GROWTH AND MORTALITY OF HERRING GULL CHICKS

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Only about one-half of the Herring Gull (*Larus argentatus*) chicks which hatch live to fledging. In a previous paper (Kadlec and Drury, 1968), we showed this to be a major factor in the current structure of the New England Herring Gull population. In that paper, we emphasized average and range of age structure, mortality, and reproduction of the Herring Gull population; here we are more concerned with the specific events which bring about the general effect during the critical period between hatching and fledging.

Many studies of gull breeding biology show that on the average a pair of Herring Gulls succeeds in rearing one young to fledging each year (see Kadlec and Drury, 1968; and Brown, 1967, for reviews). The average clutch size is nearly three, and variations are small (Keith, 1966; Brown, 1967; Kadlec and Drury, 1968). Hatching success is usually high—60-80 percent. Keith (1966) has discussed in detail the problems of accurately measuring hatching success. Paynter (1949) and Brown (1967) agree that the hatching success of 2-egg clutches is poorer than that of 3-egg clutches; 1-egg clutches are usually too uncommon to provide adequate samples. Our data (Kadlec and Drury, 1968) indicate that the success of 2-egg clutches is sometimes as great, or greater than that of 3-egg clutches. The reasons for the discrepancy in observations is not known. Because our data indicate that rearing young is not related to clutch size, we will not discuss clutch size as a factor in growth and mortality of Herring Gull chicks.

Success in raising young varies with the time of hatching. Brown (1967) found mid-season nests produced more young per nest than did early or late nests. We also found this to be true in five of six studies, but in the sixth study, the earliest nests were most productive.

Ideally, a complete analysis of growth and mortality should evaluate the relative importance of clutch size, hatching success, time of hatching, and perhaps also age of parents, as well as differences between years and areas. Unfortunately, our data, although extensive, do not permit simultaneous analysis of all these factors. To obtain reasonable samples, we combined data from different sources to show patterns and make regional comparisons.

Our data are from: a) a special study in 1964 of a few chicks in which age, growth, plumage development, and mortality were

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compared; b) records of chicks found dead in studies designed primarily to measure the number of young fledged per nest in many colonies in 1965, 1966, 1967; and c) detailed nest history data from one colony for 3 years.

METHODS

Growth and plumage development

To develop age criteria, measure growth, and observe plumage development, we marked 20 Herring Gull chicks soon after hatching on a small island (Gray's Rock) near Salem, Massachusetts, in 1964. At the first capture and every 3 to 7 days thereafter, we weighed and photographed each chick that could be located. Only six of the 20 were known to attain an age and weight (see later) which made fledging probable.

Records of chicks found dead

Using the age criteria developed in the 1964 study of growth and development, records were kept of the ages of all chicks banded in extensive studies of gull productivity in 1965-1967 (Kadlec and Drury, 1968).

The Maine study area included 22 islands from Saco Bay to Penobscot Bay. Each of these islands was visited twice. The interval between visits varied from 1 to 11 days and averaged 6.4 days. On the second visit, all chicks banded on the first visit and found either dead or alive, were recorded. The original banding data for each island gave the age distribution of chicks at the time of banding. The number of chicks in each age category was then multiplied by the interval between visits, in days, to give the number of chick-days, by age class, during which deaths could have occurred. Because the number of dead chicks found on each island was too small to give reliable results, the number of dead chicks and chick-days were summed for the entire 22-island group.

If x_{ij} = the number of chicks originally banded in the j^{th} age class on the i^{th} island.

and t_i = the interval in days between banding visits on the i^{th} island.

$$\sum_{i=1}^{n} (x_{ij}\, t_i) = \text{no. of chick-days in age class } j$$

$$\sum_{j=2a}^{4} \sum_{i=1}^{n} (x_{ij}\, t_i) = \text{total number of chick days}$$

Similar procedures were followed for a series of 10 Massachusetts islands in 1965 and for five Massachusetts islands in 1966 and 1967. In addition, many of these islands were visited a third and sometimes a fourth time to provide information on later mortality.

