well. This paper summarises the data on numbers, distribution, habitat preference, age, breeding success and mortality agents, collected between 1975 and 1978.

Numbers

The Lauwerszee area was part of the Dutch Waddensea. It was a 10 km wide estuary which, in its original state, was a salt water tidal area

characterised by sand- and mud-flats crossed by channels of varying depth. In 1969 the area was embanked; the tidal flats became permanently dry and the salt water in the channels soon turned to fresh. The embankment of the area led to marked changes in the number and species composition of the birds visiting the area. Among the many species whose numbers and distribution were influenced by the embankment is the Little Gull. Before embankment Little Gulls were mainly seen during spring and autumn migration, numbers were small and the birds never stayed in the area for long. In contrast to this situation, in the first year after the embankment more than a hundred Little Gulls invaded the area in May, remained there till the middle of June and there upon gradually decreased. Ever since the number of Little Gulls visiting the area has increased from year to year (maximum number 566 in May 1978) but the distribution over time (figure 2, upper graph) has remained unaltered.

The Little Gull population of the Lauwerszee area consists of two age categories: juveniles (second calendar-year) and adults (third calendar-year and older). Figure 2 (lower graphs) gives for both categories the maximum number of birds per 10-day period present between April and July 1978. Arrival and departure was earlier in the adults than in the juveniles. The same phenomenon was recorded in 1975, 1976 and 1977. Spring migration is thus influenced by age.

In 1970 and 1971 several adult Little Gulls

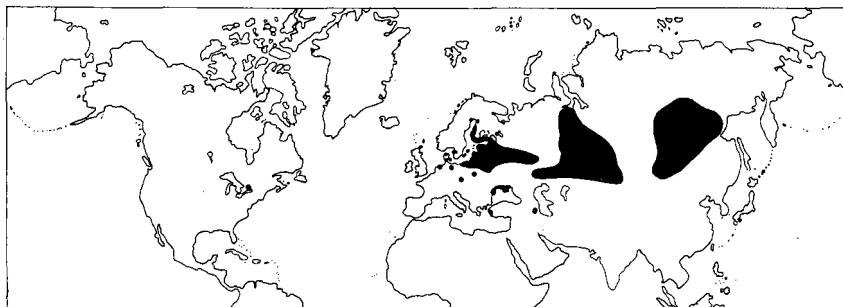


Figure 1. Breeding distribution of the Little Gull (after Voous 1960). Broedgebied van de Dwergmeeuw (naar Voous 1960).

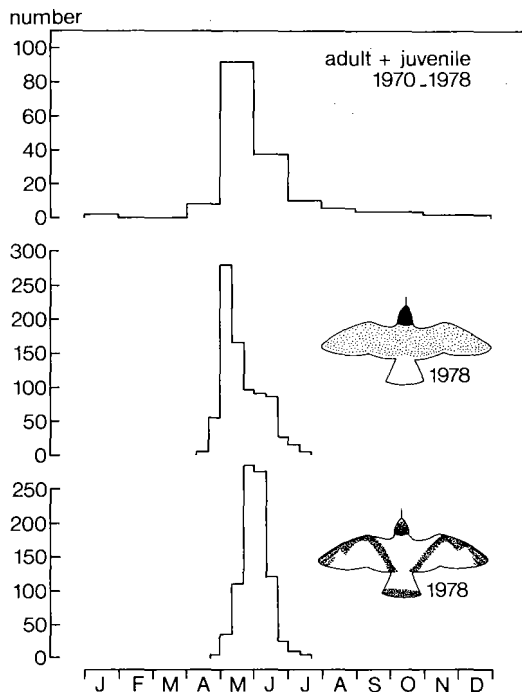


Figure 2. Monthly average number of Little Gulls recorded in the Lauwerszee area between 1970 and 1978 (upper graph) and the maximum number of adults (third calendar-year or older) and juveniles (second calendar-year) per 10-day periods in 1978 (lower graphs). Gemiddeld aantal Dwergmeeuwen waargenomen in het Lauwerszeegebied tussen 1970 en 1978 (boven) en het maximum aantal volwassen (derde kalenderjaar en ouder) en juvenielen (tweede kalenderjaar) per decade in 1978 (midden, onder).

Table 1. Number of breeding pairs of the Little Gull in the Lauwerszee area. Aantal broedparen van de Dwergmeeuw in het Lauwerszeegebied.

Year Jaar	No. of pairs Aantal paren	No. of colonies Aantal kolonies	Pairs/colony Paren/kolonie
1972	7	3	1-3-3
1973	15	3	2-4-9
1974	42	2	9-33
1975	25	3	1-7-17
1976	44	6	2-2-3-3-7-27
1977	30	1	30
1978	61	5	3-3-16-19-20

were recorded among Black-headed Gulls *Larus ridibundus*, Common Terns *Sterna hirundo* and Arctic Terns *S. paradisaea* which had started nesting in the new polder. These Little Gulls did not breed, but they did show signs of attachment with the area in the neighbourhood of the tern and gull colonies: they reacted to human disturbance by hovering above the intruder uttering weak but distinct alarm calls. The same behaviour was recorded among Little Gulls which, in later years, concentrated in the breeding area prior to egg-laying.

From 1972 onwards Little Gulls have been recorded breeding in the area (Franke & Meijer 1974). Table 1 gives for all years the number and distribution of breeding birds. Between 1972 and 1978 the number of breeding pairs has increased. Independently of the total number of breeding birds within a particular year, the gulls either settled in one colony (1977) or in several relatively small settlements (1976).

