

This is a pre peer-reviewed, pre-print (draft pre-refereeing) version of the following published document, This is the peer reviewed version of the following article: O'CONNELL, M. J., COULSON, J. C., RAVEN, S. and JOYCE, S. (1997), Nonbreeding and nests without eggs in the Lesser Black-backed Gull Larus fuscus. Ibis, 139: 252–258. doi:10.1111/j.1474-919X.1997.tb04622.x, which has been published in final form at http://onlinelibrary.wiley.com/doi/10.1111/j.1474-919X.1997.tb04622.x/full. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving. and is licensed under All Rights Reserved license:

O'Connell, Mark ORCID logoORCID: https://orcid.org/0000-0003-3402-8880, Coulson, J, Raven, S and Joyce, S (1997) Nonbreeding and nests without eggs in the Lesser Black-backed Gull. Ibis: International Journal of Avian Science, 139 (2). pp. 252-258. doi:10.1111/j.1474-919X.1997.tb04622.x

Official URL: http://onlinelibrary.wiley.com/doi/10.1111/j.1474-919X.1997.tb04622.x/full

DOI: http://dx.doi.org/10.1111/j.1474-919X.1997.tb04622.x

EPrint URI: https://eprints.glos.ac.uk/id/eprint/5061

Disclaimer

The University of Gloucestershire has obtained warranties from all depositors as to their title in the material deposited and as to their right to deposit such material.

The University of Gloucestershire makes no representation or warranties of commercial utility, title, or fitness for a particular purpose or any other warranty, express or implied in respect of any material deposited.

The University of Gloucestershire makes no representation that the use of the materials will not infringe any patent, copyright, trademark or other property or proprietary rights.

The University of Gloucestershire accepts no liability for any infringement of intellectual property rights in any material deposited but will remove such material from public view pending investigation in the event of an allegation of any such infringement.

PLEASE SCROLL DOWN FOR TEXT.

Nonbreeding and nests without eggs in the Lesser Black-backed Gull Larus fuscus

M. J. O'CONNELL, J. C. COULSON*, S. RAVEN & S. JOYCE
Department of Biological Sciences, University of Durham, South Road, Durham DH1 3LE, UK

Estimates of the number of breeding Lesser Black-backed Gulls Larus fuscus at the Tarnbrook Fell gullery, Lancashire, have been made from annual counts of nests since 1981. During all of these surveys, the mean percentage of nests which did not contain eggs has been remarkably constant from year to year (54% ± 1.9%). A study of specific nests at the colony in 1992 showed that the great majority of these "empty" nests did not subsequently receive eggs. In 1993, a study of a sample of territory-holding gulls was made on a 0.41-ha study plot to investigate and to quantify the occurrence of empty nests. Of the 62 pairs that defended a territory and constructed a complete nest, 27% subsequently failed to produce eggs. These birds attended their territory as a pair significantly less frequently than pairs that produced clutches and achieved significantly fewer apparently successful mountings. Sixty percent of pairs constructed more than one nest, and 58% of all nests built received no eggs. The construction of empty nests was not found to be related to the density of nesting gulls. Since 1981, estimates of the number of gulls in the colony have been based on the assumption that one nest represents one pair of gulls. This has been shown not to be the case, and a correction multiplier of 0.61 must be applied to counts of nests at the colony to obtain an estimate of the number of breeding

In most birds, nests are constructed solely to facilitate the incubation of eggs. However, in a few species, nests have acquired other functions such as roosting, shelter and display areas (Rosenberry & Klimstra 1970, Pettingill 1971, Dorst 1974, Ryder 1976). The occurrence of nests which never contain eggs has been reported in several gull species: Paludan (1951) and Tinbergen (1953) described unused "play" nests built by Herring Gulls Larus argentatus, but the extent of this behaviour was not quantified. In two consecutive years, Harper (1971) found that 55% and 31% of Western Gulls Larus occidentalis built nests that remained empty. In a similar 2-year study of Ring-billed Gulls Larus delawarensis, Ryder (1976) found that 22% and 43% of nests never contained eggs. In these species, the occurrence of empty nests appeared to be limited to only a few specific gulleries and was not typical of all individuals.

