

ATTENDANCE AND DIET IN RELATION TO BREEDING SUCCESS IN HERRING GULLS (*LARUS ARGENTATUS*)

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ABSTRACT.—Breeding success was studied in relation to time partitioning, and diet, in Herring Gulls (*Larus argentatus*) on Terschelling, The Netherlands, in 1992. The average fledging success of 0.5 chicks fledged/pair ($n = 26$ pairs) was lower than in the 1960s. We suspect that increased conspecific predation of eggs and chicks was the result of local food shortages. Successful pairs differed markedly in attendance patterns and diet from unsuccessful pairs. Unsuccessful pairs traveled to the feeding grounds more frequently (pre-egg and egg stages), and left the territory unguarded, for longer periods of time (egg and chick stages) than successful ones. Feeding frequency of chicks was significantly higher in successful pairs and was accompanied by higher growth rates in chicks. Overall, successful pairs ate more fish and chicks of conspecifics and Lesser Black-backed Gulls (*L. fuscus*) than unsuccessful ones, while the latter generally ate more crabs and starfish. Chicks of pairs that did not change their diet at hatching suffered higher mortality than chicks of pairs that did. We suggest that the deteriorating feeding conditions on Terschelling since the late 1960s has resulted in less synchronous territory attendance within pairs and less adequate feeding behavior, resulting in high levels of conspecific predation and relatively poor chick growth. Received 20 June 1995, accepted 20 August 1995.

DURING THE 20TH CENTURY, Herring Gull (*Larus argentatus*) numbers increased dramatically on both sides of the Atlantic Ocean (Drury and Kadlec 1974; reviews in Glutz von Blotzheim and Bauer 1982, Cramp and Simmons 1983, Vauk and Prüter 1987, Spaans et al. 1991). Similarly, the Herring Gull colony on Terschelling increased from a few thousand pairs during the late 1950s to over 20,000 pairs in the early 1980s, but has since declined to 12,000 pairs in 1992 (Zwart 1985; A. L. Spaans, State Forestry Service Terschelling, pers. comm.). Furthermore, annual breeding success has decreased by 75%, resulting from increased egg and chick predation by conspecifics and intense competition for food by both conspecifics (Spaans et al. 1987) and Lesser Black-backed Gulls (*L. fuscus*; Noordhuis and Spaans 1992).

When competition for food is intense, feeding efficiency and food choice, combined with adequate parental activities (synchronous and equitable), may be essential for successful breeding. The first week after hatching, during which these factors must be strictly attuned to each other, is the most important period. During this time, chicks are very vulnerable to predation by conspecifics (e.g. Brown 1967, Parsons

1971, Brouwer et al. 1995) and need very caloric food, especially marine fish (e.g. Spaans 1971, Annett and Pierotti 1989, Noordhuis et al. in prep.). Inadequate division of parental activities between feeding and the care of eggs and chicks markedly increases the risk of partial or total clutch and brood loss (e.g. Butler and Janes-Butler 1983, Morris 1987). A low feeding efficiency by one or both parents may result in disproportionate parental investment within the pair, and this will make the synchrony of care difficult. As a consequence, the territory and young are frequently left unattended, thus increasing the probability of egg and chick predation (Pugesek 1983, Schoen and Morris 1983). However, a low feeding efficiency negatively affects the quantity and quality of food brought to the chicks and, thus, increases the possibility that chicks die of starvation (Safina et al. 1988, Hario 1990). Hungry gull chicks also wander further from their nests thereby subjecting themselves to increased risk of predation and infanticide (Hunt and McLoon 1975, Hunt and Hunt 1976, Spaans et al. 1994, Bukaciński et al. in prep.).

The aim of our paper is to test whether patterns of parental care and diet of Herring Gull

pairs influenced breeding success in a colony where food was a limiting factor and conspecific predation pressure was high.

STUDY AREA AND METHODS

The study was conducted in the "Eerste Duintjes" (53°25'N, 05°28'E), located in the 4,400-ha Boschplaat Nature Reserve on the eastern side of the Dutch Frisian Island of Terschelling in 1992. The Eerste Duintjes consists of low undulating dunes surrounded by salt marshes intersected by large tidal creeks (for detailed description of study area, see Spaans 1971, Spaans et al. 1987).