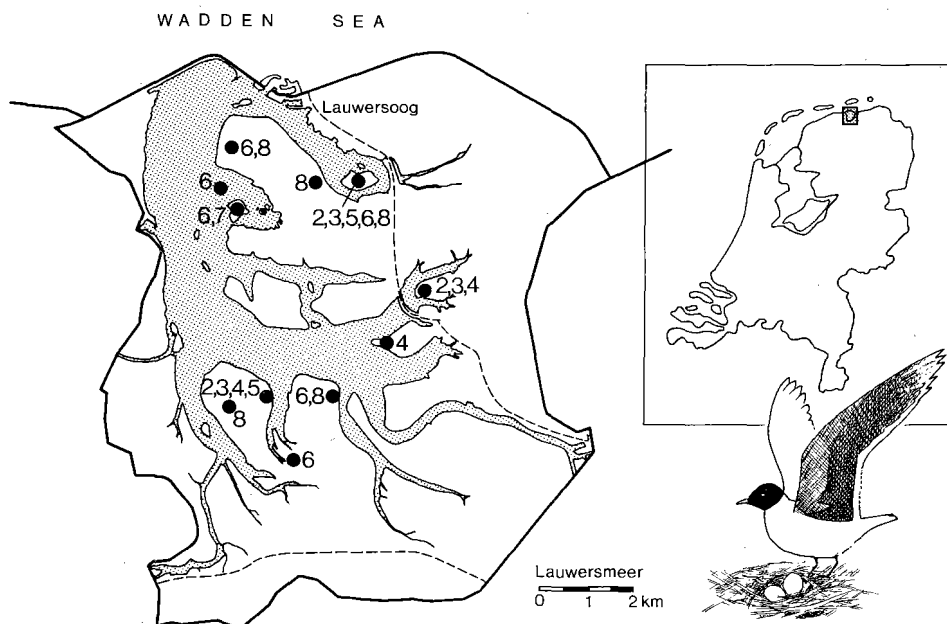


Figure 3. The distribution of Little Gull colonies in the Lauwerszee area between 1972 and 1978. Numbers refer to the year of breeding: 2 = 1972, 3 = 1973, etc. De verspreiding van Dwergmeeuwkolonies tussen 1972 en 1978. De getallen hebben betrekking op de jaren waarin gebreed werd.

Figure 3 gives the combined data on colony distribution. A relatively large number of different breeding places was chosen by the gulls. In contrast with the majority of gull and tern species of the northern hemisphere which tend to occupy the same area for breeding year after year, in the Little Gulls which nested in the Lauwerszee area the tendency to return to the same place for breeding in consecutive years was either absent or remarkably low. This might be related to (1) a lack of any strong site attachment, (2) changes in the environment from year to year, (3) the absence of breeding birds which have bred in the area before. This problem will be touched upon again in the discussion.

Arrival and settlement

Between 1975 and 1978 the first Little Gulls arrived in the area on 19, 30, 24 and 20 April, respectively. During the first days after arrival they were mainly seen foraging along the water-surface. This gradually changed, however, and in the course of May they were more and more seen hunting on insects above the land. In the course of May there also was an increasing number of Little Gulls concentrating on gathering places on land. Sometimes the gulls preferred gathering places close to a nesting site of the year before. Very often however, they concentrated on new places. The number of birds present on the gathering places and their age composition varied greatly at different times of the day and at different times of the season. Changes in numbers seemed on the one hand dependent on the weather situation which is of influence on food-availability, and on the other on the strong tendency of the birds to change from one place to another under the influence of disturbance.

Courtship displays started as soon as the first birds had arrived in the breeding area. In the beginning aerial displays dominated, but in the course of the pre-laying period ground displays, which were mainly seen on gathering places, gradually replaced them. In contrast to the majority of Larid species of the northern hemisphere, the Little Gulls on the gathering places did not behave territorially. Among displaying birds overt aggression was often recorded but aggressive behaviour could not be related to the defense of a particular place. We also have no indications that individual birds are consistently present at a particular spot. Among the Little Gulls of the Lauwerszee area colony occupation and nest-site selection did not take place until a few days before the start of egg-laying. Observations made in 1975 showed that two individually recognizable pairs suddenly changed their behaviour by vigorously defending a territory on

30 May. At the end of the same day, after several aggressive encounters, both pairs had secured a territory in which they were actively involved in nesting activities. Two days later the first egg was laid.

In the pre-laying period the gulls were very sensitive to human disturbance and, therefore, had to be approached carefully. In general, we could not predict where the gulls would settle and since the time-lapse between settlement and egg-laying was small we often had no opportunity to study the gulls in this stage. For this reason it was difficult to establish what social and environmental factors play a role in nest-site determination. According to the characteristics of a number of colonies studied, the following factors seemed of importance: (1) vegetation, (2) predation and disturbance, (3) the presence of colonies of other Larid species.

(1) The composition of plant species greatly varied between different breeding places, but topography and vegetation density were rather uniform. All colonies studied were situated close to the shore on small islets or peninsulas (figure 3), they were all on dry ground in an area with low vegetation. A small number of nests was found in a completely bare, sandy or shell-covered area, but this seemed rather uncommon. Most colonies were situated in an area covered with a sparse and homogeneous vegetation of *Salicornia spec.* and *Suaeda maritima*, or in an area with a more heterogeneous vegetation in which *Puccinellia spec.*, *Agrostis stolonifera*, *Festuca rubra*, *Atriplex hastata*, *Aster tripolium* and *Epilobium hirsutum* dominated. Sometimes the gulls nested in the neighbourhood of patches of Reed *Phragmites australis* or willow bushes *Salix spec.* Although the nests in such areas sometimes ended up in rather high vegetation, we had the impression that the gulls, in general, avoided nesting in high vegetation. Though little is known about the habitat in which the Little Gull nests in the more central parts of its breeding range, the Lauwerszee breeding area seems rather atypical. Witherby et al. (1941) mention marshes and marshy islets, Berg (1916) describes a colony in southern Sweden where Little Gulls nested in a rather wet area covered with dense vegetation of *Cladium mariscus*. In SE Friesland in the Netherlands Little Gull-nests have been recorded on floating vegetation (mainly *Stratiotes aloides*) and Voous (1960) suggests that the typical habitat of the species is on vegetation surrounded by water.

