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The biology of *Necrophorus* (Col.) and the mortality of terns (*Sterna*); an ecological study

by

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(St. Cuthbert's Society)

Being a thesis presented in
candidature for the degree
of Doctor of Philosophy of
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CONTENTS

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INTRODUCTION

INTRODUCTION

The Farne Islands have been known as a breeding area for sea birds since historic times, but the scientific description of their vertebrate fauna is only just beginning, whilst the invertebrate fauna is almost unknown. The present study examines the ecology of a highly specialised insect (*Necrophorus*, Coleoptera), in relation to the mortality during the breeding season of the arctic tern, *Sterna paradisaea* Brünn (Sternidae, Aves), whose corpses form the main food source of the beetle.

Necrophorus are nocturnal beetles flying strongly in search of carrion which they bury and on which they feed their larvae. The behaviour of *Necrophorus* was first studied by Fabre (1919), who described their burial activities and emphasised the co-operation which exists between individual beetles as they bury a corpse. Portevin (1926) described the taxonomy of the carrion beetles (*Silphidae*) but gave little biological information.

Pukowski (1933) described the behaviour of five members of the genus *Necrophorus* in detail, pointing out that the isolation of a single pair at a corpse arises from intra-specific fighting and not by co-operation as suggested by Fabre. Pukowski called attention to the stridulation of *Necrophorus*, and gives a graphic description of the predatory habits of hungry *N. germanicus* when confronted by *Geotrupes*.

The burial behaviour was studied in detail, and the work shows how the female beetle feeds the larvae during the first two instars, often driving the male from the chamber before the eggs hatch. A certain amount of habitat separation occurs within the genus, and details of the life cycles of the five species are given.

Since the study by Pukowski, little has been discovered about *Necrophorus*. A series of short papers by various authors appeared in France between 1946 and 1957 (Cantonnet, F., and Lecordier 1947, Paulian, R., 1946, Roehrich, C., 1949, Theodorides, J., 1950, 1952); and in Germany (Von Lengerken 1954).

More recently a survey of carrion beetles was carried out near Oxford (Moore 1955), and Elton (1966) discusses the biology of *Necrophorus* in general terms. Elton points out that *Necrophorus* are monopolists, making the best use of their resource by ensuring that no other animals share the resource, and by having a social system which ensures that the resource is fully utilised by themselves. *Necrophorus* are also discussed by Wynne-Edwards (1962) who discusses them in relation to property-tenure and its relationship to dispersion and the securing of an optimum population density at times of breeding.

A quantitative study of the ecology of *Necrophorus*, particularly in relation to its food supply, has been lacking.

The present work, carried out on the Inner Farne, concurrently with the study of the arctic tern, was designed to go some way towards filling this gap. The tern colonies of the Farne Islands are remarkable in that four species of terns, arctic, common (Sterna hirundo L.), roseate (Sterna dougalli, Mont.) and sandwich (Sterna (Thalasseus) sandvicensis Lath.), nest in close proximity. The arctic tern is the most numerous species, here almost at the southern limit of its breeding range. About 4,000 pairs of arctic terns breed annually, yet very little is known of their breeding biology. In North America the huge tern colonies of Cape Cod have been studied by Austin (1945), who concentrated on the biology of the common tern. The behaviour of the common tern has been studied by Palmer, (1941) and although much of this work is applicable to the arctic tern, the only worker to study the latter species was Hawksley (1950), who studied their breeding biology on Machias Island, New Brunswick.

In Europe, Marples and Marples (1920) investigated the behaviour and general biology of the terns breeding in the British Isles, and gave information on the status of tern colonies in this country. More recently Cullen (1956) studied the behaviour of the arctic tern on the Farne Islands, and Burton & Thurston (1959) reported on the breeding of the arctic tern in Spitzbergen. Belopolskii (1961) gives information on the biology of arctic terns in high latitudes, but similar information for the British Isles is lacking.

On the Farne Islands the arctic tern breeds on the beaches and in vegetation close to the sea. The Inner Farne colony was described by Bullough (1942) but has doubled in size, and now almost 1,500 pairs of arctic terns breed annually. The colony has spread considerably and birds now breed amongst tall vegetation on the flat top of the island.

II STUDY AREAS

STUDY AREAS

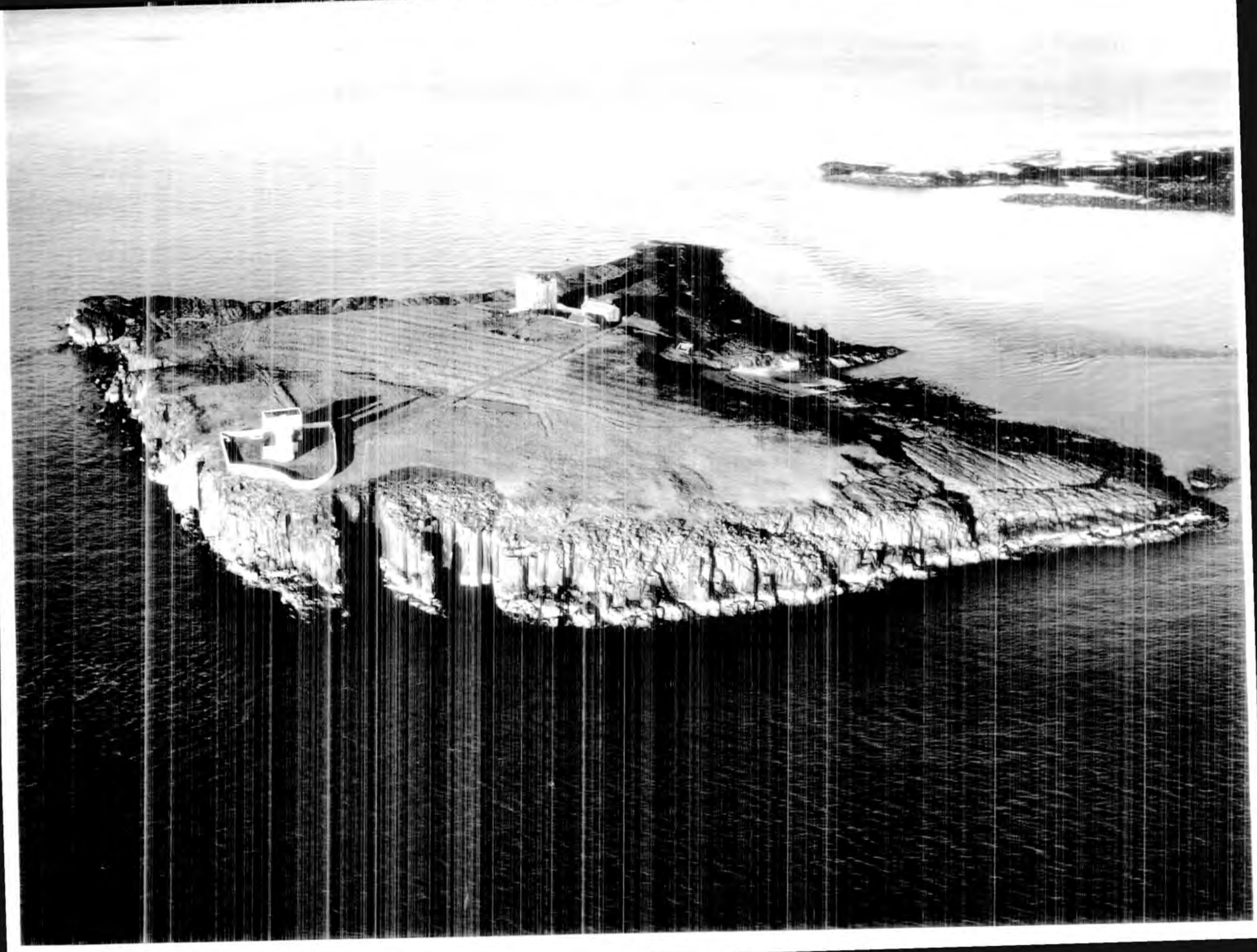
The Farne Islands are a group of rocky islands situated off the north Northumberland coast (National Grid Reference NU 220360). They represent the most easterly extension of the Whin Sill, and are composed almost exclusively of whin (quartz dolerite) which dips gradually north-east. The angle of dip results in low sea cliffs being formed on the south and west sides of the islands. The highest point (Inner Farne) is 60 feet above O.D. There are between 13 and 20 islands in the group, depending on the state of the tides, but only nine of these are covered with soil and support vegetation. The largest island, the Inner Farne, was used in the present study, and lies 1½ miles from the mainland (Figure 1).

The Farne Islands have not been colonised by ground predators recently and have supported large colonies of sea-birds for many years. Two islands, Inner Farne and Brownsman, support breeding colonies of terns, although terns have bred in the past on Longstone End, Knoxes Reef and West Wideopens (Plate 1). Visitors to the Inner Farne are not allowed into the tern colony, and landing on Brownsman is normally prohibited.

The Inner Farne was chosen for this study as being the only island, with living facilities, having a large population of both burying beetles and terns. The island has an area of about 6.4 hectares, 2.0 hectares of which are covered with soil or vegetation, the rest is bare rock. The island supports a

Plate I

The Inner Farne, looking north towards the Tower.



mixed colony of arctic, roseate and common terns, which breed most densely on the shingle beach and sandy cove of the north-east side (Fig. 1).

Two areas of the Inner Farne were chosen for detailed study of the terns and these are described below. Information from other areas was used for comparative purposes.

St. Cuthberts Cove, Figure 1

The Cove is an area of shelving sandy beach, measuring approximately 40 x 16 metres at high tide. The area is bounded to the south and west by a steep and thickly vegetated bank, to the north-west by a steep rocky outcrop and a path, and to the north-east by the sea and a concrete landing stage. The boundary to the south-east of the Cove was arbitrarily defined as where the sand left the rock uncovered. On the area, devoid of vegetation except for scattered clumps of _Silene_ _maritima_ With., about 200 pairs of _S_. _paradisaea_ nested annually.

Gut Garden, Figure 1

The Gut Garden is a small enclosure north of the tower. The area is bounded by the limit of vegetation round its north and north-west perimeter, by a high (2 m) stone wall to the south and south-east, and by the deep fissure, St. Cuthberts Gut, to the west and south-west.

The Gut Garden measures 33 x 33 m, and is thickly vegetated.

Figure 1 A map of the Inner Farne, showing the tern study areas and the areas used in the study of the distribution of *Necrophorus*

fig. 1

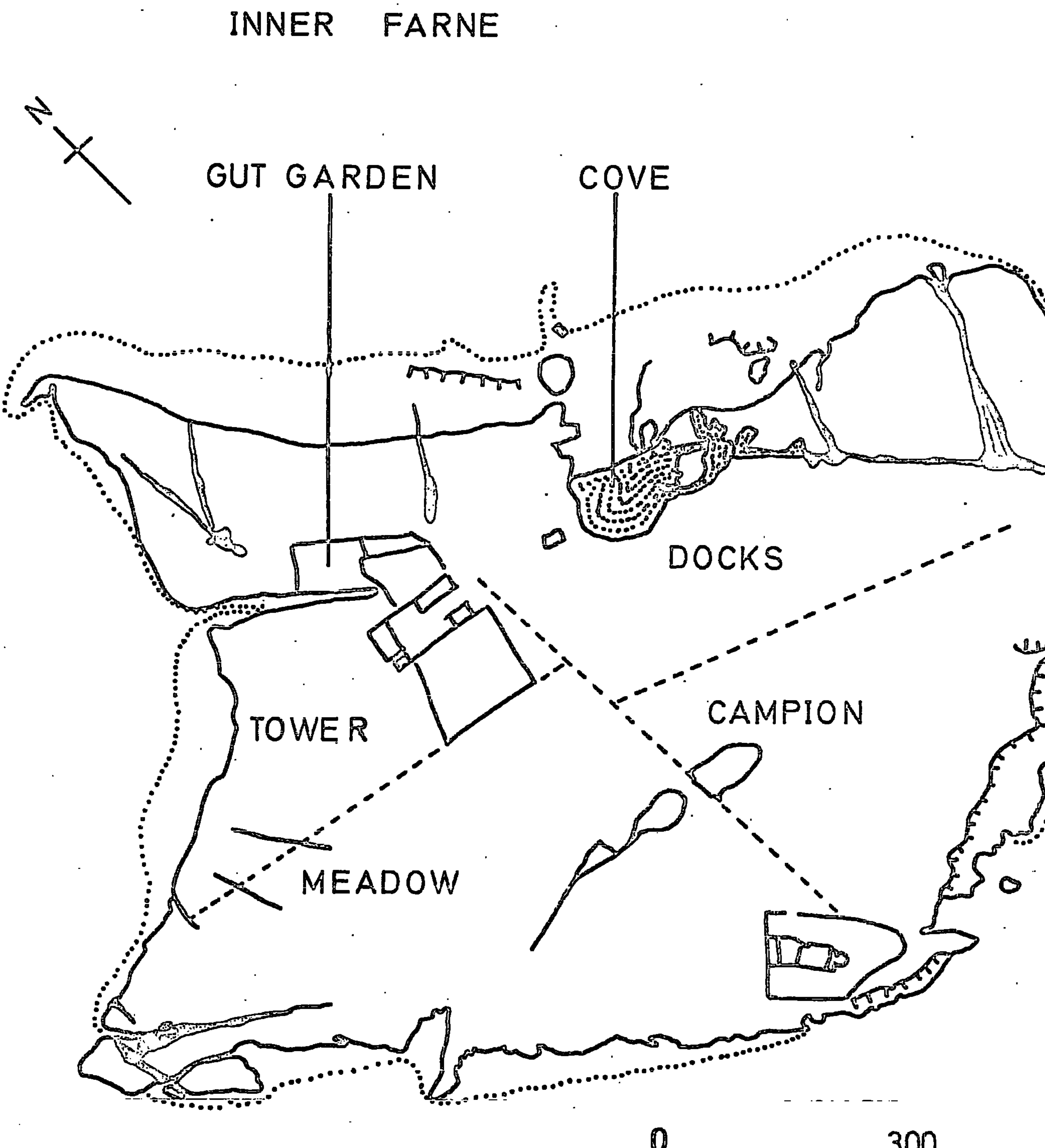
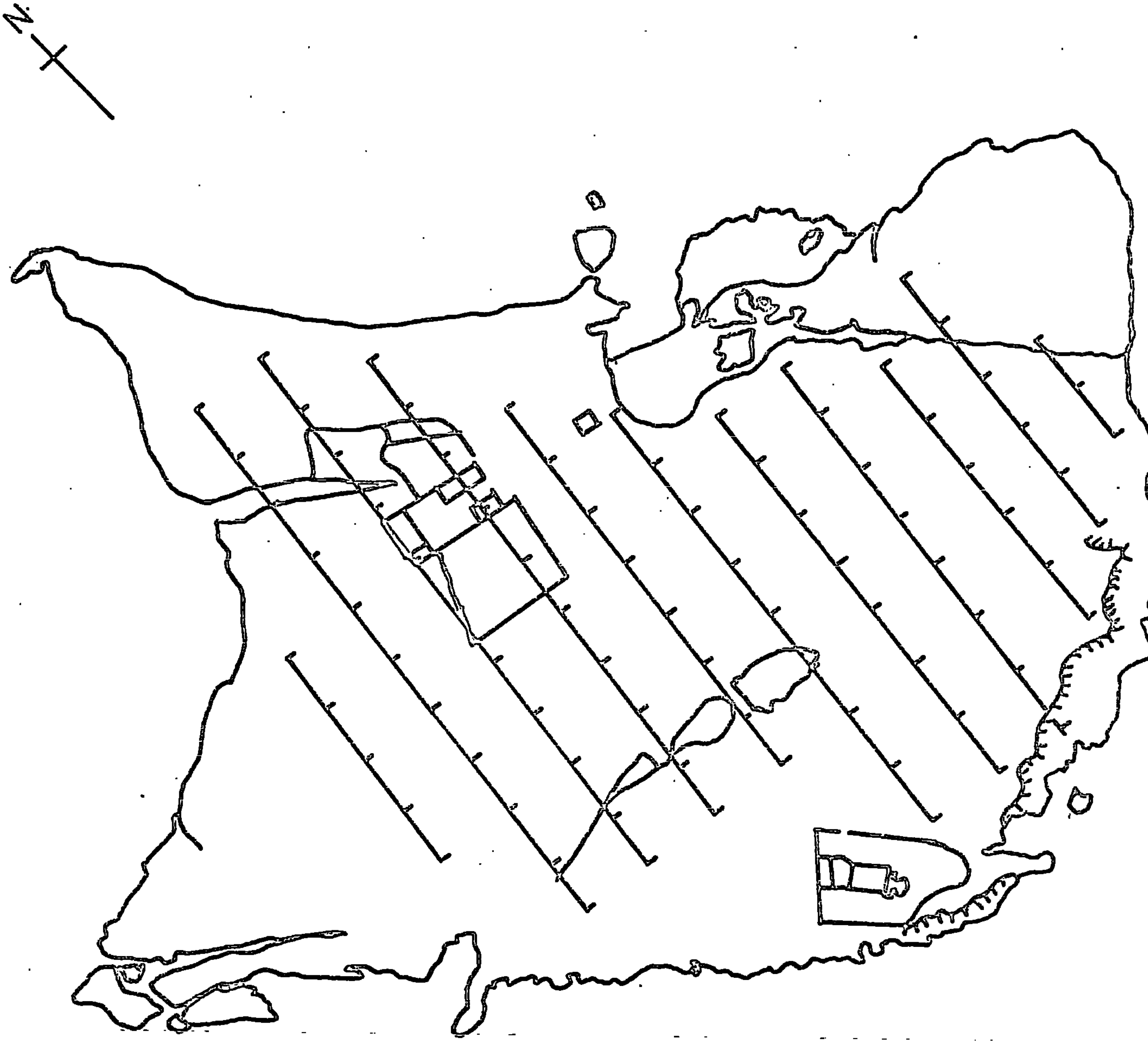

INNER FARNE
N
GUT GARDEN
COVE
DOCKS
TOWER
CAMPION
MEADOW
0
300
FEET

Figure 2 A map of Inner Farne, showing the grid of traps laid down across the island. The traps were situated at intervals of 20 m along each grid line, and are represented by short dashes at right angles to each grid line fig.2

INNER FARNE SHOWING THE TRAPPING GRID



The dominant plant is *S. maritima*, which grows here in luxuriant clumps, covering much of the ground. Between and beneath these clumps of vegetation, approximately 120 pairs of *S. paradisaea*, and 17 pairs of *S. hirundo* breed annually.

The beetles were studied in relation to the whole of the Inner Farne, and traps were laid in a grid pattern over all the vegetated areas (Fig. 2).

III THE BIOLOGY OF NECROPHORUS: METHODS

THE BIOLOGY OF *NECROPHORUS*

Taxonomy

Two species of *Necrophorus* occur on the Farne Islands. They are *N. humator* Ol, a large (18-28 mm length), black species, and *N. investigator* Zett, a medium (13-20 mm length) species, black, with four prominent orange marks on the elytra.

At the beginning of the study, difficulty was experienced in using the available taxonomic keys to the genus. Accordingly a short dichotomous key was prepared, combining the characters given by Portevin (1926), Joy (1932) and Crowson (1950). The key is reproduced on p.9.

A reliable and rapid method of sexing *N. humator* and *N. investigator* in the field was required. The method described by Portevin (1926), utilising the shape of the clypeal membrane, was satisfactory for both *N. investigator* and *N. humator*. Using forceps, each beetle was oriented so as to be head-on to the observer. In both species the clypeal membrane was orange, in the males large and campaniform, and in the females narrow and subtriangular. These differences are illustrated in Fig. 3.

Treatment of Observations

The data have been divided into three sections.

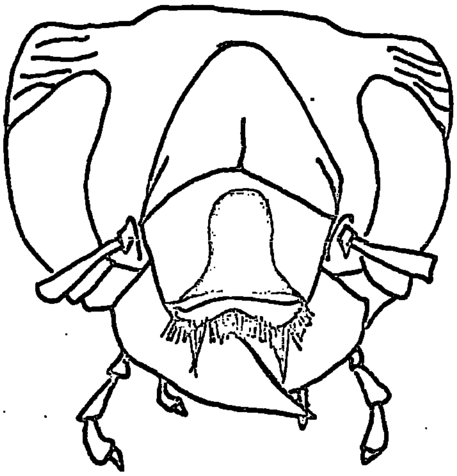
(1) The first section deals mainly with the results from the field study. Data from laboratory dissections of adults

Figure 3 A diagrammatic representation of the head views of *N. investigator*, to show the method of sexual distinction. The membranous emargination of the clypens which provides the major means of recognition is shown in solid black. The scale is approximately 100 x life size.

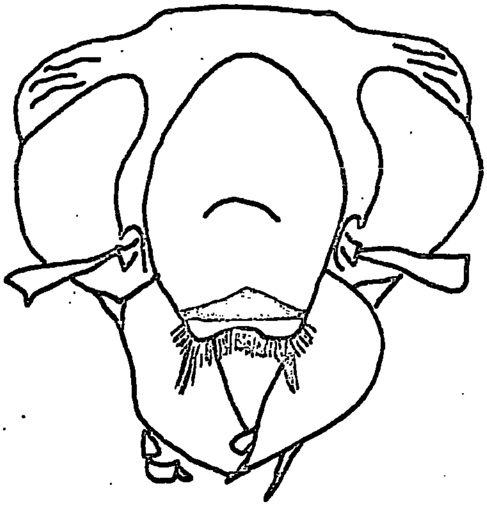
fig. 3

N. investigator: head view to show sexual features

male



female



Key to the British Necrophoridae, (Col. Silphidae)

1. Antennae slightly clubbed, front tibiae simple ... ... Necrodes littoralis

\- Antennae strongly clubbed, front tibiae with a strong tooth towards the apex ... Necrophorus ... 2

2. Colour entirely black 3

\- Colour black with two transverse reddish bands across elytra 4

3. Club of antennae black, very large (25-32 mm) ... N. germanicus

\- Club of antennae reddish-brown ... N. humator

4. Club of antennae black ... N. vespilloides

\- Club of antennae reddish-brown 5

5. Thorax with yellow pubescence 6

\- Thorax glabrous 7

6. Hind tibiae straight, thoracic pubescence on all margins ... N. vestigator

\- Hind tibiae strongly turned inward near apex, thoracic pubescence at sides and base but occasionally near middle of hind margin ... N. vespillo

7. Anterior coloured mark continued across both elytra ... N. investigator

\- Anterior coloured mark divided at suture as posterior mark ... N. interruptus caught in the field are also presented in this section, as these data clarify the results obtained by pitfall trapping.

(2) The second section presents data concerning the culturing of beetles in the laboratory, and relates these data to the field results. Some aspects of the behaviour of Necrophorus are examined.

(3) The third section deals with the relationship between Necrophorus and their associated fauna of Acarina, with the results of experiments conducted in the laboratory.

The Field Study

Methods

a. Trapping

Adult Necrophorus were caught using baited pitfall traps. Each trap consisted of a 1 lb. jam jar (11.5 cm high, 6.5 cm diameter at the mouth), sunk into the ground with the rim flush with the surface. The traps were normally baited with sheep lungs which had the advantages of being cheap, easily cut into standard-size pieces and was as attractive as other meat. Between 20-30 g of meat were used in each trap.

The effectiveness of the bait diminished with time, and re-baiting was necessary about once a week. Traps were re-baited with meat which had been kept warm and moist for two days.

No preservative or killing agent was added to the traps, which were kept dry by a ∧ shaped roof of aluminium. The traps were sited in relation to the grid (see below) and no attention was paid to vegetational boundaries.

b. The grid

A grid system was constructed with major lines running NE-SW over Inner Farne (Fig. 2). Pitfall traps were placed at 20 m intervals on each line and were marked with a bamboo cane and a peg bearing the trap co-ordinates. It was estimated that *Necrophorus* emerging in the evening were never more than 14 m from an attractive source of carrion. Danzer (1956) showed that *Geotrupes stercorarius* detect faeces from at least 10 m in a slight breeze, and *Necrophorus* may detect carrion at the same distance, and also carrion buried to 15 cm in sand (Abbott 1927).

However, a source of error, the effect of which it was difficult to estimate accurately, was the presence of naturally occurring carrion. Some measure of this was obtained by the recovery of individually marked beetles on carrion away from the traps.

c. Trapping intervals

It was found impracticable to empty all the traps daily during the field season, and to study the tern colony at the same time. Consequently the traps were emptied at intervals of not less than 7 days.

d. Trapping procedure and marking technique

In 1963, captured beetles that were alive were released after marking with a spot of cellulose paint. Dead beetles were preserved in Pampel's fluid and subsequently dissected.

In 1964, live beetles were collected in the morning and marked in the field laboratory, using a branding technique. The marked beetles were kept in buckets containing soil and vegetation and released from a central point on the evening of their capture. Dead beetles were collected and preserved as in the previous year.

In 1963, no recaptures were obtained, although 150 _N. investigator_ were marked on Inner Farne and experiments during the field season showed that this resulted from the beetles losing their marks. In 1963, each beetle received a dot of fast-drying cellulose paint, either on the elytra, the prothorax or the femora. The laboratory experiments showed that paint spots, wherever applied, only lasted up to three days from application. At the end of this time, the passage of the beetle through the soil had completely abraded the paint. Alternative methods of permanently marking beetles were tried, but a reliable method was not developed until the end of the 1963 season.

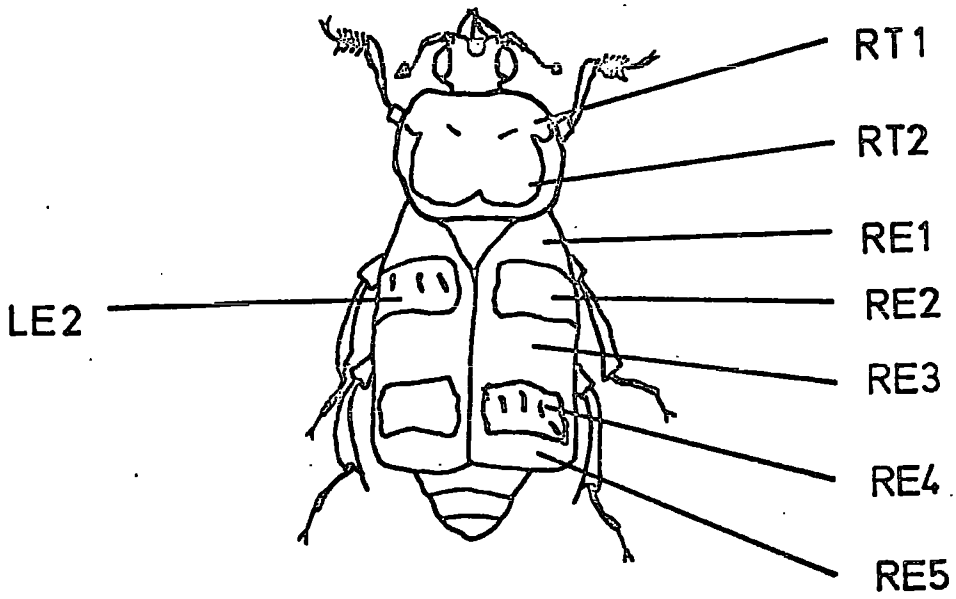
The method finally adopted was that of branding. The branding instrument consisted of a battery-operated gas lighter, from which the metal cap protecting the filament had been removed. The exposed filament was uncoiled and bent into a V-shape. The point of the V was then applied to the elytra, and small burn marks produced. The periphery of the thoracic shield was also used and in this case the edges of the shield were nicked with the filament. A similar but much improved and more sophisticated branding device has been described by Schotz Christensen (1965).

During the marking operation the beetles were held in forceps under a lens and the hot filament carefully applied. The beetles died if the filament pierced the hard parts. A hand lens was necessary to distinguish marks in the field. The behaviour and survival of marked beetles in the laboratory were identical to unmarked controls.

It was found practicable to divide each elytron of *N. humator* into three sections, and in addition the prothoracic shield was divided into quarters. Each section could receive four marks. The elytra of *N. investigator* could be divided conveniently into five smaller sections, utilising the orange patches. Each section could receive four marks, as in *N. humator*. Figure 4 shows the marking notation as used on *N. investigator*.

Figure 4 A diagram of the marking notation used for the mark and recapture study of <u>Necrophorus</u> on Inner Farne. The left hand side of the beetle was divided in a similar way to the right hand side, but only the portion which was branded in the example is labelled. The brand marks are depicted by short vertical lines in the appropriate sector. The beetle is approximately 3 x life size.

The marking notation used for <u>Necrophorus</u>



Beetle no. LE2/3 RE4/4

In both seasons, when live beetles had been marked and released, the traps were closed by replacing the original jar lid for one night in order to allow the marked individuals to disperse within the population on the island. In practice this precaution was probably unnecessary as, when released, the newly marked beetles flew strongly.

e. Trapping season

In 1963 the traps were baited on 14 April, and trapping continued until 13 October. The same period was covered in 1964. In both seasons weekly visits were made to the Inner Farne after the 25 August until the 13 October.

IV THE BIOLOGY OF <u>NECROPHORUS</u>: THE FIELD STUDY

I. The Field Study

Pitfall Data

Activity measured by pitfall trapping, 1963

N. humator

The activity of *N. humator* expressed as the weekly totals of beetles caught in pitfall traps, on Inner Farne in 1963, is shown in Figure 5. The first beetles became active in late April, when after a sharp rise, the number of captures decreased and remained low until early July. The last adult of the 1962 generation which over-wintered into 1963, was caught on 30 July 1963. A gap of five weeks followed, in which no captures of *N. humator* were made.

The first beetles of the 1963 overwintering generation were caught in the second week in September, and captures reached a peak on 6 October. These beetles had undeveloped ovaries and fat body and a few were callow. No beetles were captured after 6 October.

N. investigator

The data, expressed as the total captures in each week, are shown in Figure 6. The first beetles were active by 21 July, and captures rose to a peak during the second week in August. No *N. investigator* were captured between 12-26 August, but a peak of captures was evident during the beginning of September. No beetles were captured after 6 October.

Sex-ratio in weekly captures, 1963

N. humator

The sex-ratio, expressed as the percentage of female beetles captures in each week, is shown in Fig. 5 and Table 1. The sex-ratio departed significantly from equality only once in 1963, at the beginning of June. In that week the captures contained significantly more males than females ($X^2_{(1)} = 3.6$ $P < 0.05$). The trend throughout June was similar, with very few females being captured. A return to a 50:50 sex-ratio was found in the first week in July and thereafter there was no significant departure from equality.

N. investigator

The sex-ratio is shown in Fig. 6 and Table 2 for each weekly total.

In 1963 it may be seen that the sex-ratio differed significantly ($X^2_{(1)} = 17.04$ $P < 0.001$) from equality in the week 6-12 August, and was again low during the week 27 August-2 September. On both these occasions there were 25% of females in the captures.

Activity measured by pitfall trapping, 1964

N. humator

The weekly captures in 1964 show a close similarity to those of 1963 with a peak of captures in late April and early

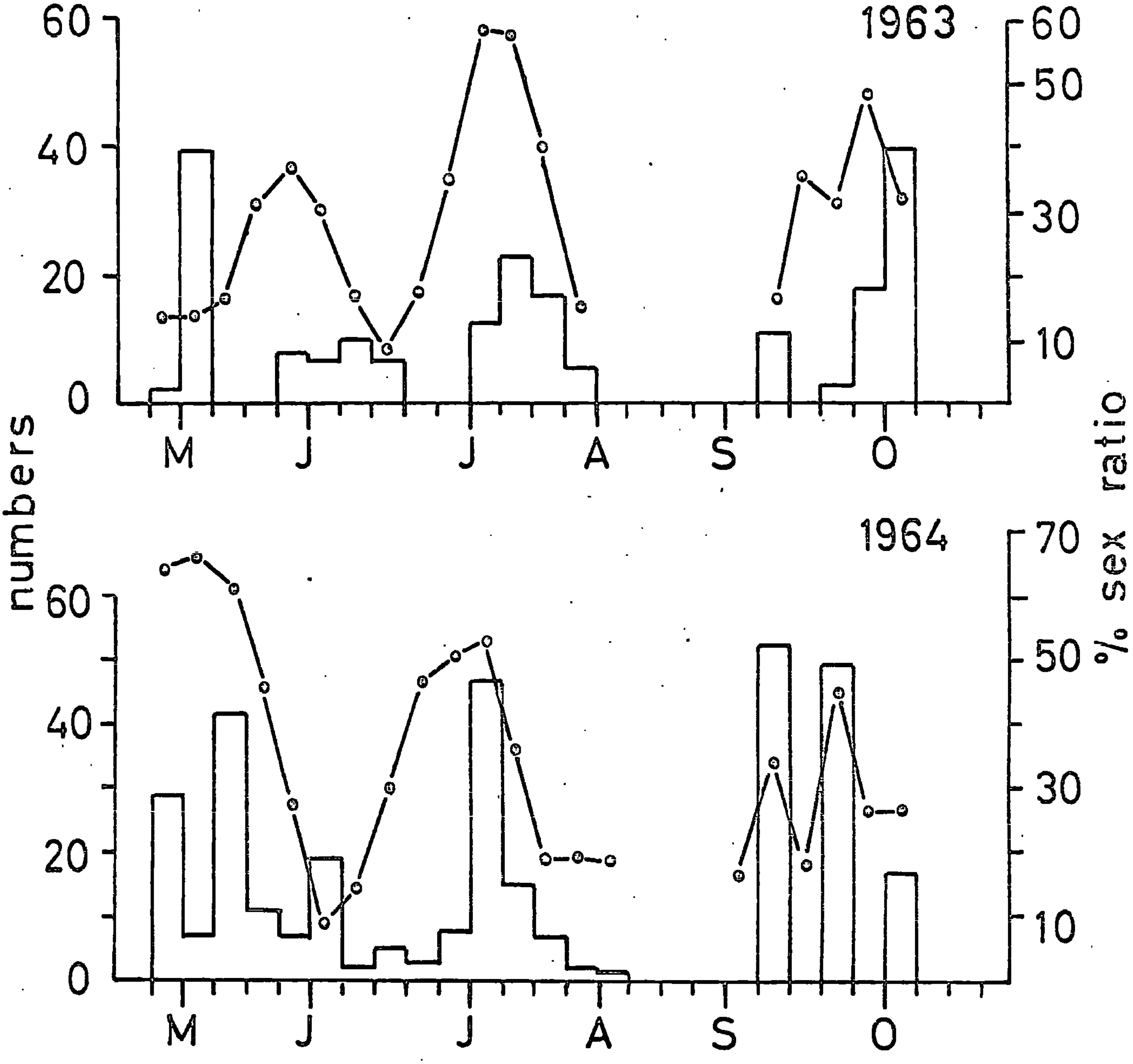
Table 1 showing the total captures and sex-ratio in *N. humator*, expressed as the percentage of females, caught in pitfall traps in 1963 and 1964.

Time	Total captures		Percentage females in each week	
	1963	1964	1963	1964
21-28 April	2	29	-	48
29-5 May	39	7	41	72
6-12 May	0	42	-	69
13-19 May	0	11	-	54
20-26 May	8	7	50	57
27-2 June	2	19	43	26
3-9 June	10	2	20	0
10-16 June	7	5	28	0
17-23 June	0	3	-	43
24-30 June	0	8	-	47
1-7 July	13	47	53	50
8-14 July	23	15	52	53
15-21 July	17	7	70	57
22-28 July	6	2	50	0
1 August	0	1	-	0
2 September	0	0	-	-
3-9 September	11	52	54	49
10-16 September	0	0	-	-
17-23 September	4	49	50	53
24-30 September	18	0	44	-
31-6 October	40	17	52	82

Figure 5 The numbers of *N. humator* of both sexes, caught in pitfall traps on Inner Farne, according to weekly intervals. The sex-ratio, expressed as the percentage of females in each week, is shown as a three point running mean.

fig.5

Numbers and sex ratio of N.humator



May, a general reduction of captures throughout June and a resurgence in July (Fig. 5).

In 1964 the last adult from the 1963 season was caught on 5 August. There was then a cessation of activity for four weeks until the first individuals of the overwintering generation appeared in the traps on 9 September. Captures decreased after that date, and the last individuals to be trapped in 1964 were found on 6 October.

N. investigator

The data are shown in Figure 6. It was apparent that activity started earlier in 1964 than in 1963, and a peak of captures was found on 28 July. Captures then decreased, but a notable resurgence occurred during the last two weeks of August. There was little activity in the first week in September, but captures once again reached high numbers in the following week. After the 9 September captures decreased rapidly and the last beetles were found on 6 October.

Sex-ratio in weekly captures, 1964

N. humator (Fig. 5 and Table 1)

During a peak of activity in early May, the sex-ratio was 69% females. This was statistically significantly different from equality ($X^2_{(1)} = 6.08$ $P < 0.02$). The preceding week, although not statistically significant, there were 72% females.

Table 2 showing the total captures and sex-ratio in *N. investigator* expressed as the percentage of females, caught in pitfall traps in 1963 and 1964.