We studied 26 pairs that formed a small subcolony within the large mixed colony of Herring and Lesser Black-backed gulls on the Boschplaat. Each nest was marked with a numbered stick and was visited every one or two days to monitor clutch size and egg fate. Eggs were marked *a*, *b*, and *c* according to their laying order and measured to the nearest 0.1 mm using Vernier calipers. Egg volume (V ; in cm^3) was calculated using the formula

$$V = 0.5035LW^2 \quad (1)$$

(Spaans and Spaans 1975), where L is length and W is width in centimeters. At hatching, chicks were individually marked with color bands. Every one or two days, chick mass was recorded to the nearest 1.0 g using a Pesola scale, and tarsus lengths of chicks were measured in study nests. Both chick measurements and behavioral observations (below) were conducted for 25 to 30 days after hatching (successful pairs) or since the loss of the clutch or brood (unsuccessful pairs). The growth rates of mass and tarsus were compared only for the first 10 days after hatching, as most of the unsuccessful pairs lost their chicks before they were 15 days old. Chicks that reached the age of 25 days were considered to have fledged. When chicks disappeared from the territory, we considered them to have been preyed upon by conspecifics, since legs with color bands of most of these chicks later were found in pellets. Moreover, we did not observe any intra- or interspecific adoptions.

From late April through July we monitored their territory attendance by continuous sampling from blinds every one or two days during 3 or 4 h for a total of 135 observation hours per nest. Behavioral observations, of all pairs simultaneously, were made at different times of day. The earliest began at 0630; the latest finished at 2130. Since we recorded exact times of arrivals and departures of each partner we could calculate the proportion of time that: (1) both partners were present on territory; (2) one bird was present (and which sex); and (3) neither was present. We used both the synchrony of parental care (defined as shifts between partners to leave territory unguarded for as short a time as possible) and the equitability of care (differences in time budgets between mates)

as measures of the pair's quality (e.g. Burger 1986). We also recorded the rate at which gulls left the territory, and the duration of an individual's absence from the territory. We assumed that only trips longer than 10 minutes were to the feeding areas (foraging trips). The shortest absence after which we observed chick feeding was 10 min. After hatching, we also recorded the rate of regurgitation food by adults directed to their chicks, which we call the rate of chick feeding (feeds \cdot chick $^{-1} \cdot$ h $^{-1}$). For analysis we partitioned the breeding cycle into three stages: the pre-egg stage (days prior to clutch initiation), the egg stage (from clutch initiation to one day before first egg hatched), and the chick stage (starting on day that first chick appeared in nest).

Since it was often difficult to identify the composition of food regurgitated by the adult gulls for the chicks, we used only pellets for diet analysis. Regurgitated pellets of undigested food were collected from territories of individual pairs almost daily from 10 days before until 9 days after hatching. Food types identified in the pellets were expressed as the average proportion of pellets per pair containing a particular type of food. Fish species were identified by the otoliths and characteristic bones (Schmidt 1968, Härkönen 1986), and were categorized as being either freshwater or marine. In total, we collected 201 pellets from unsuccessful and 231 pellets from successful pairs.

Data were statistically analyzed using the Student's *t*-test and the Mann-Whitney *U*-test for independent samples, and the Wilcoxon matched-pairs signed-ranks test and Friedman two-way nonparametric ANOVA for related samples. Normality of distribution was tested with the χ^2 -test (Zar 1984, Siegel and Castellan 1988). The level of significance was set at the 0.05 probability level.

RESULTS

Breeding parameters.—A summary of the breeding data in the study plot for 1992 is shown in Table 1. The overall fledging success was low. Only 7 of 26 all studied pairs (27%) and 7 of 19 of pairs that hatched young (37%) produced at least one fledgling (Table 1).

Successful pairs started laying eggs earlier and had a larger C-egg (third egg) volume than unsuccessful pairs (Table 1), although pairs of both groups had already arrived at the colony when the study started. Other breeding parameters were not significantly different ($P > 0.05$) between successful and unsuccessful pairs. Conspecific predation (69% of 26 eggs, and 94% of 34 chick deaths) was the main factor affecting breeding success. At least 6% of the chick deaths were attributable to starvation (Bukaciński et al.

TABLE 1. Median date on which first egg laid in each nest, clutch size, egg and clutch volume, and reproductive output of Herring Gulls on Terschelling in 1992. Comparisons between successful (at least one young fledged) and unsuccessful pairs (no young fledged) made only for three-egg clutches, because all successful pairs had three eggs.