Our study was conducted in a gullery of Lesser Blackbacked Gulls Larus fuscus (96%) and Herring Gulls (4%), where an annual census of breeding gulls has been made since 1981. These surveys have used counts of nests to estimate the number of breeding birds in the colony, based on the assumption that a well-built nest represented one pair and that the empty nests found would receive eggs in the days following the census. A repeated check of specific nests in 1992 suggested that this was not usually the case, and a more detailed study was made in 1993 with the following aims: (1) to examine the assumption that one nest represents one pair. If the assumption was incorrect, to quantify the number of pairs in relation to the number of nests and to provide a correction factor for census data; (2) to investigate whether empty nests are built only by pairs that fail to produce clutches; (3) to investigate behavioural differences between pairs that produce only empty nests and those that successfully produce a clutch and (4) to investigate behavioural differences between pairs that produce single or multiple nests.

METHODS

The Tarnbrook Fell gullery

This study was conducted at the Tarnbrook Fell gullery, situated on the western slopes of the Forest of Bowland in Lancashire (grid reference SD614595). The colony covers some 6 km² of blanket bog moorland at an altitude of about 450 m and has been in existence since the late 1930s. During the period of the study, there were approximately 18,000 breeding gulls in the gullery.

^{*} Present address: J.C. Consultancy. 15, The Links, Belmont, Durham City DH1 2AG, UK.

Study plot

Observations of the behaviour and attendance of Lesser Black-backed Gulls on a 0.41-ha study plot were made from a hide between 4 April and 30 May 1993. This period covered the pre-nesting, incubation and start of chick-rearing periods. A total of 88 h of observations were made on 22 days. Natural features and a grid of marker canes 5 m apart were used to plot the position of each gull on a map every 30 minutes during observation periods. In addition, displaying, mating and territorial fighting were also recorded throughout the observation periods. These data were used to determine the extent and boundaries of territories within the plot. Generally, each pair would remain within specific areas. and so territory boundaries were easily determined. Approximately 25% of the gulls using the plot were readily identifiable by distinctive plumage characteristics or stains. A complete survey of the study plot was made every 3 days. and all new nests were marked. A 10-m wide strip around the periphery of the plot was also searched to locate nests built outside the study area by birds whose territory extended within it. After the end of direct behavioural observations (30 May), all nests were monitored until mid-July, and chicks were ringed to determine fledging success. On 8 June 1993, a visit was made to the gullery on Walney Island, Cumbria, to compare the proportion of empty nests at that colony.

Prior to statistical analysis, count and proportional data were examined for normality, and, where appropriate, transformations were made. Mean values are shown with standard errors or 95% confidence limits.

In the text, the term "empty nest" is used to describe a fully constructed nest in which no eggs had been or were subsequently laid. Pre-nest "scrapes" were not considered. The term "clutch nest" is used to describe a nest with eggs.

The colony census and the proportion of empty nests

A variety of methods have been used to estimate the number of breeding gulls at the Tarnbrook Fell gullery since the colony was started in the 1930s. Since 1981, an annual census of gull nests has been conducted at the colony during which the number of nests in 55-65 quadrats of 50 m × 100 m were counted (Nature Conservancy Council data 1981-1988; no census in 1989; our own data from 1990 onwards). The quadrats were originally sited randomly throughout the colony, but since 1992, the distribution of quadrats has been based on a stratified grid system. The counts were made in mid-May, by which time 80% of all nests built had usually been constructed. The contents of each nest were noted as either empty or with one, two or three eggs. The numbers of nests within the quadrats and the total area covered by the gullery were used to estimate the number of breeding gulls, making the assumption that one nest represented one pair. In 1993, the number of nests on the study plot was counted at the time of the census.