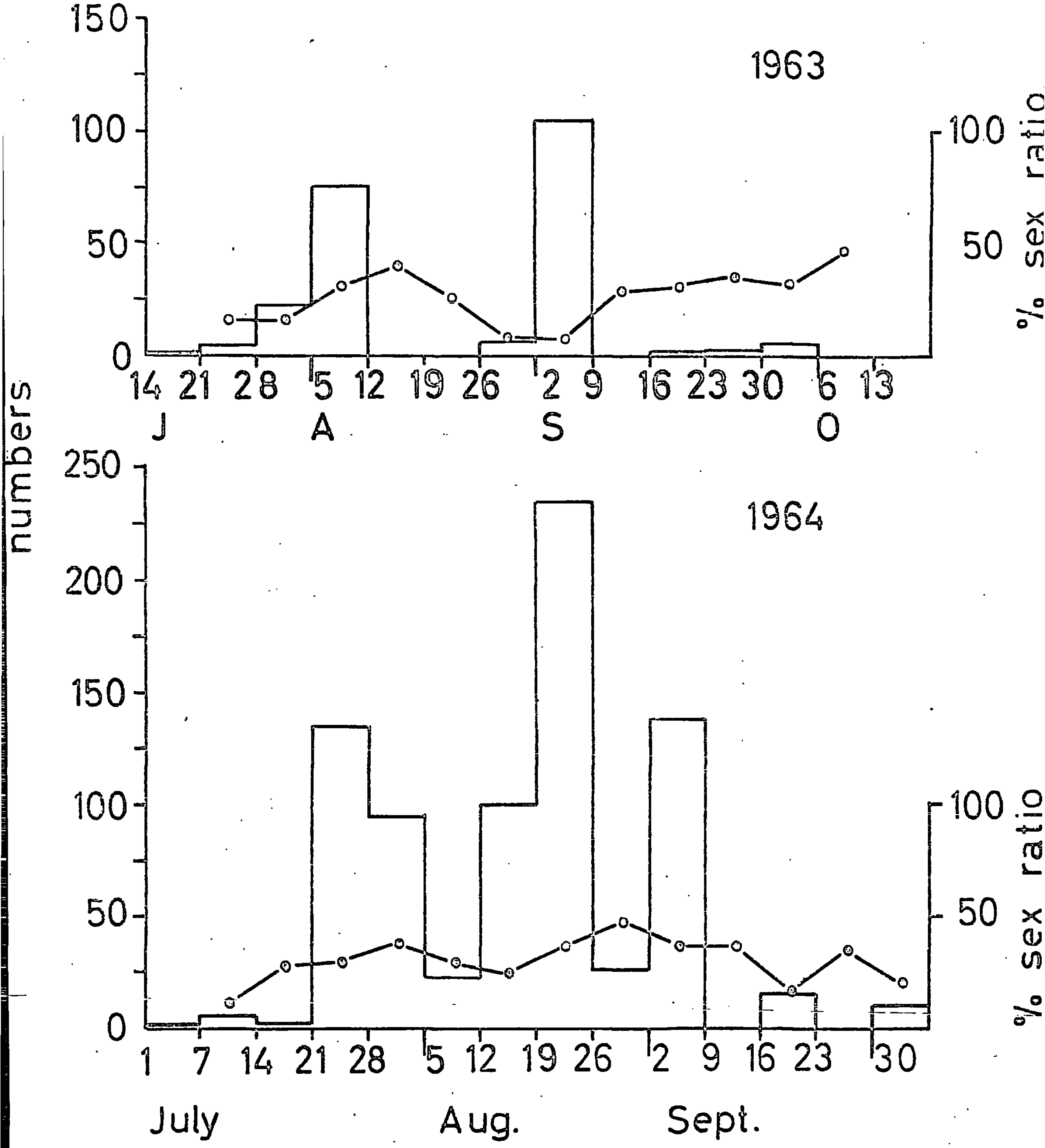
Time	Total captures		Percentage females in each week	
	1963	1964	1963	1964
7-14 July	0	5	-	40
15-21 July	1	1	0	0
22-28 July	4	134	50	50
29-5 August	21	90	48	44
6-12 August	76	21	26	27
13-19 August	0	101	-	29
20-26 August	0	236	-	34
27-2 September	12	17	25	52
3-9 September	108	138	53	52
10-16 "	0	0	-	-
17-23 "	2	17	50	48
24-30 "	4	0	50	-
31-6 October	11	10	45	60

Figure 6 The numbers of _N_. _investigator_ of both sexes caught in pitfall traps on Inner Farne, according to weekly intervals. The sex-ratio, expressed as the percentage of females in each week, is shown as a three point running mean.

fig. 6

Numbers and sex ratio of

<u>N. investigator</u>



After 19 May however, the trend was for less females than males to be caught, and on 2 June only 26% of the captures were females ($X^2_{(1)} = 4.26$ $P < 0.05$).

The sex-ratio after 2 June showed a steady trend towards equality and remained at equality until the last captures in July were made.

In September, the sex-ratio was at equality, but during the last week when the beetles were active (6 October), there were more females than males caught (sex-ratio 82% females, $X^2_{(1)} = 7.0$ $P < 0.01$).

N. investigator (Fig. 6 and Table 2)

In 1964, the sex-ratio of *N. investigator* dropped significantly below equality during three weeks in August. Captures during the week ending 12 August showed 27% females ($X^2_{(1)} = 3.8$ $P < 0.05$), 19 August showed 29% females ($X^2_{(1)} = 18.5$ $P < 0.01$) and 26 August, 34% ($X^2_{(1)} = 21.8$ $P < 0.001$).

After 26 August the sex-ratio returned to unity and remained at equality for the rest of the season.

The dearth of beetles trapped during mid-season is explicable in terms of a change in behaviour. In both species the male and female stay underground with the corpse and defend it. The female feeds the first instars of the larvae by regurgitation and during larval feeding the male may stay within the burial chamber (crypta), but it is more often chased out by the female (Pukowski 1933). Thus, during the major reproductive period, many females are underground and not at risk to the traps, whilst the male population is less affected by reproductive activities.

Results obtained from the dissection of adult beetles captured in the field

Method

Dead beetles found in the traps were collected, individually preserved in Pampel's fluid and stored in labelled containers until they were dissected. In the laboratory the beetles were pinned through the prothorax, the abdomen opened and the gonads and fat body examined under water.

When the beetles were dissected, the condition of the fat body and the gonads was scored according to their state of development. In males, only the fat body showed readily discernible changes during the flight season, the testes and accessory glands outwardly remaining unchanged. In females the condition of the ovaries could be divided into three categories. These were:

i. Immature, when many small, ill-formed and undeveloped eggs were present.

ii. Mature, when some of the eggs were large, fully formed and pearly white in colour.

iii. Spent, when small ill-formed eggs were present, combined with the presence of follicular debris at the base of the ovarioles, showing that egg laying had taken place.

The above classification of the ovarian condition in *Necrophorus* is similar to that adopted by Gilbert (1958) and Schotz-Christensen (1965) for Carabidae, and by Milne (1960) for *Phyllopertha*.

The development of the fat-body was scored as in the scheme below.

Score	State of development of fat body
A	Little or no fat body development
B	Some fat body development, tissue lying loosely within abdomen
C	Full fat body development, abdomen fully charged with tissue

Callow beetles were recognized by the softness of their cuticle and in *N. humator*, by the dark brown colour.

Few beetles died in the traps in 1963 and 1964. However, a large amount of material was collected at weekly intervals on the Inner Farne in 1961. In the results which follow, the material from the three years has been combined. The scoring for fat body development has been adapted from Milne (1960).

N. humator

a. ~~Condition of ovaries~~

It is evident from the data (Table 3 and Fig. 7) that females of N. humator emerged sexually immature in late April. The first beetles containing mature eggs in the ovary had appeared by 21 May and a high proportion of beetles caught in June and early July had mature eggs. The last female with immature ovaries was captured in the last week in June.

Female beetles with spent ovaries first appeared in late May, but large numbers were found from early July. All beetles caught after 15 July were spent. The female beetles caught in autumn, from 3 September until the beginning of October, had immature ovaries.

b. Condition of fat body in females

The state of the fat body in female N. humator is shown in Table 4. Emerging beetles had little fat body, while immature beetles caught a week after the peak of emergence activity, showed extensive fat body development, the body being full of fatty tissue, and the ovaries difficult to find. Beetles with mature eggs in the ovary showed a fat body development intermediate between little fat body and large fat body. Beetles with spent ovaries showed a similar range. Callow beetles caught in autumn had no fat body, but individuals that had been active for some time showed full fat body development.

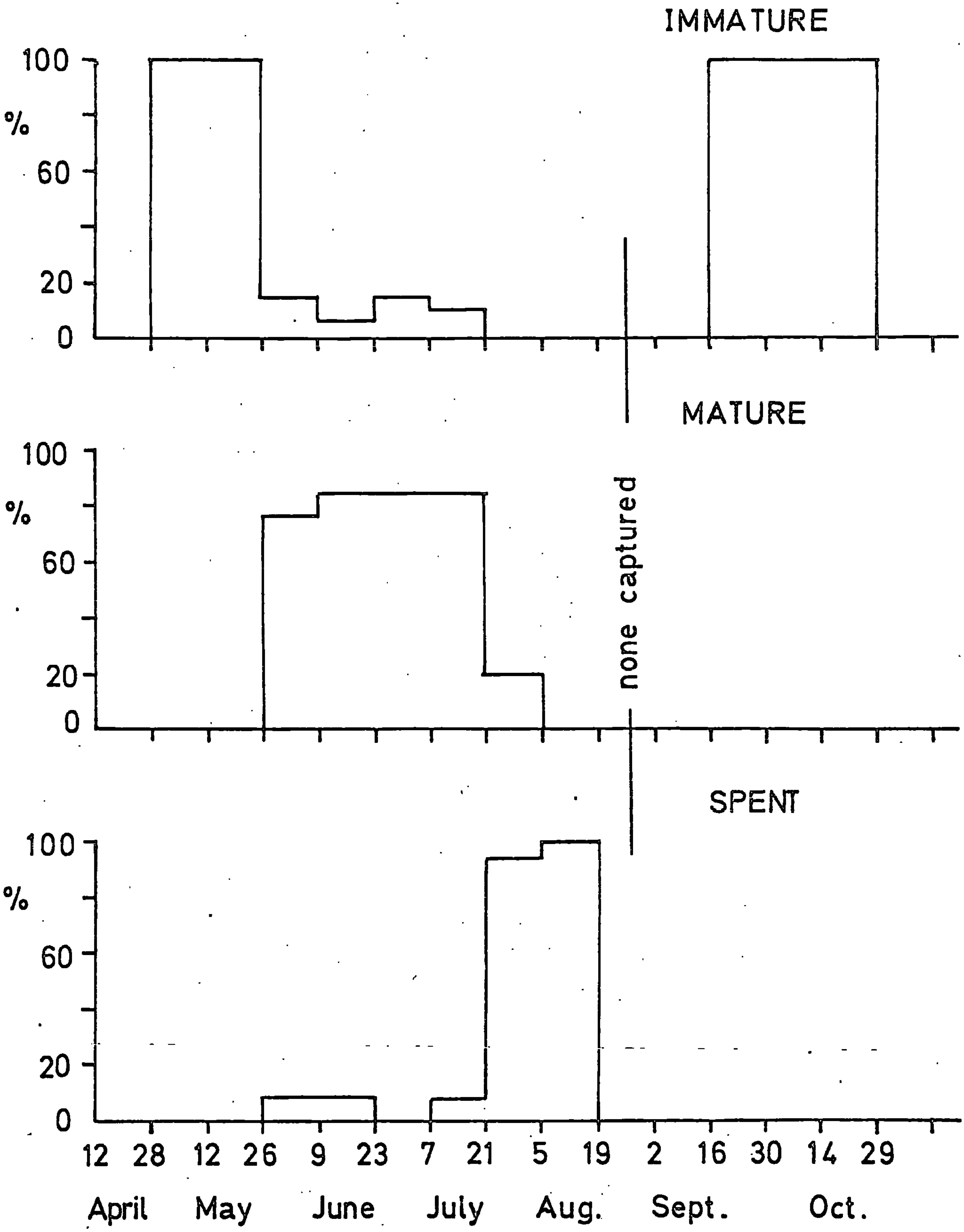
c. Condition of fat body in males

The extent of fat body development varied considerably,

Figure 7 The ovarian condition of *N. humator*, expressed as the percentage of females in each category caught each week. From 19 August to 16 September no captures of *N. humator* were made.

fig. 7

The ovarian condition of *N. humator*



as shown by the data in Table 5.

In late April and early May, male beetles showed little or no fat body development. However, extensive development had occurred in individuals caught after 5 May, and between 12 May and 28 July, the fat body of the majority showed full development. Beetles caught in autumn showed little fat body development at first, but all the beetles caught after 23 September had their fat body fully developed.

N. investigator

a. Condition of ovaries

The data are shown in Table 6 and graphically in Figure 8. Immature beetles emerging in early July showed undeveloped ovaries. The first individuals with mature eggs were caught after 14 July, and the proportion of mature beetles increased until 25 August-1 September when over 90% were mature. After 2 September the proportion of mature females decreased rapidly. Beetles with spent ovaries appeared after 28 July, and the proportion increased after 5 August until only spent beetles were present on 29 September.

b. Condition of fat body in females

The distribution of fat in *N. investigator* showed a similar pattern to that in *N. humator*. The data are presented in Table 7.

Figure 8 The ovarian condition of *N. investigator*, expressed as the percentage of females in each category, caught each week.

fig. 8

The ovarian condition of N. investigator

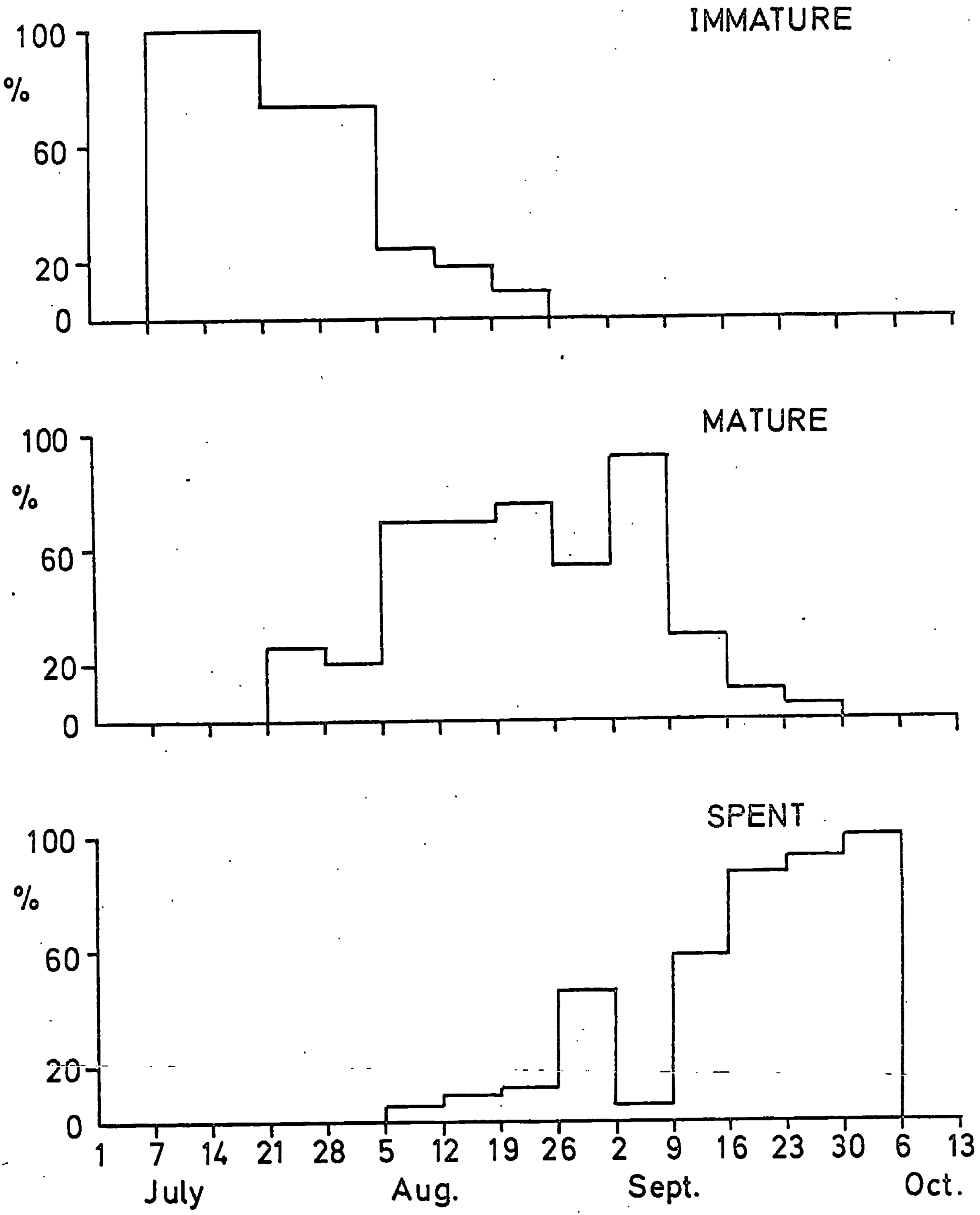


Table 3 The condition of the ovaries in N. humator caught at different times in the flight season in 1961, 1963 and 1964.

Fortnight	Number examined	Immature Number	%	Mature Number	%	Spent Number	%
12-28 April	8	8	100	0	0	0	0
29-12 May	9	9	100	0	0	0	0
13-26 May	19	3	15	15	78	1	7
27 May- 9 June	12	1	8.5	10	83	1	8.5
10-23 June	9	1	12	8	84	0	0
24 June-7 July	25	2	8	21	84	2	8
8-21 July	44	0	0	2	5	42	95
22 July-5 August	13	0	0	0	0	13	100
6 August-2 September		none		captured			
3-9 September	19	19	100	0	0	0	0
10-23 September	15	15	100	0	0	0	0
24 September-6 Oct.	15	15	100	0	0	0	0

Table 4 The condition of the fat body in females of *N. humator* according to season

Fortnight	Number examined	Condition of fat body		
		A	B	C
12-28 April	8	8	0	0
29 April-12 May	9	0	3	6
13 May-26 May	19	0	15	4
27 May-9 June	12	0	10	2
10-23 June	9	0	8	1
24 June-7 July	25	0	21	4
8-21 July	44	2	21	21
22 July-5 August	13	0	4	9
6 August-2 September		none captured		
3-9 September	19	19	0	0
10-23 September	15	5	8	2
24 September-6 October	15	0	0	15

A - Little or no fat body

B - Medium fat body

C - Full fat body

Table 5 The condition of the fat body in males of <u>N. humator</u> according to season

Fortnight	Number examined	Condition of fat body A	B	C
12-28 April	7	7	0	0
29 April-12 May	9	0	2	7
13-26 May	15	0	3	12
27 May-9 June	7	0	0	7
10-23 June	14	0	3	11
24 June-7 July	29	0	2	27
8-21 July	26	0	3	23
22 July-5 August	23	0	0	23
6 August-2 September		none	captured	
3-9 September	10	10	0	0
10-23 September	19	4	5	10
24 September-6 October	17	0	0	17

Table 6 The condition of the ovaries in *N. investigator* caught at different times during the flight season

Week	Number	Condition of ovaries					
		Immature		Mature		Spent	
	examined	Number	%	Number	%	Number	%
1-7 July	10	10	100	0	0	0	0
8-14 July	13	13	100	0	0	0	0
15-21 Suly	8	6	75	2	25	0	0
22-28 July	83	61	76	22	24	0	0
29 July-5 Aug.	46	11	22	32	70	3	8
6-12 August	31	6	20	22	70	3	10
13-19 August	30	3	10	23	76	4	14
20-26 August	18	0	0	10	55	8	45
27 Aug-2 Sept.	31	0	0	29	93	2	7
3-9 September	30	3	10	10	33	17	57
10-16 September	78	0	0	9	12	69	88
17-23 September	42	0	0	3	8	39	92
24-30 September	27	0	0	0	0	27	100
TOTALS	447	113		162		172	

Table 7 The condition of the fat body in females of *N. investigator* according to season.
(Scoring notation as in Table 4)

Week	Number examined	Condition of fat body A	B	C
1-7 July	10	10	0	0
8-14 July	13	13	0	0
15-21 July	8	6	2	0
22-28 July	83	10	73	0
29 July-5 August	46	3	41	2
6-12 August	31	1	28	2
13-19 August	30	1	10	19
20-26 August	18	0	14	4
27 August-2 September	31	0	29	2
3-9 September	30	0	10	20
10-16 September	78	10	8	60
17-23 September	42	9	3	30
24-30 September	27	3	4	20
TOTALS	447	66	222	159

Table 8 The condition of fat body in males of *N. investigator* according to season

Week	Number examined	Condition of fat body		
		A	B	C
1-7 July	8	8	0	0
8-14 July	11	4	3	4
15-21 July	7	0	0	7
22-28 July	72	0	2	70
29 July-5 August	51	0	10	41
6-12 August	38	0	7	38
13-19 August	19	0	0	19
20-26 August	23	0	0	23
27 August-2 September	41	0	3	38
3-9 September	33	0	4	29
10-16 September	84	0	3	81
17-23 September	22	0	0	22
24-30 September	29	0	0	29
TOTALS	438	12	32	394

Newly emerged immature beetles had little or no fat body, while those that had been active for some time had large, fully developed fat body. Mature females had a reduced, but still considerable, amount of fat body. The amount of fat body in spent females varied between little and full development.

c. Condition of fat body in males (Table 8)

No fat body was found in newly emerged males of N. investigator, but extensive fat body development had occurred when beetles caught after 21 July were examined. The majority of male beetles caught after 5 August had fat body fully developed and this full development was a feature of male beetles until the end of the season.

Interpretation of the results

A clear picture of the adult life-history is obtained when the results from pitfall trapping are considered in conjunction with the results from dissection. In their broad outlines, the life-histories of the two species are very similar.

In both species the beetles emerge sexually immature at the start of the reproductive season. There is little or no fat body present in beetles at this time, and the peak of activity at the beginning of the season is probably caused by the need to find carrion in order to build up fat body for gonadal development. Indeed, newly emerged beetles which fail to find food within five days of emerging, do not survive and die with no fat body.

Female beetles of both species build up fat body with the ovaries still immature, and then develop mature eggs at the expense of the store of fat body. (Laboratory experiments showed that a newly emerged female beetle could produce mature eggs within 14 days of emergence, having only been allowed to feed for two days.)

During the major part of the reproductive period in these species, female beetles are absent from the actively-flying population. This is because the female plays the active role in larval brood care.

A similar situation prevails with N. investigator from about 12 August to 2 September, when the proportion of females caught in the traps was statistically significantly below equality in 1963 and 1964 (Fig. 6). The relationship between the proportion of mature females and the numbers caught in pitfall traps is shown in Fig. 5 for N. humator and Fig. 6 for N. investigator. In both species the second peak of activity was caused by intense post-breeding activity. After they have reproduced the beetles fly strongly, probably searching for food to build up the fat body depleted by the long sojourn underground. Deeper analysis of the results from dissection of the fat body showed that immediately after reproduction

Table 9 The state of the fat body in females of _N. humator_, according to the reproductive condition of the beetles

Reproductive condition of beetle	State of fat body A	B	C
Immature, caught before 5 May	8	0	0
Immature, caught after 5 May	1	4	11
Mature	2	53	1
Spent, on emergence	10	3	0
Spent, after feeding	0	12	34
TOTAL	21	72	46

Table 10 The state of the fat body in females of _N. investigator_, according to the reproductive condition of the beetles

Reproductive condition of beetle	State of fat body A	B	C
Immature, caught before 28 July	23	6	0
Immature, caught after 28 July	0	26	58
Mature	13	149	0
Spent, on emergence	30	4	0
Spent, after feeding	0	37	101
TOTAL	66	262	159

females had little or no fat body (Tables 9 and 10). This discovery supports Pukowski's suggestion that the females do not feed when in the brood chamber.

In the laboratory spent female beetles died within a fortnight of re-appearing above ground despite being supplied with unlimited and apparently suitable food, it seems likely that similar conditions prevail in the field. The data are shown in Tables 11 and 12.

Table 11. Length of life of female *N. humator* after emergence from the 'crypta' (16-18°C)

Days after re-emergence	6	7	8	9	10	11	12	13
Number of beetles dying	1	1	2	1	5	3	6	1

Mean survival time after re-emergence = 10.3 ± 2·5 days

Table 12. Length of life of female *N. investigator* after emergence from the 'crypta' (16-18°C)

Days after re-emergence	6	7	8	9	10	11	12	13	14
Number of beetles dying	1	-	1	2	3	7	4	2	1

Mean survival time after re-emergence = 11.3 ± 2·9 days

N. humator overwinter as adults and the larvae reared during June and July emerge during early September and are very active in their search for food. Individuals caught immediately after emergence show no fat body development, but by the time ~~their activity ceases in October, these immature individuals~~

show full fat body development. This fat body must be utilised in the winter months, for the beetles emerge with little or no fat body the following April.

The length of the adult flight-season is similar in both species, three months in *N. humator* (late April - late July), and two and a half months in *N. investigator* (mid July - late September).

A striking feature of the life-cycles of the two species was that the periods of reproduction did not overlap. The last mature females of *N. humator* were caught between 7-14 July, and the first mature females of *N. investigator* appeared between 21-28 July. The major part of the reproductive period in *N. investigator* had finished by the time immature *N. humator* appeared in early September.

The analysis of the mark release and recapture data

Initially it was decided to analyse these data using the method described by Leslie, Chitty & Chitty (1953). The method involves tabulating the recaptures of individually marked animals according to the date of their last previous capture, and calculating parameters describing the population from the tabulation. The most important parameters were considered to be the total number of animals in the population and the weekly death rate.

The analysis was started, using method B of Leslie & Chitty (1951) (Appendix A) and estimates of the total population and their variances were obtained. Unfortunately the standard errors of the population estimates were large, and the death rates, estimated from the population figures were unreliable, with negative death rates being obtained in many cases.

Negative death rates were expected using these methods, because beetles disappear underground to reproduce and reappear after an interval. Thus marked animals would "die" and then reappear, causing negative death rates. The other population parameters (dilution and survival rates) utilised the death rate in their calculations, and as the death rates were unacceptable, further analysis was abandoned.

However, another method of analysis, using a similar way of grouping the recaptures and based on a stochastic model, has been developed by Jolly (1965) (Appendix A). In this method the formulae are simpler to use and the calculations less laborious than in Leslie's (1951) method, and approximate variances for the estimates of population numbers are easily obtainable. A comparison of the two methods was undertaken, and the results are given below. Negative death rates still appeared using Jolly's methods and it is obvious that the recapture data are not extensive enough to give accurate estimates of this important parameter, and that the behaviour of the beetles prevents the estimation of death rates by these methods.

A simpler way of obtaining the weekly death rates of the Necrophorus population is to arrange the capture-recapture data in a trellis diagram where the recaptures are set out according to when the beetles were first captured and marked. This method was used by Lack (1951) to calculate the annual death rate of Redstart (P. phoenicurus L.), and has the added advantage that the standard error may be attached to the calculated values. This expression is given by $SE = 1-S\sqrt{\frac{S}{N}}$, where S = death rate and N = the total number of animals. Lack's method can also be used to derive the average further expectation of life, and this has been utilised to demonstrate the change in life expectancy of beetles as the flight season progresses.

It was assumed at the start of the analysis that the capture of marked and unmarked beetles was at random, and that marking had no effect on the beetle's behaviour. Marked individuals kept in culture did not show any difference in behaviour or survival compared with unmarked animals. To allow sufficient time for the marked individuals to mingle with the unmarked population the traps were closed for one night after the marked beetles had been released. Observation showed that when released at dusk, marked Necrophorus flew strongly, and it seems safe to assume that marked individuals were mingling satisfactorily with the unmarked population.

It was also assumed that immigration was absent, and emigration negligible. A trapping series on East and West Wideopens failed to show that marked beetles from the Inner Farne population moved the 300 yards to these adjacent islands. It was considered unlikely that beetles from the mainland, 1½ miles away, would reach the Inner Farne, and conversely, that beetles on Inner Farne would reach the mainland. This was supported by the lack of other species of carrion beetle on Inner Farne which were common on the mainland, e.g. _Silpha carinata_ Herbst, _Necrodes littoralis_ L. Emigration in the form of beetles flying out to sea and perishing was a possibility, but it was felt that the numbers involved would be very small and unimportant in terms of the analysis; in any case, this can be regarded as a natural cause of mortality.

Births, in the form of a second generation, were assumed to be absent and estimates of the rate of increase, although calculated, have little meaning in this study and are not discussed. Apart from the initial emergence of the beetles, the only complication was in _N. humator_, where a new generation of overwintering beetles emerged in September. However, this generation was not marked, and no estimates of population size were obtained for it.

Results

Estimation of the total population

The estimates for the total population of each species of beetle, and for each sex, are set out in Tables 13 to 16, with their standard errors. In addition the estimates have been compared graphically in Figs. 9 to 12 where the standard errors are omitted for the sake of clarity.

N. investigator (Tables 13 and 14)

During 1964, 275 male and 157 female N. investigator were marked for the first time, corresponding to a sex-ratio of 1.0:0.6, male:female. The population estimates show that N. investigator emerged in late July and that large numbers of beetles were active throughout August and September. The estimates of the population of both sexes show a drop on 12 August, but estimates rose again on 19 August. After 26 August the male population estimates show a steady decline, and no males were caught after 6 October. The estimates for females indicate a decline in numbers from 19 to 26 August, with an increase on 9 September. The female estimates fell sharply after 9 September and no females were caught after 6 October.

The estimates obtained by the two methods of analysis are very close, indicating that the recaptures were adequate in number for these methods. At the peak times, 19-26 August, some 500 beetles of both sexes were active. This is equivalent to a density of 78 beetles per hectare.

These estimates are sufficiently accurate to show when most of the population retired underground and when the successfully reproducing females emerged above ground. The estimates for both sexes show a drop in numbers on 12 August, and at that time the male population was halved and the female population decreased by at least 20%. This is interpreted as the pre-reproductive disappearance and would be the time when fighting for corpses would take place. The emergence of the post-reproductive females probably took place between 2-9 September, when the female population increased from 123 to 180 (Leslie) or from 100 to 140 animals (Jolly).

It is evident that the bulk of the N. investigator population did not disappear underground during August and September, but were very active at that time. It will be shown later that there was an unusually high survival of tern chicks, and the consequent dearth of corpses may have given rise to a situation where many beetles competed for few corpses. It is suggested that after the initial emergence, some of the population found corpses, buried them and reproduced normally. However, many beetles would not have found a corpse, and it was probably the constant activity of these beetles that accounted

Figure 9 Population estimates of male _N_. _investigator_ according to two methods. The solid circles joined by the solid lines (•____•) represent the population estimates derived by Jolly's (1965) method, and the open circles joined by the pecked line (o----o) represent the estimates derived by the method of Leslie et al (1953).

fig. 9

Population estimates of ♂ N. investigator

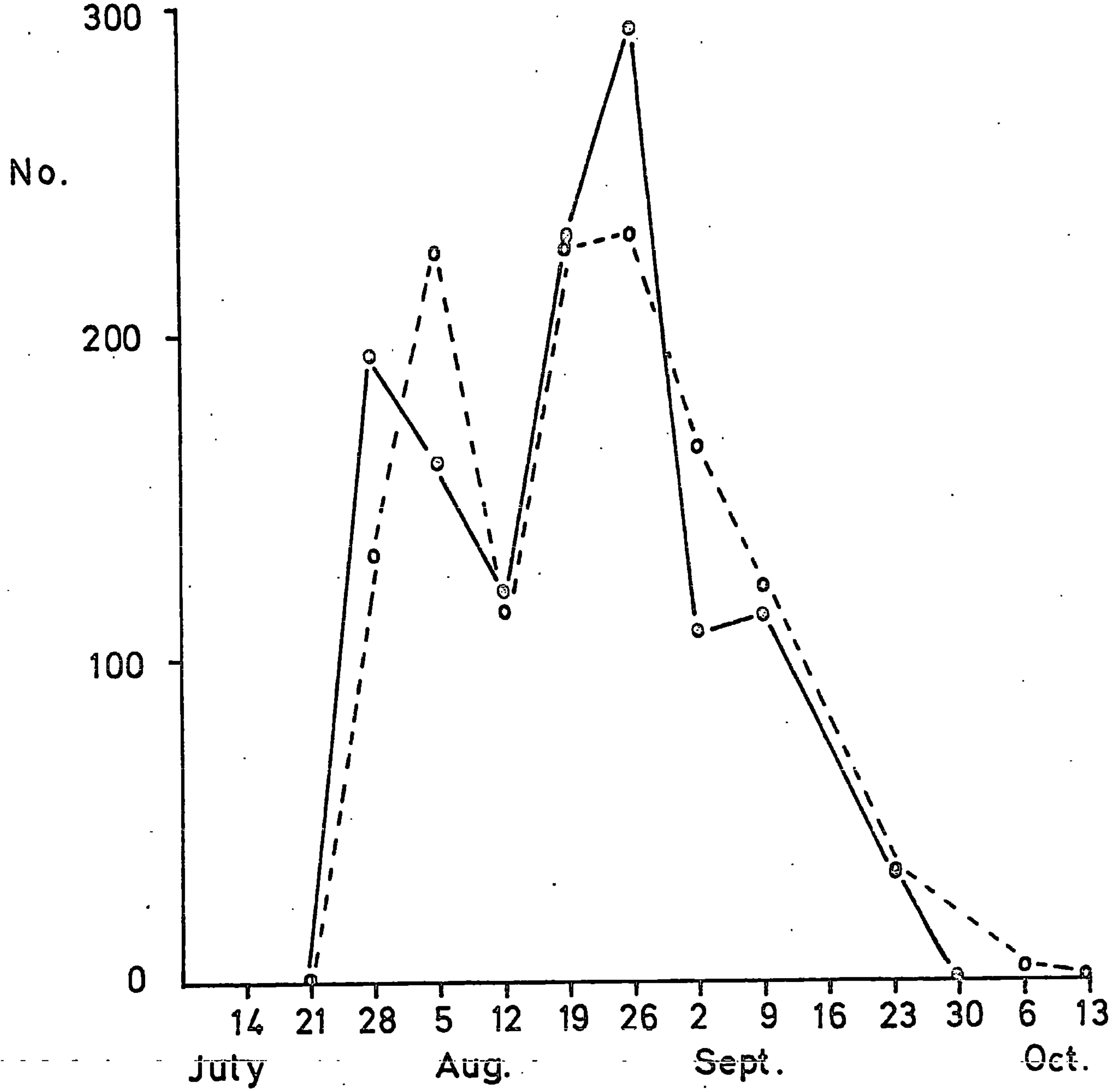


Figure 10 Population estimates of female N. *investigator* according to two methods. The estimates derived by Jolly's (1965) method are shown •____•, and the estimates from Leslie et al (1953) are shown o---o.

fig. 10

Population estimates of N. investigator ♀

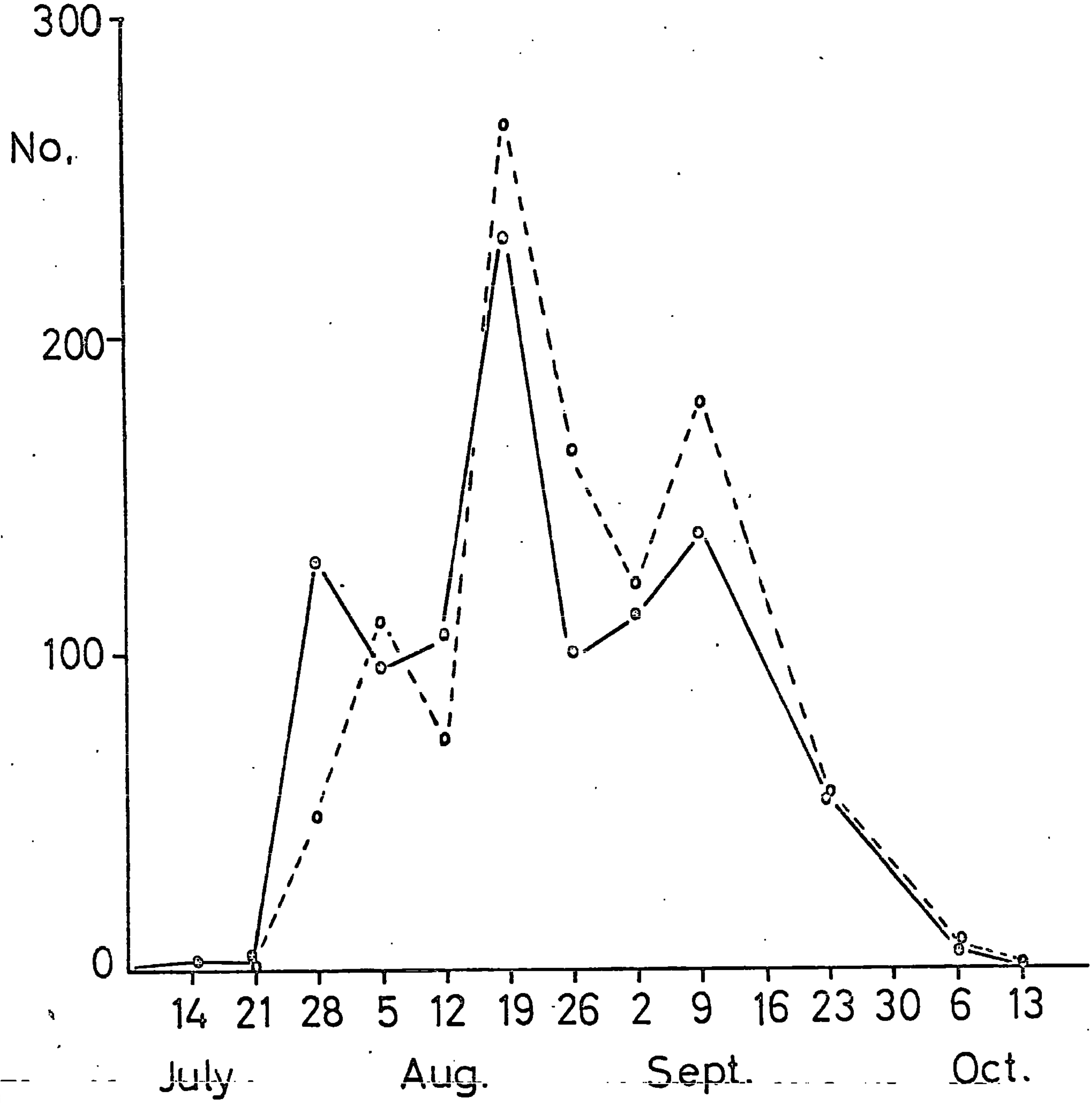


Table 13 Population estimates of male N. investigator, obtained by the methods of Jolly (1965) and of Leslie et al (1953)

	Jolly	Leslie
28 July	194.4 ± 128.3	133.6 ± 90.9
5 August	159.9 ± 107.2	226.7 ± 140.7
12 August	120.3 ± 36.0	116.0 ± 57.4
19 August	231.1 ± 44.1	227.0 ± 141.2
26 August	295.2 ± 42.8	231.2 ± 127.2
2 September	108.0 ± 16.7	166.7 ± 34.5
9 September	115.3 ± 30.9	122.0 ± 14.4
16 September	-	-
23 September	35.5 ± 29.1	34.8 ± 30.3
30 September	-	-
6 October	-	4.0 ± 4.0

Table 14 Population estimates of female N. investigator, obtained by the methods of Jolly (1965) and of Leslie et al (1953)

	Jolly	Leslie et al
28 July	128.1 ± 69.8	48.0 ± 23.2
5 August	96.5 ± 26.2	110.5 ± 71.4
12 August	105.1 ± 42.1	72.8 ± 71.0
19 August	231.6 ± 187.0	267.9 ± 79.5
26 August	99.6 ± 39.7	163.0 ± 61.3
2 September	113.7 ± 22.3	122.9 ± 42.9
9 September	138.0 ± 33.3	179.9 ± 73.2
16 September	-	-
23 September	54.0 ± 6.3	54.0 ± 47.8
30 September	-	-
6 October	-	6.0 ± 4.0

for the high population figures during August and September.

