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POST-FLEDGING SURVIVAL IN HERRING GULLS IN RELATION TO BROOD-SIZE AND DATE OF HATCHING[a]

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Many bird species suffer high mortality in the period immediately after fledging, but this mortality is difficult to study because it often coincides with dispersal or migration. Perrins (1965), studying an English population of Great Tits (*Parus major*), found that young birds hatched in the early part of the season were proportionately more numerous in the breeding area in late autumn than young hatched late in the season. Perrins attributed this difference primarily to greater mortality of the late-hatched young during the post-fledging period. However, Dhondt and Hublé (1968) and Kluyver (1970) gave evidence that in Belgian and Dutch populations of Great Tits, the late-hatched birds were much more prone to emigrate than early-hatched birds. In the Manx Shearwater (*Puffinus puffinus*), Perrins (1968) found that chicks fledging early in the season were much more likely to return to breed in the same colony in subsequent years than those fledging late in the season. Similarly, in the Pied Flycatcher (*Ficedula hypoleuca*), early-hatched birds return to breed in the same area in much greater numbers than late-hatched birds (von Haartman, 1967; Lack, 1966). In the Manx Shearwater, the lower return rate of later-hatched birds is more likely to represent differential mortality than differential dispersal, because most young Manx Shearwaters return to breed in the colony where they were hatched (Perrins, 1968). In the Great Tit, young fledged from large broods appear to survive less well than those from average-sized or small broods (Lack, 1966), but there is no conclusive evidence for such a difference in the Pied Flycatcher (Curio, 1960; Lack, 1966; von Haartman, 1967).

Between 1964 and 1970, we and our assistants banded 27,115 Herring Gull (*Larus argentatus*) chicks of known age in New England colonies, and 708 have been recovered through November 1971. In this paper we use these recoveries to estimate the relation of post-fledging mortality rates to brood-size and to the date of

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hatching. The principle of the method is as follows. If two groups of chicks from the same colony experience different mortality rates in the first few weeks or months after fledging, this should be reflected proportionately in differences in the numbers found dead during this period and reported. After a sufficiently long period, the mortality rates of the two groups are expected to become equal, and the relative numbers of birds reported (either dead or alive) are then expected to be proportional to the relative numbers that survived the period of differential mortality. Thus the group that suffers the higher post-fledging mortality is expected to yield proportionately more recoveries in the post-fledging period, and proportionately fewer subsequently.

The only assumption made above is that the probability that a dead bird will be found and reported (the "reporting rate") is the same for each group. Reporting rates of Herring Gulls are known to be biased in a number of ways (Kadlec and Drury, 1968, 1969), but it is unlikely that any of the known biases would lead to a difference between reporting rates of groups of chicks raised in the same colony in the same year. Data from different colonies can therefore be grouped, even though the mean recovery rates differ between colonies because of differences in reporting rates. Similarly, data from birds banded in different years can usually be grouped, although the recovery rates for birds banded in the more recent years are lower because more are still alive.

For this study, the recoveries were divided into four groups:

A. Birds found dead away from the colony before 1 October in the year of hatching.

B. Birds found dead away from the colony between 1 October and 31 December in the year of hatching.

C. Birds reported (dead or alive) in the second calendar year of life.

D. Birds reported (dead or alive) after the second calendar year of life, through November 1971.

The date 1 October was selected for the division between groups A and B because it is close to the time at which juveniles end their dependence on parental feeding and migrate south (Gross, 1940). The remaining dates were selected arbitrarily.

DATA FROM BLOCK ISLAND

The most detailed data are from Block Island, Rhode Island, where 200-280 Herring Gull nests were studied in each year from 1965 to 1970. Each nest was visited every two or three days, so that dates of laying and hatching were known within 1-3 days, and the clutch-size and hatching success were known with few errors. Chicks were recorded as fledged if they were known to have reached the age of 15 days, beyond which the mortality rate is very low (Kadlec *et al.*, 1969). Chicks that were not found after the age of 15 days were assumed to have died. By using this criterion the number of chicks fledging was underestimated, perhaps by as much as 15 per cent, because 11 chicks that were not found after the age of 15 days nevertheless were recovered subsequently away from the island. In these 11 cases only, we have amended the brood-size originally recorded. We then estimate that 1,890 chicks were fledged from 1,488 nests: 161 broods of 3, 436 broods of 2, and 535 single chicks.

Table 1 summarizes the recoveries in each of the four periods according to the recorded brood-size. Most (5 out of 8) of the recoveries in period A (July-September) were of birds from broods of 3. In this respect the recoveries in this period differed significantly from all subsequent recoveries (Fisher's exact probability test, $P = 0.0097$).