TABLE 1. WEIGHTS OF HERRING GULL CHICKS[1]

Days of Age	American Wild: All which reached a given age	American Wild: Only those presumed fledged	Hand-reared[2]	European Hand-reared[3]
5	97 ± 18 (10)	106 ± 15 (4)	88 ± 18 (7)	116 ± 20 (10)
10	221 ± 46 (12)	249 ± 41 (6)	189 ± 22 (7)	196 ± 57 (10)
15	393 ± 95 (12)	443 ± 75 (6)	386 ± 53 (7)	337 ± 58 (10)
20	580 ± 96 (9)	608 ± 81 (6)	375 ± 66 (7)	509 ± 86 (10)
25	697 ± 100 (9)	731 ± 88 (6)	520 ± 99 (7)	678 ± 93 (10)
30	787 ± 117 (9)	853 ± 109 (6)	668 ± 109 (7)	841 ± 116 (10)
35	914 ± 197 (8)	990 ± 157 (6)	806 ± 107 (7)	892 ± 123 (10)
40	928 ± 267 (7)	1054 ± 190 (5)	No weight data	904 ± 115 (10)
45	976 ± 268 (6)	1048 ± 237 (6)	although	857 ± 122 (10)
50	982 ± 171 (4)	982 ± 147 (4)	chicks lived	944 ± 114 (10)

[1] Mean weights ± one standard deviation. Figures in parentheses indicate sample size. In the wild birds, variations reflect our inability to find individuals, as well as deaths, and disappearances.

[2] Data courtesy of W. John Smith and George L. Hunt, Jr., of the Harvard University Biological Laboratories.

[3] Data taken from graphs of Goethe (1955) and Peters and Müller (1951).

Detailed nest history studies

A portion of the gull colony on Block Island, Rhode Island, that contained about 250 nests was studied intensively in 1965, 1966, and 1967. Each nest was numbered and was visited every 2-5 days, so that hatching dates could be determined within a day or two. The chicks in each nest were marked soon after hatching, so that ages of any found dead could be determined. Errors are inherent because hatching is spread over several days, and dead chicks are not necessarily found immediately after death. For these reasons and for ease of comparison with data from other studies, deaths were recorded by intervals of 0-5, 6-11, 12-17, 18-23, 24-40, 41-52, and 53 or more days after hatching. For deaths near the limits of the intervals, details of the schedule of visits were used to determine placement.

RESULTS

Growth and development

Table 1 gives the mean weights (at 5 day intervals) of Herring Gull chicks found on Gray's Rock three or more times and, for comparison, the mean weights of two groups of hand-reared gull chicks. Growth was rapid until about 30-35 days of age. Of six chicks which fledged, the youngest was between 35-44 days of age at fledging and the oldest was between 56-61 days. The average

TABLE 2. PLUMAGE AND LEG DEVELOPMENT IN HERRING GULLS FROM HATCHING THROUGH FLEDGING

Observations made by Goethe (1956) on hand-reared European Herring Gulls	Age in Days	Observations made in this study on wild American Herring Gulls
	0	
		Class 1 (0-5 days)
Week 1	2	Legs pink; too small to wear a size 6 band.
Egg tooth disappears in some chicks.	4	Stays in nest.
	6	
	8	
		Class 2a (6-12 days)
Week 2	10	Legs become dark; can be banded. No pinfeathers.
Egg tooth lost by rest of chicks. Pinfeathers begin to appear	12	Mobile.
Birds become mobile.		
	14	Class 2b ((12-17 days) Pinfeathers appear on wings but
Week 3	16	do not yet erupt.
Pinfeathers present on all. Lesser coverts begin to appear.	18	
Feet attain full growth.		Class 3a (18-23 days)
	20	Primary feathers erupt; tail feathers not erupted.
	22	
Week 4	24	
Final fledging weight attained.	26	
	28	Class 3b (24-40 days)[1] Tail feathers erupt; body becomes
Week 5	30	more fully feathered. Down gradually lost from all areas but the
Head spots begin to disappear with down, leaving a crest of down on the	32	occiput and flanks.
top of the head. Wing and tail feathers grow noticeably.	34	(Occasional birds which appear sick and eventually die may remain 3b's
	36	until as late as day 48)
Week 6 Contour feathers fill out.	38	
Last remnants of down are lost from neck, throat, back of head,	40	
breast and belly.	42	Class 4 (41 days-fledging) Chicks lost head down; become fully feathered. Chicks fledge. Mantle
Week 7 Last of down lost; chicks attain	44	and wings chocolate brown; body
fledging plumage. Chicks begin	46	solid dark chocolate; belly paler, mottled with tan; rump brown, barred with buff; tail all brown; eye brown; bill black.[2]
to fledge		
Weeks 8-10 All chicks fledge.		