Parameter	All pairs		Pairs	
	<i>n</i> = 21 ^a	<i>n</i> = 26	Successful <i>n</i> = 7	Unsuccessful <i>n</i> = 14 ^a
Median laying date of first egg	18 May	19 May	14 May ^b	21 May ^b
Clutch size ($\bar{x} \pm$ SD)	3.0 \pm 0.0	2.8 \pm 0.4	3.0 \pm 0.0	3.0 \pm 0.0
Egg volume (cm ³ ; $\bar{x} \pm$ SD)	79.6 \pm 6.0	84.2 \pm 5.9	82.4 \pm 4.6	78.0 \pm 6.3
C-egg volume (cm ³ ; $\bar{x} \pm$ SD)	77.9 \pm 5.0	—	81.4 \pm 5.3 ^c	74.4 \pm 6.2 ^c
Clutch volume (cm ³ ; $\bar{x} \pm$ SD)	238.8 \pm 18.1	235.1 \pm 38.9	247.3 \pm 13.8	233.9 \pm 18.9
Hatchlings/nest where young hatched ($\bar{x} \pm$ SD)	2.4 \pm 0.2	2.3 \pm 0.7	2.6 \pm 0.5	2.3 \pm 0.7
Hatching success of eggs (%)	80.4	82.1	85.7	76.7
Fledglings/pair ($\bar{x} \pm$ SD)	0.6 \pm 0.9	0.5 \pm 0.9	1.9 \pm 0.7	0.0 \pm 0.0
Nests successfully raising chicks (%)	33.3	26.9	—	—
100·nests successfully raising chicks/ nests successfully hatching eggs (%)	41.2	36.8	—	—

^a Three egg clutches only; clutch size for all unsuccessful pairs (*n* = 19) averaged 2.7 \pm 0.5.

^b Mann-Whitney *U*-test, *Z* = 2.47, *P* < 0.01.

^c Student's *t*-test, *t* = 2.49, *P* < 0.05.

in prep.). Some chicks that were preyed upon might have been starving chicks.

Frequency and duration of feeding trips.—The duration of feeding trips varied significantly during the season for successful and unsuccessful pairs combined (Friedman ANOVA; among males, $X^2_1 = 6.19$, *P* < 0.05; for pairs, $X^2_1 = 6.27$, *P* < 0.05). No difference was found for females ($X^2_1 = 2.65$, *P* > 0.05). The mean duration of a single feeding trip per individual ranged from 40 \pm SD of 54 to 100 \pm 79 min in males (*n* = 26), and from 50 \pm 58 to 125 \pm 80 min in females (*n* = 26). There were no statistical differences between males and females (Wilcoxon signed-ranks test; *P* > 0.05) and between successful and unsuccessful pairs (Mann-Whitney *U*-test, *P* > 0.05).

The rate of departures to the feeding area (Fig. 1) varied during the season too (Friedman ANOVA; among males, $X^2_1 = 8.0$, *P* < 0.02; among females, $X^2_1 = 8.0$, *P* < 0.02; for pairs, $X^2_1 = 6.38$, *P* < 0.05), with highest values occurring before egg laying and after hatching of the eggs. There were no significant differences in trip frequency between males and females, within either successful or unsuccessful pairs (Wilcoxon signed-ranks test; successful pairs, *Z* = 0.18, *P* > 0.05; unsuccessful pairs, *Z* = 1.08, *P* > 0.05). However, unsuccessful pairs left the colony more frequently during the pre-egg and egg stages than successful pairs (Fig. 1; Mann-

Whitney *U*-test; pre-egg stage, *Z* = 2.05, *P* < 0.05; egg stage, *Z* = 2.12, *P* < 0.05).

Territory attendance.—The proportion of time that the parents left the territory unguarded varied significantly over the course of the breeding season (Friedman ANOVA, $X^2_1 = 12.04$, *P* < 0.005). During the pre-egg period, mated birds spent more time together on the territory and left the territory unguarded for longer than in the other stages of the breeding cycle. Pair absence was lowest during the incubation period, while pairs were together on the territory for the shortest length of time during the chick stage.

The proportion of time each partner spent alone on the territory varied significantly over the course of the season as well (statistically different only for males; Friedman ANOVA, $X^2_1 = 7.52$, *P* < 0.02; Table 2). Both males and females spent the least time alone on the territory during the pre-egg stage.

Territory attendance of the pair also was related to their reproductive success. During the incubation period, unsuccessful pairs left their territory unguarded for longer periods of time, and spent less time together on the territory than successful pairs (Fig. 2; Mann-Whitney *U*-test; for pair absence, *Z* = 2.29, *P* < 0.05; for pair presence, *Z* = 0.77, *P* > 0.05).