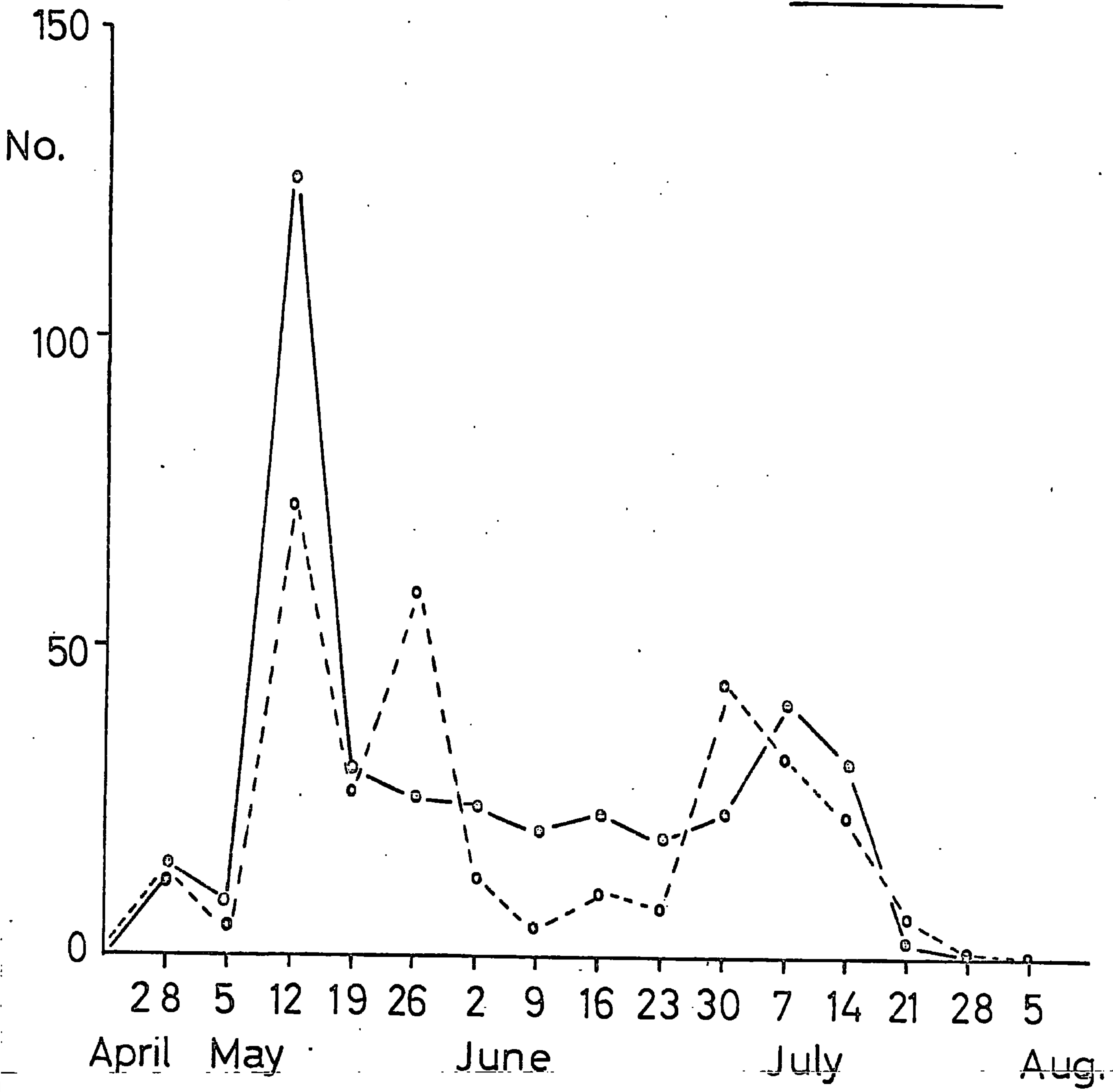
N. humator (Tables 15 and 16)

During 1964, 39 male and 52 female N. humator were marked for the first time, corresponding to a sex-ratio of 1:1.3, male: female. Both sets of population estimates (Figs. 11-12 and Tables 15-16) show that N. humator emerged in early May and was active throughout the month. In June very few beetles were caught and estimates were low. Higher estimates occurred again at the end of June, and in July the estimates show a drop in number. The pattern of population rise and fall in these species is similar to the expected pattern.

The pattern of the estimates obtained by the two methods is similar, but Jolly's method gives very high population estimates for the female population, on 2 June (170 individuals), while Leslie's method gives only 5 individuals. The estimates are unreliable in that the recaptures are small in number, but from the data it is obvious that about 100 males, and up to 200 females were active at peak times in the flight season. One way of avoiding the unreliability of these population estimates is to group the data into fortnightly intervals, but this has not been considered justified, for the flight season is so short that calculating population estimates on only six occasions during the period is bound to obscure the known biological picture.

Figure 11 Population estimates of male N. *humator* according to two methods. The estimates derived by Jolly's (1965) method are shown •___•, and the estimates from Leslie et al (1953) are shown o---o.

fig. 11



Population estimates of ♂ *N. humator*

Figure 12 Population estimates of female *N. humator*, according to two methods. The estimates derived by Jolly's (1965) method are shown •___•, and the estimates from Leslie et al (1953) are shown o---o.

fig. 12

Population estimates of ♀ N.humator

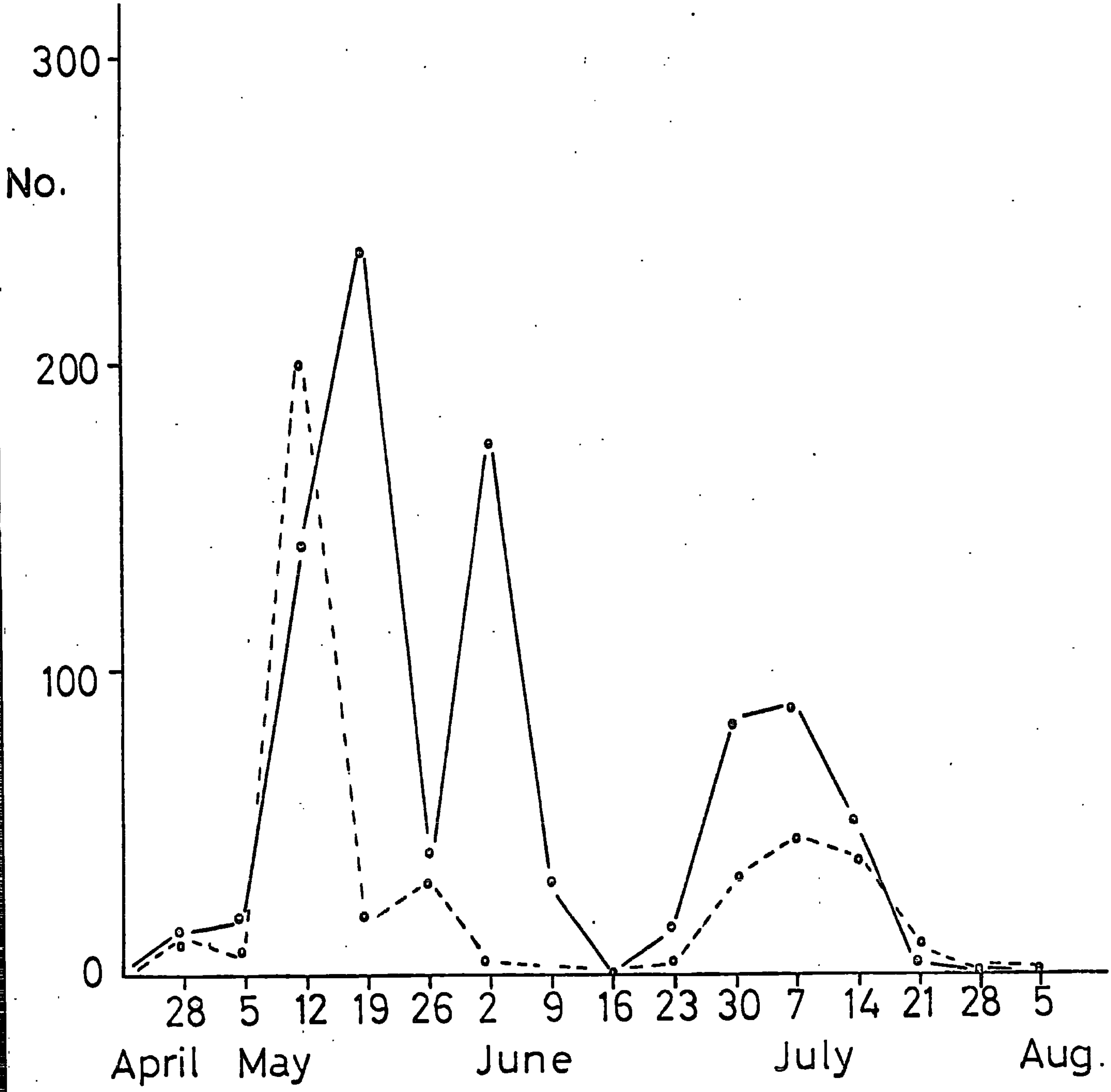


Table 15 Population estimates of male <u>N</u>. <u>humator</u>, obtained by the methods of Jolly (1965) and Leslie et al (1953)

	Jolly	Leslie
5 May	8.6 ± 4.3	4.0± 2.1
12 May	126.1 ± 62.1	72.8 ± 71.2
19 May	30.0 ± 10.4	27.0 ± 26.8
26 May	25.0 ± 23.4	58.8 ± 57.5
2 June	23.9 ± 17.3	13.6 ± 5.4
9 June	20.0 ± 19.4	5.0 ± 5.0
16 June	23.3 ± 4.8	10.8 ± 8.6
23 June	19.0 ± 17.9	8.0 ± 6.9
30 June	23.3 ± 21.6	43.8 ± 9.1
7 July	41.3 ± 13.8	32.8 ± 15.3
14 July	31.5 ± 28.5	22.8 ± 9.8
21.July	-	6.6 ± 4.6

Table 16 Population estimates of female N. humator, obtained by the methods of Jolly (1965) and of Leslie et al (1953)

	Jolly	Leslie
5 May	18.6 ± 17.2	13.0 ± 10.4
12 May	143.2 ± 59.9	198.0 ± 187.8
19 May	237.2 ± 191.5	15.7 ± 12.8
26 May	30.5 ± 28.9	10.5 ± 10.5
2 June	173.7 ± 120.9	4.8 ± 4.8
9 June	28.0 ± 27.5	4.0 ± 4.0
16 June	-	-
23 June	15.0 ± 14.5	4.0 ± 4.0
30 June	84.0 ± 54.7	32.5 ± 21.8
7 July	88.0 ± 44.4	51.3 ± 22.1
14 July	50.6 ± 43.8	38.5 ± 35.9
21 July	4.0 ± 2.0	8.0 ± 8.0

The death rate

From a consideration of the behaviour of Necrophorus, it was expected that in both species the incidence of mortality would be similar. The expected pattern was of an initial heavy mortality, caused by intraspecific fighting for corpses after emergence; little mortality for a short period, and finally an increasing mortality as the adult population declined to extinction. The initial mortality might be masked by the disappearance, and apparent mortality, of beetles underground. Female mortality was expected to be severe after the post-reproductive emergence, as experimental data showed that in culture these individuals only survived for a maximum of two weeks. Theoretically, if all the post-reproductive females emerged at once, the female population would be extinct within two weeks, but normally this situation would never arise, females reproducing as suitable corpses become available. In practice this means that females who are physiologically capable of breeding may delay doing so until corpses become available. This situation has been produced in the laboratory, and it is probable that final egg development, and perhaps successful copulation, only takes place when a pair have been isolated at a corpse.

Results

N. investigator

The weekly death rates obtained using Lack's (1951) method are set out in Table 17, with their standard errors. In addition the results are graphically expressed in Fig. 13. Death rates were initially low (50-60%), and stayed low in females until 19-26 August, when they doubled and remained high (80-98%) until the end of the season. In males a high death rate was shown on 12 August (83.3%) and the rate remained high until the end of the season. This pattern of mortality is close to the expected one, the beetles suffering heavy mortality once breeding activities cease.

The average expectancy of further life was calculated, assuming that each beetle lived half a week after its last recapture, and the results are shown in Table 18. The method of calculation is described in Appendix A and an example given.

The average life expectancy of adults was calculated, and the results are shown in Table 18. It was expected that later in the flight season beetles would have a shorter expectancy of further life, and this was found to be the case. After the 19 August the life expectancy of both sexes was halved from above one week to half a week, and this is also reflected in the mortality rates which increased sharply at that time.

_N_. _humator_

The weekly death rates are set out in Table 19 and shown graphically in Fig. 14. The weekly death rates in both sexes were relatively low from 20 April until 7 May, when the female

Figure 13 The weekly percentage mortality of male and female *N. investigator*. Male mortality is denoted •___•, and female mortality o---o. The vertical scale, (% mortality) begins at 20.

fig. 13

Percentage mortality of *N. investigator*

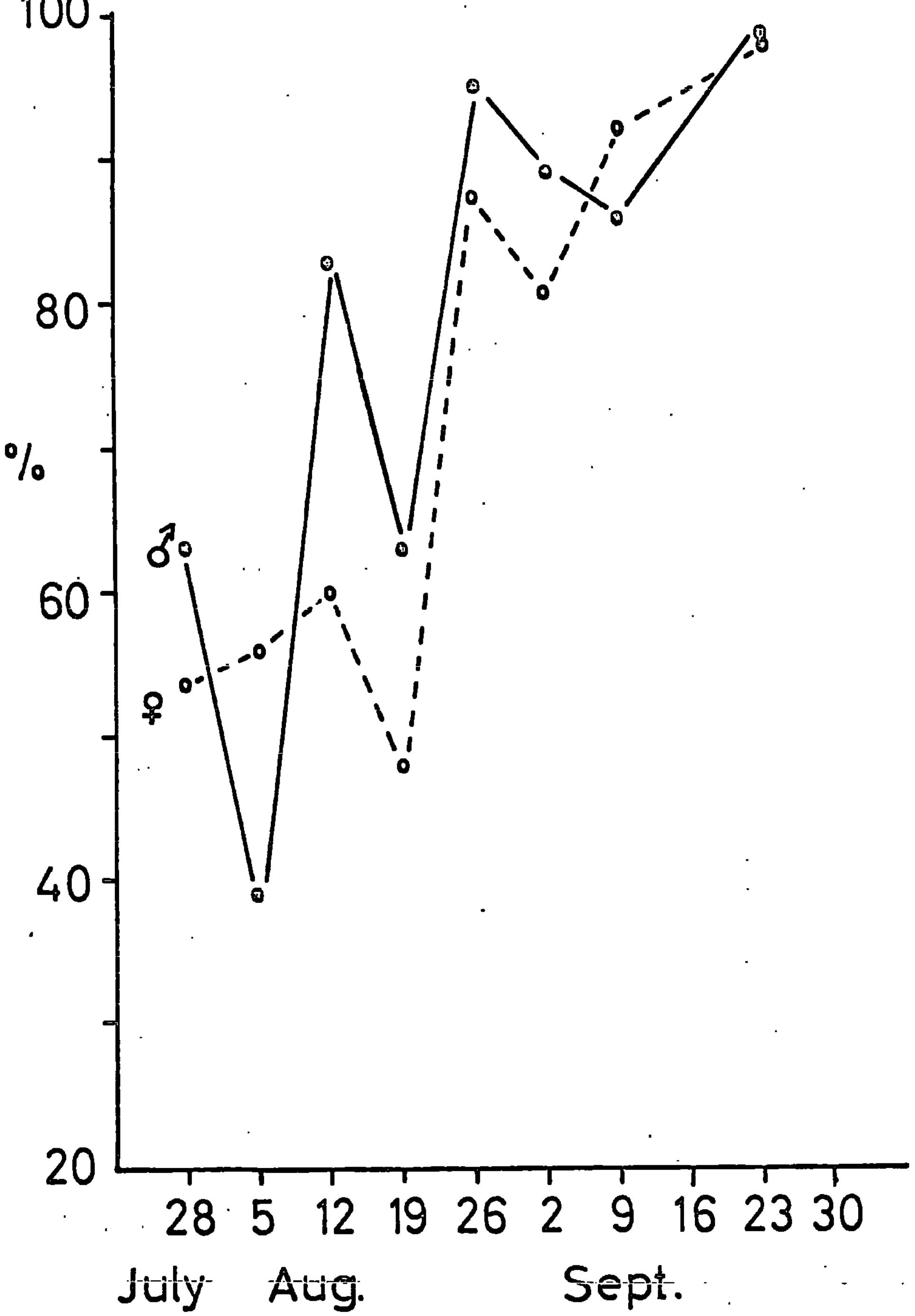
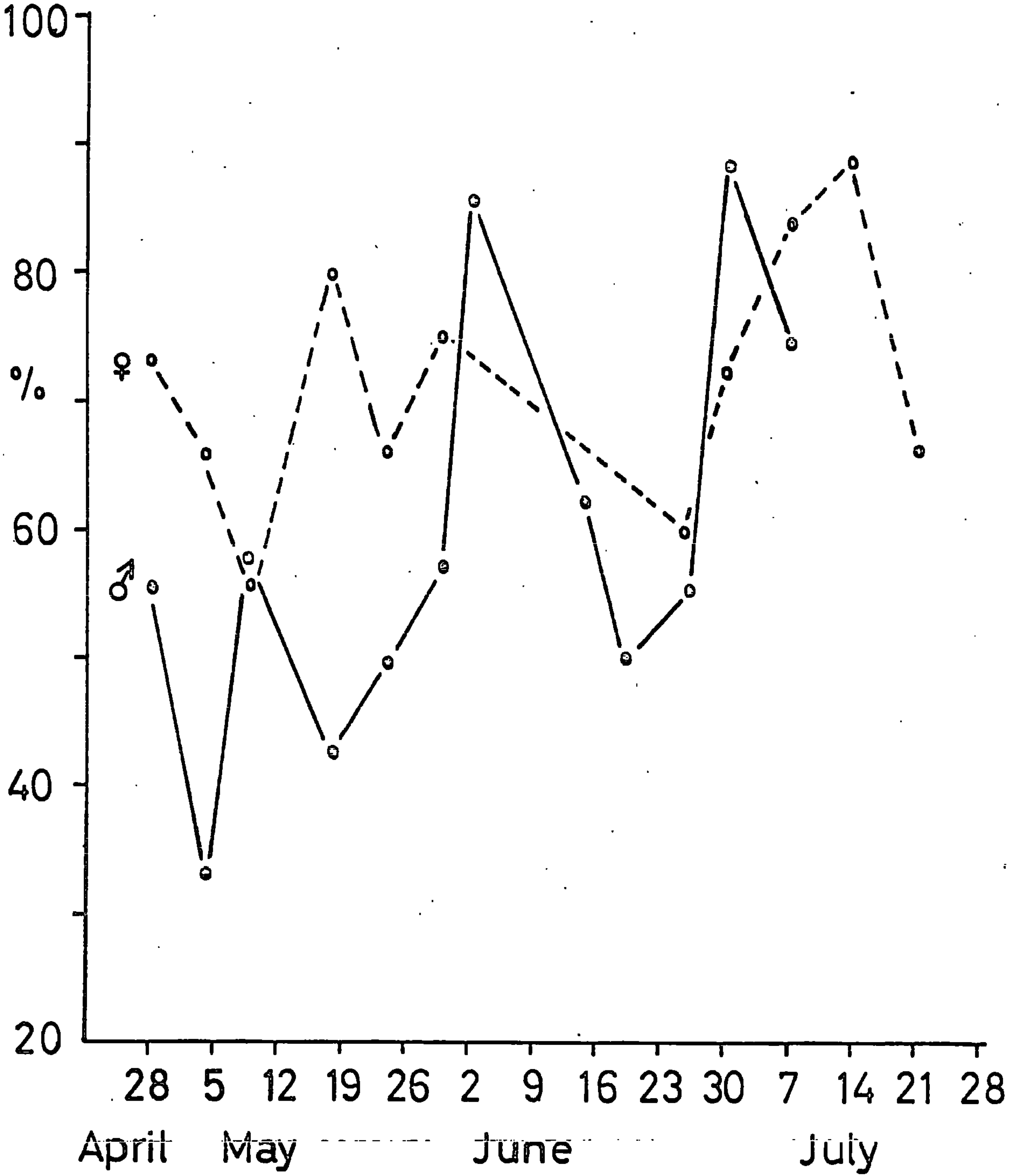


Figure 14 The weekly percentage mortality of male and female *N. humator*. Male mortality is denoted •___•, and female mortality o---o. The vertical scale, (% mortality), begins at 20.

fig. 14

Percentage mortality of N. humator



mortality increased from 56% to 80% on 18 May, whilst male mortality remained at 40 to 50%. Male mortality became more severe on 2 June (86%) but from 14-25 June remained between 55-61%. During July male and female mortality was high, between 70-90%. This pattern of mortality is very similar to that seen in *N. investigator*, initially low but high at the end of the flight season.

The average life expectancy of adults was calculated and the results are presented in Table 20. Once again a similar pattern to *N. investigator* is shown, with an initially high life expectancy decreasing as the season progressed. In this species, females appeared to have a shorter life expectancy than males, but the paucity of the original data invalidates any serious consideration of this point.

The sex-ratio

The sex ratios derived from the population estimates have been expressed as the percentage of females in the total population, and are compared with similar results derived from pitfall captures.

N. investigator

The sex-ratio in this species is tabulated in Table 21. The results show that broadly similar sex-ratios are derived from both the population estimates and the pitfall catches.

Exceptions occur on 12, 19 August, when the population estimates show 50%, but the pitfall catches indicate 27% and 29% females. This may be a reflection, in the pitfall traps, of the disappearance of females underground, which was not apparent in the estimates of the total population. The overall picture is of equal numbers of males and females in the population.

N. humator

In this species the two sets of sex-ratios disagree on several occasions, notably on 19 May, 2 and 30 June. On these occasions the proportion of females derived from the population estimates are higher than those derived from the pitfall catches (Table 22) and in these cases over 80% of the population are females, according to Jolly's method, and only 26% to 54% according to the pitfall catches. Little can be said about this phenomenon, but it seems likely, from the biology of the beetle, that many females were underground at these times. If this were so one would expect the sex-ratio to be roughly at equality, possibly with the proportion of females depressed in the flying population.

The results of these analyses show firstly that the method of Jolly (1965) provides more accurate estimates of the total population than Leslie's method, and that the former estimates have smaller standard errors attached to them. However, because of the lack of data on recaptures and the beetles' behaviour,

Table 17 The weekly percentage mortality of ♂ and ♀ *N. investigator*, during the 1964 flight season

Date	Percentage mortality ± standard error	
	♂	♀
28 July	63.1 ± 2.9	53.4 ± 3.0
5 August	39.0 ± 3.3	56.3 ± 12.3
12 August	83.3 ± 3.6	60.0 ± 10.0
19 August	62.9 ± 10.3	47.7 ± 5.3
26 August	95.1 ± 0.6	87.5 ± 1.9
31 August	88.8 ± 3.7	81.0 ± 5.1
3 September	86.6 ± 3.3	92.0 ± 0.2
6 September	98.1 ± 0.2	98.4 ± 0.3

Table 18 The average expectancy of further life in adult male and female N. investigator, throughout the 1964 flight season

Date	Average expectancy of further life in weeks ♂	♀
28 July	1.11	1.37
5 August	1.66	1.27
12 August	0.86	2.83
19 August	1.09	1.60
26 August	0.55	0.64
31 August	0.62	0.72
3 September	0.65	0.58
6 September	0.52	0.51

Table 19 The weekly percentage mortality of male and female *N. humator* during the 1964 flight season

Date	Percentage mortality ± standard error	
	♂	♀
28 April	55.5 ± 6.3	73.6 ± 5.2
4 May	33.3 ± 6.7	66.6 ± 5.1
7 May	57.8 ± 7.3	56.5 ± 4.7
18 May	42.8 ± 13.9	80.0 ± 2.5
24 May	50.0 ± 11.2	66.6 ± 5.1
29 May	57.1 ± 8.6	75.0 ± 10.7
2 June	85.7 ± 5.1	-
14 June	62.5 ± 10.6	-
18 June	50.0 ± 17.8	-
25 June	55.5 ± 10.8	60.0 ± 14.0
1 July	88.8 ± 3.7	72.7 ± 3.3
7 July	75.0 ± 5.2	84.2 ± 2.4
14 July	-	88.8 ± 3.7
21 July	-	66.6 ± 11.2

Table 20 The average expectancy of further life in adult male and female *N. humator* throughout the 1964 flight season

Date	Average expectancy of further life in weeks ♂	♀
28 April	1.30	0.85
4 May	2.50	0.75
7 May	1.22	1.65
18 May	1.83	0.75
24 May	1.70	1.00
29 May	1.50	0.83
2 June	0.66	
14 June	1.10	
18 June	1.50	
25 June	0.80	1.16
1 July	0.60	0.87
7 July	0.80	0.69
14 July	-	0.62
21 July	-	0.75

Table 21 The sex-ratio in _N._ _investigator_ in 1964 according to the population estimates, and to the pitfall catches. The ratio is expressed as the percentage of females on each occasion.

Date	Sex-ratio (Jolly)	Sex-ratio (Pitfalls)
28 July	36	50
5 August	45	44
12 August	50	27
19 August	50	29
26 August	33	34
2 September	50	52
9 September	50	52
16 September	-	-
23 September	60	48
30 September	-	-

Table 22 The sex-ratio in N. humator in 1964, according to the population estimates, and to the pitfall catches. The ratio is expressed as the percentage of females on each occasion

Date	Sex-ratio (Jolly) % females	Sex-ratio (Pitfall) % females
5 May	60	72
12 May	50	69
19 May	89	54
26 May	50	57
2 June	86	26
9 June	50	-
16 June	-	43
23 June	50	47
30 June	80	50
7 July	68	53
14 July	60	-

unacceptable death rates were derived using either method. It is concluded that in analyses of this nature, where recaptures are relatively few, Jolly's method will give more accurate population estimates, and is simpler to use, and is to be preferred to Leslie's method for this reason.

The death rates derived by Lack's method are relatively accurate for N. investigator, but are not so accurate for N. humator. Nevertheless, the death rates show what might be expected from observations in the laboratory, that is that the beetles suffer heavy mortality at the end of the season. In both male and female N. investigator the death rates show a marked rise between 19-26 August, at a time when the population estimates showed that large numbers of beetles were active. This mortality is interpreted as being caused by severe competition for the very few corpses available at that time. The 1964 season was marked by the very high survival of tern chicks (over 80% fledged) and the beetles were prevented from utilising tern corpses for reproductive purposes. A field observation supports this contention, for a tern corpse discovered on 14 August 1964 had fifteen N. investigator beneath it, where normally only four or five beetles would have been present. In the competition for the corpse only one pair could be successful and many beetles must have failed to reproduce. It is considered that these unsuccessful beetles were the ones which were actively searching for corpses in late August, and being unable to find them, dying in large numbers.

It is obvious from these data that the death rate in both species of Necrophorus rises sharply at the end of the flight season. This is particularly well marked in N. investigator where the population of 300 beetles on 7 September is extinguished by 6 October. The activity of N. humator also ceased on 6 October in both 1963 and 1964. Such a synchronous cessation of activity is possibly the result of a physical factor such as an early frost.

Larger numbers of N. investigator were caught in 1964 than in 1963, and this is probably a reflection of the success of the Necrophorus breeding season in 1963. Tern mortality in 1963 was normal, and many corpses were available to Necrophorus for reproduction. Given the normal overwintering mortality, large numbers of Necrophorus would have emerged in mid-July 1964. Theoretical consideration of Necrophorus population fluctuations indicates that in years of corpse shortage, competition for carcases will be fierce, only a few beetles will reproduce and the following year's population will be low. In years of corpse abundance the majority of the population will be able to rear a brood and the following year's population will be high. The former appears to have been the situation in 1964.

The spatial distribution of _Necrophorus_ on Inner Farne

Because of their strongly flying habit and the restricted area of Inner Farne, it was expected that catches of _Necrophorus_ would be at random. The distribution of _Necrophorus_ as reflected in the pitfall catches was compared in areas delineated by natural boundaries as follows.

1. The Dock - situated to the SW of the Cove and to the south of the Lighthouse path, the vegetation consisted of Dock (_Rumex_ sp.) with thick stands of nettle, _Urtica dioeca_ L.
2. The Campion, the remainder of the island to the south of the Lighthouse path. The vegetation consisted almost entirely of Sea Campion, _Silene maritima_ With. with Thrift, _Armeria maritima_ Willd. where the soil was shallow.
3. The Meadow, an area to the north and NW of the Light house path, the vegetation consisting of coarse grasses.
4. The Tower, the area adjacent to the buildings and including the North Point.

These areas are shown in Fig. 1.

The weekly catches of _Necrophorus_ in pitfall traps in each area are shown in Tables 23 and 24. For purposes of comparison the figures have been divided into the catches before and after breeding.

N. humator (Table 23)

During the pre-breeding spring emergence (before 19 May) of adults in 1963 and 1964, no difference in distribution was found. The same was true of the catches during the breeding season (19 May onwards). The catches of the overwintering generation, caught in September 1963, showed that although few were caught in the Campion (14) and Meadow (4), significantly more were caught in the Dock (42) ($X_1^2 = 26.8$ $P < 0.001$) and in the Tower (21) ($X_1^2 = 3.1$ $P < 0.05$). There were significantly more animals caught in the Dock than in the Tower area ($X_1^2 = 7.0$ $P < 0.01$).

A similar pattern was shown by the catches in September 1964, when catches in both the Dock and Tower areas were very similar (46:49) and were highly significantly different ($X_1^2 = 21.6$ $P < 0.001$) from the catches in the Campion and Meadow (13:11).

<u>N</u>. <u>investigator</u> (Table 24)

In 1963, during the summer pre-breeding emergence (before 19 August), significantly more animals were caught in the Dock (54) than in any other area ($X_1^2 = 7.0$ $P < 0.01$). The catch in the Tower area (29) was significantly greater ($X_1^2 = 8.6$ $P < 0.01$) than the catches in either the Campion or Meadow, which were very similar (10:9). The catches during the breeding season (19 August onwards) showed that there was no difference between the Dock and Tower catches (52:46), but

Table 23a Weekly catches of N. humator, according to area, in 1963

Area	April	May				June					July				September				Oct
	28	5	12	19	26	2	9	16	23	30	7	14	21	28	9	16	23	30	6
Docks		10			5		3				3	3	4	3	7		1	10	24
Campion		10			1	4	2	2			3	5	5	1			8	2	4
Meadow	1	11				2	2	3			2	8	4	1	1		1		2
Tower	1	8			2	1	3	2			5	7	4	1	3		2	6	10

Totals	Prebreeding	Breeding	Overwintering
Docks	10	21	42
Campion	10	23	14
Meadow	12	22	4
Tower	9	25	21

Table 23b Weekly catches of N. humator, according to area, in 1964

Area	April	May				June					July				September				Oct
	28	5	12	19	26	2	9	16	23	30	7	14	21	28	9	16	23	30	6
Docks	7	1	9	3	3	3	1	2		2	12	2	2		21		17		8
Campion	5	1	11	4	2	3		1	1		13	3	1		4		8		1
Meadow	9	3	10	2	1	8	1	1		2	10	8	2	1	3		5		3
Tower	8	2	12	2	1	5		1	2	4	12	2	2	1	24		19		6

Totals	Prebreeding	Breeding	Overwintering
Docks	17	30	46
Campion	17	28	13
Meadow	22	36	11
Tower	22	32	49

Table 24 a Weekly catches of N. investigator, according to area, in 1963

Area	July				August				September					Oct
	7	14	21	28	5	12	19	26	1	9	16	23	30	6
Docks				2	19	33			6	38		2	1	5
Campion				1		9			3	16			3	
Meadow			1			8			1	27				
Tower				1	2	26			2	37			1	6

Totals	Prebreeding	Breeding
Docks	54	52
Campion	10	22
Meadow	9	28
Tower	29	46

Table 24b Weekly catches of N. investigator, according to area, in 1964

Area	July				August				September					Oct
	7	14	21	28	5	12	19	26	2	9	16	23	30	6
Docks		2		42	51	12	22	66	10	36		4		4
Campion		1		17	5	3	26	52	3	31		2		
Meadow	1			19	28	6	16	60	4	40		2		1
Tower		2	1	63	26		37	57		31		9		5

Totals	Prebreeding	Breeding
Docks	87	142
Campion	26	114
Meadow	54	123
Tower	92	139

that these were significantly greater than the catches in either the Meadow or the Campion (28:22) ($X_1^2 = 4.2$ $P < 0.05$).

In 1964, during the pre-breeding emergence, significantly more animals were caught in the Dock (87) and Tower (92) areas than in the Meadow (54) ($X_1^2 = 8.2$ $P < 0.01$). The catch in the Meadow was significantly greater than that in the Campion (26) ($X_1^2 = 10.3$ $P < 0.01$). The catches during the breeding season were similar in all areas, and did not differ significantly.

These results show interesting departures from the expected even distribution of catches with respect to area. Apart from factors affecting flight activity, such as wind and temperature, the only variables relevant to <u>Necrophorus</u> activity are the distribution and availability of carrion. The distribution of artificially provided carrion on Inner Farne was regular over the whole island, and was constant from week to week. It is suggested that the disposition of naturally occurring carrion affected the catches, and that beetle activity was concentrated where large amounts of natural carrion occurred. From the results it may be seen that significantly more <u>N. humator</u> were obtained from the Dock and Tower areas, in both 1963 and 1964, before the breeding season. A similar distribution was shown by <u>N. investigator</u> throughout the season in 1963 and on emergence in 1964. This distribution may be explained by the occurrence of the most carrion in the areas where the majority of birds, eider ducks and arctic terns, nested. According to this hypothesis, where carrion was scarce beetle activity would be high and catches would be evenly distributed in relation to the areas. If this is the case, then it would follow that carrion was scarce for *N. humator* during the breeding season in 1963 and 1964, and scarce for *N. investigator* during the breeding season in 1964. This hypothesis appears to satisfy the facts, that is that the amount of carrion available to *N. humator* on Inner Farne is normally small, the population consequently being small. In normal years the carrion supply of *N. investigator* is large, but was much reduced in 1964, possibly accounting for the even distribution of catches in that year.