[1]In 1967 we sub-divided this age class at day 30, using the appearance of feathers on the crown as a criterion.

[2]The European Herring Gull chick's first plumage is a light buffy color, like the second-year plumage of American birds.

TABLE 3. SUMMARY OF NEST HISTORY DATA
BLOCK ISLAND, RHODE ISLAND, 1965-1967

Year	No. of nests studied	No. of Eggs	No. of eggs hatched	Known deaths, Age class 1 0-5 days	2a 6-11 days	2b 12-17 days	3a 18-23 days	3b 24-40 days	4 41-52 days	Known alive after 15 days	Disappeared during first 15 days
1965	253	714	613	43	14	7	8	8	7	359	167
1966	261	749	565	37	8	4	4	4	2	377	129
1967	259	719	548	33	18	14	4	7	1	268	203
Total	773	2,182	1,726	113	40	25	16	19	10	1,004	499

age of fledging was 51 days. These ages are consistent with the range of fledging ages (43-62 days) reported by Goethe (1956) for the European Herring Gull and by Paynter (1949) for the American Herring Gull.

The chicks that presumably fledged were consistently heavier than the average of all chicks of any given age. This, of course, means those that died were consistently lighter.[4] The non-survivors seemed to have slower rates of growth during the first 30-35 days and more erratic patterns of weight change during the remaining time. Two of three chicks weighing less than 700 grams at 30 days died before fledging.

Slow growth and being under-weight are not necessarily direct causes of mortality, for the American hand-reared birds survived in spite of both. In the wild, however, underweight chicks apparently are less able to withstand the common hazards of the environment.

The European hand-reared Herring Gull chicks (Table 1) grew faster than the American hand-reared ones but not quite as well (in general) as the American wild gulls. In addition to the factor of captivity, there may be subspecific size differences confounding comparison of the data.

Even though the rate of weight gain decreased markedly after 30-35 days of age in all chicks, at this stage the chicks could be described as "half-feathered." About 2 more weeks were needed to complete plumage development required for flying from the island. Parental care decreases throughout this period, but may continue for several weeks after the chicks have left the natal islands.

Age at various stages of plumage development is shown in summary in Table 2. Our observations agreed with those made by

[4]Because of the very small sample, these differences were not tested statistically. Similarly, standard deviations are presented to give a concept of the variability, rather than confidence limits which might imply that we thought this was an adequate sample for meaningful conclusions.

TABLE 4. MORTALITY[1] OF BANDED YOUNG HERRING GULLS

	Age class at banding[2] 2a	2b	3a	3b	4	Total	Mean
1965							
Maine—22 islands							
No. banded, first visit	465	826	1,096	942	12	3,341	
No. dead, second visit[3]	35	29	25	17	0	106	
No. of chick-days[4]	3,613	6,075	7,441	5,616	60	22,805	
Deaths per 100 chick-days	.968	.477	.335	.302	0		.464
Massachusetts—10 islands							
No. banded, first visit	129	155	539	1,410	225	2,458	
No. dead, second visit	1	4	8	26	3	42	
No. of chick-days	802	987	3,847	7,937	1,442	15,020	
Deaths per 100 chick-days	.123	.405	.207	.327	.208		.279
1966							
Massachusetts—5 islands							
No. banded, first visit	183	396	403	490	24	1,496	
No. dead, second visit	10	8	10	9	0	37	
No. of chick-days	550	1,283	1,376	1,619	77	4,905	
Deaths per 100 chick-days	1.818	.624	.727	.556	0		.754
1967							
Massachusetts—5 islands							
No. banded, first visit	[5]	172	255	145	13	585	
No. dead, second visit	—	12	4	4	0	20	
No. of chick-days	—	289	431	216	23	959	
Deaths per 100 chick-days	—	4.152	.928	1.852	0		2.086

[1]Between first and second visits to each island.
[2]According to system of age classification presented in Table 2.
[3]In 1965, second visits averaged 6-7 days after first visits; in 1966, 3 days; and in 1967, 1-2 days.
[4]Chick-days calculated as explained in text.
[5]Only 2b and older chicks banded in 1967.