TABLE 1. Recoveries of Herring Gulls banded as chicks at Block Island, Rhode Island, grouped according to the period of recovery and the brood-size at the time of fledging.

	Number of birds recovered from brood-size of		
Period of recovery	3	2	1
A. Before 1 October, hatching year	5	2	1
B. October-December, hatching year	4	9	10
C. Second calendar year	3	11	4
D. All subsequent years, through Nov. 1971	2	9	4
Totals	14	31	19

The proportion of banded chicks recovered after period A was lower among broods of 3 (9 out of 483, or 1.9 per cent) than among broods of 2 (29 out of 872, or 3.3 per cent) or of 1 (18 out of 535, or 3.4 per cent). The difference is not statistically significant ($\chi^2 = 2.23$, d.f. $= 1$, $0.1 < P < 0.2$, two-tailed test), but would probably become so if a correction could be made for the number of broods of 3 erroneously listed as broods of 2 (see above). In conjunction with the result in the previous paragraph, these data suggest that post-fledging mortality was higher in broods of 3 than in broods of 2 or 1, probably involving one additional death per brood or even more.

In about one-third of the broods, the order of hatching was known (in other cases two or three newly-hatched chicks had been found on the same visit). Among the broods of 3, the 5 birds recovered in period A included 2 known to have been hatched third, 1 known to have hatched first, and 2 hatched first or second; the 9 birds recovered subsequently included 3 hatched third, 1 hatched second or third, and 4 hatched first or second. Among the broods of 2, the 2 birds recovered in period A included 1 hatched second and 1 hatched first or second; the 29 recovered subsequently included 2 hatched third, 4 hatched second, 3 hatched first, 1 hatched second or third and 19 hatched first or second. There was thus no discernible tendency for the later chicks within a brood to suffer disproportionate mortality in the post-fledging period.

The recoveries of birds banded at Block Island were further subdivided according to the date of hatching. However, no significant differences were found between early-hatched and late-hatched birds in the periods of subsequent recovery.

DATA FROM OTHER ISLANDS

Methods

The remaining 25,225 chicks were banded on 49 other islands in New England between 1964 and 1969. (Only a few colonies were visited in all 6 of these years; the total number of colony-years was 137.) Most islands were visited two or three times during the fledging period, with an interval of from 2 hours to 10 days between visits; a few islands were visited four times or even more for special studies. The timing of the first banding visit was such that the age of the median-aged chicks was between 13 and 34 days, in most cases 20-25 days. At banding each chick was assigned to an age-class on the basis of plumage characters described by Kadlec *et al.* (1969). The age-classes corresponded to ages as follows: class 2a, 6-11 days; 2b, 12-17 days; 3a, 18-23 days; 3b, 24-29 days; 4a, 30-40 days; 4b, over 40 days. Hence, except for a few of the oldest birds, the age of each banded chick was known within 3 or 4 days.

For each island in each year, the numbers of birds banded and recovered were tabulated according to the age-class at the time of the first banding visit. In most cases relatively few birds were banded on the second banding visit, and the ages of these birds at the time of the first visit were estimated from the elapsed time between the visits. The age-class which contained the median chick was then denoted by M, subsequent age-classes (containing older birds, hatched earlier) by M+1, M+2, etc., and preceding age-classes by M−1, M−2, etc. The corresponding dates of hatching were then estimated by working back from the date of the visit by the appropriate numbers of days.

Although the range of ages corresponding to each plumage-class is known reasonably well, some overlapping necessarily results when data from different colonies are combined. For example, the boundary between age-classes 3a and 3b falls at 23-24 days. In a colony in which the median chick was 24 days old at banding, M corresponds to 3b and a 29-day-old chick is included in M. However, in a colony in which the median chick was 23 days old at banding, a 24-day-old chick is included in M+1. The expected result of this overlapping is that differences in recovery rates between neighboring age-classes will be slightly reduced.

Results

Data from three colonies experimentally disturbed are discussed in the next section. The remaining data are summarized in Tables 2 and 3, in which data from all colonies and all years are added together.

TABLE 2. Recoveries of Herring Gulls banded as chicks in 49 New England colonies, grouped according to the period of recovery and the date of hatching relative to the median date for the colony.