The significance of the preference for the Dock and Tower areas by newly-emerged *N. humator* and *N. investigator* can be explained by the distribution of carrion when the previous generation of beetles reproduced, for it is in these areas that the largest numbers of bird corpses occur. It is suggested that these results reflect the distribution of newly emerged individuals, hence also the distribution of the previous generation's reproductive activities.

After the initial emergence of the beetles, the distribution of *Necrophorus* was even in relation to the four areas, and some idea of the amount of movement was gained by comparing the number of animals recaught in the same area as their previous capture with the numbers caught in different areas. 80% of the animals which were caught twice were caught in a different area on each occasion, showing that extensive movement between areas occurs.

Such a result is not surprising when the strength and speed of flight are observed in the field. Once airborne, Necrophorus fly very rapidly, and several times individuals flying early in the evening have been followed, their flights timed and the distance measured. In one case a male N. investigator flew across the island, 450 m, in 5 minutes, an average speed of over 3 miles per hour. However, the actual flight speed was much faster than this, as the beetle did not fly in a straight line, but pursued a zig zag course.

Further data on flight distance were gathered from experiments with paint-marked Necrophorus near Durham. In these experiments 20 N. humator and 25 N. vespilloides were marked and released in the same place (Little High Wood) on the same night. Necrophorus subsequently captured at baited pitfalls set up at varying distances from the wood were examined for marks. Two beetles were recaptured, one of each species, both on the evening following release. One specimen of N. humator, a male, was recovered within the wood some 800 m away from the release point, the other beetle, a female *N. vespilloides* was retrapped in an adjacent wood, almost 2000 m from the release point. Both animals flew these distances within 24 hours of release, and probably during the 8 hours of darkness immediately after release.

Dispersal and possibly colonisation of new areas is achieved in *Phyllopertha horticola* (Milne 1960) by bee-liners, females whose behaviour differs from normal females in that they undertake long straight and very fast flights away from the natal area. The flight distances of male and female *Necrophorus* on Inner Farne were examined for any tendency on the part of one sex to fly further than the other. The data gathered from the pitfall results are presented in Table 25 and it is obvious that no sexual difference in flight distance may be discerned.

Table 25. The distances flown by male and female *Necrophorus* on the Inner Farne, 1964

Distance	*N. investigator*		*N. humator*	
	♂	♀	♂	♀
0-50 m	7	5	2	3
51-100 m	8	10	2	3
101-150 m	16	19	9	6
151-200 m	28	25	18	8
201-250 m	37	33	15	14
251-300 m	38	40	8	9
301-350 m	29	28	3	7
351-400 m	3	8	1	1
401-450 m	5	4	0	0
	172	172	58	51

Table 25 shows clearly that flights of under 50 m are not common, and this fits well with the idea that *Necrophorus* are strong fliers.

The relationship between *Necrophorus* and their food supply on Inner Farne

In this study positive evidence of the reproductive activities of *Necrophorus* on Inner Farne was obtained by carefully searching for half buried corpses at times when the beetles were reproducing. On examination it was found that the beetles were feeding principally on a single species of corpse (Table 26a). The availability of corpses to *Necrophorus* was studied by weekly 'corpse counts', from 14 April to 16 June (Table 27). Corpse counts were discontinued after mid-June because of the inability to search the thick vegetation efficiently. The results, although incomplete, are a good guide to the number of corpses available to *Necrophorus*, and taken in conjunction with the results in Table 26, show how each beetle species appears to be confined to a single type of corpse.

When half buried corpses were found, the burial activities of *Necrophorus* were not disturbed. Apart from the shag (*Phalacrocorax aristotelis*) used for reproduction by *N. humator* on 28 May 1964, the only corpses found to have been buried by *N. humator* were those of Eider ducklings (*Somateria molissima*).

Table 26 Species of animal buried by *Necrophorus* on Inner Farne in 1963 and 1964

Necrophorus species	Date	Eider adult	Eider duckling	Tern species	Shag	Rabbit
N. humator	28.5.64				+	
"	1.6.63		+			
"	8.6.63		+			
"	11.6.64		+			
N. investigator	3.8.64			+		
"	6.8.64			+		
"	6.8.63			+		
"	14.8.64			+		
"	15.8.63			+		
"	15.8.63			+		
"	16.8.63			+		
"	16.8.63			+		

The Eider ducks on Inner Farne lay their eggs during May and the ducklings hatch during June. Immediately the ducklings are dry (24 hours after hatching), the duck leads them to the water, and the family swims to the mainland 1½ miles away. During the journey from the nest to the water some ducklings are killed by gulls, and some, failing to keep up with the rest, are abandoned amongst the vegetation and die. It is probably the abandoned ducklings that were utilised by N. humator. The number of corpses available to N. humator from this source including ducklings left in the nest, was at least double that shown in Table 27 (I. K. Marshall, pers. comm.). However, it is thought that, at the most, not more than 40-50 Eider ducklings became available to N. humator in 1963 or 1964.

A possible source of carrion for both N. humator and N. investigator for which little data are available, is the rabbit (Oryctolagus cuniculus) population of Inner Farne. Apart from the rabbits found dead when observations started in April (Table 27), no dead rabbits were found. To give some idea of the size of the rabbit population, spot counts were taken from the top of the Tower in May, June and September 1964. The maximum number of rabbits counted in May/June was 94, of which 20 were recently born animals. In September the maximum number was 116, of which at least 35 were young animals. (Counts in July and August were abandoned because of the difficulties of

Table 27 The number and species of naturally occurring corpses on Inner Farne in 1963 and 1964

Week ending	Eider adult 1963	Eider adult 1964	Eider duckling 1963	Eider duckling 1964	Shag 1963	Shag 1964	Other Bird species 1963	Other Bird species 1964	Rabbit 1963	Rabbit 1964
14 April					2*		5*	1*	10*	6*
21 April	1									
28 April	1	2				4			2	5
5 May	1									
12 May										
19 May										
26 May										
2 June			8	4						
9 June	1		10	6						
16 June			2	3						

* Denotes late winter mortality

observing rabbits in thick vegetation.) The counts failed to show extensive rabbit mortality during the summer, and support the similar result obtained from the corpse counts. During bird-ringing operations in July and August, no dead rabbits were found. It was assumed that the rabbits found dead in April comprised part of the winter mortality, and that little, if any, mortality occurred during the rest of the flight season of Necrophorus on Inner Farne.

The possibility of rabbits dying underground cannot be discounted and such corpses would probably be found by Necrophorus. However, as the results from spot counts did not show any mortality, it is considered unlikely that many died under these circumstances. During the summer there was no shortage of food for the rabbits on Inner Farne, but in winter the vegetation virtually disappears, and this is likely to be the period of heavy mortality. It was concluded that the rabbits on Inner Farne did not normally provide Necrophorus with a carrion source.

The mortality in the tern colony on Inner Farne is discussed in detail later and it is significant that the pre-fledging mortality period, occurring throughout August, coincides with the reproductive period of N. investigator. In 1963 at least 10% of the chicks which hatched, died between the ages of 3 weeks and two months. This figure represents 135 large chicks (80-110 g) and does not take into account the number of younger chicks dying, which might be up to 450 birds. It is apparent that *N. investigator* have no shortage of corpses at a time when they require them.

A feature of the *Necrophorus* population on Inner Farne was the difference in numbers between the two species. The *N. humator* population was estimated at about 200-300 animals in 1964, and in the same year the estimated population size of *N. investigator* was 400-500 animals. This suggests that the small size of the *N. humator* population on Inner Farne was a reflection of the relative paucity of suitable carrion at the time when the beetle reproduces. *N. investigator*, on the other hand, could take advantage of a much larger amount of carrion, and the population size was correspondingly larger.

V THE BIOLOGY OF NECROPHORUS: LABORATORY STUDIES

2 LABORATORY STUDIES

Culture techniques

Laboratory cultures of Necrophorus humator and N. investigator were set up in 1963 in order to provide data on burial behaviour, developmental periods of eggs and larvae and the subsequent behaviour of the adults.

After some experiment, straight-sided, (1000 ml) crystallising dishes were used as culture chambers. Each dish was filled with loosely compacted topsoil to within 4 cm of the top, and the top covered by a glass plate. A suitable corpse was placed on the soil surface and a pair of Necrophorus introduced. Burial behaviour could be observed through the lid and sides of the chamber. In many cases the corpse was lowered into the soil by the beetles until the bottom of the chamber was reached, and observations on behaviour within the crypta could be made.

Physical conditions were similar to those in the field, and a temperature between 15-20°C was maintained within the culture chambers. Care was taken to maintain the relative humidity in the chambers at high levels as the beetles readily died if the soil dried out. In the chambers moisture condensed on the lid and was automatically returned to the soil.

The behaviour of the female beetle during the care of the brood was observed by a simple variation of the culture chamber. In these chambers, only 2 cm of soil was added, and in such cases the pair did not attempt to bury the carcase and feeding behaviour could be easily observed.

During the larval growth experiments, each larva was removed from the corpse with fine forceps, weighed on a torsion balance and placed inside a container with moist soil. All the larvae were treated similarly and the brood was returned en masse to the crypta.

Preference experiments in the field

A limited number of experiments were carried out in 1963 on the type of corpses preferred by Necrophorus in the natural state. Freshly dead animals were arranged in pairs one foot apart on the Meadow and inspected every 24 hours. Each pair of corpses was separated from the next pair by at least 20 m and the animals buried or visited by Necrophorus were noted daily. (During the experiments the pitfall traps were closed.) The animals presented to the beetles were the same species as those used in the laboratory experiments in 1964, and were chosen to represent the naturally occurring carrion on the Inner Farne. The animals were Eider ducklings, rabbits and tern chicks.

Results

a. *N. humator* (10 replicates, 10 successful)

Choice	Eider duckling v.	small (150 g) rabbit
No. of times chosen	8	2

(10 replicates, 8 successful)

Choice	Small (150 g) rabbit v.	large (300 g) rabbit
No. of times chosen	8	0

b. *N. investigator* (20 replicates, 16 successful)

Choice	Tern chick v.	small (150 g) rabbit
No. of times chosen	15	1

These results indicate that *N. humator* preferred eider ducklings to rabbits, and small to large rabbits. It was obvious that *N. investigator* preferred tern chicks to rabbits.

During the experiment the beetles were collected after they had been found on the corpse and were not released until the experiment had finished. This was to ensure that different beetles found the corpses each time, and the possibility of trap- or corpse-happy beetles was avoided.

Preference experiments in the laboratory

Experiments similar to those in the field were carried out in the laboratory. Two corpses were presented to one male and one female *Necrophorus*. The corpses were placed on top of 10 cm of loose soil in a tray (1 m x 1 m), the tray was covered for 24 hours and then examined. Normally the burial of one of the corpses had been started within 24 hours, but where no burial was observed the tray was left for a further 24 hours and then re-examined. In all the experiments, burial activity had started 48 hours after the introduction of Necrophorus.

Necrophorus humator and N. investigator were used in the experiments, and the animals presented in the trays were chosen to represent the naturally occurring food of Necrophorus on the Inner Farne. These animals were rabbits, Eider duckling and arctic tern chicks. Fresh material was used whenever possible, and at other times deep frozen specimens were thawed for 24 hours at room temperature before being presented.

Preliminary field experiments showed that a small (150 g) rabbit was chosen in preference to a large (300 g) rabbit. The result of 10 experiments in the laboratory, set up to demonstrate this, was 9 choices of small rabbit and 1 choice of a large rabbit, where only the head was buried. The difference was statistically significant ($X^{2}_{(1)} = 4.9$, $P \leqslant 0.05$ ~~0.02~~) and it was thought justified to use small rabbits in the main series of experiments. The weights of eider ducklings and arctic tern chicks were approximately 20-30 g and 70-90 g respectively. No Necrophorus were used twice in a choice experiment, the number of experiments being limited by the number of beetles available. The experiments were started in 1963 and continued in 1964.

N. humator

The results of preference experiments using N. humator are set out in Table 28.

Table 28 The number of times each animal corpse was chosen by N. humator in preference experiments

	Rabbit (150g) –	Tern (40-50g)	Rabbit (150g) –	Eider (30g)	Tern (40-50g) –	Eider (30g)
1963	3	10	2	8	4	6
1964	1	4	0	5	2	3
TOTAL	4.5	13.5	2.5	12.5	6.5	8.5
$X^2_{(1)}$	4.5		6.7		0.002	
P	< 0.05		< 0.01		< 0.9	

From these results it appears that N. humator prefers arctic tern chicks and eider ducklings to rabbits, but more data are needed to enable definite conclusions to be reached.

N. investigator

The results of preference experiments using N. investigator are set out in Table 29.

These results indicate that N. investigator prefers tern chicks to rabbits, but does not prefer Eider ducklings to tern chicks, or Eider ducklings to rabbits.

Table 29 The number of times each animal corpse was chosen by _N. investigator_ in preference experiments

	Rabbit	Tern	Rabbit	Eider	Tern	Eider
1963	2	12	1	8	3	8
1964	1	4	2	3	1	4
TOTAL	3.5	15.5	3.5	10.5	4.5	11.5
$X^2_{(1)}$	7.4		3.5		3.1	
P	< 0.01		> 0.10		> 0.10	

It is possible that the physical bulk of a rabbit prevents its being chosen when a smaller, more easily moved animal is present. That physical bulk is important is indicated by the results of the experiments using large and small rabbits, where smaller animals were consistently chosen. However, _Necrophorus_ do occur and reproduce beneath large animals without attempting to bury them, and burial is thus no prerequisite for successful reproduction.

Corpse burial

Pukowski (loc. cit.) described in detail how _Necrophorus_ bury a corpse, first by digging beneath it and finally by easing the corpse, neatly folded, into the shallow sloping depression. The process is repeated until the corpse has been covered with soil, and lies at the bottom of a sloping tunnel in the ground between 2-10 cm from the surface. The process is shown in diagrammatic form in Fig. 15 a-d, modified from Pukowski (loc. cit.).

Fabre (1919) noticed that during the burial, beetles emerged and moved slowly over the corpse, as if inspecting the surface. Pukowski referred this behaviour to a test of the mobility and size of the corpse before burial. At the beginning of the present study, it was suggested (C.S. Elton, pers. comm.) that this behaviour might be an adaptation to ensure that dipterous eggs are found and destroyed before the corpse is buried. However, when dipterous eggs were placed on the surface of a corpse during burial, the beetles which 'inspected' the corpse took no notice of them. This experiment was repeated 20 times and the results were always identical. A further series of experiments in which Calliphora sp. larvae were placed on the surface of a corpse,showed that these were eaten when encountered by a beetle. This result was to be expected, because, as Pukowski points out, Necrophorus adults are primarily predators of dipterous larvae found in corpses.

Another puzzling piece of behaviour is shown by Necrophorus when the corpse has been buried. At this point the rolled-up corpse is stripped of its outer covering of ~~fur, feathers, scales or skin. The outer covering~~ is pressed on to the wall of the crypta (burial-chamber), away from the corpse. The corpse thus lies in a chamber

Figure 15 Diagrammatic representation of the way in which a corpse is buried by *Necrophorus*, (after Pukowski, 1933).

A Initial position of corpse

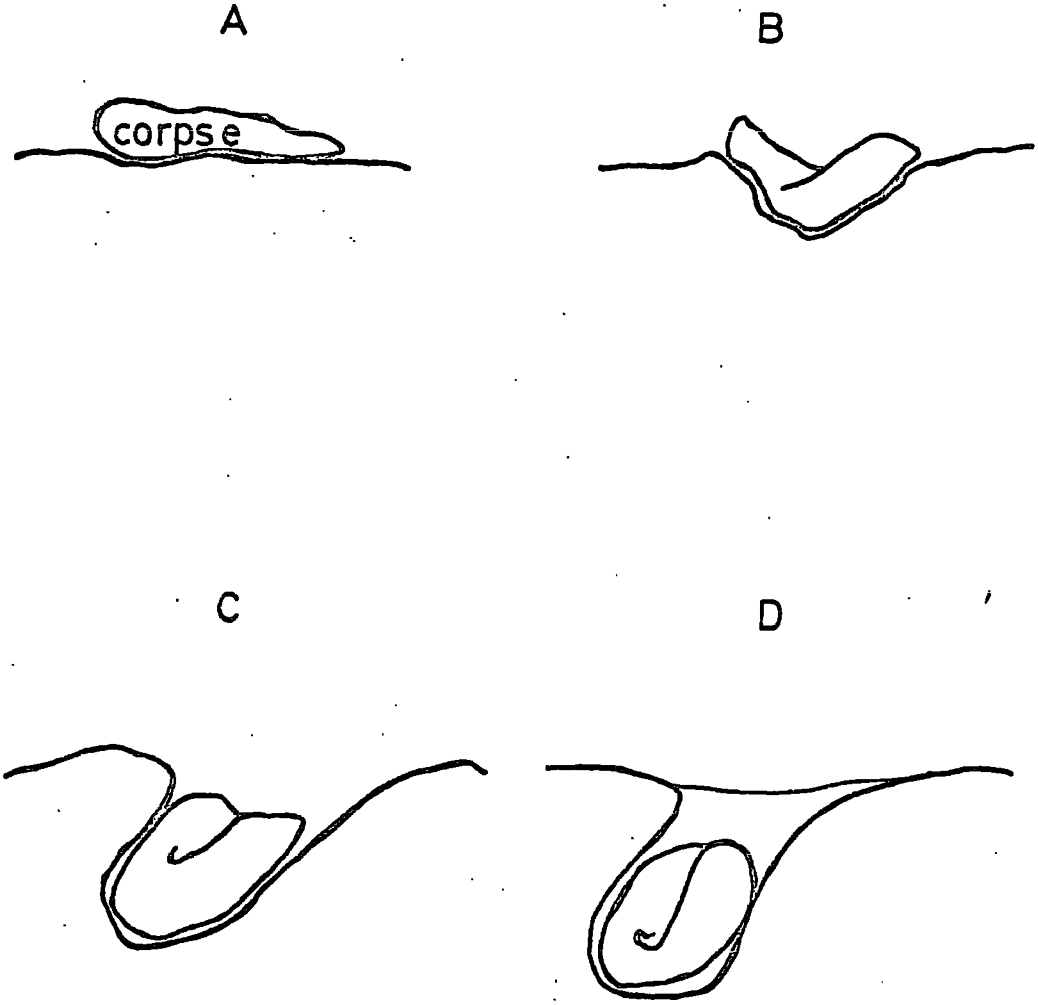
B Position of corpse about 6 hours after the arrival of *Necrophorus*

C Position of corpse between 12-18 hours after the arrival of *Necrophorus*. Note the way in which the corpse is folded.

D Final position of corpse about 24-36 hours after the arrival of *Necrophorus*.

fig. 15

Stages in the burial of a corpse
by *Necrophorus*



lined with its own external covering. This behaviour was noted by Fabre and Pukowski and was also seen in the present study, and it seems possible that under natural conditions this may be an important factor in reducing infestation by dipterous larvae.

Experimental controls (corpses exposed to dipteran egg-laying activities) showed that <u>Calliphora</u> eggs were laid inside the beak and vent, and between the feathers of birds, and in the nostrils, mouth, anus, and at the base of the fur in mammals. It is suggested that post-burial stripping behaviour by <u>Necrophorus</u> removes a large proportion of the dipterous eggs on the corpse to a distance of between 1-2 cm from the corpse. Many of these eggs will have been destroyed by the stripping process, and the small gap between fur and corpse might be sufficient to ensure that the majority of dipterous larvae fail to reach the corpse. The results from the experimental cultures to test this were inconclusive.

Many beetles may gather at a corpse and co-operate in the burial (Pukowski loc. cit., Fabre loc. cit.) but all except a single male and female are eliminated by intraspecific fighting. The possession of a corpse is a prime requisite for reproductive success, and at times of corpse shortage intraspecific competition for food will probably be fierce and many beetles may fail to reproduce. (Fighting was not observed often in this study, for normally only a single pair of beetles were placed with a corpse.) The defeated beetles disperse in search of another suitable corpse, or are eaten by the victors.

In the chamber the corpse is prepared by rolling into a ball, and is moistened with a secretion from the fore-gut of the beetles whilst it is being stripped (Pukowski loc. cit.). This fluid appears to prevent the growth of fungi and other organisms, for although the chamber is very humid, the corpse does not decay. Pukowski postulated that extra-intestinal digestion is the normal feeding method of Necrophorus, and this would seem to be highly likely, particularly as the larvae are fed by regurgitation, and when handled, Necrophorus produce a thick dark brown fluid from the mouth.

Stridulation

Stridulation by Necrophorus was mentioned by Pukowski (loc. cit.), and the stridulation is caused by the movement of paired abdominal files against the elytral extremities. The position of the files are figured in Crowson (1950 p.278 fig.32). The severity of the abdominal pumping movement determines the sound produced. Although stridulation is only produced in one way, a series of signals appears to have been evolved, each of which is elicited in a particular situation.

The 'startle' reaction can be elicited by suddenly disturbing a beetle, or by picking it up. This reaction has recently been well described by Rothschild and Lane (1964) who likened both the posture and the noise to the buzz of a somnolent bumble bee (*Bombus*). *Necrophorus* which gather at a corpse for feeding prior to gonad maturation often stridulate quietly. The beetles also stridulate prior to copulation, and in the crypta the female stridulates in a distinctive way when feeding the larvae. When the larvae beg for food by insinuating themselves between the female's anterior pair of legs, the female stridulates with regular short pauses, producing a droplet of brown fluid between her mandibles which is ingested by the larvae.

Individuals stridulate violently when fighting amongst themselves, and in such situations there are indications that the stridulation facilitates sexual recognition. When a male grasps a female, the instant the female stridulates the male stops fighting.

Studies on the function of stridulation in Coleoptera have been neglected, but it is obvious from the present study that in *Necrophorus* this form of signalling is capable of more variation than that of *Geotrupes* or *Xestobium*. It may be significant that many of the other stridulatory Coleoptera are those which live underground or in wood where they are invisible to each other.

Egg laying

In the cultures the eggs were laid in the sides of a curved horizontal tunnel constructed by the female, the

'Muttergang' of Pukowski (loc. cit.). The tunnel is blind, opening into the crypta, and is as wide as the female beetle. Its length varies from 2 to 8 cm. If the chamber is disturbed by a predator, the female will use the egg tunnel as a refuge. The eggs were laid, singly, in the soil on either side of the tunnel. The egg sometimes showed at the surface of the tunnel wall, but was more often completely buried. On the four occasions when the duration of egg laying was known, the female beetle laid all the eggs within 24 hours.

Description of eggs

The eggs of *Necrophorus* sp. are pearly white ovoids. Because of the difficulty of extracting eggs from the 'Muttergang' and the relatively small number of cultures available for experimental work, the eggs of *Necrophorus humator* and *N. investigator* were not measured accurately in this study. Pukowski (loc. cit.) gives measurements from 11 eggs of *N. vespillo*, the mean length and breadth being 2.96 mm x 1.84 mm. The mature eggs taken from preserved specimens of *Necrophorus* in the present study are in accord with these measurements.

Fecundity

The number of eggs laid by *Necrophorus* varied considerably ~~from individual to individual. Pukowski found that 20 egg~~ batches of *N. vespillo* gave an average of 14.2 ± 6.8 eggs per batch (Table 30c). The size of each batch varied from 4 to 24

Table 30 a The mean egg batch size in cultures of *N. investigator*

Batch size	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
No. of batches	1	1	2	1	2	1	1	1	2	4	2	3	1	1	2	1	1	-	-	1	1	-

n = 29. Total number of eggs = 349

Mean batch size = 11.1 ± 6.8 eggs

Table 30b The mean egg batch size in cultures of *N. humator*

Batch size	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
No. of batches	-	1	-	2	1	1	2	-	2	3	4	1	1	2	1	1	2	1	-	-	-	-

n = 25. Total number of eggs = 313

Mean batch size = 12.5 ± 4.2 eggs

Table 30c The mean egg batch size of *N. vespillo* (from Pukowski)

Batch size	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
No. of batches	2	-	1	-	3	-	1	-	3	-	1	-	2	-	1	-	-	1	2	-	3

n = 20. Total number of eggs = 285

Mean batch size = 14.25 ± 6.8 eggs

eggs. The number of eggs per batch was calculated in the present study from cultures where the eggs could be seen against the glass of the culture chamber. This figure was checked against the number of larvae which emerged, and must be regarded as a minimum figure. It was found that N. humator laid a mean egg batch of 12.5 ± 4.2 eggs, and N. investigator a mean egg batch of 11.1 ± 6.8 eggs.

The variability of the size of the egg batch was a marked feature, both species laying between 3 and 24 eggs (Table 30a, b). There was no indication of two peaks of batch size, as might have been expected if a second laying of a smaller number of eggs had occurred. This supports data obtained from the cultures, where breeding for a second time was not observed. Although data on the point are lacking, it seems possible that the amount of preliminary feeding and the consequent size of the fat body determines the number of eggs laid. Probably some beetles fail to gain enough food before reproducing to mature more than a few eggs.

Egg mortality

N. humator

Table 31b shows the number of eggs which failed to hatch, in those cultures where a minimum egg batch size was known. It can be seen that in all cases egg mortality was low. The overall mortality in this species was 14.0%. The highest incidence of mortality occurred in one batch of fifteen eggs, where three eggs (20.0%) failed to hatch. There were two

Table 31a The mortality of eggs of _N. investigator_, according to batch size

Egg batch size	3-5	6-8	9-11	12-14	15-17	18-20	21-23
No eggs laid	17	28	41	116	65	37	45
Total eggs hatched	15	24	39	108	55	32	41
Total eggs dying	2	4	2	8	10	5	4
% eggs dying	12.8	15.3	2.5	7.9	15.4	13.6	8.9

Table 31b The mortality of eggs of _N. humator_, according to batch size

Egg batch size	3-5	6-8	9-11	12-14	15-17	18-20
No eggs laid	4	27	40	102	64	76
Total eggs hatched	4	25	35	86	54	65
Total eggs dying	0	2	5	16	10	11
% eggs dying	0	7.4	12.5	15.7	15.7	14.5

cultures where no egg mortality was recorded. The percentage mortality of smaller batches (6-8 eggs, 7.4%) was half that of the larger batches (15-17 eggs, 15.7%).

N. investigator

The number of eggs which failed to hatch in cultures with egg batches of known size, is shown in Table 31a. As in N. humator, the maximum mortality in any batch was just below 20%, when three eggs from a batch of sixteen failed to hatch. In three cultures no egg mortality was observed. The mean percentage egg mortality was 10.0%. The difference between the two mean egg mortality figures (10% and 14%) was not significant.

The low figure for egg mortality is probably a direct result of the care devoted by the female to the defence of the chamber. In the natural situation it seems possible that a higher egg mortality would occur, as factors such as disturbance by large mammalian predators and predatory soil organisms were absent in the cultures.

Incubation period

Pukowski gives 4-5 days from laying to hatching in N. vespillo, and the present work supports this statement. A mean development period (from laying of first egg until hatching of that egg) of 4.9 ± 0.3 days was recorded for 29 cultures of N. investigator at 16°C and 4.9 ± 0.9 days for 25 cultures of N. humator at 16°C, and the data are shown in Table 32.

The larvae

The larvae of Necrophorus pass through three instars. The development is particularly rapid, and the larvae are fully grown within 7 days from hatching. The duration of each instar is approximately:

Instar I	0-12 hours after hatching
Instar II	12-24 hours after hatching
Instar III	24 hours - 7 days after hatching

Parental care

Pukowski found that when the larvae hatch from the eggs, they migrate along the tunnel towards the corpse, where they are fed by the female. This was observed in the present study. The larvae are fed by the female for the first 72 hours of life, and in this time pass through two instars and enter the third and last instar. The female feeds the larvae by regurgitating a drop of fluid, which is held between, and hangs from, the mandibles. The larvae stretch upwards between the female's forelegs and suck up the drop, which shrinks visibly.

Larval mortality in experimental cultures

The importance of the female to the survival of the larvae was tested in the following manner:

In five cultures of N. investigator, the female beetle

Table 32 The duration of egg development in N. investigator at 16°C

Egg development in days	4	5	6
Number of occasions	7	18	4

n = 29; mean = 4.9 ± 0.3 days

The duration of egg development in N. humator at 16°C

Egg development in days	4	5	6
Number of occasions	5	16	4

n = 25; mean = 4.9 ± 0.9 days

was removed as soon as all the eggs were laid, 48 hours after the corpse was buried. (No calculations of egg mortality in the absence of parental care are available, as the number of eggs in each culture was unknown.) In each culture the fate of the newly hatched larvae was followed. A similar experiment was conducted with five cultures of N. humator.

Results

Instar I

N. investigator

From the five cultures a total of 47 larvae were observed at the carcase. The newly hatched larvae were observed to feed on the corpse. The presence of food in the gut was confirmed by observing that when the larvae arrived at the corpse their guts showed through the cuticle as a milky white thread. After feeding the colour of the gut changed to a dark brown. However, all the larvae died within 24 hours, without passing into the second instar.

N. humator

Identical results were obtained from the five cultures (45 larvae) of N. humator, that is, all the larvae died, after feeding, within 24 hours of reaching the corpse and none passed into the second instar.

Instar II

A similar series of experiments, using five cultures of each species,was undertaken to test the effect of parental feeding on the second instar larvae. When the parent was removed directly after the larval moult from first to second instar, and although the larvae were seen to feed on the carcase, not one succeeded in attaining the third larval instar and all died within 24 hours.

It appears that Pukowski's conclusion that parental feeding is essential to the survival of Necrophorus larvae, at least until the third instar, is correct. The fact that the larvae could feed and yet not moult, would seem to suggest that the female beetle supplies the larvae with the digestive enzymes essential for food assimilation and growth.

Instar III

The female beetle was removed in five cultures of each species, after the moult to the third larval instar had taken place. In all cultures the third instar larvae fed, grew and pupated as in similar cultures where the female was present. Pupal survival was similar to that obtained in the undisturbed cultures.

Larval mortality in control cultures

N. investigator

Twenty-six undisturbed cultures (undisturbed meaning with the female present, but opened to facilitate removal of the larvae) were used as controls, and the number of larvae at each instar counted. In some cultures the larvae were removed daily for weighing. Table 33 summarises the data gained from these control cultures, and it is immediately apparent that larval mortality was slight. There is some indication of differential mortality in relation to brood size in this species, broods of less than 14 having 89% survival, and broods above 14 having 77% survival.

N. humator

Thirty-one undisturbed cultures were used as controls, and the number of larvae at each instar counted. The data are summarised in Table 34. It is obvious that larval mortality was low, and there was no indication of differential mortality in relation to brood size.

The production of adult beetles by a single pair

The number of eggs laid by a single female *Necrophorus* which survive to produce adult beetles as the next generation can be calculated by utilising the mortality of eggs, larvae and pupae as found in the cultures.

In *N. investigator*, each female lays 11 eggs (Table 30a) of which 10% fail to hatch (Table 31a). Of the 10 larvae which hatch, 17% or 1.7 die during the larval or pupal stage (Table 33), leaving 8.3 adult beetles produced from each female of the previous generation.

In *N. humator*, a similar calculation shows that from 12.5 eggs (Table 30b), 14% or 1.75 eggs fail to hatch (Table 31b).

Of the remaining 10.7 larvae, 13.5% or 1.4 die during the larval or pupal stages (Table 34), leaving 9.3 adults.

Bearing in mind that these data are provided by an artificial culture situation, with optimum conditions, a single pair of Necrophorus investigator or N. humator produce on average 8 or 9 offspring. Given a constant number of corpses available for burial, it is obvious that competition for corpses will occur, the population increasing four-fold every year. The large over-production of adults provides a reservoir of animals which are capable of taking immediate advantage of unusually large amounts of carrion which might become available, for instance during myxomatosis or a vole population crash.

The growth of Necrophorus larvae

As mentioned previously, the larvae from some cultures of N. investigator were removed daily for weighing. Only third instar larvae were used in the weighings, and 10 cultures (126 larvae) were weighed regularly.

The curve of the mean daily weight increase (Fig. 16) shows that the weight of the third instar larvae rises in a linear fashion from the second until the eighth day. Larvae then decreased in weight until the ninth or tenth day, when pupation occurred.

The drop in weight after the eighth day coincided with a period of increased larval activity. At their maximum weight

Table 33 Larval mortality in cultures of N. investigator

(n = 26)

Original brood size	3	6	7	8	9	10	11	12	13	15	16	17	18	22	23	TOTALS	% survival
No. 1st instar larvae	6	6	7	8	36	20	33	24	26	30	16	34	18	44	23	331	
No. 1st surviving to 2nd instar	6	6	7	8	36	20	33	24	26	26	16	34	18	44	23	327	98.7
No. 2nd surviving to 3rd instar	6	6	6	8	34	19	30	23	26	22	13	33	18	40	21	308	91.1
No. 3rd instar pupating successfully	6	6	6	8	34	19	29	23	26	19	12	31	18	38	20	295	95.8
No. pupae emerging as imagines	6	6	5	8	32	18	29	20	24	18	10	29	17	35	18	275	93.2

Survival from 1st instar - imago = 83.0%

% mortality = 17%

Table 34 Larval mortality in cultures of *N. humator*

(n = 31)

Brood size	4	5	6	8	9	10	11	12	13	14	16	17	18	19	21	22	24	TOTALS	% Survival
No. 1st instar larvae	8	5	12	8	18	30	22	60	26	14	16	34	18	19	42	22	48	402	
No. 1st surviving to 2nd instar	7	5	12	8	16	29	22	55	25	14	14	31	18	18	41	22	41	378	94.0
No. 2nd surviving to 3rd instar	7	5	11	8	16	29	22	55	25	12	13	31	18	17	41	22	41	373	96.0
No. 3rd instar pupating	7	5	11	8	16	29	21	55	25	12	13	31	18	17	40	22	40	370	99.3
No. pupae emerging as imago	6	4	10	7	15	27	21	53	22	11	12	30	18	16	38	20	38	348	94.0

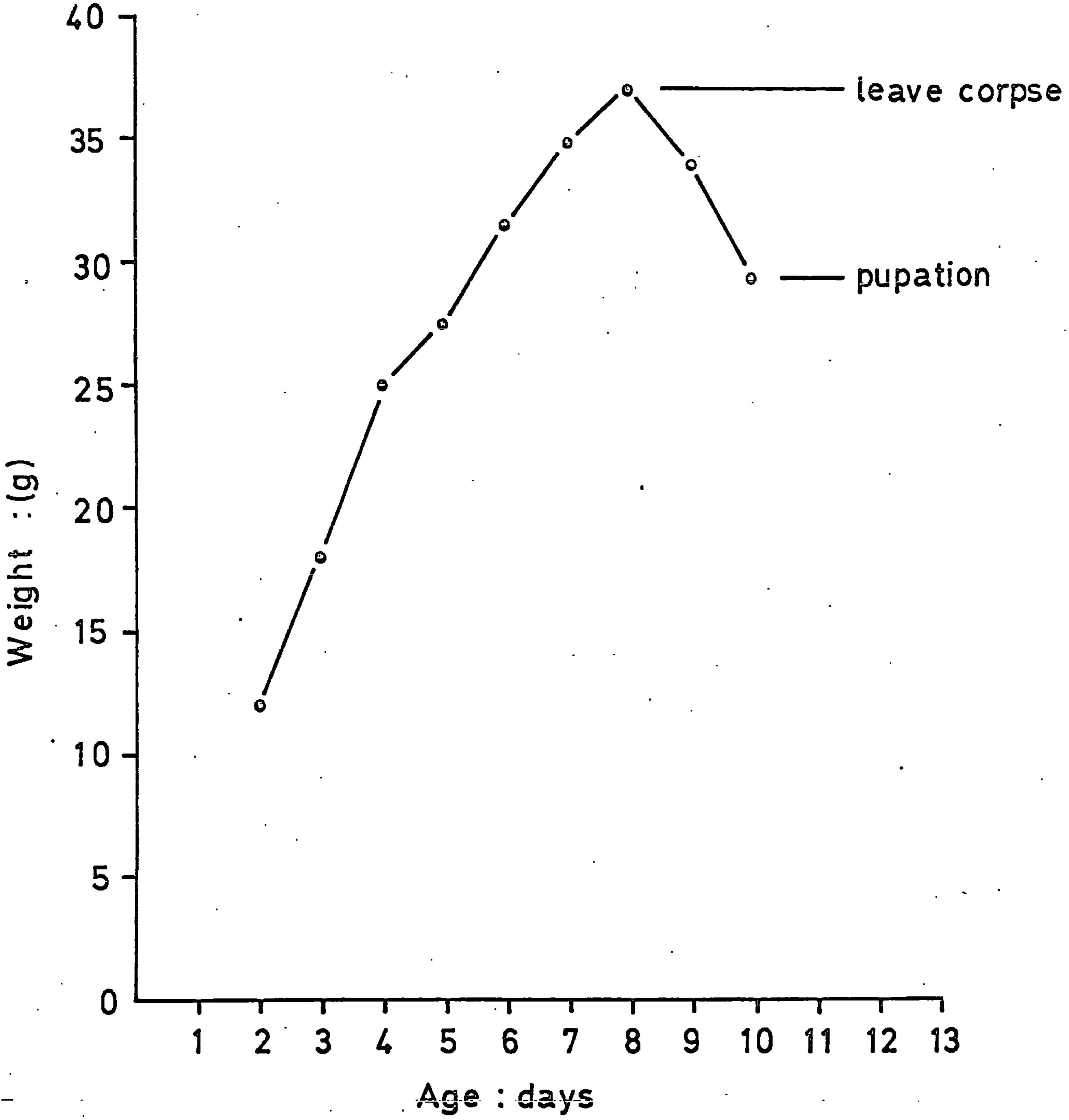
Survival from 1st instar ÷ imago = 86.5%

% mortality = 13.5%

Figure 16 The mean daily weight increase of _N. investigator_ larvae. The vertical scale is in milligrams. The time when the larvae leave the carcase and when they pupate is also shown.

fig. 16

Mean daily weight increase of *N. investigator* larvae



the larvae became restless and left the corpse, often wandering round and round the sides of the culture chamber on the surface. Larvae kept in a large terrarium (1 m x 1 m) wandered up to 5 cm away from the corpse at this time, and rapidly lost weight. This behaviour was thought to be similar to the dispersal shown by Lucilia larvae from a corpse (Cragg 1955). Even where cultures were reared in 1000 ml crystallising dishes, the beetle larvae always migrated as far away from the corpse as possible and would be found very close to the sides of the dish. Larvae were never found to pupate within the crypta, and this migration may be an adaptation, as suggested by Cragg (loc. cit.), to escape predation.