Table 1. The percentages of empty nests and completed (threeegg) clutches at the time of the annual census of Lesser Black-backed Gull nests at Tarnbrook Fell gullery; mid-May 1981–1989 and 1990–1994 (no census in 1989)

Census year	Nests exam- ined	Empty nests (%)	Three-egg clutches (%)
1981	1421	53	27
1982	1060	56	13
1983	1095	56	27
1984	650	34	46
1985	560	54	31
1986	464	61	31
1987	396	54	35
1988	426	50	30
1990	849	56	27
1991	486	56	28
1992	1239	57	27
1993	953	56	23
1994	1281	63	26
Mean ± s.e.		54.3 ± 1.9	27.6 ± 2.7

The actual number of pairs on the plot was also known from mapped territories, and this was compared with the estimates from the nest census. A correction factor for the nest-counting method was then calculated from the difference between the two estimates.

RESULTS

Percentage of empty nests at the Tarnbrook Fell gullery

Between 1981 and 1994, the percentages of empty nests and of nests with completed (three-egg) clutches within the gullery at the time of the annual census remained remarkably similar (Table 1). The mean percentage of empty nests each year during this period was $54\% \pm 1.9\%$, and the mean percentage of three-egg clutches was $28\% \pm 2.7\%$. The census data for 1992-1994 showed no significant relationship between the number of nests in a census quadrat and the proportion of empty nests it contained (Fig. 1), indicating that empty nests were found in the same proportions in areas of high or low nest densities.

Empty nests at the Walney Island gullery

The Walney Island gullery is approximately 40 km west of the Tarnbrook Fell gullery, and in 1993, it contained some 23,000 breeding pairs of gulls (65% Lesser Black-backed Gulls, 35% Herring Gulls; T. Dean, pers. comm.). On 8 June 1993, only 2% of 141 nests investigated were empty. On the study plot at Tarnbrook Fell on this date, 64% of the 109 nests were empty, and it is important to note that none

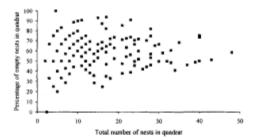


Figure 1. Number of Lesser Black-backed Gull nests in a 50-m × 100-m census quadrat and the percentage of empty nests in that quadrat. Tarnbrook Fell gullery census 1992–1994 (n = 172 quadrats); Y = 35.6 - 0.13x, r = 0.01.

of these empty nests subsequently received eggs. The difference in the proportions of empty nests between the two colonies was large and highly significant (χ^2 ₁ = 107, P < 0.001; Table 2).

Territories on the "empty nest" study plot

Sixty-two pairs established territories on the study plot, and 109 nests were built. Of these nests, 64 (58%) remained empty. Four types of territories could be identified: (1) territories with a clutch nest only = 16 (26%); (2) territories with empty nest(s) only = 17 (27%); (3) territories with one clutch nest and empty nest(s) = 29 (47%) and (4) territories without nests = 0 (0%). Thus, of the 62 pairs of gulls that established a territory, 73% produced eggs, but 27% failed to produce a clutch and were nonbreeding.

Multiple nest building

None of the territories contained more than one clutch nest. A total of 37 (60%) territories contained multiple nests. Table 3 shows the percentage of territories with one, two, three or four fully built nests. There was no significant difference in the proportion of pairs with these numbers of nests that laid eggs and those that did not $(\chi^2, = 2.5, n.s.)$.

When considering the 45 pairs that laid clutches, there were no significant differences in the mean nest-building date or mean date of egg laying for those building single nests and those building multiple nests (Table 4).

Empty nests and nests with clutches

There was no significant difference in the mean date by which a nest was fully built when comparing all empty nests (n=64) and nests which received clutches $(n=45,t_{107}=0.1,n.s.;$ Table 5). For 20 of the 29 pairs that laid a clutch and also built one or more empty nests, the order in which the empty and clutch nests were built was known (Table 6). There was no significant difference in the proportions of clutch nests that were built before or after the empty nest(s)

Table 2. Percentages of Lesser Black-backed Gull nests that were empty, contained a clutch or contained chicks at the Turnbrook Fell and Walney Island gulleries on 8 June 1993

Gullery	Empty nests (%)	Nests with eggs (%)	Nests with chicks (%)
Tarnbrook Fell (n = 109 nests)	64	18	18
Walney Island (n = 141 nests)	2	52	46

had been constructed on the same territory ($\chi^2_1=0.2,$ n.s.). After a clutch had been laid, none of the pairs built further nests. In several cases, selection of the nest in which the clutch was to be laid occurred after two or more nests had been built. The mean time between construction of the final nest and one of the nests receiving eggs was 8.6 ± 1.5 days.