	Age-class at the time of banding†						
	M+4 and M+3	M+2	M+1	M	M−1	M−2	M−3 and M−4
Number banded	339	2420	4289	10006	4789	1854	890
Number recovered:							
A. Before 1 October,	4	8	31	58	29	11	3
hatching year	1.18%	0.33%	0.72%	0.58%	0.61%	0.59%	0.34%
B. October-December	0	6	18	39	28	9	1
hatching year	0%	0.25%	0.42%	0.39%	0.58%	0.49%	0.11%
C. Second calender	1	16	42	63	34	16	4
year	0.30%	0.66%	0.98%	0.63%	0.71%	0.86%	0.45%
D. All subsequent years, through	4	24	40	76	40	10	5
Nov. 1971	1.18%	0.99%	0.93%	0.76%	0.84%	0.54%	0.56%

†M is the age-class containing the median-aged chick in the colony in the year concerned. (M+1), etc., are the age-classes of successively older birds; (M−1), etc., are the age-classes of successively younger birds. Each age-class corresponds to about 6 days, but overlap of up to 5 days is introduced by grouping data from different colonies (see text).

In Table 2 the numbers of birds banded and recovered are grouped according to their ages relative to the median age-class in the same colony in the same year. That is, all data from class M are summed in one column, all data from class M+1 in the next, etc.

The distribution of recoveries from the various age-classes is generally similar in each of the four recovery periods, but there is one significant exception. The recovery rate of birds from the oldest age-classes (M+2 to M+4) is relatively low in periods A and B, and relatively high in period D. Comparing recoveries from these age-classes with those from M−1 to M+1, the difference is statistically significant (χ^2 = 4.31, d.f. = 1, $P < 0.05$). This suggests that the oldest birds survived the post-fledging period significantly better than birds hatching at the peak period.

Another noteworthy feature of Table 2 is that the recovery rates of the younger birds (classes M−2 to M−4) are lower than those of birds in M−1, M and M+1, at least in periods A, B, and D. Such a difference had been expected, because most of the former birds were banded at ages 6-18 days (age-classes 2a and 2b), at which time chick mortality is still substantial. The differences in Table 2 are not statistically significant, but they are consistent with the 10-25 per cent mortality in these age-classes recorded by Kadlec *et al.* (1969).

TABLE 3. Rceoveries of Herring Gulls banded as chicks in 49 New England colonies, grouped according to the period of recovery and the estimated date of hatching.

	May 21-26	27-31	June 1-6	7-12	13-18	19-24	25-30	July 1-6	7-12	13-18	19-24	25-30
Number banded†	127	1015	2475	5082	6913	4785	2240	1263	563	97	24	3
Number recovered:												
A. Before 1 October, hatching year	0	2 0.20%	11 0.44%	39 0.77%	51 0.74%	25 0.52%	9 0.40%	6 0.48%	0 0%	0	0	1
B. October-December, hatching year	0	2 0.20%	4 0.16%	23 0.45%	37 0.54%	27 0.56%	4 0.18%	3 0.24%	1 0.18%	0	0	0
C. Second calendar year	0	7 0.69%	12 0.48%	48 0.94%	55 0.80%	27 0.56%	21 0.94%	5 0.40%	1 0.18%	0	0	0
D. All subsequent years, through Nov. 1971	2	14 1.38%	24 0.97%	42 0.83%	66 0.95%	30 0.63%	12 0.54%	6 0.48%	1 0.18%	2	0	0

†Each column includes all chicks in the age-class whose median fell into the corresponding range of dates. Overlap of up to 5 days is introduced by grouping data from different colony-years (see text).

Table 3 summarizes the recoveries according to the estimated dates of hatching. (It differs from Table 2 in that relatively early birds in late colonies are grouped with relatively late birds in early colonies.) The differences in the recovery pattern of the early hatched birds are much more pronounced in Table 3 than in Table 2. Comparing birds hatched before 6 June with those hatched during the peak period 7-24 June, the mean recovery rate in periods A and B was about 60 per cent less and that in period D was 30-35 per cent higher: the difference is highly significant ($\chi^2 = 13.98$, d.f. $= 1$, $P < 0.001$). The difference between Tables 2 and 3 suggests that the absolute date of hatching is more important than the relative date in determining the probability of surviving the post-fledging period. Or, to state the matter differently, the factors that favor early-hatched chicks favor primarily those from early colonies. Table 3 shows further that the recovery rate of birds hatched before 6 June was lower than that of birds hatched during 7-24 June in period C also. In this respect the pattern of recoveries in period C was significantly different from that in period D ($\chi^2 = 4.54$, d.f. $= 1$, $P < 0.05$), but not significantly different from those in periods A and B. This suggests that the period of differential mortality continued through at least part of the second calendar year of life. The number of recoveries in period C was insufficient to determine the precise date at which the pattern of recoveries changed, but the recovery rate of the early-hatched birds was low in at least the first two quarters of the year.