During the chick stage, however, unsuccessful pairs spent more time together on the ter-

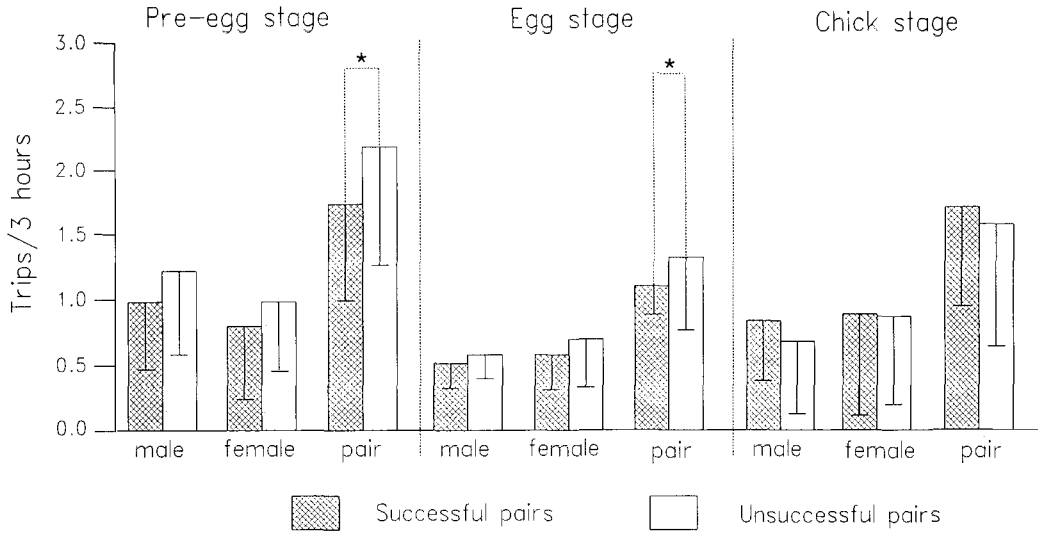


Fig. 1. Mean number of times per 3-h observation period that Herring Gulls left colony to feed in relation to breeding phase and fledging success. Whisker indicates SD. Statistical differences between groups indicated by asterisks (Mann-Whitney *U*-test; *, *P* < 0.05).

ritory and left their chicks unguarded for longer periods of time than successful pairs (Fig. 2; Mann-Whitney *U*-test; pair presence, *Z* = 3.23, *P* < 0.001; pair absence, *Z* = 2.12, *P* < 0.05). In that period, males of unsuccessful pairs spent less time alone on the territory than males of successful pairs (Table 2; *Z* = 2.46, *P* < 0.01).

Feeding frequency and growth of chicks.—Feeding frequency varied according to breeding success and the chick age (Fig. 3). Although young chicks (<10 days old) were fed more frequently than older chicks, the difference was not significant (all brood combined, *n* = 9, 0.31 ± 0.38 vs 0.15 ± 0.23 feeds·chick⁻¹·h⁻¹; Wilcoxon signed-ranks test, *Z* = 0.84, *P* > 0.05). No significant difference was found in feeding frequency in relation to the number of chicks per

nest. Chicks of successful pairs were fed more often than chicks of unsuccessful pairs, particularly during the first 10 days after hatching when the feeding rate by successful pairs was almost twice as high as that of unsuccessful ones (Fig. 3; Mann-Whitney *U*-test, *Z* = 2.36, *P* < 0.02).

Daily mass increment, particularly after the fifth day after hatching, was significantly higher for chicks of successful pairs than for unsuccessful ones (Table 3; Student's *t*-test, *t* = 4.19, *P* < 0.01). There was, however, no difference in tarsus length between chicks of successful and unsuccessful pairs (Table 3; *P* > 0.05).

Diet.—The diet of Herring Gull pairs was very diverse. Over the entire period successful pairs ate more fish (Mann-Whitney *U*-test, *Z* = 2.30,

TABLE 2. Proportion of time (percentage, $\bar{x} \pm$ SD) partners of Herring Gull pairs present solitarily at territory in relation to fledging success (successful pairs fledged at least one young; unsuccessful pairs did not fledge young).

Breeding stage	Pair			
	Successful (<i>n</i> = 7)		Unsuccessful (<i>n</i> = 19)	
	Females	Males	Females	Males
Pre-egg	10.5 ± 16.5	4.0 ± 7.9	6.5 ± 14.3	12.6 ± 19.9
Egg	24.0 ± 39.3	34.0 ± 38.7	28.6 ± 39.9	36.6 ± 42.1
Chick	28.2 ± 39.3	47.7 ± 41.9*	19.6 ± 32.6	23.7 ± 30.4*

* Significantly different (Mann-Whitney *U*-test, *Z* = 2.46, *P* < 0.01). Other differences not significant (*P* > 0.05).