Goethe (1956) on hand-raised European Herring Gulls. Table 2 also tabulates the leg and plumage characteristics we used to classify chicks into age classes in the field, and the ages included in each class.

Detailed nest history studies

Our most complete information on chick mortality was obtained from detailed nest history studies (Table 3). Regular and frequent searches gave a good record of the distribution of mortality from hatching to fledging. The data in Table 3 clearly indicate that most of the known mortality occurred very soon after hatching, over half (51 percent) within 5 days. Close observation at the time of hatching showed that nearly 80 percent of the eggs hatched. In a less detailed study, much of this early loss would have been missed and it would have been concluded that hatching success was much lower than it really was.

Another indication of the heavy early mortality was that 499 of the 1,641 marked chicks were last seen fewer than 15 days after hatching. If, as seems likely, they all died within fewer than 17

TABLE 5. MORTALITY[1] OF BANDED YOUNG HERRING GULLS ON MASSACHUSETTS BAY COLONIES

	Age class at banding[2] 2a	2b	3a	3b	4	Total	Mean
1965—10 colonies							
No. banded	186	220	573	1,616	277	2,872	
No. found dead	7	11	21	45	7	91	
No. of chick-days	1,761	2,067	6,754	13,707	2,109	26,398	
Deaths per 100 chick-days	.397	.532	.310	.328	.331		.344
1966—5 colonies							
No. banded	224	453	461	612	33	1,783	
No. found dead	16	27	22	29	1	95	
No. of chick-days	4,519	8,500	9,954	12,652	619	36,043	
Deaths per 100 chick-days	.354	.318	.226	.229	.162		.264
1967—5 colonies							
No. banded	—[3]	190	287	200	16	693	
No. found dead	—	16	13	17	1	47	
No. of chick-days	—	5,059	7,901	6,042	502	19,504	
Deaths per 100 chick-days	—	.316	.165	.281	.199		.241

[1]Based in part on data in Table 4, but additional information from third and fourth visits included.
[2]According to system of age classification presented in Table 2.
[3]Only 2b and older chicks banded in 1967.

days, then 677 of the 1,726 chicks that hatched (39.3 percent), died during this period. It seems incredible that three-fourths of the dead chicks were simply overlooked; alternative explanations are that they were eaten or carried away by the adult gulls, or that they died in hiding and decomposed to the extent that they were overlooked.

Mortality in the older age classes was much lower, with only 45 known deaths during the last 20-35 days (depending on exact fledging age) in the colony. Although older chicks are very mobile and skilled at hiding, they are also larger, easier to see, less easily swallowed whole or carried off, and take longer to decompose.

The last two age categories in Table 3 are longer than the previous ones. Thus, the higher numbers of deaths in class 3b does *not* reflect an increase in mortality but rather a longer time interval. As mentioned earlier, the age classes used were selected to permit direct comparison with other studies.

Records of chicks found dead

Our banding operations were conducted mainly to measure productivity, so we delayed the first visits until most of the chicks were of age class 3a or 3b, over 3 weeks old. Early mortality was known to be heavy, and we wished to avoid this complication in measuring productivity. In the process we lost a great deal of information on early mortality.

Known mortality among the banded chicks (Table 4) was very low; only 2-3 percent of those banded were found dead. The chicks

TABLE 6. LIFE TABLE ANALYSIS OF BLOCK ISLAND CHICK MORTALITY (1965-1967) AND CONVERSION TO DEATHS PER 100 CHICK-DAYS

Age	No. Alive	No. Die[1]	Death rate	No. of Chick-days	Deaths per 100 chick-days	Found dead[2] per 100 chick-days
Hatch	1,726	434	.251	10,356	4.191	1.091
2a	1,292	153	.118	7,752	1.974	0.516
2b	1,139	95	.083	6,834	1.390	0.366
3a	1,044	48	.046	6,264	0.766	0.254
3b	996	57	.057	16,932	0.348	0.112
4	939	30	.032	11,268	0.266	0.089
Fledge	909					

[1]Mortality data from Table 3.
[2]Found dead differs from deaths by the exclusion of those chicks which disappeared.

in Maine had progressively lower mortality rates as they grew older, which is biologically reasonable. The mortality rates for Massachusetts were much more variable, partially, no doubt, due to the small numbers of birds found dead. One difference between years was the interval between visits. The death rates were highest in 1967 when the interval between visits was shortest perhaps because most of the mortality occurred immediately after the first visit, probably due to the disturbance of banding. Alternatively, a shorter interval between visits may have resulted in finding more of the dead chicks, probably because they were less likely to have been carried off or to have decomposed beyond recognition.