Territory attendance

Occupation of territories

The mean proportion of established territories occupied at any one time during the eight observation days prior to the start of egg laying was 76% (95% confidence limits, 73-78%) for pairs that successfully produced eggs. This was appreciably and significantly higher than the 71% (95% confidence limits, 68-73%) found during the same period for pairs that established a territory but failed to lay eggs $(t_{14} = 3.9, P < 0.01;$ Table 7). After egg laying, the mean percentage of established territories that were occupied at any moment was 80% (95% confidence limits, 79-78%) for pairs that successfully produced eggs. This percentage was significantly higher than the 61% presence (95% confidence limits, 60-63%) found during the same time for pairs that established a territory but failed to lay eggs ($t_{24} = 2.8$, P < 0.01). Table 7 shows that the attendance of birds with clutches significantly increased after 3 May ($t_{19} = 9.3$, P <0.001), whereas the attendance of pairs without eggs significantly decreased ($t_{19} = 5.8$, P < 0.001).

Table 3. Percentages of Lesser Black-backed Gull pairs building single or multiple nests, for pairs that biid clutches and those that did not. Tarnbrook Fell gullery study plot. 1993

	Number of nests built in the territory			
	1	2	3	4
Pairs with clutches (n = 45)	37%	44%	13%	6%
Pairs without clutches $(n = 17)$	53%	41%	6%	0%
All pairs $(n = 62)$	40%	43%	11%	5%

Table 4. Lesser Black-backed Gull nest-building and egg-laying dates (mean \pm s.e.) for clutch-laying pairs that built single nests or multiple nests. Tarnbrook Fell gullery study plot, 1993

	Pairs building single clutch nest only (n = 16)	Pairs building clutch nest and empty nest(s) (n = 29)	Significance
Mean date nest completed	4 May ± 2.9 days	7 May ± 1.9 days	t ₊₁ = 0.8, n.s.
Mean egg-laying date	15 May ± 2.4 days	17 May ± 2.5 days	$t_{45} = 0.6$, n.s.

Table 5. Lesser Black-backed Gull nest-building dates (mean ± s.e.) for empty nests and clutch nests

	n	Nest-building date	Range	Total number of days over which nests were built
Empty nests	64	5 May ± 1.6 days	14 April-30 May	47
Nests with clutches	45	6 May ± 1.7 days	15 April-22 May	38

Table 6. Order in which clutch and empty nests were built on Lesser Black-backed Gull territories where clutches were laid and multiple nests were built

Nests built on territory	Pairs	Clutch nest built first	Empty nest built first	Building sequence unknows
Clutch and one empty nest	19	6	6	7
Clutch and two empty nests	7	2	3	2
Clutch and three empty nests	3	1	2	0
Total	29	9 (31%)	11 (38%)	9 (31%)

Table 7. Mean percentage of established Lesser Black-backed Gull territories that were occupied on observation days prior to and after the start of the egg-laying period for pairs that produced a clutch and those that did not. Tarnbrook Fell gullery study plot, 1993 (95% confidence limits shown in parentheses)

	Geometric mean percentage of established territories occupied on observation days			
	Territory-holding pairs that produced eggs	Territory-holding pairs that did not produce eggs	Significance	
Before start of egg laying (n = 8 observation days				
between 4 April and 2 May) After start of egg laying (n = 8 observation days	76% (73–78)	71% (68–73)	$t_{14} = 3.9, P < 0.01$	
between 3 May and 30 May)	80% (79-81)	61% (60-63)	$t_{14} = 2.8, P < 0.01$	
Significance	$t_{19} = 9.3, P < 0.001$	$t_{19} = 5.8, P < 0.001$		