Pupation

The larvae pupate underground, and create a hardwalled cell by rotating upon their long axis. The resulting chamber is smoothwalled and slightly larger than the larva. Within this chamber the moult from last larval instar to pupa takes place.

Pukowski (loc. cit.) mentioned that the pupal period in N. humator and N. investigator, among other species, lasted for 14-15 days. In the present study, however, the mean length of the pupal period from pupation until emergence on the soil in N. humator was 29.4 ± 2.3 days at 16°C and of

N. investigator 25.6 ± 2.1 days at 16°C (Table 35 a and b). Although N. investigator overwinters as an immature stage, it does so as a prepupa, that is a last-instar larva with the gut cleared, and pupation occurs shortly before the emergence of the adult the following year. In this part of the study there was no evidence to suggest that males and females of Necrophorus emerged at different times.

The emergence of the adult from the pupal cell

The emergence of adult Necrophorus from a pupal cell was noted on only nine occasions, all of them with N. humator. The procedure was similar in all cases, beginning three days before emergence with a wave of pigmentation. Pigmentation started at the anterior and passed posteriorly, changing the pupae from creamy white to light brown. Two days before emergence the beetles had broken out of the pupal cell at 4.5 cm, and were lying 3 cm below the surface of the soil. Pigmentation proceeded rapidly and on the evening of emergence, the beetles were a uniform dark chocolate-brown, with orange eyes. At this point the beetles lay just below the soil surface with the eyes and antennae visible from above. Final emergence occurred during late evening, and the beetles were active on the surface during the night.

Apart from being very dark brown in colour, newly emerged N. humator had a soft cuticle. The beetles were

Table 35a The mean pupal period in *N. humator*

(from pupation to emergence on the surface) at 16°C

Pupal period in days	22	23	24	25	26	27	28	29	30	31
Number of occasions	1	1	3	2	6	11	7	4	1	1

n = 37

Mean pupal period = 29.4 ± 2.3 days

Table 35b The mean pupal period in *N. investigator*

(from pupation to emergence on the surface) at 16°C

Pupal period in days	21	22	23	24	25	26	27	28	29	30
Number of occasions	1	2	2	1	6	8	3	1	1	2

n = 27

Mean pupal period = 25.6 ± 2.1 days

fully pigmented within 24 hours of appearing on the surface, and the cuticle had hardened by that time. When handled, newly emerged beetles exuded a drop of clear greenish-yellow liquid from the anus, whilst older individuals, which had fed, produced a thick brown fluid from the anus.

To discover how long newly emerged beetles survived without food, 15 N. humator were starved from emergence until they died. The results (Table 36) show that N. humator survived less than a week under these conditions. It is obviously important for Necrophorus to find food as rapidly as possible after emergence, and this is clearly reflected in the peak of activity at that time (Fig. 5, 6).

Table 36 The survival of newly emerged N. humator at 16°C when starved

Survival in days	1	2	3	4	5	6	7	8
Number dying	1	-	-	2	8	3	-	1

n = 15, mean survival time without food = 5.0 ± 0.4 days

Sex ratio of emerging beetles

The sex ratio of 275 N. investigator when the beetles emerged from pupation was 140 males: 135 females. This does not differ significantly from a 1 : 1 ratio of males to females. A similar situation was found in 348 adult N. humator, there being 160 males : 188 females.

VI THE BIOLOGY OF *NECROPHORUS*: THE RELATIONSHIP BETWEEN *NECROPHORUS* AND THEIR ASSOCIATED ACARINA

3 THE RELATIONSHIP BETWEEN NECROPHORUS AND THEIR ASSOCIATED ACARINA

At the beginning of the study it was noticed that Necrophorus beetles invariably carried several mites. Interest in the mites was stimulated by the discovery that, in a Necrophorus culture, the mites preyed upon the artificially introduced eggs of Calliphora sp.

The mites most commonly found on Necrophorus were identified as Parasitus (Poecilochirus) necrophori Vitzt, 1930. The biology of P. necrophori as a phoretic associate of N. humator has previously been described by Neumann (1943). Neumann described P. necrophori as a symphorist and paraphage, using the beetle for transport and feeding on fly-maggots and the carrion encountered by the host. Neumann's description was essentially that of a loose association between the beetle and the mite. The discovery by Costa (1964) of a close relationship between the dung beetle Copris hispanus L and the mite Parasitus copridus Costa, prompted the writer to undertake a closer study of the relationship between Necrophorus and Parasitus (Poecilochirus) necrophori.

Beetles caught in the field were preserved in Pampel's fluid in individual containers. When the beetles were dissected the mites were examined, identified and counted.

Results from the preserved material

The data presented in Table 37 shows the average number of P. necrophori deutonymphs present on N. humator, counted at the time of dissection in the laboratory. The beetles were all caught and preserved on the Inner Farne. Similar data are presented for *N. investigator* in Table 38.

These data indicate that infestations ranging from 10 to 30 mites per beetle are common in both species. This may be compared with a maximum infestation of *Parasitus copridus* on *Copris hispanus* of 6.6 deutonymphs per beetle. However, Hyatt (1959) describing mites from *Geotrupes stercorarius* (L) found that the infestation on 4 beetles was 157.7 mites per beetle.

The data also suggest that the infestations (the numbers of mites per beetle) rise as the reproductive cycle progresses. Thus for *N. humator* (Table 39a), the numbers rose from 12 to 35 mites per beetle, during the season, and in *N. investigator* (Table 39b) from 11 to 38 mites per beetle. In *N. humator*, the newly emerged adults caught in September showed infestations similar to those found at the beginning of the season (April-May), that is, about 10 mites per beetle, These data suggested that the mite was reproducing at the same time as *Necrophorus* and were utilising the emerging, spent, *Necrophorus* as a convenient dispersal mechanism.

Results from laboratory experiments and cultures

Data from cultures in the laboratory showed similar results to those observed in the field. However, the infestations of deutonymphs on spent female *Necrophorus* from

Table 37 The number of mites per beetle shown at weekly intervals during the flight period of *N. humator*

Week ending	Number of beetles examined	Number of mites found	Number of mites/beetle
21 April	8	92	11.5
5 May	6	75	12.5
12 May	3	46	15.3
19 May	7	83	11.8
26 May	12	170	14.1
2 June	8	99	12.3
9 June	4	62	15.5
16 June	7	103	14.7
23 June	2	40	20.0
30 June	15	317	21.1
7 July	10	210	21.0
14 July	18	370	20.5
21 July	6	210	35.0
28 July	3	82	27.6
August	-	-	-
1 September	6	62	10.3
8 September	19	211	11.1
15 September	7	68	9.7
22 September	8	66	8.2
29 September	9	103	11.4
6 October	6	71	11.8
TOTAL	164	2541	15.4

Table 38 The number of mites per beetle shown at weekly intervals during the flight period of _N_. _investigator_

Week ending	Number of beetles examined	Number of mites found	Number of mites/beetle
7 July	10	93	9.3
14 July	13	150	11.5
21 July	8	86	10.7
28 July	83	870	10.5
4 August	46	502	10.9
11 August	31	587	18.9
18 August	27	460	17.0
25 August	18	320	17.9
1 September	31	773	24.9
8 September	38	860	22.6
15 September	78	1708	21.8
22 September	42	1520	36.1
29 September	27	1030	38.1
TOTAL	452	8959	19.8

Table 39a The number of mites per beetle according to the reproductive state of beetles, (*N. humator*) caught in the field

Necrophorus humator	Reproductive state of beetle				
	Immature		Mature		Spent
	♂	♀	♂	♀	♀
No. of beetles	39	40	25	31	29
No. of mites	451	452	310	372	955
No. of mites/beetle	11.5	11.3	12.4	11.0	32.9

Table 39b The number of mites per beetle according to the reproductive state of beetles, (*N. investigator*) caught in the field

Necrophorus investigator	Reproductive state of beetle				
	Immature		Mature		Spent
	♂	♀	♂	♀	♀
No. of beetles	27	25	69	93	172
No. of mites	388	412	1130	1152	5477
No. of mites/beetle	14.3	15.7	16.3	16.6	31.8

successful cultures were relatively enormous. For example, approximately 800 deutonymphs of *P. necrophori* were counted on a single spent female of *N. humator*. The average numbers of deutonymphs per infestation of spent females from successful cultures was 650.

It was thought that the major factor contributing to these very high mite infestations was the enclosed conditions of the cultures, which prevented the escape of both deutonymphs and beetle. It seemed likely that under natural conditions when the beetle emerged and took flight, a large proportion of the deutonymphs would be dislodged and dispersed, and an experiment to test this hypothesis was undertaken.

In a greenhouse (10 m x 5 m), a spent female *Necrophorus* with a known number of mites (either *N. humator* or *N. investigator*) was allowed to fly freely. After 5 minutes the beetle was collected, killed and the mites counted. This was repeated, with different spent beetles, on five occasions. The data are shown in Table 40, and it is obvious that after even a short flight, over 90% of the deutonymphs had been lost. The differences between the high numbers of deutonymphs on each beetle found in the laboratory and the relatively low numbers found in the field are thus explained.

A choice experiment was devised in order to determine whether the deutonymphs of *P. necrophori* preferred *Necrophorus* to other beetles. A large aluminium tray (1 m x 1 m) with

Table 40 The reduction in numbers of deutonymphs of *P. necrophori* on spent *Necrophorus*, after five minutes flight

Female *Necrophorus*	Original number of deutonymphs	Final number of deutonymphs	Estimated number of deutonymphs lost in flight	Percentage reduction
N. humator	c. 800	49	751	94%
N. humator	c. 360	28	332	92%
N. investigator	c. 520	33	487	94%
N. investigator	c. 710	47	663	93%
N. investigator	c. 450	38	412	92%
TOTALS	2840	195	2645	

vertical sides 10 cm high was filled with 5 cm of level topsoil. Six live specimens of Carabus sp. caught in pitfall traps, were released in the tray. In addition, six live N. investigator with no mites (three male, three female, all immature), were released in the tray, which was covered and left undisturbed. The mites (all deutonymphs of P. necrophori) were kept in a glass container and after 24 hours a known number were shaken at random on to the soil surface. The beetles were removed and inspected six hours after the addition of the mites and the results are shown in Table 41a. No mites were found on theCarabus sp. beetles, but 159 were found on the Necrophorus. The experiment was repeated three times, using different beetles, with identical results. It was concluded that deutonymphs of P. necrophori choose Necrophorus in prefefence to Carabus sp.

A similar experiment was conducted to show whether P. necrophori prefer Necrophorus to other beetles found in corpses. Specimens of N. vespilloides Herbst and Silpha carinata were used in this experiment, and the data are presented in Table 41b. This experiment was regarded as important, for although the result of the previous preference experiment, Necrophorus v. Carabidae, was predictable, the outcome of Necrophorus v. Silpha was not. If the relationship between P. necrophori and Necrophorus was as loose as Neumann (loc. cit.) suggested, then one might expect that any carrion beetle would be a suitable host, and that the mites would sort

Table 41a The results of preference experiment, involving deutonymphs of *P. necrophori*, (Acari), *N. investigator* and Carabidae (Col.)

Number of mites released	Number of mites on *Necrophorus*	Number of mites on Carabidae
c. 150	159	0
c. 100	98	0
c. 50	52	0
c. 300	309	0

Table 41b The results of preference experiments involving deutonymphs of *P. necrophori* (Acari), *N. investigator* (Col.) and *Silpha carinata* (Col.)

Number of mites released	Number of mites on *Necrophorus*	Number of mites on *Silpha*
c. 40	36	1
c. 50	54	0
c. 90	85	3
c.180	175	4

themselves out equally amongst all the beetles. However, that was not the case, and the preference of the mites for Necrophorus throws further doubt upon the looseness of the association.

Further information upon the life-cycle of P. necrophori in relation to Necrophorus investigator was gained from a series of experimental cultures, set up in 1963 and 1964. In order to isolate the factors affecting the relationship between the mite and the beetle, various combinations of mites, beetles and Calliphora eggs were placed with a "standard" corpse. The Calliphora eggs were obtained by exposing meat to gravid Calliphora and carefully transferring suitable numbers of eggs from the meat to the corpse. The eggs were placed on the eviscerated corpse in two positions, about 50 eggs into the mouth and ears, and a similar number into the body cavity. Live mites were obtained by brushing them from Necrophorus into tubes. The combinations of animals used in the cultures were as follows:

Type A. Vole carcase, c. 30 deutonymphs of P. necrophori, c. 100 Calliphora eggs.

Type B. Vole carcase, c. 30 deutonymphs of P. necrophori, c. 100 Calliphora eggs, one male and one female N. investigator.

Type C. Vole carcase, c. 100 Calliphora eggs, ~~one male and~~ one female N. investigator, (no P. necrophori).

Type D. Vole carcase, c. 100 *Calliphora* eggs.

Type E. Vole carcase, one male and one female *N. investigator* (no *P. necrophori*).

Type F. Vole carcase, c. 30 deutonymphs of *P. necrophori*, one male and one female *N. investigator*.

Type F cultures, the "Standard" culture arrangement, were considered as controls for the other arrangements. During 1963 each culture was replicated four times, and the same number of replicates with identical conditions was repeated in 1964. The physical conditions of the cultures were similar to those described previously.

Results

The results from both years are similar and have been combined and presented in Table 42.

Type A cultures (8 replicates) Vole carcase, c. 30 deutonymphs of *P. necrophori*, c. 100 *Calliphora* eggs

Immediately the deutonymphs of *P. necrophori* were introduced into the chamber, they ran rapidly over the surface of the corpse. Their movement was apparently at random, but within 30 minutes of their introduction, some of the mites had found and were attacking the two batches of *Calliphora* eggs with their chelicerae. Four hours after the introduction of the mites, all the *Calliphora* eggs had been discovered and eaten. Although the experiment was allowed to continue for six weeks, the mites failed to reproduce during this time.

Type B cultures (8 replicates) Vole carcase, c. 30 deutonymphs of *P. necrophori*, c. 100 *Calliphora* eggs, pair of *Necrophorus*.

The results from these cultures were similar to those in Type A. The mites rapidly found the *Calliphora* eggs and attacked and ate them, and in all the cultures the mites reproduced successfully. In six cases, the *Necrophorus* buried the carcase and reared a brood of larvae. In the other two cases, the carcase was buried, but no eggs were laid. The females were dissected and found to be spent.

Type C cultures (8 replicates) Vole carcase, c. 100 *Calliphora* eggs, pair of *N. investigator*, (no P. necrophori)

In all cultures of this type, the *Calliphora* eggs hatched successfully and the larvae invaded the carcase, after burial by *Necrophorus*. In all cases, *Necrophorus* reproductive efforts failed, only three female beetles laid eggs, and these deserted their eggs before they hatched. In the remaining cultures no eggs were laid. In four of the cultures, the beetles were seen to attack and eat *Calliphora* larvae, and this observation was confirmed when the numbers of emerging adult flies were compared with pure cultures of *Calliphora* (Table 43). It is also possible that post-burial stripping behaviour reduced the success of the *Calliphora* larvae.

Type D cultures (8 replicates) Vole carcase, c. 100 *Calliphora* eggs (no *P. necrophori*)

A high survival of fly larvae and adults was noted in these cultures. The results are shown in Table 43, compared with similar results from Type C cultures.

Type E cultures (8 replicates) Vole carcase, pair of *Necrophorus*
(No mites)

In these cultures the beetles were brushed free from mites before being placed in the culture chamber. In the cultures of this type all *Necrophorus* raised a brood successfully.

Type F cultures (8 replicates) (Control)
Vole carcase, c. 30 deutonymphs of *P. necrophori*, pair of *Necrophorus*.

In the majority of these cultures, *Necrophorus* were successful in rearing a brood. In one culture the corpse was buried but no eggs were laid and the female was afterwards found to be spent. In all cultures of this type, *P. necrophori* reproduced successfully.

A striking feature of these experimental cultures was that whenever deutonymphs of *P. necrophori* and adults of *Necrophorus* were together on a corpse, both mites and beetles were able to reproduce (Table 42). Further, whilst *P. necrophori* never reproduced without the beetle, *Necrophorus* were able to reproduce without the mite, but only successfully in the absence of dipterous larvae. Where dipterous eggs were present on a corpse which was buried, *Necrophorus* appeared to depend upon the mite for reproductive success.

A similar series of cultures using small (3 mm) *Calliphora* larvae instead of *Calliphora* eggs was carried out in 1966, and the results are given in Table 44. These cultures tell a different story from the previous set, for in all the cultures inoculated with fly larvae (A, B, C, D,) the beetles failed to rear a brood. Only where *Calliphora* larvae were absent did *Necrophorus* reproduce successfully, although in cultures with *Necrophorus* and *Calliphora* larvae, the beetles were observed to eat fly larvae when they found them. In some cases, the mites also attacked and killed fly larvae, but only those under 5 mm long. In all these cases, some fly larvae escaped attention, growing to a large size, and then invaded the corpse whereupon the beetles would abandon it.

These cultures reinforce the idea that the mites are important to *Necrophorus*, and also that the mites are in some way dependent on *Necrophorus* for reproductive success.

Another observation which points to the close relationship between *Necrophorus* and *Poecilochirus* is the infestation of beetle larvae with mite deutonymphs. This phenomenom was observed in *N. humator* and *N. investigator*, and occurred in the same fashion in both species. Third instar larvae which had finished growth and had empty guts, were observed moving around the culture chamber bearing mite deutonymphs with them. These mites were clinging on to the dorsal shields of the larvae, and continued to hang on when the larvae finally went underground to construct pupal cells. Throughout the pupal period these mites could be seen to be active within the cell, and newly emerged beetles carried these deutonymphs when they

Table 42 The results of experimental cultures set up to determine the relationship between *Necrophorus*, *Parasitus* and *Calliphora*, using *Calliphora* eggs. Eight replicates were used throughout

	Culture Type	Number of successful *Necrophorus* cultures	Number of successful *Necrophorus* cultures	Number of successful *Necrophorus* cultures
A	Corpse Mites *Calliphora* eggs	-	0	0
B	Corpse *Necrophorus* Mites *Calliphora* eggs	6	8	0
C	Corpse *Necrophorus* *Calliphora* eggs	0	-	8
D	Corpse *Calliphora* eggs	-	-	8
E	Corpse *Necrophorus*	8	-	-
F	Corpse *Necrophorus* Mites	7	8	-

Table 43 The number of flies emerging from two different types of experimental cultures

	Culture (8 replicates)	Original number of <u>Calliphora</u> eggs on 8 carcases	Number of flies emerging from 8 carcases	% success
C	Carcase <u>Calliphora</u> eggs <u>Necrophorus</u>	c.800	c.580	72%
D	Carcase <u>Calliphora eggs</u>	c.800	c.711	89%

Table 44 The results of experimental cultures set up to determine the relationship between *Necrophorus*, *Parasitus* and *Calliphora*, using *Calliphora* larvae. Eight replicates were used throughout

	Culture Type	Number of successful *Necrophorus* cultures	Number of successful mite cultures	Number of successful *Calliphora* cultures
A	Corpse Mites *Calliphora* larvae	-	0	8
B	Corpse *Necrophorus* Mites *Calliphora* larvae	0	0	8
C	Corpse *Necrophorus* *Calliphora* larvae	0	-	8
D	Corpse *Calliphora* larvae	-	-	8
E	Corpse *Necrophorus*	8	-	-
F	Corpse *Necrophorus* Mites	8	8	-

arrived at the surface.

The length of time that deutonymphs stayed within the pupal cell was approximately two months in N. humator, and a maximum of ten months in N. investigator. It should be noted that this imprisonment is not voluntary, for once inside the pupal cell the mites cannot break out through the hardened walls. However, this behaviour ensures the survival of another generation of mites, in close contact with the beetle, and has obvious advantages for the beetle in terms of ensuring the reproductive success of the next generation. The relationship between the beetle and the mite is not as loose as suggested by Neumann (1943),and it appears that a certain amount of synchronisation has occurred between the life histories of the two species.

VII THE MORTALITY OF ARCTIC TERNS ON THE BREEDING GROUNDS:

EGG LAYING, INCUBATION AND HATCHING.

EGG LAYING, INCUBATION AND HATCHING

Methods

Observations of the terns in the Cove averaged 12 hours daily in 1964, but were less intensive in 1963. In 1964, the observer watched from 13 May until the majority of birds left in mid-August. Certain observations were made in 1965. The birds were observed from a hide at a minimum range of 20 metres and a maximum of 60 m. Optical equipment included 10 x 50 binoculars and a prismatic telescope giving a magnification between 15 and 60 times.

Adult birds were caught and colour banded, and approximately half of the pairs on the Cove were colour-ringed by the end of 1964. Nests were marked with an aluminium peg, numbered so as to be visible from the hide. The eggs were marked with lead pencil, according to the order in which they were laid, The contents of each nest were noted monning and evening throughout the incubation period.

On the Farne Islands, arctic terns normally return during the last week in April. At first they avoid the breeding areas and roost in large numbers on nearby rocky islets. Occupation of the colony is gradual, and the first eggs are normally found during the last week in May.

Start of laying

The mean date when the first eggs were found, for 13 years (1951-1964) is 23 May (Farne Island Ornithological Reports 1951-1960, pers. obs. 1961-1964) (Table 45). This date is 25 days earlier than the mean date for 6 years in the Murman Sea (17 June) area recorded by Belopolskii (1961). The reason for the difference in these laying dates is probably that conditions for laying were unsuitable in the Arctic areas until June and Belopolskii mentions that on Bear Island in 1948 the protracted nature of egg-laying may have been caused by nesting conditions. Belopolskii also mentions that in 1950, the exception to the early laying observed in many birds was the arctic tern, which laid late and deserted the breeding colonies during the incubation period.

Territorial activities

During the initial occupation of the Inner Farne colony in 1964, from 10 May to 17 May, the breeding areas were occupied throughout the day and night. During this time pairing took place, and the territories occupied by colour-ringed birds were noted.

This phase of intense activity finished abruptly on 17 May when the island was deserted during the early morning, the birds roosting at night on adjacent islets. Gradual re-occupation of the colony occurred during the next four

Table 45 The date of laying the first egg in arctic tern on Inner Farne, for 13 years

Year	Date first egg seen
1952	28 May
1953	20 May
1954	23 May
1955	24 May
1956	22 May
1957	22 May
1958	30 May
1959	19 May
1960	23 May
1961	17 May
1962	29 May
1963	24 May
1964	22 May

days 18-21 May, and the first eggs were laid on 22 May. The territories defended by colour-ringed birds during the first phase (10-17 May) were not necessarily the same as those defined by the same birds during the second phase, when the eggs were laid.

Table 46 shows how many individually marked birds changed territories between 17 May and 22 May, and also the numbers whose territories remained the same.

Table 46

Number of birds changing since 17 May	25
Number of birds remaining since 17 May	10
TOTAL	35

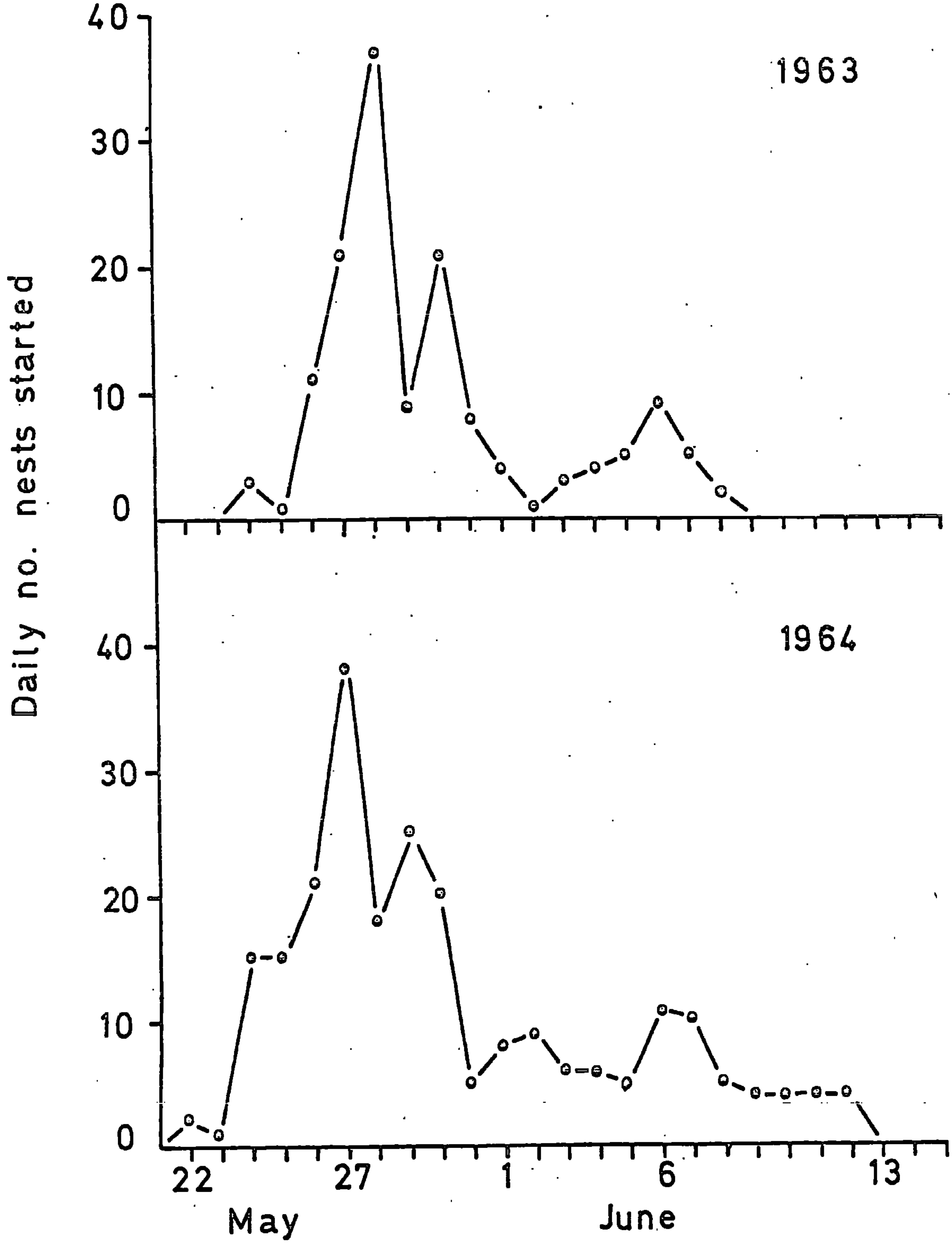
These data suggest that pairing territories are set up and defended and that these are often different from the final breeding territories.

The number of new nests started daily

In the Cove study area, the peak of laying the first eggs of a clutch occurred between 4 and 5 days after the first egg was found (Figure 17). In both years the form of the curve was similar, that is a sudden sharp rise to a peak with a slower fall off and a long tail. This indicates that the birds lay synchronously, and presumably some type of communal mechanism must co-ordinate them in this way.

Figure 17 The number of eggs of arctic tern laid daily in the Cove in two years, 1963 and 1964.

Daily laying pattern : cove



Comparison of the number of new nests started in 10 day periods on Inner Farne and in the East Murman Sea area shows a similar pattern (Figure 18). Laying in both areas was highly synchronised, and in both cases the major part of the colony laid their eggs over a period of 9-10 days after the start of egg-laying. Figure 17 shows a subsidiary peak occurring two days after the main peak, and there are fluctuations in the number of nests started daily because of temporary increases in the rate of laying. These increases were unexplained in 1963, but were thought to have been caused by the laying of replacement clutches. Belopolskii (loc. cit.) states that the slow drop in laying rate after the peak indicated "a prolongation of the period on account of second clutches", but gives no further information.

The laying interval

Observations on the laying intervals of arctic terns were made at 0800, 1400 and 2000 G.M.T. daily, when the birds' nests were inspected by walking through the colony. The laying interval was thus known to within 6 hours during the day, and 12 hours during the night. The data were obtained from 82 clutches of two eggs in 1963; single eggs and 3-egg clutches were disregarded. The data are presented in Table 47, and the laying interval between first and second eggs may be seen to be 44.3 hours, (1.8 days).

Figure 18 The percentage of total clutches of arctic tern started in each ten day period in two widely separated areas, the E. Murman Sea (after Belopolski, 1961) and the Farne Islands. Note the similarity of the laying patterns.

fig. 18

Comparison of laying patterns in two areas

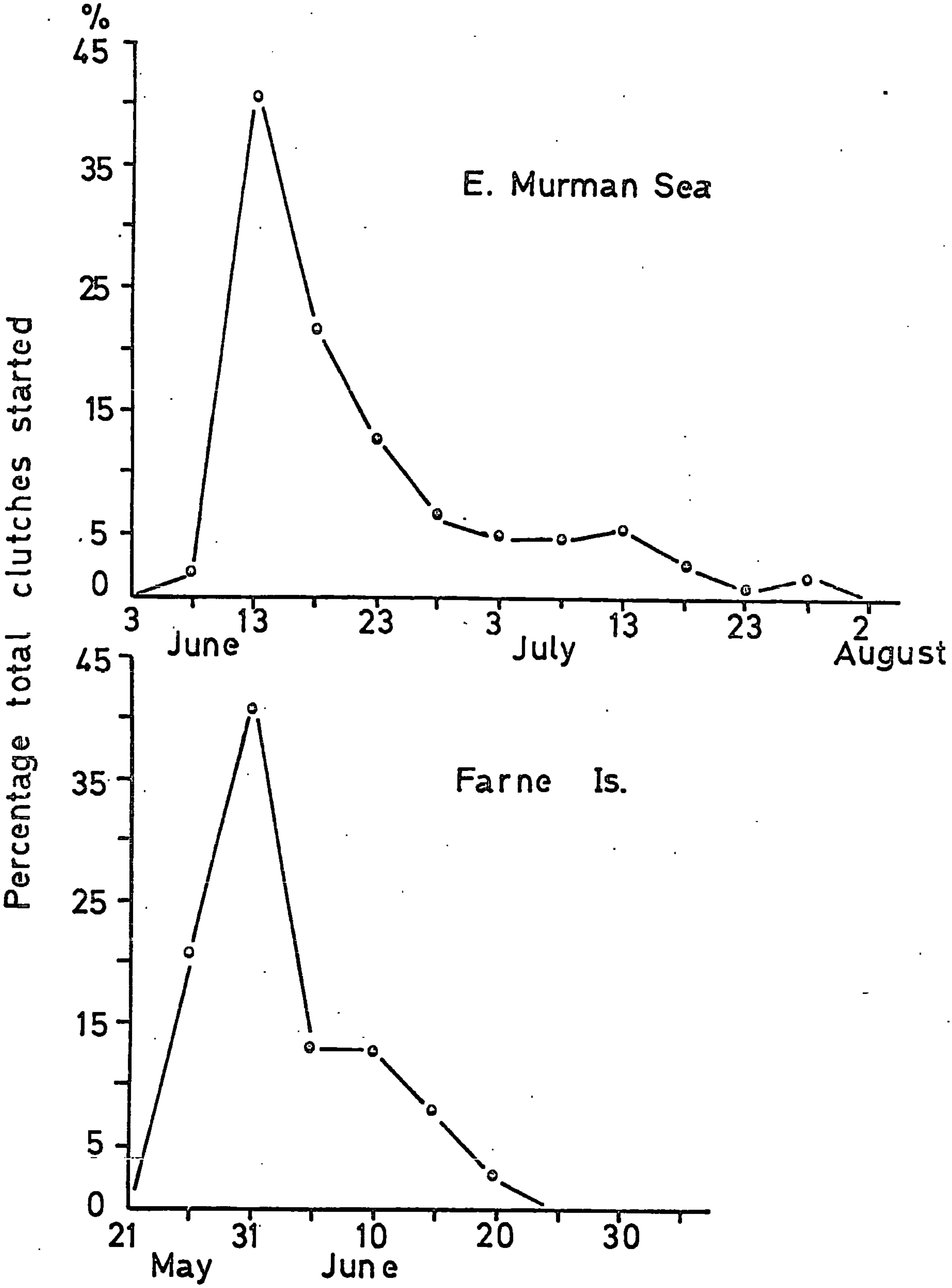


Table 47 The interval between laying 1st and 2nd eggs in arctic tern, Inner Farne, 1963.

Hours after laying 1st egg	6	12	24	30	36	48	54	60	72	78	84	96
Number of occasions	0	0	13	15	8	17	5	3	11	2	0	6

The laying of replacement clutches

a. Where both eggs were lost after incubation had started

By observation of colour-ringed birds in 1964, it was shown that the small fluctuations of 1-2 and 6-7 June could be explained by the laying of the first egg of a replacement clutch, after the first completed clutch had been lost. Single-egg clutches were disregarded in this analysis.

The mean time taken to lay the first egg of a replacement clutch was 8.6 ± 1.3 days. The data are presented in Table 48, which also shows the relationship between the length of time the original clutch was incubated, and the time taken to relay. This relationship is expressed as a graph in Figure 19.

Figure 19 shows how the period between the loss of the eggs and relaying varies proportionately with the length of time the original clutch was incubated. Insufficient data were gathered to extrapolate beyond an original incubation time of 7 days.

In the case of a bird incubating its first clutch for longer than 7 days and then losing it, it would seem that the chicks would have little chance of survival, and would

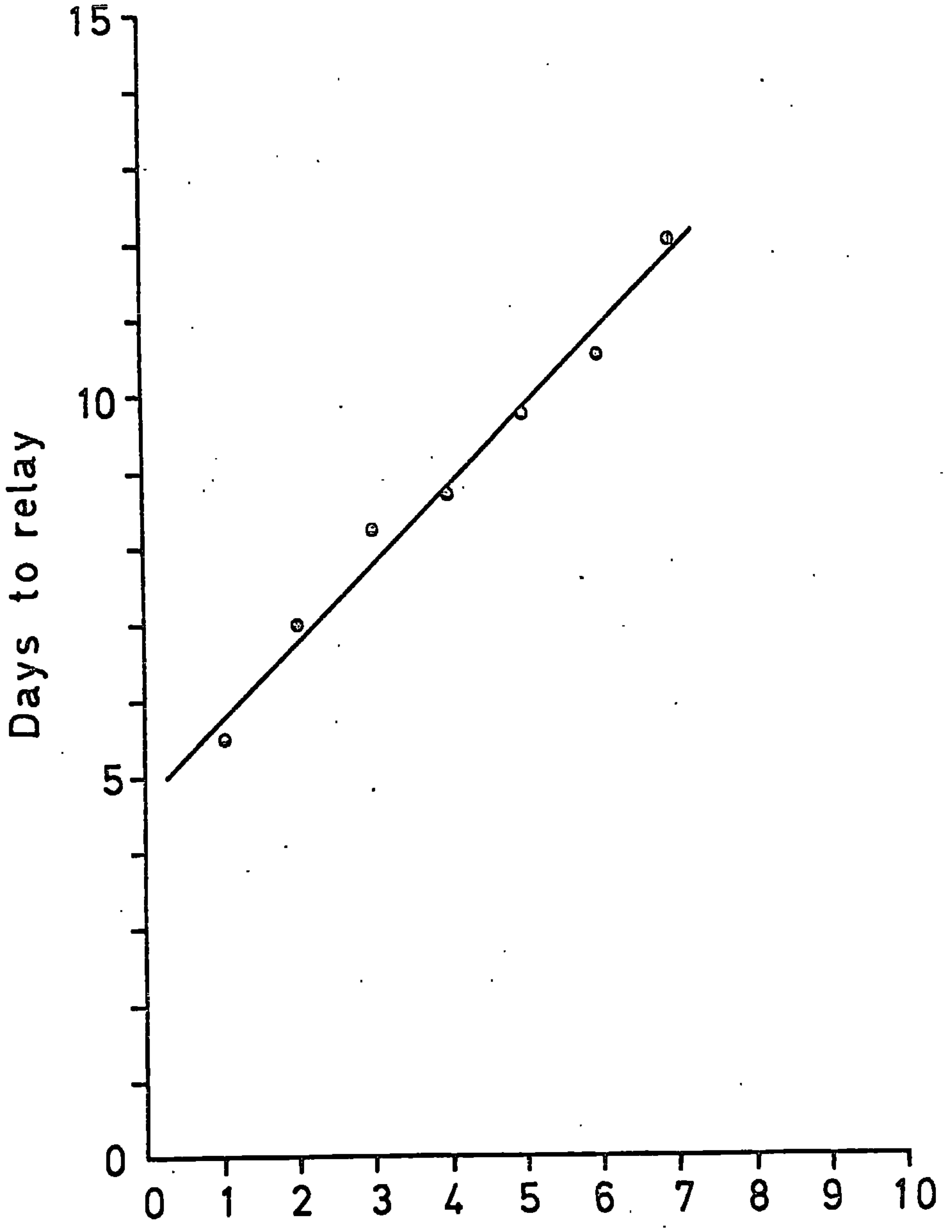
Table 48 To show the time taken to lay the first egg of a replacement clutch after the first completed clutch had been lost

Days original clutch incubated	Time taken to relay after loss of original clutch											
	1	2	3	4	5	6	7	8	9	10	11	12
1					1	1						
2						1	2	1				
3								4	2			
4								2	5			
5									2	4	1	
6										1	1	
7												1
Totals					1	2	2	7	9	5	2	1

Figure 19 The time in days taken to lay the first egg of a replacement clutch in relation to the number of days the original clutch was incubated, in 1963 and 1964.

fig. 19

Relationship between incubation of original clutch and relaying



Incubation of original clutch : days

probably not reach fledging age. It is obviously important that loss of the clutch should not occur after full time (effective) incubation has started. Harris (1964) shows that the ovary in Larus marinus decreases rapidly in weight after laying of the first egg, but points out that this is nothing to do with relaying ability.