When later mortality was included by adding data from third and fourth visits to the calculations for the Massachusetts colonies (Table 5), variability was reduced. More important, the mean death rates declined from 1965 to 1967, indicating that the increases in Table 4 can be attributed largely to the variations in the interval between visits.

In Tables 4 and 5 mortality is presented in relation to age at banding. For the data in Table 4, the first and second visits were close enough together so that most of the mortality probably occurred during the age class interval of banding. Relating much later mortality, derived from third and fourth visits, to the age at banding, as was done in Table 5, meant that many of the deaths occurred in age classes after the one of banding. For example, some (if not most) of the seven deaths recorded in the 2a age class in 1965 undoubtedly occurred in older age classes. Our method of calculation adjusted for different numbers of chicks banded in the different age classes and different intervals between visits on different islands, but not for the fact that a chick might change age class between banding and death. To be completely accurate, we would have needed to know: a) the ages at death of all chicks found dead, and b) the exact size of an age class when each death occurred, or c) the average number of chicks which passed through each age class.

TABLE 7. COMPARISON OF AGE-SPECIFIC DEATH RATES BASED ON KNOWN DEATHS ONLY

Age	Block[1] Island	Maine[2]	Massachusetts 2 visits[3]	Massachusetts All visits[4]
1	1.091			
2a	0.516	0.968	0.814	0.366
2b	0.366	0.477	0.938	0.346
3a	0.254	0.335	0.389	0.229
3b	0.112	0.302	0.399	0.281
4	0.089	0	0.195	0.279

[1]Data from Table 6
[2]Data from Table 4
[3]Data from Table 4, average for 1965-1967
[4]Data from Table 5, average for 1965-1967

Synthesis of mortality

As a first step in attempting to synthesize the data into a composite picture of chick mortality, the data from Block Island were subjected to life table analysis (Table 6). For this, it was necessary to make some assumptions about the pattern of mortality of chicks which simply disappeared. This was done in two parts: a) the 499 chicks not seen after day 15 (Table 3) were assumed to have died during the first three age classes in the same proportion as those found dead; and b) the number of chicks found dead in the three oldest age classes were assumed to represent one-third the true number of deaths. Several variations of these assumptions were tried and found to have no important effect; in fact, it was necessary only to assume that the pattern of known deaths was a rough sample of the total deaths.

The life table construction gave values for the numbers of chicks entering each age class, which in turn permitted calculation of the numbers of chick-days in each class. Death rates comparable to those derived from other data were then calculated for both known and inferred deaths. Age-specific mortality rates based on known deaths are compared in Table 7. Although there are obvious variations, some due to small samples, the agreement is good, in general. There appear to be two exceptions: a) the absence of a decline in mortality rates for all visits in Massachusetts, and b) the low mortality in the older age classes in the Block Island studies. Both may reflect differences in the ecology, but the samples are small and the method of calculation indirect.

DISCUSSION

These studies clearly establish two facts: 1) most of the chick mortality occurs in the first week after hatching, and 2) most of the dead chicks disappear even when searches are frequent and thorough. In considering the possible causes for these phenomena, it should be kept in mind that we are dealing with elusive mortality factors. At no time in these studies have we found evidence of mass mortality due to weather or to disease epidemics.

Our first finding is in accord with Paynter (1949), Paludan (1951), Harris (1964), and Brown (1967). Brown also found most of the chicks "disappear without a trace", corresponding to our second finding. Obviously, these are real characteristics of mortality of Herring Gull chicks. The causes, however, are less clear. Brown (1967) considered gulls other than the parents the chief cause of mortality. Paynter (1949) and Paludan (1951) considered the Great Black-backed Gull (*Larus marinus*) to be the chief cause. Weaver (*in litt.*) in detailed observations from a blind in 1966 on one of the colonies studied by us in 1965, did not observe any direct predation. Indeed, he observed one pair of Herring Gulls protect its chick when it wandered into the territory of a Great Black-backed Gull. In contrast, most of the known mortality in his study could be attributed to failure of the adults to make an adequate behavioral transition from incubation to care of young. As examples, some chicks died of exposure to rain (inadequate brooding), one was built into nest material, and one was "adopted" by an incubating pair who were unsuccessful in solving the behavioral dilemma of whether to incubate their own eggs or care for the wanderer.