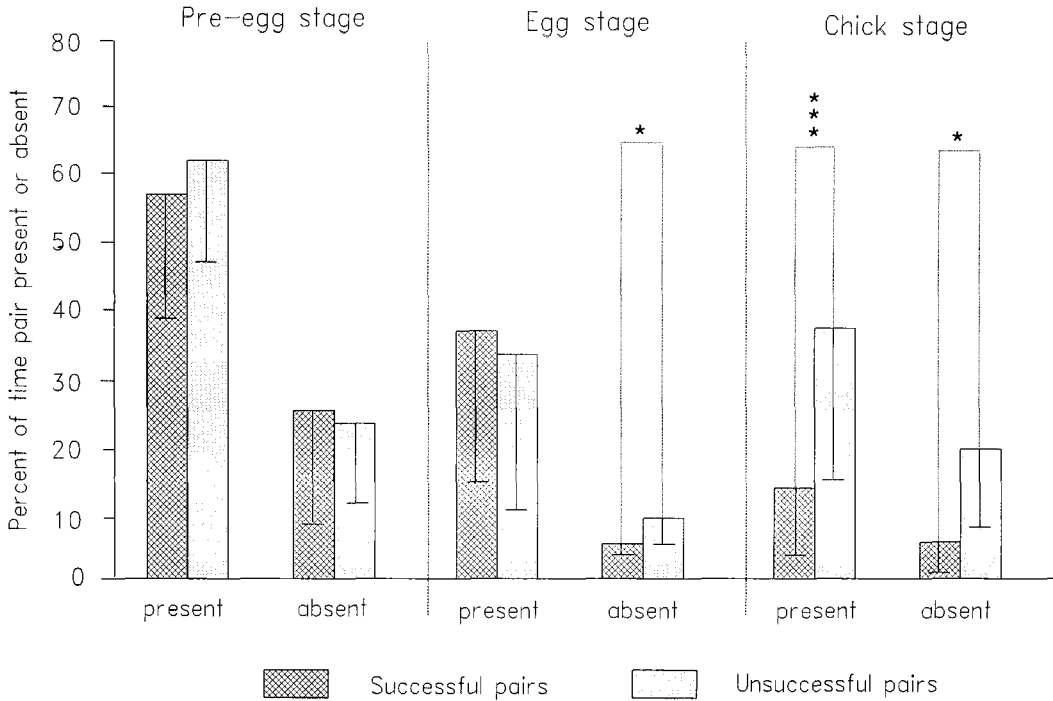


Fig. 2. Pair presence at and absence from territory, of Herring Gulls in relation to nesting success. Whisker indicates SD. Statistical differences between groups indicated by asterisks (Mann-Whitney *U*-test; *, $P < 0.05$; ***, $P < 0.001$).

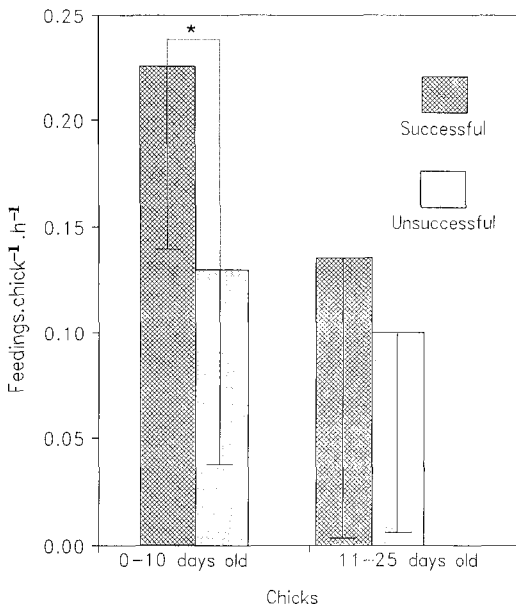


Fig. 3. Mean number of feeds · chick⁻¹ · h⁻¹ by Herring Gull pairs in relation to nesting success. Whisker indicates SD. Statistical differences between groups indicated by asterisk (Mann-Whitney *U*-test; *, $P < 0.05$).

$P < 0.02$) and gull chicks ($Z = 1.95, P < 0.05$) than unsuccessful pairs, whereas the latter ate more crabs ($Z = 2.35, P < 0.02$) and starfish ($Z = 1.97, P < 0.05$; Table 4).

The diet of unsuccessful pairs changed little from the last 10 days of incubation to the first 10 days after hatching. Only the average percentage of total marine invertebrates was significantly lower after hatching (Wilcoxon signed-ranks test, $Z = 2.11, P < 0.05$). After hatching, both the percentage of bivalves and total marine invertebrates were significantly higher in the diet of unsuccessful than of successful pairs (Mann-Whitney *U*-test; bivalves, $Z = 2.41, P < 0.01$; marine invertebrates, $Z = 2.26, P < 0.05$; Table 5).