Another striking feature of Table 3 is that the recovery rate declined sharply for chicks hatched after 24 June, and that extremely few hatched after 6 July were subsequently reported. Because these trends were noted in all four recovery periods, they evidently result from mortality before the chicks had left the island, before or very soon after fledging.

In case the grouping of data from many different colony-years had obscured some real trends, the data in Table 2 were subdivided in several ways. First, the data from the 6 different years were examined separately. Second, the data from the southern colonies (Massachusetts and Rhode Island) were separated from those from the northern colonies (Maine). Third, data from colony-years in which the median age at the time of banding was low (M = 3a or 2b) were separated from those in which it was higher (M = 3b or 4a). Fourth, data from the more successful colonies (mean productivity greater than 1.05 chicks per pair) were separated from those from the less successful colonies. However, in each case, the pattern of recoveries was similar to that in Table 2 (except that the statistical significance of the differences was weaker in the subdivided samples). In particular, the differential survival of the earliest chicks was pronounced in at least three years and in all the other subdivided samples except the low productivity islands (most of which had late median hatching dates).

DATA FROM EXPERIMENTAL ISLANDS

Table 4 summarizes recovery data from three colonies in Massachusetts (Egg Rock, Nahant; Cat Island, Marblehead; and Kettle Island, Manchester) that were the subject of experimental treatment in 1964 (Drury, 1967). After the main crop of eggs was broken in early June, many pairs renested and 638 young were reared and banded 3-4 weeks later than usual.

TABLE 4. Recoveries of Herring Gulls banded as chicks on three islands in Massachusetts where breeding was delayed by egg-breaking.

	Estimated dates of hatching						
	June 19-24	25-30	July 1-6	7-12	13-18	19-24	25-30
Number banded	31	16	68	262	226	34	1
Number recovered:							
A. Before 1 October, hatching year	0	0	2	5	1	0	0
B. October-December hatching year	0	0	0	4	0	1	1
C. Second calendar year	0	0	2	3	0	0	0
D. All subsequent years, through Nov. 1971	0	1	3	1	0	0	0

The pattern of recoveries in Table 4 differs in several ways from that in Table 3. First, substantial numbers of birds hatched as late as 1-12 July (but few hatched subsequently) were subsequently recovered away from the colony. This suggests that renesting adults were able to raise young to fledging up to 6-12 days later than the usual latest date for successful breeding, but no later. Second, the ratio of 14 recoveries in periods A and B to only 5 in period D is significantly different from that for birds banded on 12 other islands in 1964 (36 in periods A and B, 80 in period D; $\chi^2 = 10.67$, $P < 0.005$). Third, although the recovery rate for these and neighboring islands (situated in a populous region) is always relatively high (averaging 1.96 per cent in periods A, B and C for birds banded 1965-69), it was much higher for the birds hatched before 12 July in 1964 (4.24 per cent, $P < 0.05$).

Together, these data suggest that a substantial number of the birds raised on these experimental islands fledged, but an unusually large proportion of the fledglings died before 31 December of the same year. Although birds that renest after egg-breaking appear to do so with moderate success, raising about 0.54 young per pair to the point of fledging (Drury, 1967), it appears that only 10-20 per cent of the expected number of these late young survived their first winter.

DISCUSSION

The principal conclusion of this study is that most groups of Herring Gull chicks (those in broods of 2 and 1, and those hatched between 7 and 24 June) show a similar temporal pattern of recoveries, and hence appear to suffer generally similar mortality in the post-fledging period. They thus differ from other bird species whose post-fledging mortality has been analyzed (see INTRODUCTION). In one sense this result was expected, because Herring Gull chicks have many artificial food-sources available to them, so that their survival might be largely independent of minor physiological or social differences at the time of fledging.

There are, however, two significant exceptions. First, the earlier-hatched chicks in the earlier colonies appear to suffer markedly lower post-fledging mortality, perhaps only 40 per cent of that of the chicks hatched at the peak period (Table 3). It is remarkable that this advantage appears to be maintained throughout the first winter and perhaps into the next spring and summer. One possible explanation is that the earliest chicks establish dominance over younger chicks and maintain dominant status throughout the winter.

Second, chicks in broods of three appear to suffer significantly higher post-fledging mortality than those in broods of two or one (Table 1). It is known that in at least one Herring Gull colony the third chick in a brood of three grows slowly and fledges at a lower weight than its siblings (Harris, 1964). However, our data showed no discernible tendency for the third chicks in broods of three to suffer greater post-fledging mortality. Hence it is unlikely that the differential losses from the larger broods can be attributed to lower weights at fledging, as Perrins (1965) suggested for Great Tits. It seems more probable that two Herring Gull parents cannot care adequately for a brood of 3 flying chicks.