In this respect, it is interesting to note that in 1963, small colonies were established on East Wideopen and on Knoxes Reef, and that egg-laying commenced on 22 June, chicks hatching on 14-15 July. Two of the adults had attempted to breed earlier in the season on Inner Farne, but none of the chicks from these eggs fledged.

Although replacement clutches were not recognised in 1963, it seems likely that egg-losses on 26-29 May might produce replacement clutches on 5-7 June, and it is suggested that the fluctuations apparent on that later date might be attributed to the laying of replacement clutches (Figure 20).

b. When the first egg of a two-egg clutch was lost

The subsidiary peak in laying, mentioned previously, occurred in 1963 and 1964. By observation of colour-ringed birds in 1964, it became evident that this phenomenon could be explained by the laying of the second egg in a clutch of which the first egg had been lost. These eggs were laid in a new scrape within the same territory as the original egg, and in 1963 were probably counted as the first eggs of new

Figure 20 The diagram shows the number of arctic tern nests started daily in the Cove in 1964. The cross-hatched parts (29-31 May) represent the second eggs of a clutch, laid in a different scrape from the one where the original egg had been destroyed. The dotted parts represent the first eggs of replacement clutches when the first complete clutch had been destroyed.

Analysis of egg laying : cove : 1964

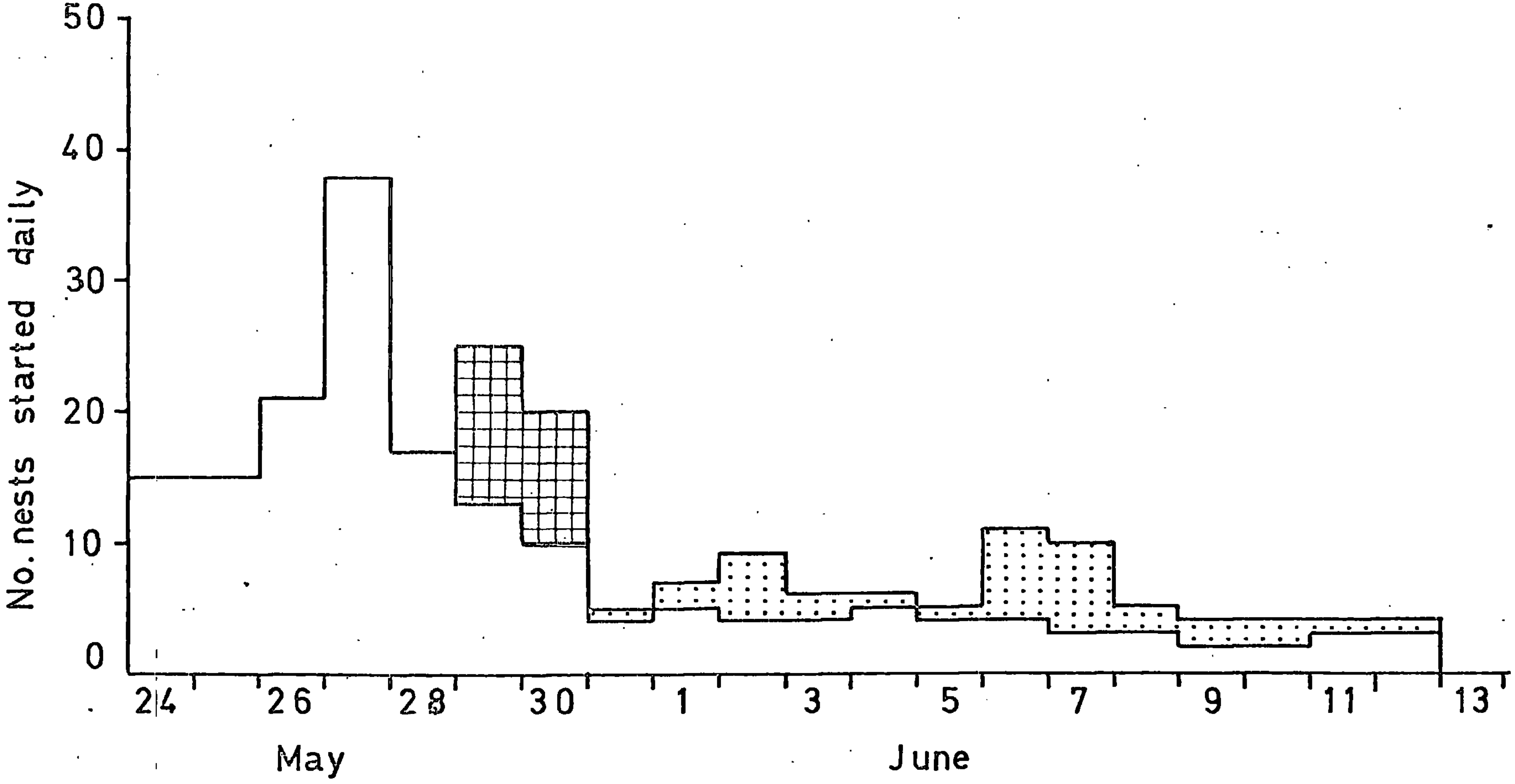


fig. 20

clutches. This phenomenon was only noticed on 29 and 30 May, 1964, (Figure 20), and on these two days the number of second eggs laid in different scrapes from the first egg were the same as the number of new nests started. This means that egg loss must have been particularly severe when the first eggs of these birds were laid, that is from 26-28 May, and this will be seen to have been the case.

Arctic terns were not found to lay a third egg when the first had been lost, that is a bird would not still attempt to lay a clutch of two if the first egg were removed within 24 hours of laying. The arctic tern would appear to be a determinate layer, laying a definite number of eggs irrespective of the number in the nest. In this it is unlike the Herring gull (Larus argentatus) which will continue to attempt to lay a clutch of three eggs if the first is removed, (Paludan (1951), Harris (1964)).

Clutch size

An accurate count of the number of eggs in each nest has been carried out for 4 years, in which the mean clutch size has ranged from 1.61 to 1.85 eggs. The overall mean, for 3,354 clutches for the 4 years, 1961, 1962, 1963 and 1964 was 1.74 ± 0.4. The data are presented in Table 49.

As Belopolskii (1961) has pointed out, the number of eggs found in each nest does not necessarily correspond to the number laid, and egg losses can cause the mean number of

Table 49 The frequency distribution of eggs in each clutch, and the mean clutch size for four years in arctic terns on the Farne Islands

Place	Year	C/1	C/2	C/3	Total	Mean clutch size
Inner Farne	1961	190	676	57	923	1.85
Inner Farne	1962	274	414	11	699	1.61
Inner Farne	1963	240	595	30	864	1.75
Inner Farne	1964	221	632	15	868	1.76
Totals					3354	1.74

Table 50 The mean clutch size, taken by spot checks according to different authorities, of the arctic tern

Place	Authority	Year	Nests	Mean clutch size
Scolt Head	Marples	1934	92	1.9
Machias Island	Pettingill	1939	100	1.4
Machias Island	Hawksley	1950	225	1.4
Greenland	Eklund	1944	279	1.7
S.E. Alaska	Williams	1947	127	2.0
British Isles	Bickerton	1909	209	1.7
Southampton Is.	Sutton	1932	127	1.8
Bolshoi Litskii Island	Belopolskii	1961	82	2.0
Totals			1241	1.7

eggs per nest to decrease. For instance, a close study of 50 nests in 1961 showed that all birds laid two eggs but the clutch size was reduced from 2.0 (50 nests, 100 eggs) to 1.4 (50 nests, 74 eggs), by egg losses during incubation.

The mean clutch size of arctic tern from spot checks by numerous authorities is shown in Table 50. It is considered reasonable to assume that, normally, arctic terns lay two eggs.

The incubation period

The data presented in this section deals with the incubation period, up to and including hatching. Particular attention has been paid to egg losses during this time.

1. Length of incubation

The mean incubation period was taken as being from the laying of the last egg of a clutch to the hatching of that egg (Heinroth, 1922, in Landsborough-Thom~~p~~son, 1964). The data were collected from 70 2-egg clutches (C/2) in 1963, and were determined with a maximum error of ± 6 hours. The mean incubation period, as defined above was 21.6 ± 1.8 days. The data are shown in Table 51.

Table 51 The mean incubation period in arctic tern

Incubation period in days	20	21	22	23	23
Number of instances	6	28	22	12	2

Mean = 21.6 ± 1.8 (n= 70)

The incubation period of the arctic tern, calculated by Hawksley (1950) from data obtained from 8 nests, was 22 days.

Witherby et al (1940) give 21 to 23 days, and these results agree with the present work.

The incubation period of the first egg of C/2 (from laying to hatching of first egg) determined for 50 clutches in 1963, was 22.5 ± 2.1 days. The data are shown in Table 52.

Table 52 The incubation period of the first egg in C/2 of arctic tern

Incubation period in days	21	22	23	24
Number of instances	3	17	23	7

Mean = 22.5 ± 2.1 days (n = 50)

2. Intensity of incubation

Although the mean laying interval in C/2 was 1.8 days, the mean hatching interval was only 0.9 days. This supports the idea that brooding does not normally reach its greatest intensity until the second egg has been laid, and Table 53 shows the number of birds which continuously brooded the first egg, and the number in which brooding was intermittent until the second egg had been laid. A third category, birds which failed to incubate the first egg and started incubating when the second egg was laid, is also included. The incubation period was taken as being from the laying of the first egg until the hatching of that egg.

Table 53 The intensity of brooding of the first egg of C/2, and the mean incubation period of 10 eggs in each category

Category of incubation	1963	1964	Incubation period
1st egg continuously brooded	8	5	21.8
1st egg intermittently brooded	30	20	22.6
1st egg never brooded	15	11	23.3
TOTALS	53	36	22.6 (n = 30)

Table 53 also shows the mean incubation period for 10 eggs in each category. It may be seen that, as might have been expected, where the first eggs were brooded continuously, they hatched in a shorter time than eggs brooded intermittently or not at all. The intensity of brooding is an important factor in the consideration of the effect of predation on eggs.

3. Hatching success

Reliable data for hatching success, the number of chicks which successfully hatched, are shown for 1961,1963 and 1964 in Table 54. The only comparable study giving reliable data for hatching success, is that of Hawksley (loc. cit.). Hawksley showed that in three years the mean hatching success for 308 eggs was 64%. The maximum success achieved in any one year was 82.8% in 1947. These figures are higher than the mean hatching success, 52%, on Inner Farne.

Table 54 Hatching success of the arctic tern in three years, 1961, 1963 and 1964

Year	Number of eggs laid	Number of eggs lost	Number of eggs hatched	% Hatching success
1961	103	40	63	51.9 ± 4.9
1963	526	281	245	46.1 ± 2.1
1964	577	257	320	55.4 ± 2.0
Mean	1206	578	628	51.1 ± 1.4

In the present study, the standard error of the difference between the mean hatching success, and the hatching success in any of the three years, 1961, 1963 and 1964 was not significant. However, hatching success in 1963 was significantly lower ($P < 0.05$) than hatching success in 1964. Reasons for this difference are discussed in the section dealing with egg losses.

4. Egg losses during incubation

The fate of eggs which failed to hatch was examined in the Cove in 1963 and 1964, and supporting observations were made from the Gut Garden in 1964. Observation was less intensive in 1963, but a careful watch was kept from the hide in 1964. Eight categories of egg loss were recognised in 1963, but only five in 1964. The mortality of eggs in two seasons is analysed in Table 55. The characteristics of each category of egg loss, and the effect on the breeding biology of the arctic tern are discussed.

a. Disappeared

This category was created in 1963 to account for the large numbers of eggs which disappeared without trace between visits to the Cove. Normally, when eggs had disappeared, the scrape continued to be recognisable by the numbered nest marker.

b. Starling predation

Starlings (Sturnus vulgaris L.) had only been seen to

Table 55 To show egg loss according to each category, expressed as the number lost, and the percentage of the total number of eggs laid during each season. (Cove, Inner Farne)

Category of egg loss	1963		1964	
	Number	% Total eggs	Number	% Total eggs
Disappeared	113	36.0	0	0
Starling predation	8	2.5	122	34.9
Punctured by terns	5	1.6	10	3.5
Infertile	14	4.4	8	2.2
Died on hatching	12	3.8	14	3.9
Destroyed by rabbits	4	1.2	2	0.5
Destroyed by humans	6	1.9	0	0
Abandoned	3	0.9	0	0
Total	165	52.3	156	45.0

take 8 tern eggs in 1963. In 1964 starlings were observed to destroy 105 eggs, and 17 more were attributed to them but were not observed.

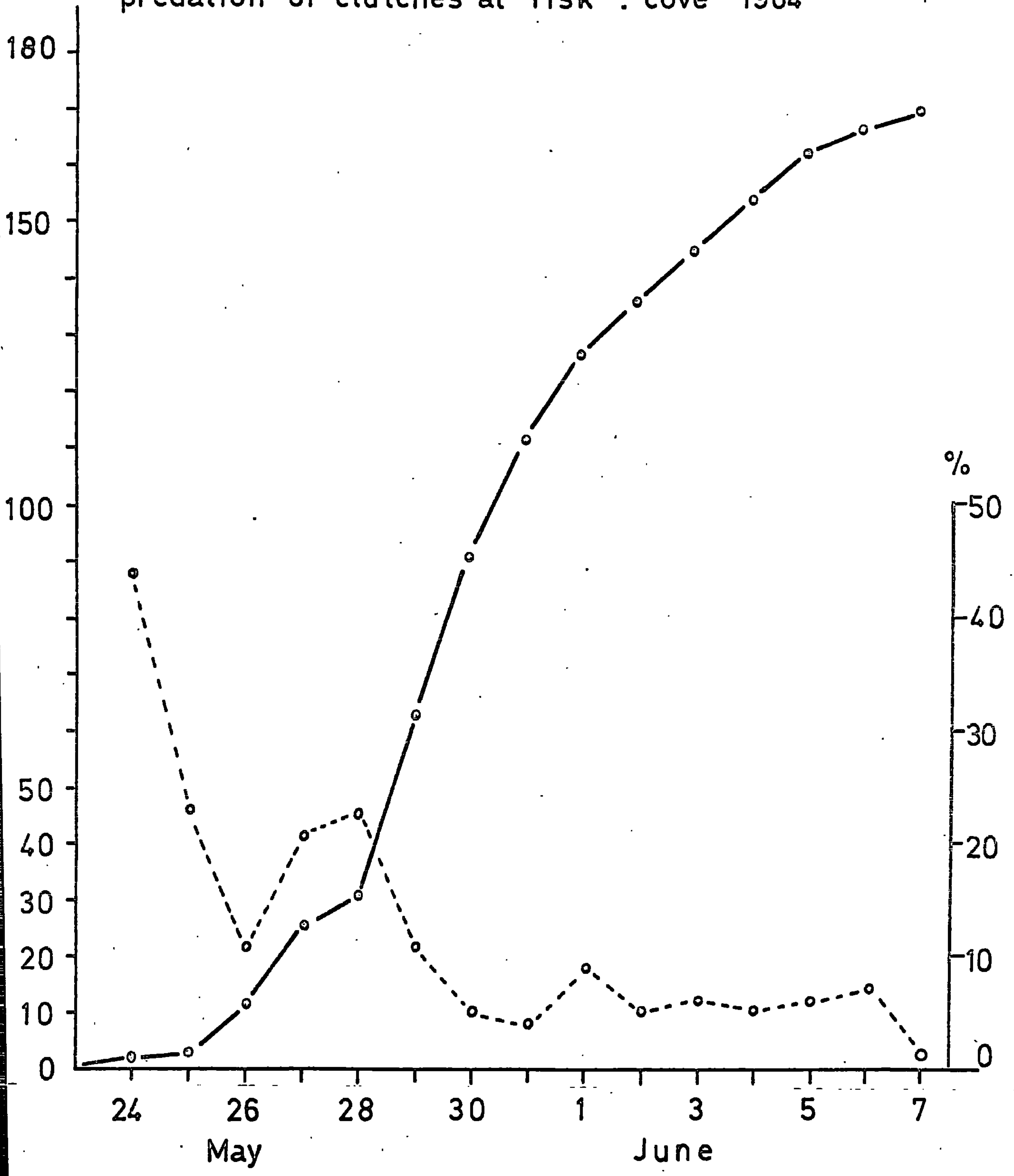
The following data have been compiled from field notes, and show the typical sequence of events during predation by starlings:

A starling would fly into the Cove and forage, taking no notice of the surrounding incubating terns. When an unoccupied scrape with eggs was seen, the starling would walk or fly to it, break the egg or eggs with its beak and eat the contents. Often the starling would be disturbed by the return of the parent tern or by adjacent incubating birds. When menaced by a tern the starling would fly away, and the pieces of egg shell would be removed by terns, not necessarily the owners of the clutch. The same starling would return at intervals and attempt to eat more of the egg contents, now congealed and sunk into the sand.

The destruction of a clutch of eggs would take about one minute. Eight hours after an egg had been broken the only indication that one had been present was a congealed patch of sand in the nest scrape and the numbered nest marker. In windy conditions, the congealed patch would be concealed by sand within 3-4 hours after egg-breakage. The numbers of eggs predated daily reached a peak on 28 May 1964. Predation of eggs in relation to the number of clutches started daily is shown in Figure 21. It is significant that igure 21 The number of arctic tern clutches completed daily in the Cove 1964 is shown by the solid line and solid circles. The percentage predation of clutches at risk is indicated by a pecked line and open circles. The scale indicating the percentage predation is drawn on the right hand side of the graph.

fig. 21

No. clutches completed daily and percentage predation of clutches at risk : cove 1964



the highest predation rate was recorded at the start of incubation when brooding intensity was at its lowest. The predation rate fell sharply and remained low when effective incubation started.

Egg predation by starlings continued at a low level throughout the incubation period, but increased when the largest number of chicks were hatching (16-17 June). This was probably because incubating birds grew restless at this time, and eggs were often unattended for short periods, allowing predation to occur.

It is believed that there is sufficient evidence for the 'disappeared' category of 1963 to be attributed mainly to starling predation. If this is the case, starlings accounted for up to 38%of the total number of eggs laid in 1963, and 35% of the total in 1964.

c. Punctured by adult terns

Adult terns were seen to puncture their own eggs by stabbing them with the bill. Punctured eggs were characterised by a round hole where the beak had been forced through the shell. Such eggs were entire save for the puncture, were not eaten and were often subsequently incubated normally. The embryo always died. This egg-puncturing phenomenon has been observed by Hawksley (1950), but egg-puncturing by terns other than the owners,(Pettingill ~~(~~1939), was not observed.

d. Infertile

Infertile eggs were taken to be those eggs incubated for the full period which showed no signs of hatching.

In the present study the incidence of infertile eggs was 2.4%. Other workers have observed 5% (Pettingill loc. cit.), and 10% (Hawksley loc. cit.), for infertile or "early addled" eggs.

e. Died on hatching

This category refers to eggs completing normal development and beginning to hatch, but which finally failed to hatch. This study showed 4%, and Hawksley (loc. cit.) found 7% failed to hatch. In one case in 1964, a half-hatched chick was lifted by its parent's premature attempts to remove the egg shell, and carried 4 m from the nest, where it subsequently died.

f. Mammalian interference

In 1963 and 1964, rabbits feeding at night scattered and broke six eggs. In 1963 a human visitor to the islands entered the tern colony in the Cove and broke six eggs. Egg losses from these causes, although considerable in other tern colonies, Austin (1948), are regarded as negligible on the Farne Islands.

g. Abandoned

In 1963, three birds abandoned single eggs.

5. ~~Comparison with other studies~~

The only study with comparative figures is that of Hawksley (loc. cit.). A comparison of the two studies is

Table 56 To show the causes of egg mortality in two studies of arctic tern

Cause of egg loss	Hawksley 1950		Present study	
	Number lost	% Total eggs laid	Number lost	% Total eggs laid
Infertile or addled early	31	10.1	22	3.3
Death of embryo	23	7.5	26	3.9
Abandoned	3	1.0	3	0.4
Disappeared	20	6.5	0	0
Punctured by terns	10	3.2	15	2.3
Rolled from nest	4	1.3	Not observed	
Mammalian destruction	20	6.5	12	1.8
Predation by starlings	Not observed		243	37.0
TOTALS	111	36.1	321	49.2

shown in Table 56. The data from Hawksley are for three years, data from the Farnes for two years.

It may be seen from Table 56 that the major differences between the studies are related to predation by starlings which appear to have caused up to 78% of the total egg mortality on the Farnes. The other causes of egg mortality are substantially similar.

VIII THE MORTALITY OF ARCTIC TERNS ON THE BREEDING GROUNDS:

MORTALITY OF CHICKS AND JUVENILES

MORTALITY OF CHICKS AND JUVENILES ON THE BREEDING GROUNDS

Methods

Observations which included daily counts and post mortems of dead chicks were made in three years, 1961, 1963 and 1964. All chicks in the study areas were ringed with a small leg ring within 24 hours of hatching. In an attempt to minimise disturbance, ringing, the collection of dead chicks, weighing and the gathering of other data were carried out twice daily, normally in the early morning and evening.

Post mortem examination of chicks was carried out as soon as possible after collection, and was normally within 24 hours of death. In 1963, a number of dead chicks were sent to the Veterinary Laboratories, Lasswade, for examination, and the findings are incorporated in this study.

Fledging success and chick mortality

Fledging success, the number of chicks which successfully left the island, has been calculated for three years from the figures shown in Table 57.

Table 57 shows that there is a significant difference between fledging success in 1963 and 1964, although success in different areas within each year is similar. Hawksley loc. cit. recorded 34.7% fledging success on Machias Island, and it appears likely that the high fledging success in 1964 was abnormal.

Table 57 Fledging success of arctic tern in three years on Inner Farne

Area	Year	Number of eggs hatched	Number of chicks dying	Number of chicks fledged	Success %
Ladies Path	1961	63	20	43	67 ± 6.0
Cove	1963	149	55	94	62 ± 3.9
Gut Garden	1963	104	42	62	59 ± 4.8
Cove	1964	195	23	172	88 ± 2.3
Gut Garden	1964	125	22	103	82 ± 3.4

The factors affecting mortality are examined in detail in this section.

Factors affecting mortality

1. Mortality and age of chick

The ages of chicks which died in the study areas were known to within 12 hours. Preliminary observations in 1961 suggested that while most of the mortality fell during the first week of life, there was an increased mortality at fledging, about 24 days after hatching.

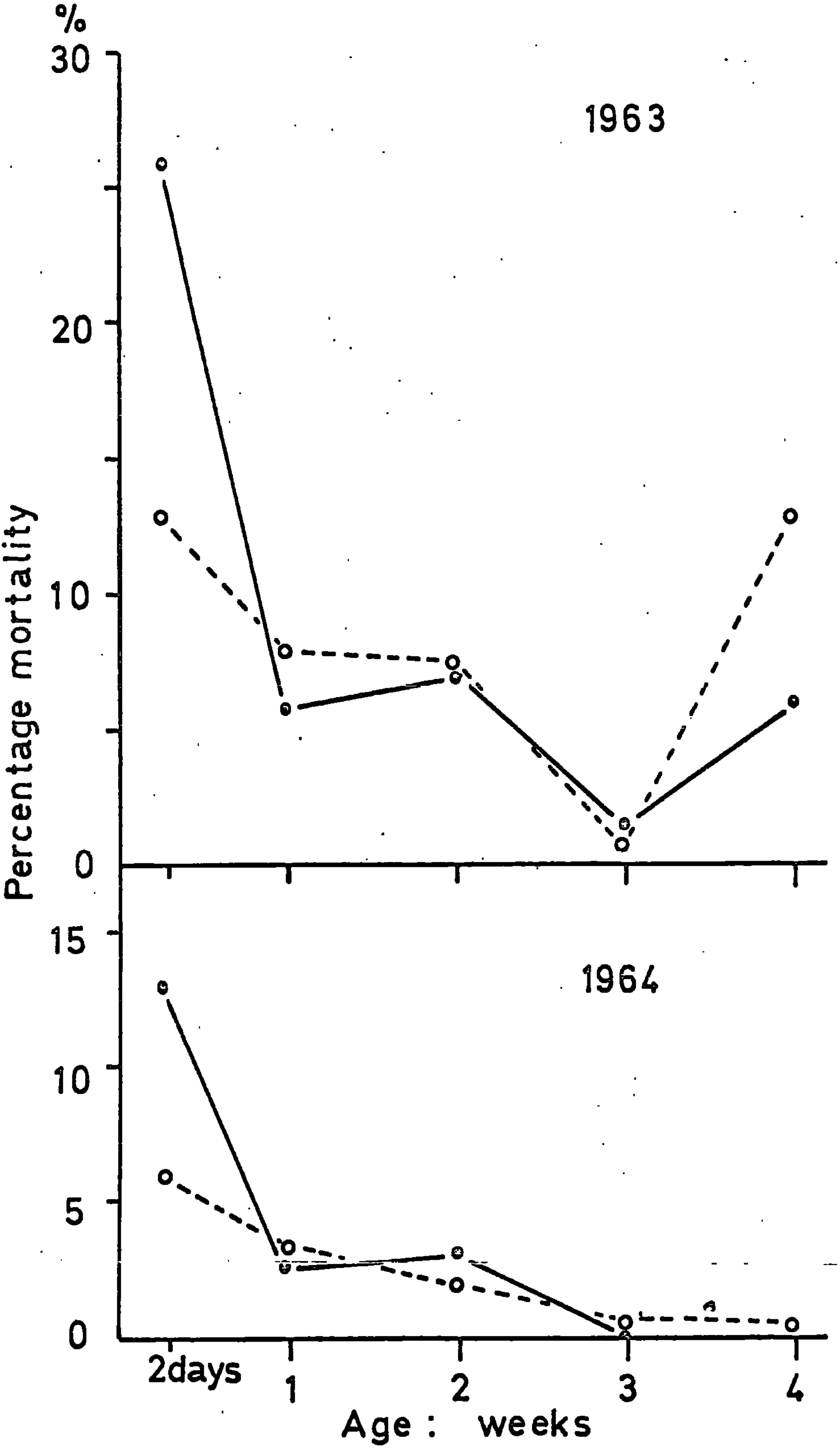
Figure 22 shows the mortality of chicks, expressed as the percentage of the total chicks at risk, according to age. Apart from the generally lower incidence of mortality, in 1964 the fledging and post-fledging mortality was absent.

Figure 22 also shows that the mortality amongst young chicks in the Gut Garden was double that in the Cove. The difference was statistically significant in 1963 ($P < 0.05$) but was not significant in 1964 ($P < 0.1$). However, mortality in 1964 amongst young chicks in the Gut Garden was again double that in the Cove. It seems likely that some factor adversely affecting the survival of young chicks was present in the Gut Garden, but absent in the Cove.

The mortality of chicks according to their age is shown for two seasons and two areas in Tables 58 and 59. These results show that mortality was heaviest during the first week of life, and that there was an increased mortality during

Figure 22 The mortality of arctic tern chicks according to the age at which they died, expressed as a percentage of the chicks at risk, in two areas of Inner Farne in 1963 and 1964. The mortality of chicks in the Gut Garden is indicated by the solid line and solid circles, the mortality in the Cove by the pecked line and open circles.

Mortality of chicks according to age



the fledging period in 1963, but not in 1964.

Tables 58 and 59 also show the unequal distribution of mortality between the Cove and the Gut Garden. For example, in 1963 chicks between hatching and two days old in the Gut Garden suffered double the mortality of those in the Cove, and fledged chicks in the Cove suffered heavier losses than the same age-group in the Gut Garden. The reasons for this unequal distribution of mortality are discussed later.

A manner of presenting these results for easier comparison is to convert the figures into the number surviving from 1000 individuals, and to plot the results as survivorship curves. The results for the two areas in 1963 and 1964 are shown in Figure 23, plotted on an arithmetic scale.

From these curves it is immediately obvious that mortality in both areas was greater in 1963, and consequently fewer chicks survived to leave the island. This is reflected in the 28 days + age category, which includes all birds dying on the breeding grounds after fledging.

Mortality and season

Figures 24 and 25 show the mortality of chicks according to the season, expressed as the number of chicks at risk dying in each period. It is obvious that some periods have

Table 58 To show relationship between mortality and the age of arctic tern chicks in 1963

Age of chick	COVE		GUT GARDEN	
	No. found dead	% mortality of those at risk	No. found dead	% mortality of those at risk
0-2 days	19	12.7	27	25.9
3-7 days	11	8.4	5	6.1
8-14 days	9	7.8	5	6.9
15-23 days	1	0.9	1	1.5
24+ days	14	12.9	4	6.0
TOTALS	54	42.7	42	46.4

Table 59 The relationship between mortality and age of arctic tern chicks in 1964

Age of chick	COVE			GUT GARDEN		
	No. at risk	No. found dead	% mortality of those at risk	No. at risk	No. found dead	% mortality of those at risk
0-2 days	224	12	6.1	136	16	12.8
3-7 days	212	7	3.8	120	3	2.5
8-14 days	205	5	2.8	117	4	3.4
15-23 days	200	1	0.5	113	0	0
24+ days	199	0	0	113	0	0
TOTALS		25	13.2		23	18.7

Figure 23 The numbers of arctic tern chicks surviving at weekly intervals for every 1000 hatched on Inner Farne in 1963 and 1964. In both graphs the 1963 figures are denoted by a solid line and solid circles, and the 1964 figures by a pecked line with open circles.

fig. 23

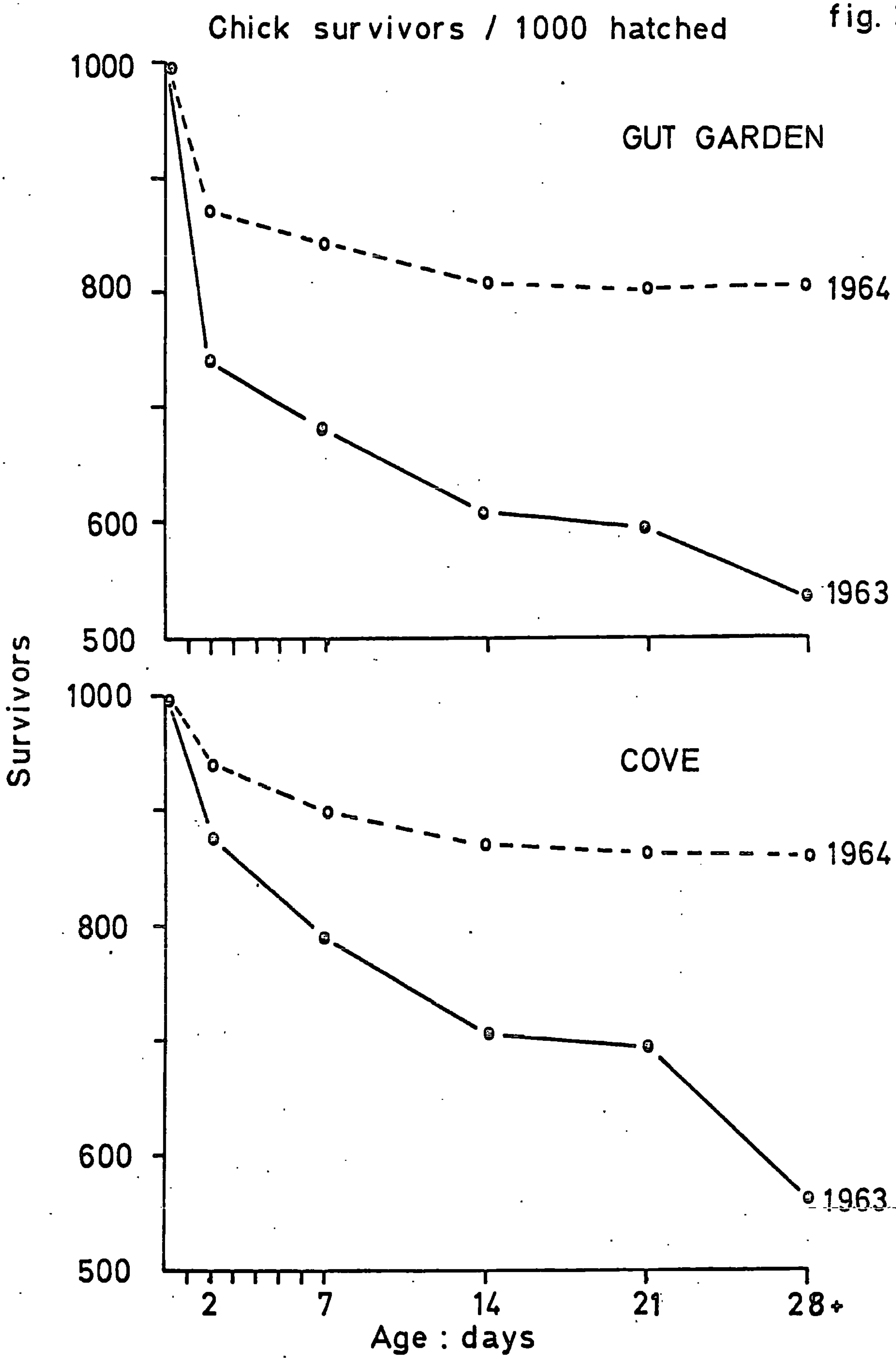

Chick survivors / 1000 hatched
GUT GARDEN
1964
1963
COVE
1964
1963
Survivors
1000
800
600
500
1000
800
600
500
2
7
14
21
28+
Age : days

Figure 24 The mortality of arctic tern chicks in 1963 in two areas on Inner Farne. The actual number of deaths per period is shown, and the rainfall in inches is also figured.