In contrast, successful pairs showed a much larger dietary switch at the time of hatching than unsuccessful pairs. During the chick stage, successful gulls fed less on freshwater fish (Wilcoxon signed-ranks test, $Z = 1.97, P < 0.05$), bivalves ($Z = 2.39, P < 0.02$) and total marine invertebrates ($Z = 2.18, P < 0.05$), and ate more crabs ($Z = 2.80, P < 0.01$) and gull chicks ($Z = 2.09, P < 0.05$; Table 5). After hatching, the average proportion of pellets per pair that con-

TABLE 3. Daily increases ($\bar{x} \pm SD$, with no. nest sampled [*n*] in parentheses) of mass and tarsus length of Herring Gull chicks in relation to fledging success (successful pairs fledged at least one young; unsuccessful pairs fledged no young) and age of chicks.

Daily increment	Pair		<i>t</i> -value*
	Successful	Unsuccessful	
Mass (grams · day⁻¹ · chick⁻¹)			
0-5 days	9.0 ± 3.1 (7)	7.2 ± 4.7 (10)	0.951 ^{ns}
6-10 days	24.4 ± 5.3 (7)	14.9 ± 3.0 (8)	4.191 ^{**}
Tarsus length (centimeters · day⁻¹ · chick⁻¹)			
0-5 days	0.11 ± 0.03 (7)	0.09 ± 0.01 (10)	1.614 ^{ns}
6-10 days	0.16 ± 0.04 (7)	0.14 ± 0.05 (8)	0.821 ^{ns}

* Student's *t*-test. ^{ns}, *P* > 0.05; ^{**}, *P* < 0.01.

tained gull chicks varied even within successful pairs. Among successful Herring Gull pairs (*n* = 7), three pairs specialized in predated gull chicks. Over 50% of the 111 pellets collected from these three nests (average 33.6% pellets per nest) contained the remains of gull chicks compared to 2.1% of the 95 pellets collected from the other four successful pairs (average 2.3% pellets per nest; Mann-Whitney *U*-test, *Z* = 2.31, *P* < 0.01). The chicks of cannibal pairs grew at a significantly faster rate ($\bar{x} = 17.01 \pm 2.2$ g/day), than the chicks of other successful pairs ($\bar{x} = 10.5 \pm 3.4$ g/day; Student's *t*-test, *t* = 3.55, *P* < 0.01). There was no significant difference between cannibal pairs and other successful pairs in the rate of chick feeding (Mann-Whitney *U*-test, *Z* = 0.65, *P* > 0.05).

DISCUSSION

Breeding parameters.—In 1992, the average fledging success of Herring Gulls nesting on Terschelling (0.5 fledged young/pair) was similar to the breeding success on the island in 1983-1984 (0.3-0.4 young/pair), but lower than that in the same colony in the late 1960s (1.3-1.5 young/pair; see Spaans et al. 1987). The 1992 reproductive success on Terschelling also was lower than average values found for the species elsewhere in Europe (Harris 1964, Davies 1975, Parsons 1975, Hario et al. 1986, Kilpi 1990). In our study, as in 1983-1984 (Spaans et al. 1987), the low productivity resulted mainly from increased conspecific predation of eggs and, in particular, of chicks.

The decline in reproductive success on Terschelling during the last 20 to 25 years was

TABLE 4. Mean proportion of pellets per pair (percent ± SD) containing a particular type of food of Herring Gulls on Terschelling in relation to fate of brood (successful pairs fledged at least one young; unsuccessful pairs fledged no young).

Type of food	Pair		<i>z</i> -value*
	Successful (<i>n</i> = 7)	Unsuccessful (<i>n</i> = 19)	
Fish			
Freshwater	7.8 ± 14.8	9.7 ± 29.2	0.27
Marine	4.1 ± 7.5	5.9 ± 18.9	0.76
Total ^b	31.9 ± 20.6	23.5 ± 19.9	2.30*
Marine invertebrates			
Crabs	25.3 ± 17.6	32.9 ± 20.2	2.35*
Bivalves	51.9 ± 23.8	55.4 ± 21.1	0.39
Starfish	0.9 ± 1.9	6.9 ± 9.7	1.97*
Total ^b	67.9 ± 20.0	74.4 ± 28.5	0.75
Others			
Grass	7.0 ± 12.5	6.3 ± 14.0	1.22
Chicks	11.9 ± 9.1	4.1 ± 10.9	1.95*
Refuse	5.1 ± 17.7	1.6 ± 4.9	0.60
Berries	0	1.6 ± 5.7	1.85
No. pellets	231	185	

* Mann-Whitney *U*-test. *, *P* < 0.05; others *P* > 0.05.