(2) Little Gulls are remarkably tame after they have settled and laid their eggs. However, probably as a consequence of the lack of any strong site attachment in the pre-laying period, groups concentrated on gathering places were easily disturbed by predators and human intruders. On several occasions we had the impression that the regular presence of predators

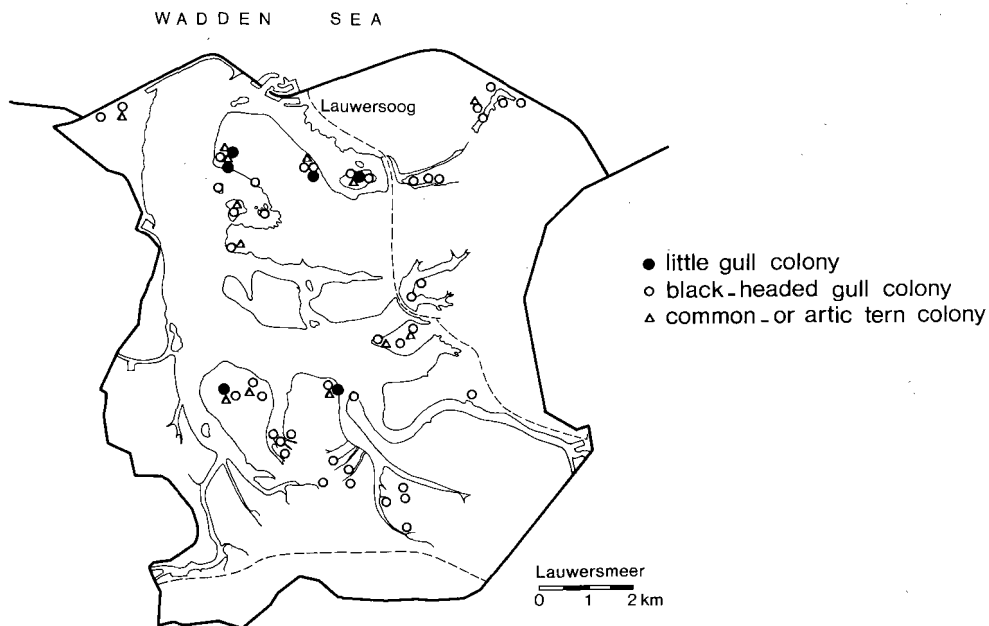


Figure 4. Map of the Lauwerszee area with the colony distribution of Little Gull, Black-headed Gull, Common- and Arctic Tern in 1978, showing that Little Gulls tend to nest in the neighbourhood of colonies of other Larid species. *Kaart van het Lauwerszee-gebied met de verspreiding van de kolonies van Dwergmeeuw, Kokmeeuw, Visdief en Noordse Stern in 1978, illustrerend dat Dwergmeeuwen de neiging hebben in de omgeving van kolonies van andere Laridae te nestelen.*

within a particular area caused the birds to move to another place. The places selected for nesting were in all cases rather isolated and were relatively difficult to reach for terrestrial predators.

(3) All Little Gulls colonies studied were situated in the neighbourhood of colonies of Black-headed Gulls ($n = 19$), Common or Arctic Terns ($n = 17$) or Avocets *Recurvirostra avosetta* ($n = 13$). On 10 occasions the Little Gulls settled in an area where the species mentioned were all present together (figure 4 gives the 1978 situation as an example). Very often the Little Gulls nested in the middle of the Common Tern colony, which in turn was situated at the border of a Black-headed Gull colony. As a consequence they usually nested nearer to the terns than to the Black-headed Gulls. They were never seen to nest in the middle of a Black-headed Gull colony, as for instance Sandwich Terns *Sterna sandvicensis* very often do (Veen 1977).

Nest, eggs and chicks

Among the Little Gulls nesting in the Lauwerszee area inter-nest distances were highly variable. In small colonies neighbouring pairs usually nested at more than 10 m from each other, whereas in the larger colonies the nests usually were much closer together. In 1978 measurements were taken in four colonies (together 58 nests). Minimum inter-nest distances varied

between 1.5 and 120 m; 43% of the birds nested at distances between 2 and 4 m from each other.

At the beginning of the breeding season the nest usually is no more than a shallow depression in the ground, either bare or covered with a thin layer of straws and twigs. During the incubation period the breeding bird usually were very active with nest-building activities before and after nest-relief. This often resulted in a marked increase of nest material in the course of the season.

The seasonal distribution of egg-laying is given in table 2. There were no marked differences in the mean date of egg-laying of different colonies within the same year. For the Lauwerszee breeding population as a whole egg-laying was highly synchronized with a marked peak between 21 and 30 May.

The majority of pairs had a clutch of 3, but 2-egg clutches were common as well (table 3). Nests with 4 (1976 and 1978) and 5 (1977) eggs have been recorded, but in all cases the colouration of the eggs within such nests suggested that they

Table 2. Laying date (first egg in nest) of Little Gulls in the Lauwerszee area. *Legdatum (eerste ei in nest) van Dwergmeeuwen in het Lauwerszeegebied.*

Period Periode	1975	1976	1977	1978
11-20 May	1	2	2	1
21-31 May	15	23	15	54
1-10 June	2	10	13	3
11-20 June		2		1

Table 3. Clutch size of Little Gulls in the Lauwerszee area. *Legselgrootte van Dwergmeeuwen in het Lauwerszeegebied.*

Clutch size <i>Legselgrootte</i>	1975	1976	1978
2	5	8	5
3	13	26	53
4	0	1	1

originated from more than one female.

Since nest checks were made with intervals of at least one day, my data on laying interval between first, second and third egg of a clutch are not very accurate. In general second eggs were laid 1 to 3 days after the first, while third eggs were laid 1 day after the second.

Little Gulls start incubation after the first egg is laid. The incubation period for a number of first, second and third eggs within a clutch is given in table 4. The incubation period averages 21–22 days; no differences are apparent between first, second and third eggs.