Mortality of all chicks 1963

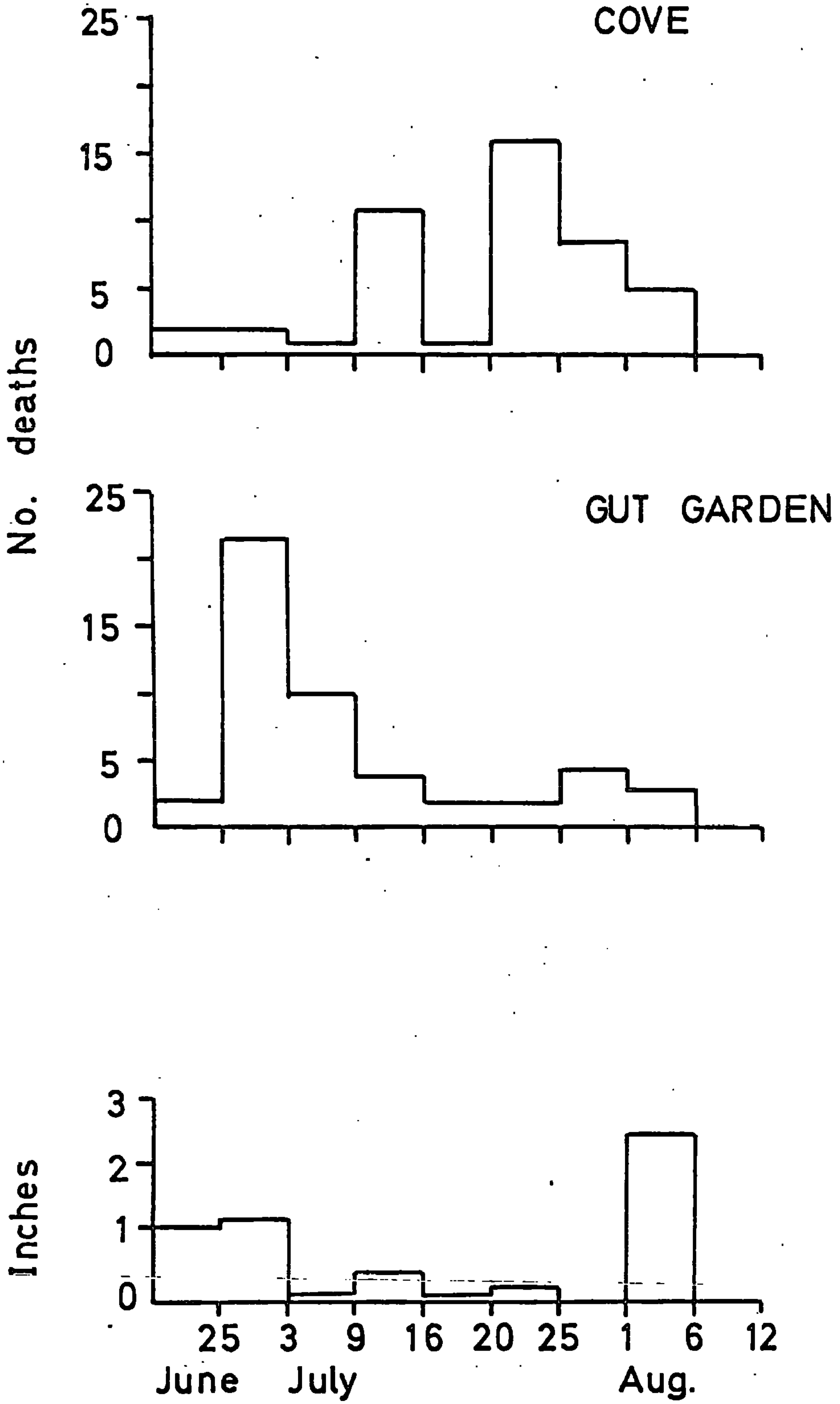
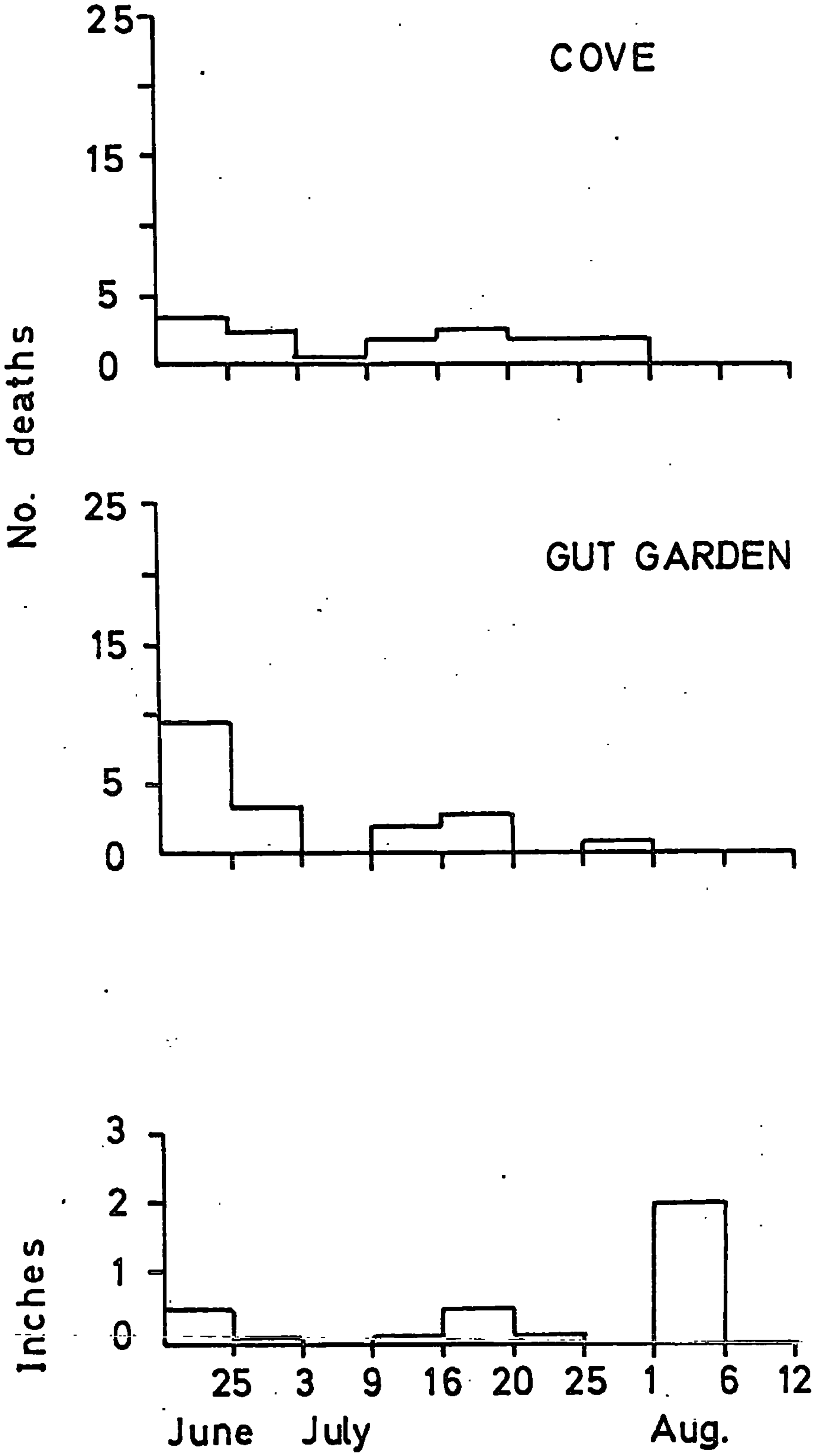


Figure 25 The mortality of arctic tern chicks in 1964 in two areas on Inner Farne. The actual number of deaths per period is shown, and the rainfall in inches is also figured.

fig. 25

Mortality of all chicks
1964



a heavier mortality than others, and that mortality can be heavy in one area and light in another area, at the same time. For instance, mortality between 25 June to 3 July in 1963, Figure 24, when mortality was heavy in the Gut Garden but light in the Cove.

Mortality according to age of chick and season

The mortality of arctic tern chicks appears to be related to the age of the chick, and to the weather, particularly rainfall. The two factors are closely linked, the younger chicks succumbing more rapidly to wet weather than older chicks. This is clearly demonstrated in the Gut Garden in 1963, when many chicks less than 48 hours old died during a period of cold wet weather (Figure 26). The mortality of chicks less than 48 hours old, and the rainfall are shown in Figures 26 and 27 for 1963 and 1964.

Mortality and cause of death

The death of chicks in the study areas could be attributed to one of five causes. These were: killed by adults, exposure, starvation, desertion and one where no cause of death could be found. The manner in which chicks were seen to die, and the diagnostic characters used to determine the cause of death are described fully below.

a. Killed by adult terns

Chicks over 24 hours old were not continuously brooded by their parents, and were prone to wander outside the

Figure 26 The mortality of arctic tern chicks 48 hours old and younger in the Cove and Gut Garden in 1963. The actual number of deaths per period is shown, and the rainfall in inches is also figured. The occurrence of a cold period of heavy rain and strong east winds is denoted by the triangle below the Gut Garden histogram.

Rainfall & mortality of 48 hour old chicks 1963

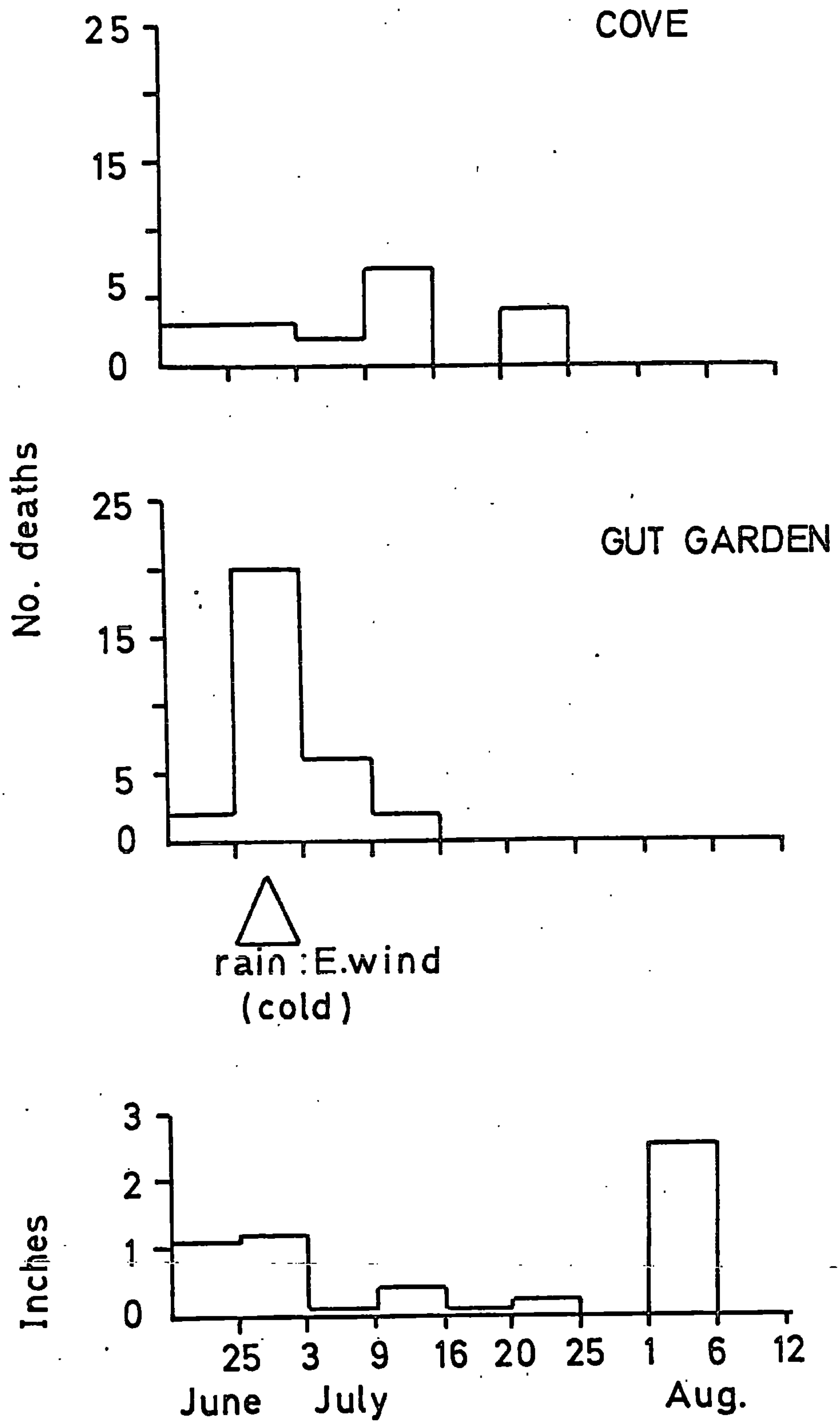
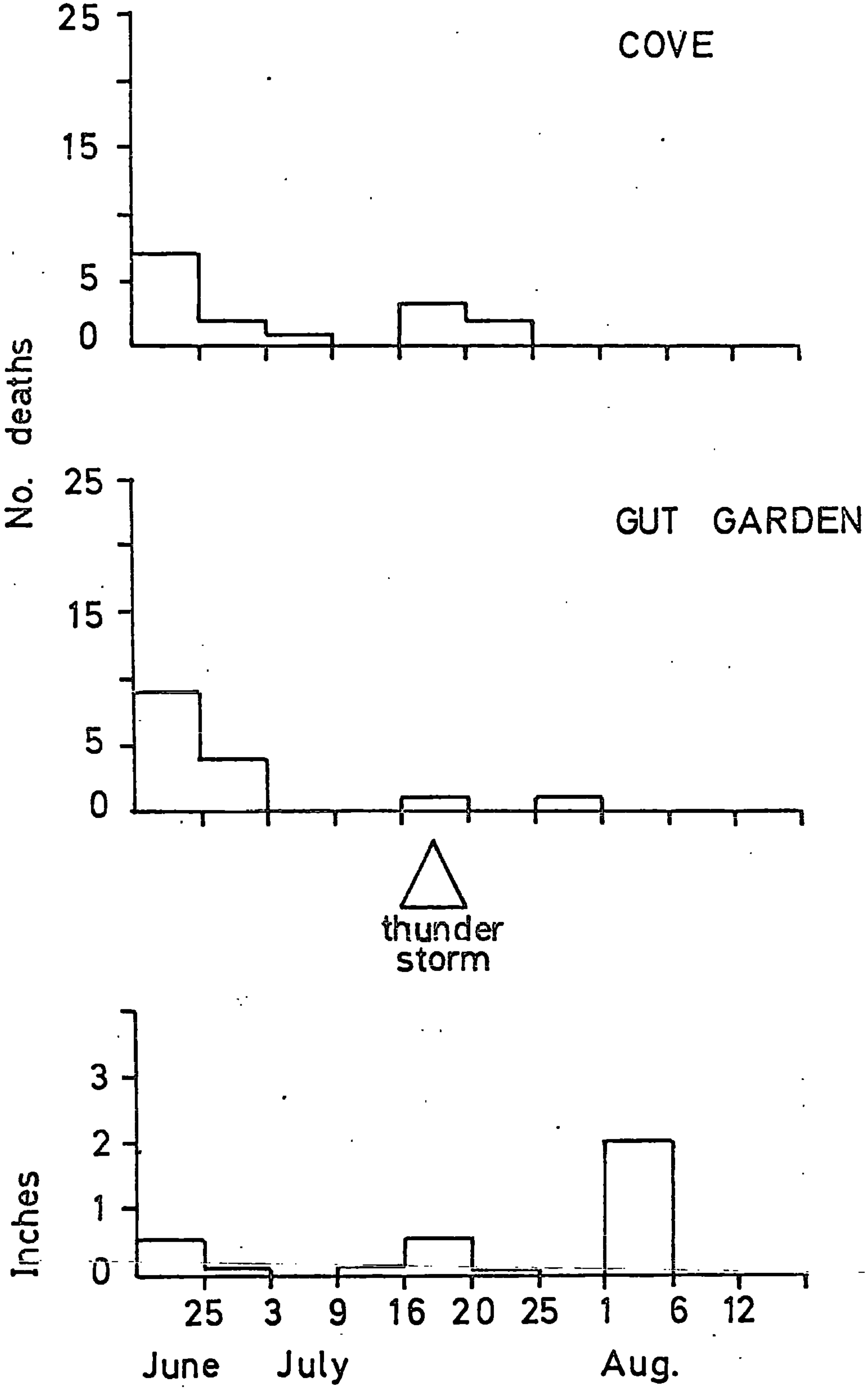


Figure 27 The mortality of arctic tern chicks 48 hours old and younger in the Cove and Gut Garden in 1964. The actual number of deaths per period is shown, and the rainfall in inches is also figured. The occurrence of a severe thunderstorm is indicated below the Gut Garden histogram.

Rainfall & mortality of 48 hour old chicks 1964



parental territory. Incursions into a neighbouring territory provoked violent attacks upon the chicks by adults defending the territory. Trespassing chicks were chased by the adults and rapidly struck with the bill. The usual target was the head, and an attack would continue until the chick lay still, or retreated into its own territory.

The rapid blows to the head of chicks resulted in more or less extensive brain damage. This was manifest externally by loss of co-ordination in the chick's movements and an inability to stand upright. Death sometimes occurred rapidly, as in two instances in 1963 and one in 1964, when an adult's bill penetrated the brain of a chick through the eye and caused direct damage. More normally the adult's bill fractured the skull and extensive bruising and haemorrhage occurred. The chicks fell over, failed to regain their feet and kicked feebly whilst opening and closing the bill. In such cases death occurred within 12 to 24 hours after the initial attack, probably with exposure as a major contributory factor.

Older chicks survived these attacks, and mortality from this cause was not diagnosed in chicks older than 5 days. In both seasons older chicks were observed to provoke attacks by adults, and these chicks survived and fledged, although they were often found with large fluid-filled swellings on the nape (10 cases in 1963, 5 in 1964). The number of chicks killed by adult terns is shown in Table 60.

Although Hawksley (1950) does not mention attacks by adults as a cause of mortality, similar behaviour has been described by Palmer (1941) for the common tern, *S. hirundo*. Pettingill (1939) mentions kidnapping of young by adults, and this may refer to the attacks described above.

In the present study, mortality caused by attacking adults was mainly confined to the Cove (Table 59), where wandering chicks might be clearly seen by adults. In the Gut Garden, the virtual absence of mortality from this cause was attributed to the tunnelling habit of tern chicks reared in tall vegetation. These chicks make tunnels into the herbage surrounding the nest and hide in them until an adult returns with food, (Norrevang, 1960).

b. Exposure

Observations in 1961 and 1962 showed that after heavy showers or prolonged periods of rain, young tern chicks were often found dead. This mortality was almost completely confined to the Gut Garden. It is suggested that mortality after rain was caused by severe chilling or hypothermia, and that this effect was more intense in the Gut Garden because of the water-retaining properties and dense growth of the dominant plant, sea campion. This latter factor would prolong chilling, and would substantially increase the time taken to regain the normal body temperature.

Heavy rain and strong winds have been mentioned as the

Table 60 The number of chicks killed by adult arctic terns in two areas in 1963 and 1964

Area	Year	No. at risk	Number killed	% Mortality of those at risk
Cove	1963	146	18	12
Gut Garden	1963	98	2	1.9
Cove	1964	195	13	6.6
Gut Garden	1964	125	0	0

cause of mortality amongst young terns by the compiler of the Farne Islands Ornithological Reports, 1956, 1957, 1961, 1962 and 1963. Conversely, in 1959, "weather had little effect on young birds." Palmer (1941) noted that chilling probably killed many chicks when a Great Horned Owl (*Bubo virginianus*) prevented adults from brooding overnight, but Paynter (1949) found little evidence for exposure as a cause of death in Herring gull chicks. Paludan (1949) mentioned that heavy rain and hot sun affected the mortality of young Herring gull chicks, and Harris (1964) points out that although young gull chicks may be adversely affected by rain and strong sun, it is only during and immediately after hatching that these factors are important. Hawksley (1950) stated that "7 chicks died from exposure in periods of cold rain", but did not base his diagnosis on any particular characteristics. The results of Jennings and Soulsby (1958), where 35 out of 53 Black-headed gull chicks died of chilling, support the view that adverse weather may cause heavy losses in nestlings. These authors also say that similar mortalities occurred in tern colonies during the same season.

Data on weather conditions have been gathered for 1963 and 1964. As has been pointed out previously, the terns in 1964 enjoyed an abnormally high fledging success, and it is believed that this was because of the lack of rain, particularly during the early part of the hatching period.

The incidence of mortality amongst chicks less than 48 hours old has been presented in Figures 26 and 27, and the rainfall is also shown.

In 1963, over an inch of rain fell in each of the first two periods. Hatching had barely begun by the end of the first period (16 June-25 June), but was in full swing from 26 June onwards. During this time (from 26 June to 3 July) 1.17 inches of rain fell, and easterly winds caused a marked drop in temperature. In the Gut Garden 20 chicks died during this period, over 20% of the birds at risk at that time. Although 3 chicks died in the Cove during this second period, they did not die from exposure. The long "tail" of mortality in the Gut Garden is attributed to the ability of Sea Campion to retain moisture for long periods after rain. Later periods of heavy rain (2-11 August) had no effect on the chick mortality.

In 1964, although the rainfall during June, July and August was much reduced compared with 1963, 0.5 inches of rain fell during the first period (16-25 June), and mortality of young chicks in the Gut Garden was again high. From 26 June to 3 July there was little rain (0.06 inches) and little mortality. A thunderstorm during the period 17-20 July killed three well-grown chicks in the Cove. These chicks were well and active before the storm, but were afterwards found dead in an exposed position. It is surprising that so few chicks were killed, as large quantities of hail fell during the storm. However, there were very few chicks less than 48 hours old at risk during this period. A period of heavy rain (2-11 August) did not cause any mortality.

Jennings and Soulsby's pathological findings showed pulmonary congestion, dark and imperfectly clotted blood, and distended gall bladders with a mottled liver. They mentioned that young chicks showed no lesions. As mortality on the Inner Farne was mainly confined to chicks less than 48 hours old, little pathological evidence for exposure, as opposed to any other cause of death, can be advanced. The evidence for exposure being the cause of death is summarised below.

I Deaths occurred during periods of rain and wind.

II Deaths were almost completely confined to the Gut Garden, where the vegetation remained wet for long periods after rain, and where the greatest chilling effect might have been expected.

III Weights of dead birds were within the normal range for each age. This discounted starvation, where a weight loss might be expected.

IV The bruising and lacerations typical of attack by adults were not found in these chicks.

V Predation was discounted, as the recovery of corpses mutilated and eaten in a fashion characteristic of the predator did not occur.

A recent paper by Nye (1964) is relevant to the present work. Nye studied the degree of hypothermia obtained when ducklings and domestic fowl chicks were immersed in water. She showed that the average temperature depression per minute of immersion was 1.5°C, but found large unexplained variations among individual birds exposed to similar experimental conditions. The average time taken to regain the original temperature, after immersion, was 34 minutes in ducklings, and 31 minutes in chicks. The animals were dried beneath a light bulb.

In the present study it is interesting to note that a tern chick left unbrooded during a ten-minute shower of rain, might be expected to lose up to 15°C, or even more when the chilling effect of the wind is taken into account. Such a bird would be suffering from severe hypothermia, and its chances of recovery at environmental temperatures would probably be very small.

c. Starvation

In 1963, over 18% of the chicks hatched in the study areas, starved to death. In 1964, less than 3% of the chicks died from this cause (Table 61).

In 1963, most of the birds which starved to death were free-flying juveniles over 24 days old. No bird which later died was seen to feed, or to be fed by adults. Some 24 hours

Table 61 The number of arctic tern chicks dying from starvation in 1963 and 1964

Area	Year	No. at risk	Number dying	% Mortality of those at risk
Cove	1963	149	28	18.7
Gut Garden	1963	105	8	7.6
Cove	1964	195	1	0.5
Gut Garden	1964	112	3	2.4

before death, these dying birds flew weakly when disturbed, and often overbalanced when alighting. Long flights were not attempted. About 6 hours before they died, juveniles were easily caught and handled. Such birds were too weak to stand upright and rested on the sand with their necks retracted and their eyes half-shut. There were no convulsions at death, and in many cases the birds were found tipped forwards on to their bills, supporting the body on partially relaxed wings.

The weights of dead birds and normal, live, birds of the same age are compared in Table 62. It may be seen that in most cases the weight of the starved birds was between 30% and 40% below that of normal birds. Gross dissection showed that the gizzard was empty, the digestive system shrunken, and in none of the birds was subcutaneous fat present.

An opportunity to examine the weight loss of starving chicks occurred in 1964, when several birds of known age wandered from their nest sites and fell into gullies where they were hidden from their parents. The "wandering" birds were weighed twice daily until they died or recovered and of 17 birds found in this condition, only 2 survived.

The daily loss of weight as a percentage of their original weight in these "wandering" birds that starved to death is shown graphically in Figure 28. The average daily

Figure 28 The percentage weight loss of starving arctic tern chicks of all ages from one week to four weeks plotted at 12 hour intervals from the time of desertion until death.

Percentage weight loss of "wandering" birds

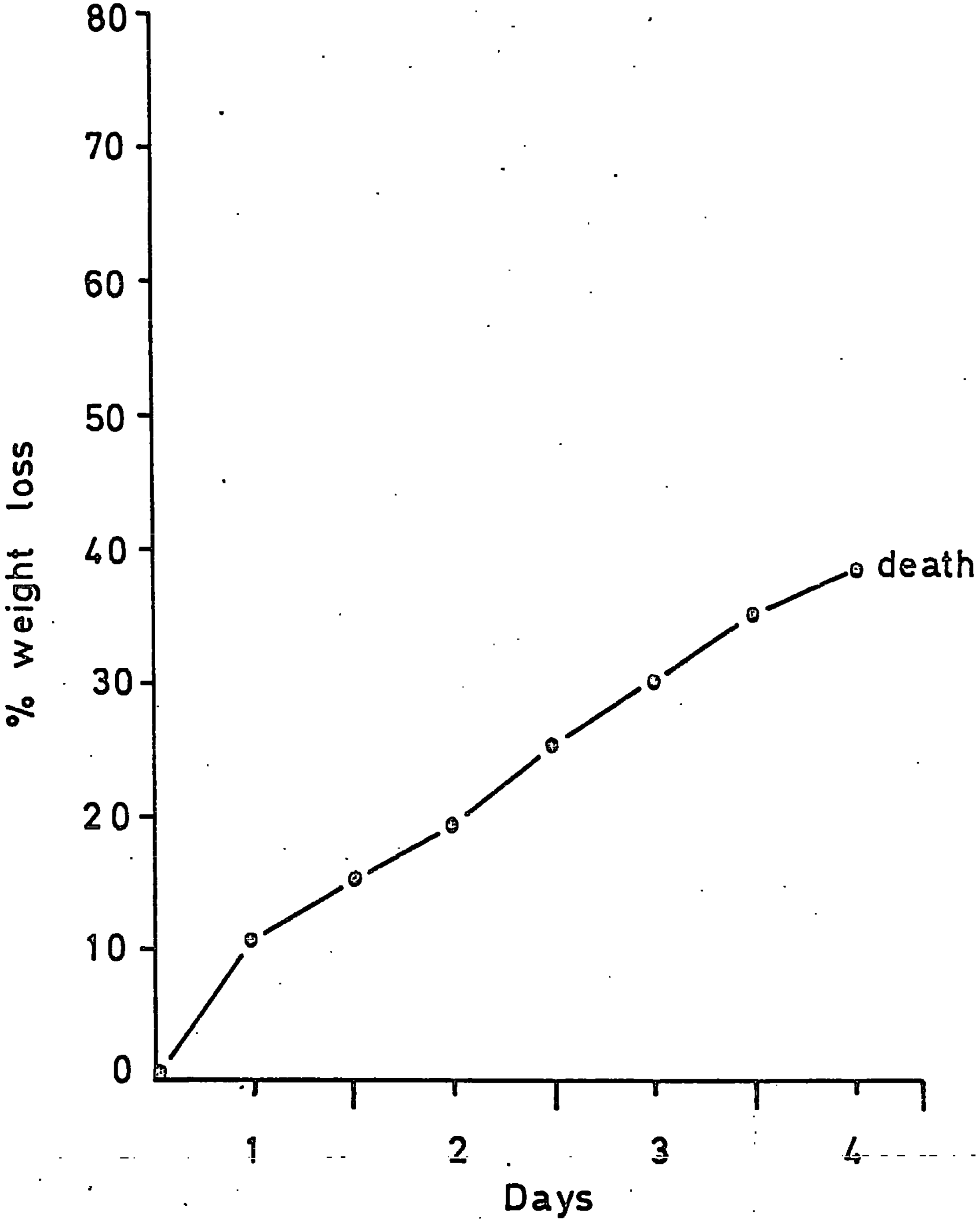


Table 62 Weights of dead, (starved), and normal live birds of the same age compared

Age in days	Wt. of dead bird in grams	Wt. of 'normal' live bird in grams (% as from 100 gms)	Approx. wt. loss as % normal wt. of live bird
44	57	90-110	43
39	53	90-110	47
36	58	90-110	42
36	57	90-110	43
36	55	90-110	45
35	81	90-110	20
34	63	90-110	37
33	54	90-110	46
29	73	90-110	25
Fledged 23+	70	90-110	30
"	67	90-110	33
"	63	90-110	37
"	59	90-110	41
"	57	90-110	43
"	57	90-110	43
"	55	90-110	45
"	55	90-110	45
"	54	90-110	46
5	29	36	8
3	25	c.25	0

loss in weight was 10 grams.

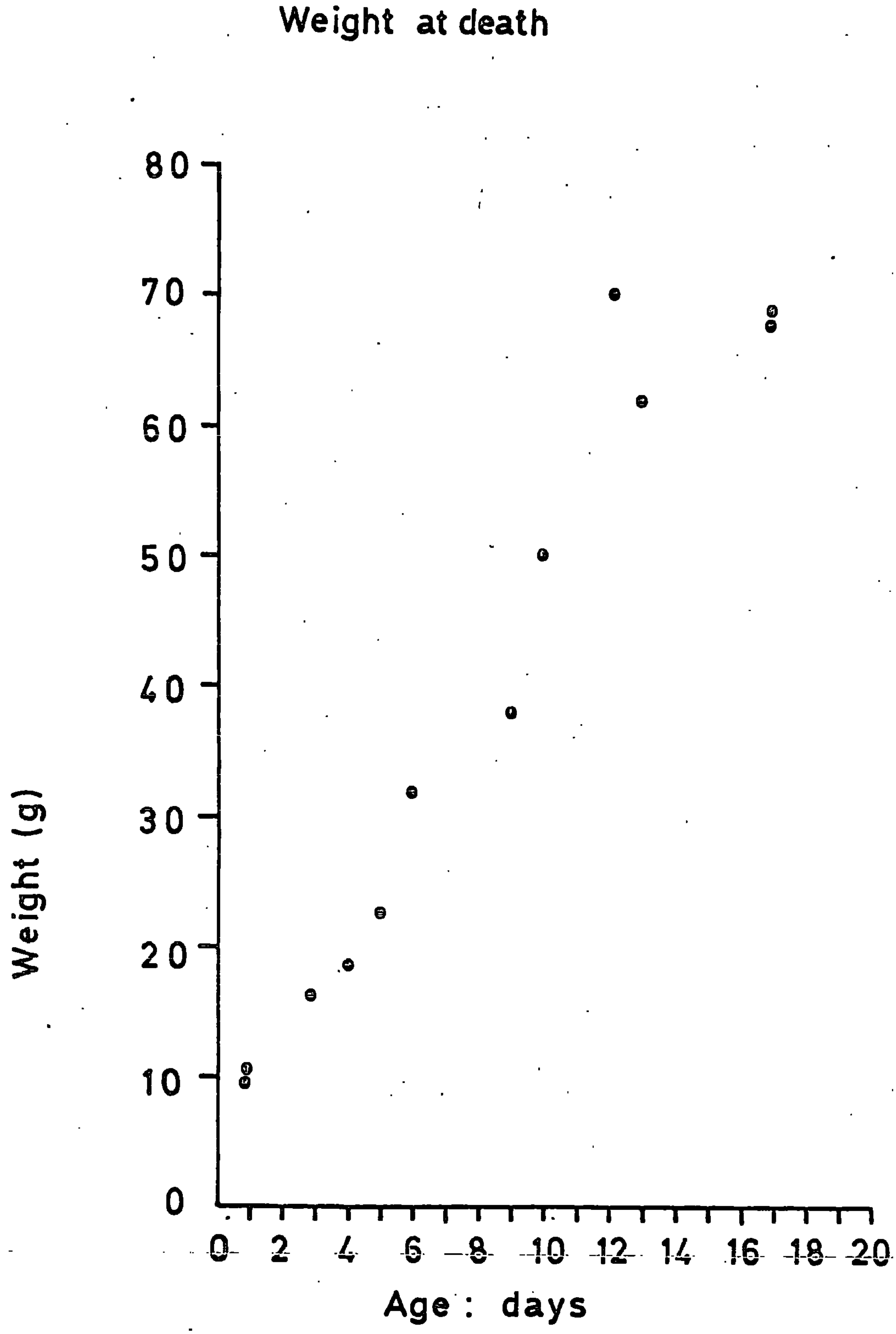
Data gathered from "wandering" birds are presented in Figure 29 where the weights of dead birds are plotted against the age of each bird. The results indicate that (a) older birds lose proportionately more of their body weight before dying than younger birds. For example, a 17 day old chick lost 40% of its initial weight before it died, but a 5 day old chick only lost 24% before dying. If chicks lost a constant proportion of their body weight before dying, irrespective of age, the slope of the line in Figure would have been at 45 degrees. In fact the line is at a shallow angle; and (b) older birds survived longer than young birds when they starved.

Birds which had wandered and starved to death showed, on gross dissection, similar features to the birds found dead in 1963, that is empty gizzards, shrunken digestive systems and lack of sub-cutaneous fat.

Whilst it was definitely known that "wandering" birds in 1964 died from starvation, the same cannot be said of the 1963 birds. Although the final cause of death was certainly starvation, it is impossible to say what caused the original loss of condition. Virus infection may be discounted, as the post-mortem reports from Lasswade were negative in this respect. It is unlikely that failure of the food supply could be the answer, for adult terns were still successfully feeding

Figure 29 The weight in grams at death of arctic tern chicks of known age on Inner Farne, 1964.

fig. 29


Weight at death
Weight (g)
80
70
60
50
40
30
20
10
0
0
2
4
6
8
10
12
14
16
18
20
Age : days

unfledged young at this time. Lacking any evidence to the contrary, it must be assumed that these birds died as a result of their inability to capture food for themselves.

Mortality and brood size

The death of the second chick in broods of two is characteristic of the Sandwich tern and also according to Hawksley (1950), of the arctic tern. However, the latter author had insufficient evidence to support his contention. More recently it has been established by Vermeer (1963), that fledging success was independent of brood size in the Glaucous Winged Gull (Larus glaucescens). Supernormal broods in this species were reared as successfully as normal broods.

In the present study it was found that in two years (1961, 1964) broods of two fledged as successfully as broods of one, but that in a third year (1963) B/2 were much less successful than B/1. These data are presented for three years on Inner Farne, according to brood size, in Table 63.

Further analysis of the 1963 data shows that the mortality of chicks fell into two well-defined periods, from 26 June to 3 July in the Gut Garden, and from 21 July to 1 August in the Cove (Figure 24). The causes of mortality in each period were different, and affected the chicks in different ways.

In the Gut Garden, early mortality was caused by a period of heavy rain and northerly winds, which killed almost a

Table 63 To show fledging success of arctic terns in four years, according to brood size

Year	Area	No. in brood	No. hatched	No. fledging	% fledging success	No. fledged per brood
1961	Farnes	1	18	13	72 ± 10.5	0.7
		2	36	24	66 ± 7.8	1.3
1963	Cove	1	57	56	82 ± 1.8	0.8
		2	74	27	36 ± 5.5	0.7
1963	Gut Garden	1	48	31	64 ± 6.9	0.6
		2	50	25	50 ± 6.1	0.5
1964	Cove	1	55	50	92 ± 3.6	0.9
		2	140	122	87 ± 2.8	1.7
1964	Gut Garden	1	27	25	92 ± 5.0	0.9
		2	98	78	79 ± 4.0	1.6

quarter of the chicks at risk younger than 48 hours. This mortality was spread evenly between B/1s and B/2s, 14 dying from B/1s and 15 from B/2s. Chicks of the same age in the Cove suffered no mortality from exposure during this period.

In the Cove, the numbers of B/2 were reduced by attacks from adults, and at the end of the season, by starvation which mainly affected the second chick in B/2. Very few chicks in B/1 died from either cause. These results are set out in Tables 66 and 67.

Data on the growth of chicks in different brood sizes were gathered by Hawksley (1950). From a study of the weights of chicks in 5 B/2 and B/1, he concluded "that the survival rate of the young may very well be affected by the number of chicks in the nest". In 1964, it was found that the daily weight increments of chicks in B/1 were no greater than those in B/2, except under adverse conditions. Under such conditions, although being fed by their parents, second chicks in B/2 gained less weight than other chicks, and some even lost weight. Although none of these chicks died, it would appear that at times when adult terns find fishing difficult, the survival of the young is definitely influenced by the number of chicks in the nest.

It is probably that seasons occur when food is in such short supply that only the first hatched chicks in B/2 survive. This type of situation may well have developed in 1965, when an unprecedented mortality of young chicks occurred during a spell of good weather. Daily weight gains in the surviving chicks did not show a marked decrease during this period (17 to 29 June) and the majority of chicks which died were the young, second hatched, chicks in B/2 (Table 64).

Table 64 The number of arctic tern chicks dying in the Cove in the twelve-day period after the start of hatching in 1964 and in 1965

Chick category	1964 Number dying	1965 Number dying
Single chicks	2	9
First chicks in B/2	2	7
Second chicks in B/2	4	23
TOTALS	8	39

The mortality in the Cove between 17 - 29 June (from hatching of the first chick in 1965 until twelve days afterwards) was 24% of the birds ringed. This may be compared with the similar period in 1964, from 14 to 26 June, when 4% of the birds died. (The figures are comparable as the ringing effort in the two years was similar, that is all chicks were ringed at hatching.) Mortality after 29 June, 1965 was slight, (J. Spriggs, pers.comm.). It is suggested that the synchrony which exists between terns and their food supply, _Ammodytes_ sp., was maladjusted early in 1965. It seems likely that the few fish that were available were not enough to supply the sudden post hatching demands of the tern colony.

Mortality and broods of two chicks

The number of 1st and 2nd chicks dying in B/2s are shown below in Table 65. If first and second chicks are assumed to have an equal chance of survival, an equal distribution of mortality might be expected. In fact this is not so, and second chicks hatched in B/2s have significantly less chance of fledging than first hatched chicks.