Even in Weaver's detailed study, many of the chicks just disappeared. The question remains: Were these taken by other gulls? The absence of any traces led Weaver to hypothesize that they were eaten or carried off by other gulls. Brown (1967) implies he considers the same phenomenon important. Both observed, as we have, that many of the corpses show evidence of being severely pecked. Yet in our experience this is often attributable to our own disturbance of the colony, as frightened chicks often run into strange territories. We have observed that the adults usually give the long call (Tinbergen, 1959) when attacking chicks. This association clearly indicates that predation is not the object of the attack, because a long call is characteristically given during territorial, not predatory, behavior.

Perhaps more significantly, few of the dead young showed signs of attempts having been made to eat them. Only on islands where there was other evidence of food shortage (low productivity), have we found evidence of actual consumption—skeletons rather than whole carcasses. This suggests that prior to man's provision of excess food, in form of waste materials, eating of chicks by adult Herring Gulls or Great Black-backed Gulls may have been much more prevalent. We cannot say whether this took the form of predation, or whether it is primarily scavenging. Obviously, the distinction is of considerable importance, for scavenging simply takes advantage of mortality from other causes.

Thus, the evidence for heavy predation (Brown [1967] called it "cannibalism") by adult gulls on chicks remains largely circumstantial. We suggest that the problems of the behavioral transition from incubation to care of young may be equally important, and perhaps fundamental, even when the actual cause is predation; i.e., predation is possible only when the parents do not make an adequate transition.

The study of the growth of chicks also showed that the chicks which ultimately died grew more slowly from the start. The implication clearly is that they were not as well fed. Food was not critical in the colony studied, so differences in the amount of food brought to the chicks must have been due largely to differences in how hard the adults worked at feeding their young. Clearly, this is also a behavioral difference.

The rate of mortality after the first week of life is low for chicks. This alone suggests that there is no one major direct cause of mortality. It is, however, probably what we should expect if the behavioral adaptations to the care and feeding of young follows some sort of spectrum. We suggest that most adults do moderately well, a few do very well, and some do poorly.

In sum, we suggest that problems of behavioral adaptation are the ultimate cause of the pattern of mortality in Herring Gull chicks and that the proximate causes are fortuitous in that they simply "take advantage" of the basic behavioral lapses.

SUMMARY

About one-half of the Herring Gull chicks which hatch die before fledging, most of the deaths occurring during the first 5 days after hatching. A large proportion of the chicks which die are never found, even when the colony is searched regularly and intensively. Possible causes of the disappearance of chicks are predation, scavenging or the rapid decomposition of young chicks. No direct evidence for any of these causes was found. It is suggested that problems of behavioral adaptation of the adults are the ultimate cause of the mortality and that the proximate causes such as predation simply reflect these basic behavioral lapses.

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A TECHNIQUE FOR CAPTURING NESTING GRASSLAND BIRDS WITH MIST NETS

By STEPHEN G. MARTIN

Careful investigations of the social behavior and population dynamics of birds often require the capture and marking of individuals so that they may be recognized and followed. Studies of this nature on grassland bird species are faced with the task of capturing sufficient numbers of individuals in a habitat which affords little or no concealment for mist nets arranged in the standard linear fashion. In mature forests, secondary growth, or forest edge, net lines can be positioned so that the vertical elements of the vegetation disrupt the net pattern and provide a dark backdrop into which the mesh appears to blend. Mist nets arranged in this manner in an open grassland, however, are silhouetted against the light background of sky and are highlighted by reflected sunlight. In addition, even slight breezes increase the visibility of nets and greatly reduce netting efficiency in open areas, while breezes upon woodland nets are buffered by the surrounding flora. Netting in woodlands may thus be carried on under conditions which inhibit field netting. To capture an adequate number of birds in an open situation one must therefore use a large number of nets arrayed in a pattern such that birds become confused and blunder into one net while attempting to avoid another. The work involved in