Both male and female incubate. In the beginning the female sits for considerably longer periods than the male. When the season progresses, however, male and female take equal shares and both make sitting stints of roughly 0.5–2 hours.

Since incubation starts after the first egg is laid, the chicks hatch asynchronously. Within a few days after hatching, the chicks tend to leave the nest walking around in the neighbourhood. Chicks from the same nest usually each go their own way and, as a consequence often sit at relatively large distances from each other. The tendency to walk away from the nest is strongly influenced by human disturbance. Observations from a hide showed that even one- and two-days old chicks may react to human disturbance by walking a few meters from the nest. Chicks of

Table 4. The incubation period of Little Gulls in the Lauwerszee area. *De broedduur van Dwergmeeuwen in het Lauwerszeegebied.*

Order in which eggs were laid <i>Volgorde waarin eieren werden gelegd</i>	Incubation period in days <i>Broedduur in dagen</i>		
	21	22	23
first <i>eerste</i>	6	5	1
second <i>tweede</i>	4	2	1
third <i>derde</i>	2	1	

three days old invariably do so and a 5-day old chick has been recorded walking away from the nest more than a hundred meters, after it had been disturbed for the third time within a few hours. In the first week of life the chicks come back to the nest to be fed and brooded, but as they get older they usually leave the nesting area. On a number of occasions groups of chicks varying in age between 1 and 2 weeks were found at a distance of several hundred meters from the nesting area. Our data on the age at which the chicks are able to fly are based on observations of only two chicks. For both the fledging age was between 3½ and 4 weeks.

Age of breeding birds

In all years of observation we noticed breeding birds with a plumage pattern characterized by immature traits, e.g. white feathers on the head, black tips on the outer primaries and light underwings. Details on the moult of the Little Gulls are only available from a field study made by Tinbergen (1933, 1937). According to Tinbergen in spring and summer of their second calendar-year Little Gulls are characterized by a predominantly white and grey plumage except for a varying amount of black feathers on the head, a

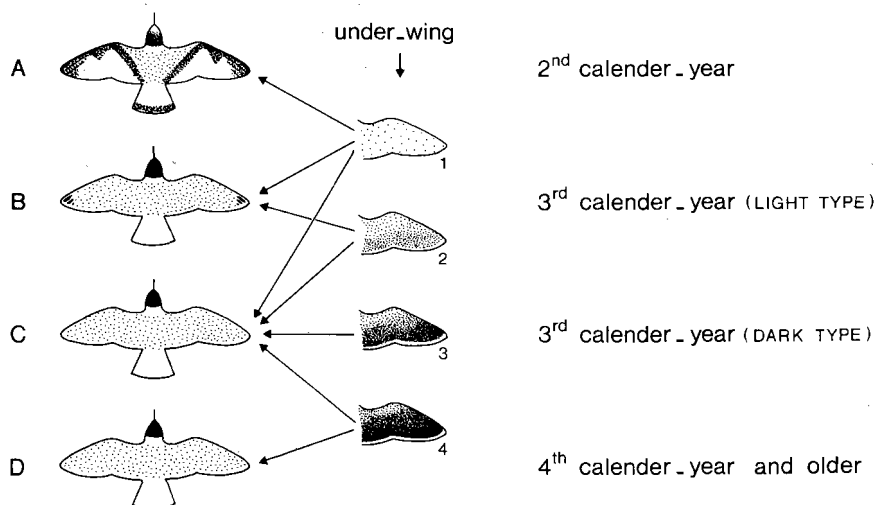


Figure 5. Plumage patterns of Little Gulls nesting in the Lauwerszee area between 1975 and 1978. *Verenkleden van Dwergmeeuwen nestelend in het Lauwerszeegebied tussen 1975 en 1978.*

black V formed by dark upper wing-coverts and a black band at the end of the tail. At the end of the same year, after the moult has taken place, two different plumage-types can be distinguished: in some birds the under-wings change to dark grey or black and all dark feathers characteristic for the juvenile pattern disappear. In others, the under-wings become only partly black or remain even white, while the new outer primaries often have a black spot at the end. No information is available on the moult from the sub-adult to the adult plumage. It may be assumed, however, that all Little Gulls adopt the adult plumage at the end of the third calendar-year.

Figure 5 gives the various plumage patterns recorded among the breeding birds present in the Lauwerszee area between 1975 and 1978. The arrows indicate possible combinations. Age-determination has been based on Tinbergen's data. According to the information available individuals with a completely adult plumage pattern may be either in their third calendar-year or older.

Between 1975 and 1977 no attempt has been made to quantify the occurrence of different age-groups within the breeding population. Once an individual in its second calendar-year (figure 5A) was found on the nest. We also found that the majority of females belonged to the light type third calendar-year category (figure 6) while many males belonged to the dark type of this category (figure 7). In 1978, to obtain more detailed information, 86 breeding birds were examined from a hide. The first column of figure 8 shows that juvenile characteristics in the head, wing-tip and under-wing occurred in 3, 16 and 74% respectively of the birds observed. White feathers on the head occurred in only two individuals. Both were males, who except for the white on the head, showed no other juvenile characters. Since in other species of hooded gulls a small number of white feathers on the head often occurs in combination with an otherwise completely adult plumage pattern, it is doubtful whether this character is a reliable measure of immaturity and, as a consequence, of age determination. Dark wing-tips often occurred in combination with a pre-dominantly white underwing, sometimes with an intermediate shade, but never with a dark underwing. So dark wing-tips (16% of birds examined) only occurred in combination with juvenile characteristics in the colouration of the under-wings (74% of birds examined). Therefore, altogether 74% of the birds studied should be regarded as in their third calendar-year. The age of the remaining 26% with adult plumage cannot be determined with certainty.