^b Unidentifiable items included.

paralleled by a decrease in egg volume and daily chick growth (Spaans and Spaans 1975, Spaans et al. 1987). These data suggest that Herring Gulls on Terschelling were having more difficulty obtaining food than in the late 1960s (cf. Kadlec and Drury 1968, Murphy et al. 1984). Van Klinken (1992) attempted to test the food hypothesis by providing Herring Gulls nesting on nearby Schiermonnikoog with additional food. The reproductive output of his experimental pairs was significantly higher than that in controls and reached a level similar to that on Terschelling in the late 1960s. Noordhuis and Spaans (1992) suggested that the present food shortage results from increased competition for food by both conspecifics and Lesser Black-backed Gulls off the islands.

The importance of food competition on breeding parameters is indicated through comparison of the breeding ecology of successful and unsuccessful pairs. The volume of the C-egg was significantly lower for unsuccessful pairs, suggesting reduced food availability (Salzer and Larkin 1990, Hiom et al. 1991) and a lesser body condition of unsuccessful females during the pre-egg and egg laying stages. It is very likely that there was the shortage of food in this group because of their inability to compete successfully for food with both conspecific and Lesser

TABLE 5. Mean proportion of pellets per pair (percent \pm SD) containing a particular type of food of Herring Gulls on Terschelling during (A) the last 10 days before and (B) the first 10 days after hatching of the eggs in relation to fate of brood (successful pairs fledged at least one young; unsuccessful pairs fledged no young).

Type of food	Successful pairs			Unsuccessful pairs		
	A (n = 7)	B (n = 7)	z-value ^a	A (n = 19)	B (n = 12)	z-value ^a
Fish						
Freshwater	19.3 \pm 19.1	2.1 \pm 5.7	1.97*	16.3 \pm 25.8	4.7 \pm 10.7	0.54
Marine	0	5.5 \pm 8.4	1.34	7.2 \pm 22.7	3.8 \pm 9.9	0.36
Total ^b	28.6 \pm 33.4	33.4 \pm 20.2	1.01	21.3 \pm 29.9	27.7 \pm 25.6	0.07
Marine invertebrates						
Crabs	0 ^c	34.3 \pm 29.5	2.80**	36.0 \pm 22.1 ^c	26.8 \pm 28.0	0.26
Bivalves	80.0 \pm 44.7	36.5 \pm 20.2 ^d	2.39*	60.4 \pm 38.5	54.7 \pm 21.8 ^d	0.42
Starfish	0	1.5 \pm 3.1	1.14	9.6 \pm 12.0	0	0.03
Total ^b	88.0 \pm 24.7	49.4 \pm 22.1 ^c	2.18*	80.2 \pm 36.5	61.5 \pm 30.4 ^e	2.11*
Others						
Grass	10.0 \pm 22.3	5.9 \pm 7.7	0.18	6.4 \pm 14.2	6.1 \pm 14.2	0.16
Chicks	0	16.2 \pm 10.8	2.09*	1.6 \pm 5.0	10.2 \pm 19.9	0.74
Refuse	0	2.2 \pm 5.6	1.14	1.4 \pm 4.7	9.8 \pm 28.8	0.27
Berries	0	2.1 \pm 6.7	0.73	0	0	
No. pellets	50	181		115	70	

^a Wilcoxon's signed ranks test. *, $P < 0.05$; **, $P < 0.01$; others $P > 0.05$.

^b Unidentifiable items included.

^{c,d,e} Mann-Whitney U -test ($Z = 2.51$ and 2.41 , $P < 0.01$; and $Z = 2.26$, $P < 0.05$, respectively).

Black-backed Gulls. Unsuccessful pairs began laying later and laid smaller C-egg than successful pairs because they either needed more time to gain proper condition for laying eggs (Drent and Daan 1980, Arcese and Smith 1988), or were younger than successful breeders (e.g. Pugesek 1983, Nisbet et al. 1984, Sydeman et al. 1991). The lack of difference in mean clutch size, mean egg volume, and total clutch volume, as well as the simultaneous arrival of all study pairs in the colony earlier in the year, indicate that the delay of egg laying in unsuccessful pairs was related to the condition of the birds rather than to their age. The more frequent feeding trips by unsuccessful pairs compared with successful ones supports this idea.

Parental-care behavior.—In contrast to Burger (1986), we found no evidence for equitability in time partitioning of parental care between partners in either successful or unsuccessful pairs. Overall, males spent significantly more time alone on the territory than females. Attendance also was higher in successful than unsuccessful males during the egg and chick stages. It was likely that low food availability was responsible for these behavioral patterns (Spaans et al. 1994). As a consequence, high energetic investment of females in egg laying could not be supplemented later, regardless of the female's quality (in both groups females had to go

to the feeding areas more frequently than males). High predation pressure could be the other reason (though also related to poor feeding conditions) of stronger male attendance (Pierotti 1987). Therefore, the equitability of care was not only affected by pair quality (e.g. Burger 1986, Morris 1987), but also by local feeding conditions.