Table 8. Attendance by pairs on Lesser Black-backed Gull territories. Attendance expressed as percentage of total number of 30-minute observation periods (shown in parentheses) summed for all territories. Turnbrook Fell gullery study plot, 1993

		Attendance as a pair	
	Before egg laying (4 April-2 May)	During egg laying (3 May-30 May)	Whole period (4 April-30 May
Pairs that produced eggs	69%	41%	48%
	(624)	(2015)	(2639)
Pairs that did not produce eggs	58%	42%	47%
	(199)	(457)	(656)

Attendance as pairs

For the entire study period, there was no significant difference in the proportions of the total number of observation periods (summed for all pairs) in which a territory was occupied by a single bird or a pair for pairs which produced clutches (48% attendance as pair) and those that did not (47% attendance as pair, χ^2) = 0.02, n.s.; Table 8). Prior to the start of the egg-laying period on the plot (3 May), territory holders that managed to produce eggs were present as pairs for 69% of the total number of observations. This percentage is significantly higher than the 58% attendance as pairs for birds that did not produce eggs (χ^2) = 7.9, P < 0.01). After 3 May (when egg laying had started), the attendance of pairs with clutches dropped significantly, from 69% to 41% of observations (χ^2 ₁ = 146, P < 0.001). The attendance of pairs not producing eggs also dropped significantly but to a lesser extent at this time (58% to 51% attendance as pairs, $\chi^2_1 = 13.6$, P < 0.001), suggesting that they were becoming less motivated to attempt to breed as the season progressed.

Mating behaviour

A total of 69 attempts at mating in which the male mounted the female were recorded on the study plot. Two types of mounting were classified: those that were apparently successful and those that were definitely unsuccessful. Successful mounting was recorded when copulation appeared to be completed through cloacal contact.

For pairs that produced eggs, the recorded number of mounts attempted per pair was 1.2, and 90% of mountings were apparently successful (Table 9). For pairs that failed to produce clutches, the number of mounts per pair was 0.3, and only 56% of mountings were apparently successful. The first successful mountings for pairs that established a territory but did not produce a clutch were recorded on 5 May. The median dates of successful mounting were not significantly different between the two groups; 2 May for birds with clutches and 6 May for those without clutches (Mann-Whitney U=114, n.s.).

Territory size

The total area of the study plot occupied by the 62 gull territories was 0.26 ha, which was 63% of the total area (0.41 ha). The remaining areas were largely comprised of peat hags or boggy areas and were unsuitable for breeding gulls. There were no significant differences in the mean area of territories defended by pairs that produced eggs and those that did not or between pairs that built a clutch nest only and those that built a clutch nest plus one or more additional empty nests. The results are shown in more detail in Table 10.

Table 9. Comparison of mounting behaviour by Lesser Black-backed Gulls that produced a clutch and those that did not. Tambrook Fell gullery study plot, 1993

	Pairs that produced clutches (n = 45)	Pairs that did no produce clutches (n = 17)
Total number of observed mountings	60	9
Number of successful mounts	54	5
Percentage of mounts that were successful	90%	56%
Number of mounts per pair	1.2	0.3
Successful mounting date		
Median	2 May	6 Мау
Range	7 April-25 May	5 May-8 May

Table 10. Territory area for Lesser Black-backed Gull pairs producing or not producing a clutch and for pairs with a single clutch nest or a single clutch nest plus one or more empty nests. Tarnbrook Fell gullery study plot, 1993

	Territory area (m ²)		
	Mean ± s.e.	Range	Significance
Pairs producing a clutch (n = 45)	35.2 ± 1.8	12-91	
Pairs not producing a clutch $(n = 17)$	35.3 ± 2.3	21-56	$t_{so} = 0.01$, n.s
Pairs with single clutch nest $(n = 16)$	30.8 ± 1.9	16-43	1 - 1 50
Pairs with clutch nest and empty $nest(s)$ ($n = 29$)	37.7 ± 3.3	12-91	$t_{4} = 1.50, \text{ n.s}$

Productivity of pairs with clutches

All chicks hatched on the study plot were ringed and were checked every 3 days to determine the survival to fledging. For those birds which laid eggs, productivity was high, with 1.53 chicks fledging per pair. Even including the territory holders which did not lay, the productivity per pair (1.11 young) was still high.