In individual pairs of the Little Gulls males are probably always bigger than females. The role of the male and the female during courtship display

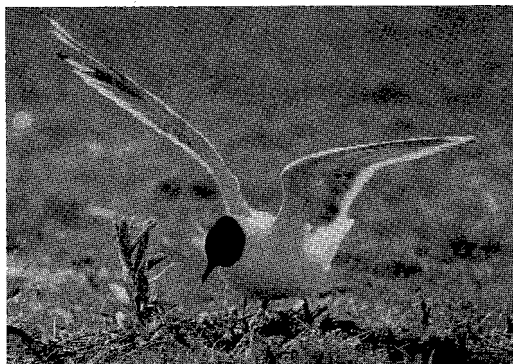


Figure 6. Female Little Gull (breeding bird) with light underwings and black tips on the outer primaries, Lauwerszee area, June 1976 (J. Veen). *Vrouwje Dwergmeeuw (broedvogel) met lichte ondervleugels en zwarte stippen op de buitenste grote slagpennen.*



Figure 7. Male Little Gull (breeding bird) with dark underwings, Lauwerszee area, June 1976 (J. Veen). *Mannetje Dwergmeeuw met donkere ondervleugels.*








	total n=86	males n=20	females n=19
	97%	90%	100%
	3%	10%	0%
upper wing			
	84%	100%	63%
	16%	0%	37%
under wing			
	26%	60%	0%
	44%	40%	37%
	30%	0%	63%

Figure 8. Occurrence of plumage characteristics among male and female Little Gulls nesting in the Lauwerszee area in 1978. *Het voorkomen van verenkleed kenmerken bij mannelijke en vrouwelijke Dwergmeeuwen nestelend in het Lauwerszeegebied in 1978.*

and care of the brood is different. These differences made it possible to distinguish between male and female on a number of occasions (figure 8). Dark wing-tips and light under-wings were only found in females. Dark under-wings were only seen in males, while intermediate under-wings occurred in both males and females. The combination of the colouration of under-wings of male and female within pairs ($n = 38$) was not different from randomness ($X^2 = 1.39$, $p < 0.1$).

Breeding records described by Berg (1916) all refer to either individuals in their third calendar-year or older ones. Since we have only one record of a Little Gull breeding in its second calendar-year, it is likely that Little Gulls, as a rule, do not breed before their third calendar-year. With respect to the Lauwerszee situation this means that in 1978 probably all females and at least 50% of the males studied were recruit breeders. The same phenomenon was found in 1975, 1976 and 1977. I therefore conclude that the Little Gull population of the Lauwerszee area each year mainly consisted of individuals which had not bred before.

Breeding success

Little information is available on the breeding success of the Little Gulls nesting in the Lauwerszee area between 1972 and 1974. Newly hatched chicks were found in all years (A. Timmerman Azn. pers. com.) but in most cases these chicks disappeared from the colony area within a few days after hatching. In 1973 and 1974 in three colonies groups of chicks varying in age between 1 and 2 weeks were recorded in the neighbourhood of the nesting area (G. P. Baerends and A. Timmerman Azn. pers. com.). In 1974 7 chicks reached the fledging age (M. R. van Eerden pers. com.).

Between 1975 and 1977 most breeding places were visited throughout the breeding season. In all cases the majority of eggs hatched (estimate 70% for all years), but we never found chicks of more than a few days old, neither inside the colony area, nor in the neighbourhood. Since the

majority of Little Gulls nested on small islets surrounded by wide channels, the chicks could not have left the neighbourhood of the colony. Therefore, we conclude, that no chicks fledged between 1975 and 1977 (Veen 1978).

In 1978, to determine breeding success, nests were marked upon appearance with a small wooden peg. Each nest was checked for its contents twice a week; chicks in the nests were given an aluminium ring. The results are given in table 5. Only a small number of eggs disappeared during the first 20 days of incubation or failed to hatch, but a remarkably high number of eggs disappeared around hatching time. It has been emphasized before that even small chicks tend to leave the nest under the influence of human disturbance and the presence of non-ringed chicks in the colony area showed that a number of chicks hatched and left the nest between successive nest-checks. To determine what proportion of the eggs disappearing from the observation in the hatching period referred to this situation, in one colony, shortly after the last egg had either hatched or disappeared, a census was made of the chicks present. The ratio ringed: non-ringed chicks captured during the census led to an estimated total number of 32 non-ringed chicks — i.e. the category missed during the nest-checks — for the whole colony. In the same colony 34 eggs disappeared from the nests during the hatching period, which means that nearly all must have hatched. This conclusion seems reasonable in view of the small number (4.6%) of eggs lost during the first 20 days of incubation. If we assume egg-loss to be constant during the whole incubation period, in 1978 hatching success comes out at slightly more than 80%.

In 1978 three colonies were completely deserted shortly after the hatching of the last eggs. In two other colonies 20 chicks varying in age between 1 and 2 weeks were seen. Finally, only 5 of them reached the fledging age, which brings breeding success down to a level of 0.1 chick/pair.

Mortality agents

Eggs preyed upon. 10–20% (estimate for 1975, 1976 and 1977) and 4.6% (1978) of the eggs laid disappeared during the incubation period. Observations from a hide showed that a clutch temporarily left runs great risk to be taken by predators. In all colonies repeatedly watched from a hide, we discovered one or two Black-headed Gulls which had specialized in stealing eggs or chicks whenever an opportunity arose and cases of egg-stealing by such predators were recorded from Little Gull, Common Tern, Arctic Tern, Black-headed Gull, Redshank *Tringa totanus* and Avocet nests. In 1975 and 1978 I saw Black-

Table 5. Breeding results of Little Gulls in the Lauwerszee area in 1978. *Broedresultaten van Dwergmeeuwen in het Lauwerszeegebied in 1978.*

No. of nests checked <i>Aantal nesten gecontroleerd</i>	59	
eggs laid <i>eieren gelegd</i>	173	100.0%
eggs disappeared <i>eieren verdwenen</i>	8	4.6%
hatching failure <i>niet uitgekomen</i>	19	11.0%
chicks in nest <i>kuikens geboren</i>	146	84.4%
chicks recovered <i>kuikens teruggevonden</i>	20	11.6%
young fledged <i>jongen uitgevlogen</i>	5	2.9%
breeding success <i>jongenproductie</i>	0.1 young/pair	

headed Gulls taking 7 Little Gull eggs from 4 different nests. These observations suggest that the eggs disappearing from the nests in the incubation period were in all probability all taken by Black-headed Gulls. *Eggs died in hatching*. In all years a small number of eggs (2.9% in 1978) was found with a full grown dead embryo.