These differences in mortality rates do not have great demographic significance. Birds hatched before 7 June comprise only 15 per cent of those in our sample (Table 3) and broods of three comprise only 25 per cent of the chicks fledged even at Block Island, one of the most successful colonies in our area. However, they may be significant for analysis of the evolution of breeding season and clutch-size. In our sample, the parents that nest very early and raise two young appear to give rise to the most mature offspring. In this sense, they are much more successful than those nesting a few days later, and probably more successful than those raising three young to fledging.

Although experimental studies have not yet demonstrated that Herring Gulls can raise more than 3 young to fledging (Harris and Plumb, 1965), the closely related species *L.* (*a.*) *glaucescens* and *L. fuscus* can raise broods of 4-6 to fledging under experimental conditions (Vermeer, 1963; Harris and Plumb, 1965), and in *L. occidentalis* experimental broods of 4-7 give rise to more fledged young, on the average, than normal broods (Coulter, 1969). Hence it might appear that gulls that could lay and hatch clutches of

4-7 eggs would be favored by natural selection. The most frequent clutch-size is 3, however, and clutches of 4 are very rare in all gulls.

Vermeer (1963) found that chicks of *L.* (*a.*) *glaucescens* from experimental broods of 4-7 were subsequently seen on a dump 70 km away in significantly greater numbers than those from broods of 1-3. However, the dates of these sightings were not given, and they do not necessarily demonstrate survival through the first winter (indeed, it is possible that the appearance of the chicks at a dump may have reflected inadequate parental care). In *L. argentatus* our data suggest that even broods of 3 were at a disadvantage in the post-fledging period. Hence clutches of 4 or more laid by Herring Gulls in our population might in fact give rise to fewer mature young than clutches of 3.

It thus seems likely that the optimum number of fledging chicks in the Herring Gulls of our area is 2. Herring Gulls that lay clutches of 3 eggs raise 2 young to fledging much more frequently than those laying 2 eggs, because of the rather frequent accidental loss of one egg or one chick (Brown, 1967; Nisbet and Drury, unpublished data). Hence it seems likely that 3 might be the optimum clutch-size in the Herring Gull, even if locally abundant food might permit raising of more chicks to fledging.

One other important result of this study is the indication that very few chicks hatched after 6 July in fact survived to leave the island where they were hatched. In the ordinary way, these late clutches are probably laid either by young birds or by birds that have lost clutches earlier in the season. When other birds were forced to nest late by experimental egg-breaking, the effective breeding season was extended by 6-12 days (Table 4). However, even in this case the last 40 per cent of the nests apparently gave rise to few independent young. It is unlikely that the abrupt ending of the effective breeding season is due to external factors, because food remains abundant throughout the summer near these colonies, and most of the chicks had passed the age at which they are vulnerable to adverse weather. It seems more likely that their failure to reach the age of independence is due to neglect by the parents at the end of the breeding season. Evidence for the waning of parental attention is provided by the results of egg-breaking experiments on other islands (Drury, 1967). Herring Gulls will lay three or more clutches if eggs are broken repeatedly in May and June, but extremely few re-lay if their second clutches are broken after 1 July. In addition, comparatively few chicks hatched after 12 July were raised to fledging, even by renesting birds.

The analysis in this paper has been based on rather small numbers of recoveries. Many of the banded birds are still alive, and the recovery rate in period D is expected to increase following the introduction of durable bands in 1968. We plan to repeat this analysis in 5-10 years.

SUMMARY

27,115 Herring Gull chicks of known age were banded in 50 New England colonies, 1964-1970. Chicks raised in broods from which three chicks fledged were recovered in greater numbers than those raised in broods of two or one during the first 2-3 months after fledging, and in smaller numbers thereafter. Chicks hatched before 6 June were recovered in smaller numbers than those hatched later during the first 6-12 months after fledging, and in greater numbers thereafter. These differences indicate differences in mortality rates in the post-fledging period. Parents that nest very early and raise two young appear to give rise to the greatest number of mature offspring.

After experimental egg-breaking, many pairs of Herring Gulls re-laid and raised young with moderate success 3-4 weeks later than usual. However, an unusually large number of these young was recovered soon after fledging, and their survival rate during their first winter appears to have been only 10-20 per cent of that for chicks from undisturbed colonies.

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