Under poor feeding conditions the synchrony of pair activities, which determines how long the territory is left unguarded and exposed to predators, forms a better measure of pair quality (Morris and Black 1980, Schoen and Morris 1983). Similar to Burger (1986) and Morris (1987), we found that successful partner rarely were absent from the colony simultaneously. In contrast, the parental activity patterns of unsuccessful pairs were poorly coordinated. During incubation, unsuccessful pairs left the territory unguarded for almost twice as long as successful pairs. After hatching, unsuccessful parents were either both on the territory at the same time or went to feeding areas together, leaving the nest unguarded for three times as long as successful pairs. As a result, chicks of unsuccessful pairs were left alone by their parents for longer periods of time (20% of observation time) than young of successful pairs. Hungry chicks wandered around more often than young of successful pairs (pers. obs. on Herring Gulls in this

study, as well as on Lesser Black-Backed Gulls; Spaans et al. 1994) and became easy prey for conspecific adults (Pierotti and Murphy 1987, Morris and Chardine 1990, Spaans et al. 1987). As a consequence, most of the unsuccessful pairs had no young after 15 days.

Diet.—Differences in diet of successful and unsuccessful pairs probably reflected differences in hunting efficiency and food competition between these two groups of pairs. Successful pairs more frequently had remains of highly calorific food in their pellets, such as gull chicks and fish (Spaans 1971, Kirkham and Morris 1979, Pierotti and Annett 1987). The proportion of gull chicks in pellets was much higher than at the same colony in previous years (Noordhuis and Spaans 1992, Noordhuis et al. in prep.), as well as higher than at colonies in other regions (Fox et al. 1990). Over 50% of all pellets from pairs with fast-growing chicks contained remains of chicks. Even the proportion of fish in the pellets of successful pairs was lower than recorded at colonies of this species in the Great Lakes of North America (Fox et al. 1990) or in the food offered by adults to chicks at marine colonies (Chudzik et al. 1994, Hillström et al. 1994).

During incubation, the diets of successful and unsuccessful pairs differed only slightly. However, after hatching, successful pairs ate fewer marine invertebrates, in particular bivalves, than unsuccessful pairs. Bivalves are of relatively low nutritive value and are difficult for chicks to handle (Spaans 1971, Niebuhr 1983, Pierotti and Annett 1987, 1990, 1991, Noordhuis et al. in prep., pers. obs.). The change of diet composition by successful pairs after the eggs had hatched (Rooth 1957, Spaans 1971, Pierotti and Annett 1987, Annett and Pierotti 1989, Noordhuis et al. in prep.) reflects the distinctive food requirements of chicks relative to adults. The average proportion of freshwater fish in the pellets from successful pairs decreased after hatching. The freshwater fish probably were caught in the reservoirs of the mainland as far as 15 to 25 km from the breeding colony (Spaans 1971). The decline in freshwater fish remains after hatching was less marked in unsuccessful pairs and may indicate the difficulties the gulls had in hunting near colony for food with high nutritive value. They lost the competitive battle for high-quality food near their breeding areas and were forced to use one of two feeding strategies: (1) to eat low-quality food (bivalves) near

the colony (McCleery and Sibly 1986); or (2) cover a longer distance to feeding areas for more nutritive food (i.e. freshwater fish).

In our study, the feeding rate of chicks by successful and unsuccessful pairs were distinctly lower than in other colonies of this species (e.g. Graves et al. 1991). Feeding rates were twice as high for successful pairs than for pairs that lost their chicks and the higher daily mass increment of chicks of successful pairs was an obvious result of better food (i.e. higher nutritive value) and higher feeding rates. However, chick growth rate was lower than measured in the same colony in the 1960s (Spaans 1971).

ACKNOWLEDGMENTS

We thank Harry Horn, State Forestry Service, Terschelling, for permission to conduct this study in the Boschplaat Nature Reserve, and the bird wardens Leo Bot, Jan Bunnink, Oene de Jong, Jan Peereboom, Jan-Piet Rijk, and Jan Vis for logistic support. Kazimierz A. Dobrowolski, Director of Institute of Ecology, Polish Academy of Sciences, gave M.B. and D.B. opportunity to carry out this study. Ruurd Noordhuis was helpful in analyzing the pellets. Miriam Hall corrected the English text. We thank also K. Brown, J. Graves, R. Pierotti, and our colleagues at the two Institutes for helpful comments on earlier versions of the paper.

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