Added eggs. Eggs remaining unhatched beyond the maximum incubation period as a consequence of infertility or early embryonic death, were classed as added. The proportion of added eggs was as follows: 13% ($n = 6$) in 1975, 25% ($n = 5$) in 1976, 10–20% (estimate) in 1977 and 8.1% ($n = 14$) in 1978. In general the added eggs were incubated for a much longer period than normal. Since in 1978 nest checks were regularly made it is unlikely that many added eggs escaped attention in that year. Between 1975 and 1977, however, nest checks were made irregularly which makes it possible that a number of added eggs disappeared from the nests before we noticed them. The figures given for 1975, 1976 and 1977 thus should be regarded as minima.

Marked differences have been found in the number of addled eggs among different species of breeding birds. Nelsen (1966) mentions 7.0—8.0% (three years of observation) for the Gannet *Sula bassana*. Drent (1967) reports 13.0—14.5% (three years of observation) for the Herring Gull *Larus argentatus*, while in the Sandwich Tern 4.0—5.4% (five years of observation) has been recorded (Veen 1977). Despite the great variation between species, the proportion of addled eggs found in the Little Gull between 1975 and 1977 is relatively high. Besides, differences between years were high as well.

In the Gannet, Nelson (1966) found that recruit breeders had a higher proportion of addled eggs (12.5%) than recidivist breeders (6.3%). The same phenomenon was found in the Sandwich Tern (Veen unpubl.). This suggests that the high proportion of addled eggs among the Little Gulls might be related to the high number of recruit breeders within the population.

Chicks found dead. In all years of observation less than 5% of the chicks hatched was found dead in or near the nest. These chicks were all less than 5 days old except for one 14 day old chick found in 1978. Some of the chicks found had small wounds on head and neck which were probably caused by the pecks of adult Little or Black-headed Gulls nesting in the neighbourhood. The majority, however, did not show any external defect and for this category the cause of death remains unknown.

Chicks preyed upon. I all years of observation most chicks disappeared within a few days after hatching. Although the cause of death remains unknown for most of these chicks, it is likely that they were all taken by predators. Table 6 gives information on the occurrence of a number of

Table 6. The occurrence of predator species in colonies of the Little Gull in the Lauwerszee area between 1975 and 1978. *Het voorkomen van predatoren in kolonies van de Dwergmeeuw in het Lauwerszeegebied tussen 1975 en 1978.*

	1975 Sennerplaat	Robbengat	1976 Achter Zwartén Z	Achter Zwartén Z	Robbengat	1977 Achter Zwartén Z	1978 Rug	Blikplaat	Robbengat
blue heron	△	○	□	□	□	□	□	□	□
black-headed gull	●	●	○	●	○	○	●	●	●
herring gull	△	△	△	△	○	△	○	△	△
marsh harrier	△	○	○	○	○	○	□	△	○
kestrel	?	○	—	—	○	—	●	△	○
stoat	○	—	—	—	—	—	?	□	—
rat	△	—	?	△	—	△	—	—	△

Symbols used: (●) predation recorded on Little Gull; (Δ) predation recorded on Black-headed Gulls and terns in the neighbourhood of the Little Gulls; (○) recorded in colony area; (□) recorded in neighbourhood of colony; (-) not recorded, presence unlikely; (?) presence unknown. *Gebruikte symbolen:* (●) *predatie op Dwergmeeuwen waargenomen*; (Δ) *predatie op Kokmeeuwen en sterns in de omgeving van de Dwergmeeuwen waargenomen*; (○) *in kolonie waargenomen*; (□) *in kolonie-omgeving waargenomen*; (-) *niet waargenomen, aanwezigheid onwaarschijnlijk*; (?) *aanwezigheid onbekend*.

predator species and the extent of predation in the neighbourhood of the Little Gull colonies. It had been emphasized before that the Little Gulls in all cases nested in the neighbourhood of Black-headed Gulls and Common Terns. Since it is likely that the species mentioned have common predators, data on predation on Black-headed Gulls and Common Terns have been included in the table. The table shows that Black-headed Gull, Herring gull, Marsh Harrier *Circus aeruginosus* and Grey Heron *Ardea cinerea* have been recorded in all colonies studied, while Brown Rat *Rattus norvegicus* and Stoat *Mustela erminea* were present in only part of the colonies examined. Predation by Herring Gulls on eggs and chicks of Black-headed Gulls and Common Terns was high in all years; Black-headed Gulls preyed upon eggs and chicks (only new-born ones) on a much smaller scale, while Marsh Harrier, Kestrel *Falco tinnunculus* and Grey Heron preyed on chicks only occasionally. The extent of predation by Brown Rats was difficult to assess because of their nocturnal feeding habits. In a number of colonies we found a large number of Black-headed Gull eggs and chicks, which were no doubt collected by Brown Rats. Three Black-headed Gull colonies heavily preyed upon by Brown Rats were deserted by the gulls during the incubation period. So, Brown Rats probably took a heavy toll in certain colonies, though not in the ones where Little Gulls were present.

Altogether I have at my disposal eight observations in which predators rob a small chick

from the Little Gull colonies. In all cases the predators were Black-headed Gulls. The behaviour of the Black-headed Gulls suggested that egg and chick predators probably were the same individuals. The predatory gulls apparently had little difficulty in catching a chick once it had strayed to more than a few metres distance from its parents. On a number of occasions, when two Black-headed Gulls hunted together, a chick was caught by one predator, while the parents of the chick chased the other. The number of observations of chicks eaten by Black-headed Gulls is low, but this may be explained by the small amount of time spent in a hide watching the Little Gulls in the period when chicks were present. The determined behaviour of the predatory Black-headed Gulls and the easy way in which they obtained their prey, strongly suggest that the majority of the chicks disappearing from the colony shortly after hatching, i.e. all chicks in 1975, 1976 and 1977 and many in 1978, were eaten by Black-headed Gulls.