Correction factor for census data

This study has shown that the assumption on which previous surveys at Tarnbrook Fell have been based is not correct. i.e. one nest does not represent one pair. The previously used method for calculating the number of breeding pairs during the census would have estimated 101 breeding pairs on the study plot at the time of the colony census in mid-May, whereas our detailed study showed that there were only 62 territory-holding pairs attempting to breed on the plot at that time. A correction multiplier of 0.61 must therefore be applied to the past census data to obtain the correct number of breeding pairs. As a result, the size of the colony has been overestimated in the past by about 39%.

DISCUSSION

This detailed study of a sample of territory-holding Lesser Black-backed Gulls at Tarnbrook Fell has revealed two points of considerable interest and consequence. First, an appreciable proportion (27%) of the gulls failed to lay eggs in 1993. Second, substantial nests were built by both pairs that laid eggs and those that did not. In many cases, pairs built more than one nest, and 58% of all nests failed to have eggs laid in them.

Although this study was conducted in only a single year, there is extensive information that the proportion of empty nests within the colony has been high and virtually constant since the first surveys of nests in 1981. The similarity in the year-to-year proportion of empty nests at the time of the annual census suggests that the pattern of nest building is likely to have been much the same over the 13-year period. There is no indication that the construction of empty nests is in any way related to the density of nesting gulls because empty nests were found in similar proportions in

all areas within the gullery. In turn, this suggests that climate or food supplies were unlikely to have been the main factors in causing this effect unless food was difficult to obtain in each and every breeding season. Even if food shortage was involved, it was unlikely to have persisted over the entire breeding season because those pairs that managed to produce a clutch had a high breeding success.

In general, birds that failed to produce eggs attended their territories as pairs significantly less frequently than pairs with clutches and had significantly fewer apparently successful mountings. However, some of these differences were rather small, and it is questionable whether they were by themselves sufficient to inhibit egg laying, particularly since laying and nonlaying pairs overlapped in the frequency of their attendance and copulatory behaviour.

The presence of many empty nests has been reported in other gull species but not, as far as we are aware, in Britain or in the Lesser Black-backed Gull. The empty nest phenomenon is not likely a feature of all colonies, but it does suggest that more checks are necessary before future census work on gulls is based solely on nest counts. In the case of the Tarnbrook colony, the counts of nests have to be multiplied by 0.61 to obtain a realistic estimate of the number of pairs. Since there is good evidence that this empty nest phenomenon has been present since at least 1981, it is likely that the annual estimates of the size of the colony have been appreciably exaggerated.

This study was made possible by a contract from the Grosvenor Estates and the kind permission of the Duke of Westminster. We also gratefully acknowledge the considerable assistance of all staff on the Abbeysted Estate, in particular Rod Banks, Ian Savage and Steve Barker.

REFERENCES

Dorst, J. 1974. The Life of Birds, Vol. 1. New York: Columbia University Press.

Harper, C. 1971. Breeding biology of a small colony of Western Gulls (Larus occidentalis wynami) in California. Condor 73: 337– 343.

Paludan, K. 1951. Contributions to Breeding Biology of Larus argentatus and Larus fuscus. Kobenhavn: I Kommision hos Enjar Marksgaard.

- Pettingill. O. 1971. Ornithology in Laboratory and Field, 4th ed.
- Minneapolis, Minn.: Burgess, Rosenberry, J. & Klimstra, W. 1970. The nesting and reproductive performance of the Eastern Meadowlark. Wilson Bull. 82: 243—
- Ryder, J. 1976. The occurrence of unused Ring-billed Gull nests.
 Condor 78: 415–417.
 Tinbergen, N. 1953. The Herring Gulls World. London: Collins.

Submitted 2 December 1995; revision accepted 25 February 1996