In 1978 20 chicks reached an age of 1–2 weeks. Since Black-headed Gulls have great difficulties swallowing chicks of over 3 days (Veen 1977), it is unlikely that this predator was responsible for the death of Little Gull chicks beyond 1–2 weeks. During visits to the area where the older chicks were present we often saw Herring Gulls which, in reaction to human disturbance, approached the area flying around in a way typical for a hunting gull. In 1974, in a simulation, Herring Gulls made several predation attempts and succeeded in catching a chick of approximately 3 weeks old (van Eerden pers. com.). In 1978 Kestrels were also recorded in the area where the older Little Gull chicks were present. Observations on hunting Kestrels and pellet analysis (Daan pers. com.) showed that some Kestrel pairs fed their young almost exclusively with the chicks of terns and gulls. The rings of four Little Gull chicks captured at the age of 1–2 weeks were found in the pellets. Since about half of the chicks were ringed, it can be surmised that Kestrels accounted for approximately 8–10 chicks, thus half of the chick mortality in this period.

We conclude that hatching failure and predation were the major causes of egg mortality in all years of observation. The proportion of added eggs was relatively high, but overall egg loss was low and hatching success (roughly between 70 and 80% in all years) was high in comparison to data for other Larid species (cf. Sandwich Tern 54–70% over six years, Veen 1977; Black Noddy *Annous tenuirostris* 58%, Ashmole 1962; Herring gulls (from different localities) 66%, 71%, 70% and 64% cited by Drent 1967; Glaucous-winged Gull *Larus glaucescens* 67%, Vermeer 1963; Arctic Tern 64%, Hawksley 1957; Common Tern 69%; Veen unpubl.). Chick mortality was extremely high in all years. Nearly

all chicks were robbed by Black-headed gulls when they were still very young. The majority of those who survived the age at which they were vulnerable to Black-headed Gull predation fell victim to Herring Gulls and Kestrels.

Discussion

The extremely low breeding success of the Little Gulls in the Lauwerszee area raises the question of what environmental or behavioural factors are responsible for it. The Netherlands lie at the periphery of the breeding distribution of the Little Gull, which implies that it can be expected to be an unfavourable place for breeding from an ecological point of view. The breeding distribution of a species is primarily determined by food availability (Lack 1954) but we never found an indication that food was a limiting factor in the Lauwerszee situation. In the Lauwerszee area predation by Black-headed Gulls was the main factor determining breeding success. Since the presence of preying Black-headed Gulls is a direct consequence of the presence of breeding colonies of this species (Veen 1977), nesting in the neighbourhood of a Black-headed Gull colony seems disadvantageous for a Little Gull. However, Little Gulls tend to nest in the neighbourhood of Black-headed Gulls and other Larid species all over their breeding range (Voous 1960). In the Lauwerszee area the Little Gulls selected a nesting site when the Black-headed Gulls had already settled. Moreover, changes in the distribution of Little Gull colonies between different years coincided with changes in the colony distribution of the Black-headed Gull. So the Little Gulls settled near the Black-headed Gulls and not vice versa and it is very likely that associative nesting of both species is not a question of similar habitat preference but of inter-specific attraction. Assuming that the Little Gull seeks the company of Black-headed Gulls for breeding one might expect a beneficial effect of this behaviour.

Various authors have shown that nesting in association with another species may have both beneficial and deleterious effects. Olsson (1951) showed that Eiders nesting in Herring Gull colonies were protected by their hosts from crow predation and consequently hatched a much higher percentage of their eggs (43% against 13%) than Eiders nesting outside the gulleries. Similarly, the deleterious effects of predation by Black-headed Gulls on the brood of Sandwich Terns nesting in the neighbourhood of Black-headed Gull colonies is lower than the benefit obtained from the gull's protection from predators (Veen 1977). The positive influence on breeding success of the antipredator behaviour of the Black-headed Gull has been shown for a variety of predator species (Kruuk 1964 and it

seems a reasonable assumption that the Little Gull seeks the company of Black-headed Gulls and other Larids for breeding, to gain protection from predators. Since we could not compare the breeding results of Little Gulls with and without Black-headed Gulls nesting in the neighbourhood, we cannot say whether in the Lauwerszee situation the beneficial effects of associative nesting outbalance the benefits or vice versa. If, for instance, in absence of Black-headed Gulls the Little Gulls would have lost all their eggs to predation the benefits of associative nesting would have outweighed its deleterious effects. The only thing we can say, is that the Lauwerszee situation the deleterious effects of associative nesting are extraordinary high. In general, Little Gulls must be capable of defending themselves more effectively against Black-headed Gull predation, otherwise one cannot understand how the species can survive in coexistence with Black-headed Gulls. We thus have to answer the question: „Why are the Little Gull chicks in the Lauwerszee situation so vulnerable to Black-headed Gull predation?“

In a great number of bird species including several Larids, recruit breeders have been shown to be less successful breeders than recidivists (Kittiwake, Coulson & White 1958, 1960, 1966; Common Tern, Austin 1945; Sandwich Tern, Veen 1977). Recruit breeders differed from recidivists with respect to clutch size, quality of the egg, laying date, breeding synchrony and nest density. In a number of cases egg loss in recruits probably resulted from incomplete incubation or inadequate treatment of the young (Gannet, Nelson 1966; Kittiwake, Coulson & White 1958). In 1978 a small number of Little Gull chicks fledged. These fledgelings were seen being fed by at least four adult birds, all of them having completely dark under-wings. (According to figure 6 these adults must have been all males. It is possible, however, that a few females with dark under-wings were present among the breeding birds but not represented in the data.) Although the age of these adults is not known with certainty, they fall in the only category including recidivist breeders (see figure 5). Since the dark-winged birds were represented in the breeding population with only 25%, the high proportion of these birds raising young to my opinion suggests that in the Little Gulls nesting in the Lauwerszee area breeding success was also correlated with age. Since we could not distinguish with certainty recidivist breeders within the population no attempt has been made to compare the behaviour of different breeding birds in order to determine whether behaviour differences were responsible for differences in success. In many cases, however, we were struck by the fact that even very small chicks walked away from the nest remaining at a relatively great distance from the adults for periods as long

as an hour. Since in many colonies there was little cover for the young these chicks were often exposed to predation by Black-headed Gulls. It has been emphasized before, that that habitat selected by the Little Gulls in the Lauwerszee area is atypical. I therefore suggest that insufficient care of young in combination with a habitat which provides little cover, must be held responsible for the remarkably low breeding success. Apparently, Little Gulls are only capable of defending themselves effectively against Black-headed Gulls, when breeding birds are involved in which predator-defense mechanisms are fully developed, including the selection of a habitat which provides sufficient cover for the young. First-time breeders probably fail in this respect.

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Summary

The reclaiming of the Lauwerszee area in 1969 had led to a sudden increase of the number of Little Gulls visiting the area during spring migration (maximum 566 birds in May 1978). Groups of Little Gulls visiting the new polder consist of juveniles (second calendar-year) and older ones (third calendar-year and older). Figure 2 shows that the juveniles visit the area somewhat later than the older birds. From 1972 onwards an increasing number of Little Gulls has nested in different places within the area (table 1, figure 3). Nest-site selection seemed importantly influenced by the structure of the vegetation, the occurrence of predators and the presence of breeding habitat of the Little Gulls in the Lauwerszee area can be regarded as atypical for the species.

Data on laying date, clutch size and laying interval are given in table 2, 3 and 4. An investigation of the plumage pattern of the breeding birds has revealed that between 1975 and 1978 nearly all females and the majority of males were first-time breeders (figure 5, 6). This means that the Little Gull colonies in the Lauwerszee area are inhabited by new birds each year.

Breeding success has been extremely low in all years (table 5). In general, eggs hatched successfully, but nearly all chicks were preyed upon by Black-headed Gulls and, to a lesser extent, by Herring Gulls and Kestrels (table 6). Only in 1974 and 1978 a small number of chicks fledged. The high proportion of Little Gull chicks robbed by Black-headed Gulls is of special interest, since Little Gulls tend to seek the company of Black-headed Gulls for breeding. The behaviour is also known from other Little Gull colonies and suggests that nesting in the neighbourhood of a Black-headed Gull colony is advantageous. The extremely low breeding results of the Little Gulls in the Lauwerszee area have been related to the age of the breeding birds. It is hypothesized that a lack of breeding experience causes that the breeding birds

often leave their young unguarded. This makes the chicks highly vulnerable to predation, especially in the open breeding habitat in the Lauwerszee area.

Samenvatting

De inpooling van het Lauwerszeegebied in 1969 is gepaard gegaan met het plotselinge verschijnen van grote aantallen Dwergmeeuwen gedurende de voorjaarstrek (maximum 566 ex. in mei 1978). De groepen Dwergmeeuwen die het gebied bezoeken zijn samengesteld uit juveniele (tweede kalenderjaar) en oude vogels (derde kalenderjaar en ouder). Figuur 2 toont aan dat de juveniele vogels iets later doortrekken dan de oudere individuen. Vanaf 1972 heeft een toenemend aantal Dwergmeeuwen op verschillende plaatsen in het Lauwerszeegebied gebroed (tabel 1, figuur 3). De nestplaatskeuze van deze vogels leek in belangrijke mate bepaald door de aard van de vegetatie, het voorkomen van predatoren en het al dan niet aanwezig zijn van kolonies van andere meeuwachtigen (figuur 4). Het broedbiotoop van de Dwergmeeuwen in het Lauwerszeegebied is atypisch voor de soort.

Gegevens over legdatum, legselgrootte en leginterval tussen eieren in eenzelfde legsel zijn weergegeven in tabel 2, 3 en 4. Een studie van het verenkleed van de broedende vogels heeft aan het licht gebracht, dat in de periode 1975-1978 vrijwel alle vrouwelijke en het merendeel der mannelijke broedvogels betrekking had op individuen die voor het eerst tot broeden kwamen (figuur 5, 6). Dit betekent dat de Dwergmeewkolonies in het Lauwerszeegebied elk jaar grotere delen door nieuwe broedvogels bevolkt worden.

De broedresultaten van de Dwergmeeuwen zijn steeds slecht geweest (tabel 5). In de meeste gevallen werden de eieren wel met succes uitgebroed, maar verdwenen de jongen als gevolg van predatie door Kokmeeuwen en in mindere mate ook door Zilvermeeuwen en Torenvalken (tabel 6). Uitvliegende jongen zijn alleen in 1974 en 1978 waargenomen. Het feit dat de meeste jonge Dwergmeeuwen door Kokmeeuwen worden opgegeten is opmerkelijk, omdat er aanwijzingen zijn dat de Dwergmeeuwen de neiging hebben om zich in de omgeving van een Kokmeewkolonie te vestigen. Dit gedrag is ook bekend uit andere broedgebieden en doet vermoeden dat het broeden in de omgeving van Kokmeeuwen voordelen met zich mee brengt. Dat de Dwergmeeuwen in het Lauwerszeegebied zo weinig succesvol zijn wordt in verband gebracht met de jeugdige leeftijd van de broedende vogels. Mogelijk is het gemis aan voorafgaande broedervaring er de oorzaak van dat de Dwergmeeuwen hun jongen soms gedurende lange tijd in open terrein onbewaakt achterlaten, met als gevolg dat de jongen gemakkelijk aan predatie worden blootgesteld.

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