Table 65 to show the unequal distribution of mortality within broods of two chicks (B/2)

Area	Year	Number of 1st chicks dying	Number of 2nd chicks dying	Total	Probability
Cove	1963	12	35	47	<0.001
Gut Garden	1963	10	15	25	$<0.5 >0.30$
Cove	1964	4	14	18	<0.02
Gut Garden	1964	4	16	20	<0.01

Mortality and cause of death in relation to brood size

In connection with the data showing the unequal mortality in B/2s, it is of interest to see how the known causes of death affect single chicks, and first and second chicks in B/2s.

Tables 66 and 67 show how the casualties were affected by the cause of death. It may be seen that, in the Cove,

Table 66a To show incidence and cause of mortality in arctic tern chicks in Gut Garden in 1963

Cause of death	Single	1st	2nd	Total
Killed by adults	0	1	1	2
Exposure	14	5	10	29
Desertion	3	1	1	5
Starvation	0	1	2	3
Unknown	0	2	1	3

Table 66b To show incidence and cause of mortality in arctic tern chicks in Cove in 1963

Cause of death	Single	1st	2nd	Total
Killed by adults	3	5	10	18
Exposure	0	0	0	0
Desertion	4	1	1	6
Starvation	3	3	22	28
Unknown	0	3	2	5

Table 67a To show incidence and cause of mortality in arctic tern chicks in Gut Garden in 1964

Cause of death	Single	1st	2nd	Total
Killed by adults	0	0	0	0
Exposure	0	3	12	15
Deserted	1	0	0	1
Starvation	0	0	3	3
Unknown	1	1	1	3
Totals	2	4	16	22

Table 67b To show incidence and cause of mortality in arctic tern chicks in Cove in 1964.

Cause of death	Single	1st	2nd	Total
Killed by adults	2	2	9	13
Exposure	2	1	2	5
Deserted	0	0	0	0
Starvation	0	0	1	1
Unknown	1	1	2	4
Totals	5	4	14	23

second chicks in B/2 have twice as many casualties caused by pecking and starvation as first and single chicks. In the Gut Garden, although mortality from pecking was absent, second chicks suffered twice as badly as first chicks from exposure. The mortality of the first chicks in B/2 was very similar to that of chicks in B/1.

It is possible that the heavy mortality inflicted upon second chicks in B/2 was the result of hunger, causing these chicks to wander more frequently. However, as second-hatched chicks in B/2 were normally fed as much as first-hatched chicks, this hypothesis may be discounted.

Mortality in broods of two chicks in relation to the age of the chicks.

Second-hatched chicks in broods of two, as shown previously, have less chance of survival than their elder siblings. The incidence of mortality within broods of two chicks, in relation to their ages, is shown in Table 68, a and b.

Table 68a. Chick mortality in broods of two, in relation to age, 1963

Age (days)	1st chick		2nd chick	
	Cove	Gut Garden	Cove	Gut Garden
0-7	5	4	10	10
8-14	2	3	3	1
15-23	2	1	10	3
24 +	3	2	12	1

Table 68b. Chick mortality in broods of two, in relation to age, 1964

Age (days)	1st chick		2nd chick	
	Cove	Gut Garden	Cove	Gut Garden
0-7	3	2	13	10
8-14	0	0	0	1
15-23	1	1	2	2
24 +	0	1	1	1

These data clearly show that during the first week of life, the second-hatched chicks in broods of two suffer at least double the mortality of the first-hatched chicks. After the first week of life, in 1963, chicks in broods of two in the Gut Garden had a similar mortality, and this was the case in both areas throughout 1964. In the Cove in 1963, although mortality of first and second hatched chicks was similar during the second week of life, starvation decimated second-hatched chicks during their third and fourth weeks of life.

It appears that in seasons when tern survival is normal, and above normal (1964), second-hatched chicks in broods of two have a heavier mortality than first-hatched chicks during their first week of life. However, mortality after the first week of life falls equally upon first and second-hatched chicks in a brood, except at times of adversity, as in the Cove in 1963 and early in 1965, when the first-hatched chick survives at the expense of its younger sibling.

IX THE MORTALITY OF ARCTIC TERNS ON THE BREEDING GROUNDS: THE GROWTH OF ARCTIC TERN CHICKS UNDER FIELD CONDITIONS

The growth of arctic tern chicks under field conditions

In 1964 the study of the survival of arctic tern chicks was expanded to include a weighing programme. This programme was designed to supplement data on chick survival and mortality, and particular attention was paid to the growth of single chicks and chicks in broods of two.

Methods

The major difficulty experienced in this part of the study was the daily location of chicks. After experiments, wire mesh barriers surrounding the nests were discarded, as they caused too much disturbance. The final solution was to weigh a large sample of chicks daily, and although every chick was not found every day, on average each chick was weighed once every two days. The method for weighing was as follows. Each chick, as it was found, was placed in a numbered compartment in a deep tray, and a stake with a corresponding number was placed where the chick was found. Experience showed that many individual chicks preferred the same hiding places from day to day, and could be easily found. The tray of chicks (twenty-five in all) was carried out of the study area to the weighing machine which was kept under cover. (The weighing machine was a battery operated Mettler pan balance, weighing up to 800 g. and accurate to within 0.1 g.) The time spent within the colony, collecting and setting down chicks, was approximately two hours every day. It was found possible to weigh approximately fifty chicks from each study area each morning, and a total of four hours was spent each day, from 0600 - 1000 G.M.T., on the weighing programme.

The relatively small amount of vegetation in the Cove made it easier to find chicks there than in the Gut Garden, and more chicks were weighed in the former area. A total of 408 birds were weighed at least twice, and the weights of these birds were used to construct the curve of mean daily weight increase, plotted against age in Figure 30.

Curve of weight increase with age

The form of the curve of weight/age is sigmoid, and the weight of chicks increases slowly from hatching until the third day. From the third day to the thirteenth day, the chicks gain weight rapidly and apparently linearly. At about fourteen days the daily weight increase slows down, and a loss of weight is apparent at about the time that the birds fledge, that is from twenty-one to twenty-six days after hatching.

Methods of analysis

The daily weighings showed large fluctuations when the chicks were weighed after the first feed of the day. Birds which had been fed could weigh from 10-15 g more than similar birds which had not been fed. In addition, the overnight loss in weight was up to 8 g. To avoid errors from these sources, the chicks were weighed in the early morning, between 0600 and 0900, and the mean daily weight increase throughout the linear period of weight increase used for comparative purposes. In this way the daily weight fluctuations were unimportant, and figures obtained for the mean daily weight increase according to brood size could be compared. Similarly, the mean daily weight increase over the first half of the linear period could be compared with a similar figure for the second half of the linear period. Finally, the mean daily weight increase for the whole of the linear period (three to thriteen days) could be examined for seasonal trends.

The data were also examined on a daily basis, and here daily figures for mean weight increase according to chick category were derived and compared using Student's 't' test. The data were analysed to determine whether daily fluctuations in mean weight increase were correlated with weather conditions.

In the analysis of the daily mean weight increase, it was thoughtreasonable to assume that the daily weight increase of chicks was a reflection of the fishing ability of the adults. Fluctuations in the availability of fish could thus be expected to be mirrored in fluctuations in the daily mean weight increase of the chicks.

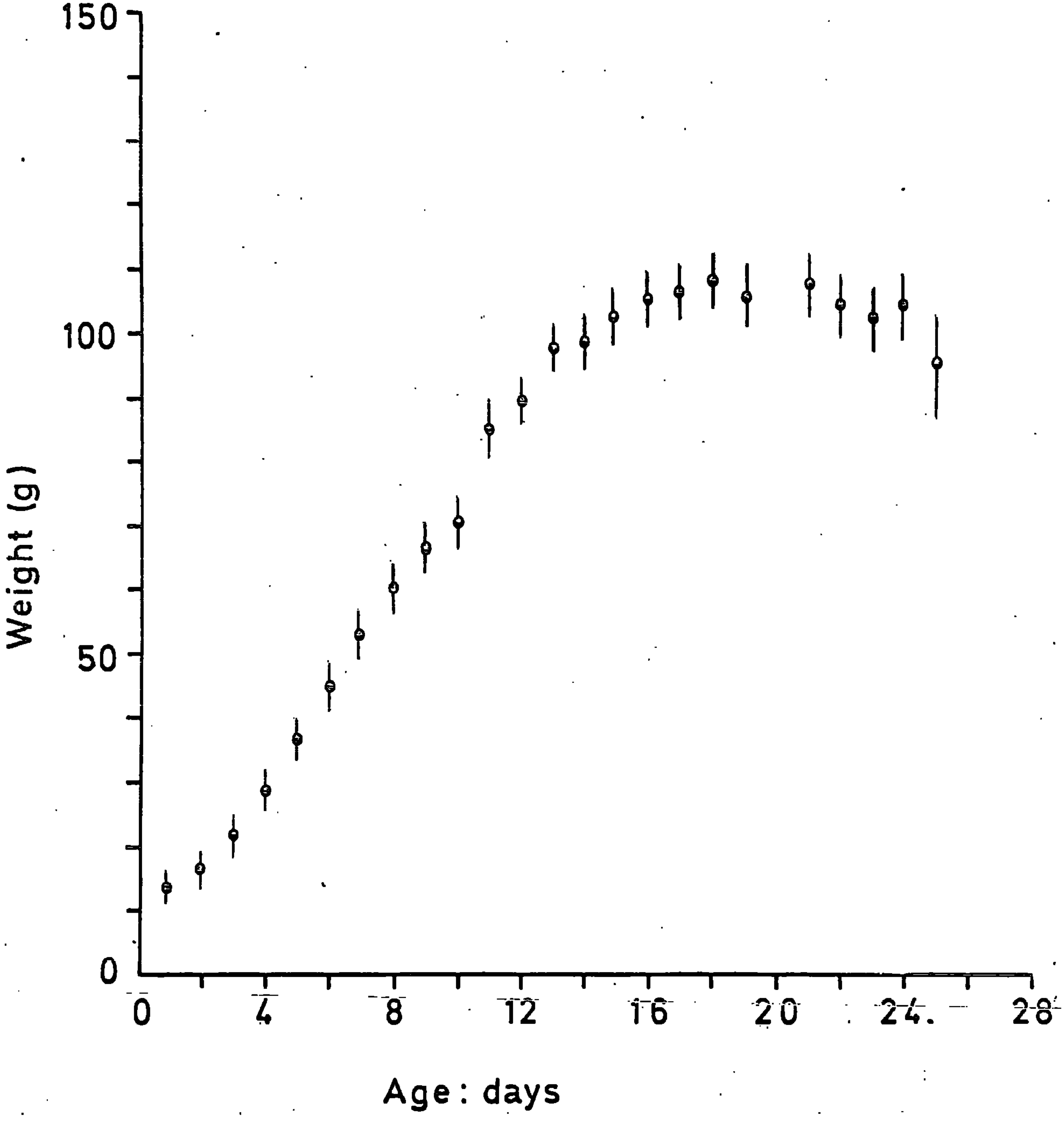
The linearity of daily weight increase from 3-13 days

As mentioned previously, it was decided to compare the daily weight increase of chicks of different categories over the period when weight increased linearly in relation to age. The linearity of the weight increase was tested by dividing

Figure 30 The mean daily weight increase of arctic tern chicks on Inner Farne, 1964.

fig. 30

Mean daily weight increase



the period in half, from the third to the seventh day, and from the eighth to the thirteenth day. The mean daily weight increase of all chicks for these two periods was then calculated, and the difference between the two periods tested for statistical significance. It was found that the mean daily weight increase from third to the seventh day was 7.3 g per day, and from eighth to the twelfth day was 7.1 g. When tested, using Student's 't' test, it was found that $t_{(8)} = 0.039$, $P > 0.90$, and it was concluded that the small difference observed did not affect the linearity of the growth curve.

The mean daily weight increase as a percentage of the adult weight

The mean daily weight increase, measured over the linear portion of the curve of weight increase, was 7.2 g/day. The mean weight of 90 adult arctic terns was found to be 104.3 ± 7.75 g. The mean daily weight increase in chicks, expressed as a percentage of the adult weight, was 6.9 per cent. A similar and comparable figure, derived from weight increase from fifth to fifteenth day in arctic terns, is 6.5 per cent, quoted by Belopolskii (loc. cit.). It would appear that tern chicks of this species increase in weight at much the same rate on the Farnes as they do in the East Murman Sea.

The mean daily weight increase, from the third to the thirteenth day, according to the category of the chick.

In this analysis all the available data were used, including the weights of chicks which had only been weighed twice within the period. It was found that single chicks had a mean daily weight increase significantly greater than the first-hatched chicks in broods of two ($P < 0.05$). Also, second hatched chicks in broods of two had a significantly lower mean daily weight increase than their elder siblings ($P < 0.05$). These data are shown in Table 69.

Table 69 The mean daily weight increase, from 3-13 days, according to chick category

Chick category	No. weighed	Mean daily weight increase in g per day, ± S.D.
Single	101	6.83 ± 1.33 g
1st in B/2	181	6.21 ± 1.79 g
2nd in B/2	108	5.80 ± 1.39 g

The mean daily weight increase from three-seven days compared with the mean daily weight increase from eight-thirteen days

A comparison of the first and second halves of the linear period of weight increase was carried out. A limited amount of data were available, as chicks that had not been weighed consistently were excluded. For the analysis a category was erected to include first hatched chicks in broods of two, where the second chick had died. It was thought that these data might illuminate the differences between single chicks and first hatched chicks in broods of two. Unfortunately, in all cases where data were available, the younger sibling died at an early age. Comparative data on weight increase before and after the death of a younger sibling are lacking. The results of this 'two-period' analysis are presented in Table 70.

The results shown in Table 70 show interesting differences between the categories of chicks. It is apparent that single chicks gain weight at a similar rate throughout the 3-13 day period. However, first hatched chicks in broods of two where the sibling died, show an appreciable difference in mean daily weight increase between the periods, gaining significantly more weight per day during the second period than during the first ($P < 0.001$). In broods of two, first hatched chicks gained weight at a similar rate throughout, whilst their younger siblings increased in weight slower during the first period and faster during the second period, than first hatched chicks ($P < 0.001$).

The results shown in Table 70 also reveal a bias in the data used to calculate the mean daily weight increase according to chick category (Table 69). This bias artificially lowers the value of the mean daily weight increase for second hatched chicks in B/2, and is caused by the disproportionately small numbers of weighings of second

Table 70 The mean daily weight increase in grams in four categories of tern chicks during the first and second half of the period of linear weight increase

Chick category	Mean daily weight increase in grams		
	Period I (3-7 days)	Period II (8-13 days)	Number of chicks
Single chicks	6.6 ± 1.6	6.8 ± 0.9	36
First chicks in B/2 where sibling died	6.6 ± 1.4	7.3 ± 1.3	24
First chicks in B/2	6.6 ± 1.3	6.3 ± 1.2	44
Second chicks in B/2	5.8 ± 1.5	7.0 ± 0.5	45

hatched chicks in B/2 during the second half of the curve of daily weight increase. Thus, an artificially large number of low readings were used. The mean daily weight increase shown in Table 70 has been corrected for this bias, as no chick was included unless it had been weighed at least twice in each half of each period. The values in Table 70 are more accurate than those in Table 69, and it is interesting to note that, after correction, the overall mean daily weight increase in both chicks in B/2 is closely similar.

The mean daily weight increase between 3-13 days in relation to the date of hatching

The mean daily weight increases for the four categories of chicks were examined for seasonal trends by plotting the mean daily weight increase on a scatter diagram according to the date of hatching of each chick. The scatter diagrams showed no discernible trends and it was concluded that chicks hatching at the end of the season (14-15 July) had a mean daily weight increase no different from those chicks hatched a month previously. This was true for all four categories of chicks.

The analysis of daily fluctuations in the mean weight increase of chicks

~~The number of days when sufficient data were available~~ for this analysis was 35. However, the availability of chicks within each category varied from day to day, and on days when only two weighings in any category were available, that category was excluded from the analysis.

The effect of weather on the daily mean weight increase in tern chicks

Three major components of weather which might affect the fishing of adult terns, and hence the amount of food presented to the chicks, were recognised. These were:

a. Wind, which was so correlated with sea conditions as to be inseparable.

b. Rain

c. Temperature

It was also considered that thick fog might hamper fishing activity, but there were no foggy days during the period in question in 1964. Other components of weather were considered unimportant in relation to the birds fishing activities, and were disregarded.

Daily weather observations, mainly of a subjective nature, were made on the Inner Farne. These observations were checked against accurate daily records taken at Belford (5 miles west of Farnes), R.A.F. Acklington (15 miles south of Farnes) and Tynemouth (40 miles south of Farnes). It was found that the temperature readings taken at Tynemouth were very similar to the few readings taken on Inner Farne, and the Tynemouth temperature readings have been used in the analysis. The daily data for rainfall at Belford were used throughout. The wind speed observations from Belford and Inner Farne were so similar that the Inner Farne readings have been used. The observations from Acklington bore little relationship to conditions on Inner Farne. It was thought that this was a result of the geographical position of Acklington, a mile inland, when compared with Tynemouth (observations taken on the pier), and the Farne Islands.

Methods of analysis

A mean daily weight increase for each category of chick according to a particular component of weather was calculated. These data are presented in tabular form in the text. The mean daily weight increases of each category were examined for significant differences in relation to the weather, and because there were less than 30 samples in each category, Student's 't' test was used for this purpose. (Statistical significance was determined at the 0.05 level). Particular attention was paid to the effect of each component of weather on the mean daily weight increase of second chicks in broods of two, as it was thought that these could be used as sensitive indicators of food shortage.

Results

a. The effect of wind on the mean daily weight increase of tern chicks

The effect of wind was analysed in four categories according to Beaufort's Scale of wind speed. The categories were Force 0-1, 2-4, 5-7 and 8. These categories roughly correspond to the following classes of sea conditions,

Force 0-1, little or no breeze, sea flat or slightly rippled
Force 2-4, medium winds, sea choppy
Force 5-7, strong winds, foam-flecked, short and steep seas
Force 8, very strong winds, white-topped waves with strong swell

The results, presented in Table 71, show that calm conditions adversely affected the daily mean weight increase of single chicks, and of second hatched chicks in B/2. On calm days, the mean weight increase of chicks in these categories showed a statistically significant decrease, compared with days when wind speed was above Force 2. It is interesting that, although not statistically significant, a drop in the mean weight increase of the other categories of chicks was observed during calm conditions.

When differences between the mean weight increase on calm days were tested, it was found that second hatched chicks in B/2 gained significantly less weight per day than any other category of chick ($t_{(8)} = 3.5$ $P < 0.01$).

It should be noticed that because all the data were used for this analysis the bias depressing the mean daily weight increase for second hatched chicks in B/2 is present in the

Table 71 The mean daily weight increase of tern chicks in grams, according to the wind speed in 1964

	Wind speed (Beaufort scale)							
Chick category	n	0–1	n	2–4	n	5–7	n	8
Single chicks	5	5.2 ± 0.7	15	6.6 ± 0.9	15	6.9 ± 1.1	3	6.8 ± 0.6
First chicks in B/2 where sibling died	4	5.8 ± 0.8	14	7.6 ± 1.2	11	6.9 ± 0.8	3	6.6 ± 0.5
First chicks in B/2	5	5.8 ± 1.1	15	6.7 ± 0.8	12	7.1 ± 1.2	3	6.3 ± 0.4
Second chicks in B/2	3	3.1 ± 0.4	15	5.8 ± 0.4	12	5.8 ± 0.7	3	5.4 ± 0.8

results in Table 71. The bias was corrected by separating the daily weights of chicks younger than eight days from those of chicks of eight days and older. The means of these two sets of weights were combined to give an unbiased mean weight increase for each day.

Days when only chicks younger than eight days were weighed were excluded, as were days when only chicks of eight days and older were weighed. The corrected daily mean weight increase for calm days, and days with wind conditions of Force 2 and more were compared and the result was unchanged, with second hatched chicks in B/2 still gaining significantly less weight (3.3 g) on calm days than on days with wind (6.7 g).

b. The effect of rain on the mean daily weight increase of chicks

There was no significant difference in the mean daily weight increase between rainy days and dry days. Adult terns' fishing activities did not appear to be hampered by rain and the data support this observation. The mean daily weight increases on rainy and dry days are presented in Table 72. The data were corrected for the effect of wind by excluding days when wind speed was Force 1 or less.

c. The effect of temperature on the mean daily weight increase of chicks

The daily temperatures were grouped as follows:

10-15°C
16-19°C
20-25°C

Table 72 The mean daily weight increase of tern chicks in grams, according to days with and without rain in 1964

		Days with and without rain		
Chick category	n	Rain	n	No rain
Single chicks	7	7.0 ± 0.8	27	6.4 ± 0.6
First chicks in B/2 where sibling died	5	7.1 ± 0.3	22	6.7 ± 0.6
First chicks in B/2	6	6.7 ± 0.5	24	7.1 ± 0.8
Second chicks in B/2	6	5.9 ± 0.4	20	5.7 ± 0.9

Using the corrected mean daily weight increase for second hatched chicks in B/2 and allowing for the effect of wind by excluding days with calm or Force 1 winds, the data are shown in Table 73. It was concluded that temperature had no effect on the feeding of tern chicks.

The daily mean weight increase of chicks according to season

The daily mean weight increase of chicks least affected by wind provided a useful check on the result obtained on p. where no seasonal trend in the mean daily weight increase was found. The daily data for first hatched chicks in B/2, and for first hatched chicks in B/2 where the sibling had died, were plotted as scatter diagrams, but there were no discernible trends.

Two hypotheses may be derived from these results. Firstly, that the availability of fish was similar throughout the season. Secondly, that the availability of fish decreased but that fishing effort and efficiency of the terns increased throughout the season. The net result is, of course, similar. It seems very unlikely that fishing efficiency would increase when the chicks hatch, for the adults have been on the Farne Islands for at least two months and have had ample opportunity to become fully proficient at fishing. However, there is no evidence either way, and in the absence of any information about the fish populations around the Farnes no conclusions may be reached.

Table 73 The mean daily weight increase of tern chicks in grams, according to the temperature, in 1964

		Temperature (°C)				
Chick category	n	10–15	n	16–19	n	20–25
Single chicks	6	6.2 ± 1.3	22	6.2 ± 0.7	7	7.1 ± 0.8
First chicks in Broods of two where sibling died	4	7.3 ± 0.9	16	6.5 ± 0.6	5	6.8 ± 0.5
First chicks in Broods of two	6	7.1 ± 0.9	18	6.5 ± 1.2	6	7.4 ± 0.4
Second chicks in Broods of two	6	5.6 ± 0.8	17	4.9 ± 0.7	5	6.3 ± 0.6

Table 74 The number of days on which first hatched chicks in B/2 gained significantly more weight than second hatched chicks in B/2

	No. days	% Total
1st hatched gained significantly more than 2nd	11	30
1st and 2nd chicks not different	21	70
Totals	32	100

The daily comparison of the mean weight increments of first and second hatched chicks in B/2

The mean weight increase of first and second hatched chicks in B/2 were compared on a daily basis. Data from 32 days were tested. Student's 't' test was used to determine significance for samples of below 30 weighings, and 2 x S.E. of the difference between the means for samples of above 30 weighings. Significance was determined at the 0.05 level. The results are shown in Table 74.

On no occasion did the younger chicks in B/2 gain significantly more weight than their elder siblings. The older chicks gained significantly more weight than younger chicks on eleven occasions. Seven of these days were during or immediately after calm conditions. The remaining four days had weather which was apparently unremarkable.

It is obvious that in summer on the Farne Islands there is normally no shortage of food for broods of tern chicks, and that both chicks are fed broadly similar amounts. However, it is equally obvious that during times of food shortage, however caused, the younger chick suffers most, and gains significantly less weight than its elder sibling. In other words, there is competition for food between nest siblings, at times when food is in short supply.

X GENERAL DISCUSSION

GENERAL DISCUSSION

In the past hundred years few ecological themes have been more discussed than that of competition, particularly competition between apparently ecologically similar animals. The debate on this fundamental problem is by no means exhausted, and its history and recent developments need to be discussed further in relation to this thesis.

The word 'competition' has been used in biological literature with so many vague and ambiguous meanings that Birch (1957) was driven to say that "the word has largely lost its value as a scientific term". Birch (loc. cit.) proposed to restrict the term to a narrow meaning, very close to the etymology of the word, and his definition is "competition occurs when a number of animals (of the same or different species) utilise a common resource which is in short supply." This definition is basically the same as those of Darwin (1857), Crombie (1947), Park (1954) and the latter half of Milne's (1961). Competition in the narrow sense has been used recently by Bakker (1961), Klomp (1961, 1966), Solomon (1964) and Reynoldson (1966).

However, a wider definition of competition has been proposed by Odum (1959) who says that competition refers to the interaction of two organisms striving for the same thing, such interactions involving space, predation, food or nutrients, disease, exudates or light. Still wider is Elton's (1946) definition where competition is used as an objective description of the interplay of various factors favouring one species at the expense of another. (However Elton and Miller (1954) use the word in the narrower sense). De Bach and Sundby (1963), and De Bach (1966) have complicated matters by stating that competition occurs when a resource is utilized by two or more organisms, "even if one does not harm or interfere with the other in the process". Reynoldson (1966) points out that the distinction between De Bach's and other workers 'competition' is in definition only, and that in the particular situation studied by De Bach and Sundby (1963), local food shortages may have arisen.

It seems logical to use the word 'competition' in the sense in which it is understood in every day speech. Thus people compete for a prize, or prizes (in a competition) and the prizes are limited in number. In fact in everyday speech the word is used in the narrow sense, and it is less confusing if the word 'competition' is limited to describing situations where animals strive for a common resource in short supply.

Nicholson (1957) drew attention to the 'contest' and 'scramble' types of competition. In the contest type, successful individuals lay claim to a supply of requisites sufficient to maintain them and to enable them to produce offspring, while in the scramble type of competition, animals obtain different quantities of the requisite according to their individual ability. It has been pointed out (Bakker, 1961) that a small difference in 'competitive ability' is much more serious for the losers in a contest situation, for the unsuccessful ones have nothing, whilst in the scramble situation less successful animals may get some of the supply and be able to survive and perhaps breed. However, when the number of scrambling animals exceeds a certain limit, wastage occurs, and some or all individuals which have secured part of the requisite may die or fail to reproduce because they have secured less than the minimum for survival or reproduction, and the food or part of the requisite such animals have secured, is lost to the species. With the contest type however, the wastage is greatly reduced. In these two sorts of competition the 'quality' of the individual, that is its competitive ability, is involved, and this aspect of competition has not been sufficiently emphasised in the literature.

Competition has been divided into two components, "exploitation" and "interference" by Brian (1956) and Park (1962). Exploitation is defined as "the ability of a species to find, occupy and retain vacant resources" (Brian, 1956). However, as the resource is defined as 'vacant' it is difficult to see how the species could compete for it. De Bach's (1966) definition of competition is open to the same criticisms (Reynoldson, 1966). The second component of competition "interference" is "the ability of a species to damage another, either directly, by attacking its individuals or indirectly by harming its resources or blocking its access to them". (Brian, 1956). It is the direct and indirect aspects of this second component which are similar to the "active" and "passive" components of Birch (1957) and the "direct" and "indirect" categories of Knight-Jones and Moyes (1961). As direct competition in this sense is in fact fighting and as fighting usually occurs intra-specifically it follows that intra-specific competition can be both direct and indirect whereas inter-specific competition is most likely to be indirect.

One of the conclusions drawn from Hairston, Smith and Slobodkin (1960) is that inter-specific competition for a resource exists amongst the producer, carnivore, and decomposer populations in each trophic level, but not among herbivores, which are limited below the levels at which resources are exhausted by predation. Their argument is based on several points, including the observation that green plants are hardly ever depleted by herbivores except when the situation is unnatural (protection by man or introduction into new habitats) and that the vagaries of weather cannot control herbivore numbers. The remaining method of control is by predation, which when removed (spraying with toxic chemicals or shooting out for example), allows the herbivore population to increase and deplete its resources.

From these observations and others, Hairston et al (l.c.)

conclude that predators (and parasites), plants and decomposers are limited by nutrients and space. According to Hairston et al (l.c.) adaptations for inter-specific competition are common in decomposers (antibiotics) and in producers (crowding, shading and zonation). Carnivores are suggested to have side-stepped the problem to some extent by niche diversification as a result of inter-specific competition. It is also pointed out that it is among herbivores "that we find examples of co-existence without evidence of competition for resources".

Although Hairston et al (l.c.) imply that herbivores do not compete for resources, the argument of niche diversification as an indication of previous inter-specific competition can be used against this view. In the case of three congeneric grasshopper species apparently feeding on the same food, it was found by Caplan (1966) that the "overall usage of foods of each species formed a preferential pattern sufficiently different from the patterns of the other two species to indicate that the three grasshopper populations occupy separate niches in the community and are not in complete competition for food". Certain of the other observations suggest that the populations of these three species were also separated in space and the population peaks in time. Data collected from ungulates in E. Africa point to the same sort of conclusion, that although a particular herbivore species may take many plants, a particular plant species is often preferred (Grizmek 1960). Such a preferred plant species amounts to a 'food refuge' similar to that found in triclads (Reynoldson 1966). This can be taken to show that inter-specific competition does, or has, occurred in at least some herbivores, resulting in niche diversification.

Certain of the observations of Hairston et al (1960) refer to competition or co-existence between animals with similar ecology. The idea that no two animals with similar ecology can exist together in the same place for long has been hotly debated since Darwin (1857). Grinnel (1904) grasped the principle in relation to woodpeckers (Udvardy 1959), Volterra (1926) stated the principle and was followed independently, by Lotka (1932) who provided the formal proof using calculus. Gause (1934) freely acknowledged earlier workers, but Lack (1947) was the first to call the principle by its popular name, Gause's hypothesis. More recently Hardin (1960) proposed the term 'competitive exclusion principle' but De Bach and Sundby (1963) and De Bach (1966) prefer the term 'competitive displacement principle' and the converse is called the 'competitive co-existence principle'.

The formulation of the principle has had a chequered history. Following the symposium on 'The ecology of closely allied species' (Anon 1944), Lack (1946) suggested that "two species with the same ecology cannot persist together in the same region" whilst Crombie (1945) stated that two species with "the same ecological niches cannot survive together in the same environment". Mayr (1948) points out that competition (with eventual extinction of one species) would occur if two species had identical ecological requirements and the same has been said by Hutchinson and Deevey (1949) about species with the same niche requirements. The latter definition has been put in a strong form by Savage (1958) who defines Gause's hypothesis as: no two species with identical niches (identical environmental relations) can occur together without one form being eliminated within a few generations by competition".

The terms 'similar ecology' and 'identical ecology' have been dismissed by Gilbert, Hobart and Reynoldson (1952) and Park (1954). These authors point out that two species differentiated by natural selection cannot be ecologically identical, and that animals which are ecologically identical only compete intra-specifically. Reynoldson (1966), Klomp (1961) and Pontin (1961, 1963) mention how the existence of two different species with identical ecology in the same place is extremely improbable. Two of the most recent statements of Gause's hypothesis are those of Mayr (1963) in which it is stated that 'no two species can co-exist at the same locality if they have identical ecological requirements, and De Bach (1966) in which the competitive displacement principle is defined as 'different species having identical ecological niches cannot co-exist for long in the same habitat'.

De Bach's definition is of interest because it shows the difficulty in interpreting definitions where the key words may be misinterpreted. 'Niche' is such a word, having been used in the widest sense to describe habitat or biotope (Udvardy 1959, Savage 1958) and in the narrow sense by Crowell (1962). Crowell (l.c.) used the definition of Parker and Turner (1961) that is: 'niche is the complement of the activities (active, reactive and interactive) of the organism in a given habitat or biotope at a given time'. It is clear that De Bach (l.c.) uses 'niche' in this restricted sense, and habitat in the sense of the large area where particular organisms are found. It should be emphasised that animals have only to be identical in one aspect of their niche before competition occurs, and as pointed out previously, it is extremely unlikely that animals will have identical ecologies.

There are many examples of work which provide evidence for the competitive co-existence principle (De Bach 1966) which is that species which co-exist indefinitely in the same habitat must have different ecological niches. This principle has been stated in different words by Andrewartha and Birch (1954), Hutchinson (1957) and Hardin (1960).

Although conclusive field evidence for this principle has been poor, Orians and Collier (1963), the studies of Lack (1945, 1946), MacArthur (1958) and Crowell (1962), on birds, Carpenter (1952) and Hairston (1957) on reptiles, Heatwole and Davis (1965) on insects and Reynoldson (1966) on triclads have demonstrated the truth of the co-existence principle. Thus in every case where two animals might have been sharing the same niche, further work has shown that in all important essentials the two animals do not compete.

Competition and population regulation are facets of the study of animal populations which cannot be wholly separated. Animal populations are limited in numbers by two main mechanisms, by the destruction of a constant proportion of the population, independent of the population (density independent), and by the destruction of a proportion that increases as the density increases (density dependent). These terms were coined by Smith (1935), and since then there has been much discussion, and argument, as to the relative importance of these factors in regulating animal numbers.

One school of thought is that the most important factors regulating (or controlling) animal numbers are climatic and edaphic (density independent), and that populations are not governed by self-imposed checks (Thompson 1929, 1956). Andrewartha and Birch (1954) advanced a similar idea, their theme being that within the range of an animal species there will be areas of high density in favourable places, while at the edge of the range the distribution will be patchy and the numbers smaller.

The second school, led by Nicholson (1954 a,b,) believes that although the gross distribution of animals is determined by physical factors such as climate, within their range animals survive independent of the environment. Animals regulate their own numbers in relation to the prevailing environmental conditions. Such arguments have recently been supported by Klomp (1962) and Hairston et. al. (1960).

The differences between the two schools of thought are largely due to differences in emphasis and definition (Varley 1963). Some authors (Milne 1957, Cragg 1961) have suggested that populations may be regulated for long periods without invoking density dependent mechanisms, and this might be the case particularly in an area with a severe climate. Such a view is quite compatible with both schools of thought, and a recent paper by Bosch, Schlinger, Lagace and Hall (1966) has emphasised how easily density dependent interactions between animals are overshadowed by weather, other biotic agents or agricultural practices. The situation with regard to the regulation of animal numbers has been summed up by Elton (1966), who says: "For if one fact is certain it is that somewhere at some time in some species everyone of these factors will be found acting as the chief or even the only limit to numbers. Similarly, somewhere at some time in some species, almost every conceivable combination of these factors will be operating in complex interaction. And a particular species may not be limited in the same fashion at different times and places.'

The relevance of competition and population regulation to the present study is most obvious in *Necrophorus*, which provide a good example of a population apparently limited in numbers by competition for a resource. The limited resource is food, or rather, a corpse on which to rear the young. The number of corpses on Inner Farne utilised by *Necrophorus* appears to be much less than the number of corpses produced each season. Closer examination shows that this situation on Inner Farne is caused by the unavailability of corpses, because they appear before *Necrophorus* emerge or after the beetles die, or during the period of pre-reproductive feeding, or that corpses occur on the rocks or in the sea where they cannot be utilised, or even that too many corpses in relation to mature *Necrophorus* appear at once. Superficially the large mortality of terns should provide enough corpses for beetles to reproduce without competition but in practice this never happens. As Bakker (1962) pointed out, competition occurs because the demand exceeds the immediate supply. In fact there is a relative shortage of suitably aged and sited corpses available for *Necrophorus* on Inner Farne, and this causes the competition for the corpses which are suitable.

The corpse is buried co-operatively, often several beetles of both sexes are present and there is no fighting. However when the corpse is finally below ground the majority of the beetles are eliminated by fighting, either escaping or being killed and eaten underground. Beetles only grapple with those of the same sex, and as there is only one brood per corpse,the number of corpses available at the right time determines the number of broods and hence the size of the population in the next year. During the competition for the corpse, the beetles of either sex with the most appropriate "competitive ability" (Bakker 1961) oust the others and are able to reproduce in isolation.

The present study has now shown what are the most appropriate competitive abilities for Necrophorus, but observation indicates that size is of little importance, small beetles of either or both sexes often being victorious over larger individuals of their own sex. Possibly the most pugnacious beetles are victorious, and if the behavioural change is associated with a gonadal change, then the victors may be those with the most mature gonads. This would ensure that the corpse is utilised immediately, an advantage in situations where the food can quickly deteriorate.

It is difficult to see where the major factors controlling or regulating Necrophorus population density occur. It is tempting to describe the competition for a corpse on which to reproduce as the final regulating factor, the severity of the competition increasing at high beetle densities and decreasing at low densities. Although this much is true, the nature of the corpses available to Necrophorus on emergence is a factor which determines how many beetles areable to mature their gonads. Adult Necrophorus are primarily predators of dipteran larvae found on corpses, and it is possible that the ability of Necrophorus to destroy its major competitors, fly larvae, decides the reproductive success of a population, and hence its density, or there may well be a major parasite of Necrophorus undiscovered in this study which depresses their numbers. The role of fly larvae in the ecology of Necrophorus is equivocal, the larvae being the main food source for the beetles as well as their main competitors. However, as long as there is sufficient food available for gonad maturation, and so long as the mites deal successfully with dipteran infestations, it is fairly certain that the major factor limiting the number of Necrophorus populations is the availability of suitable corpses.

With a constant supply of suitable corpses at a restricted period in time during the reproductive period, there will always be competition for them, and this situation is perpetuated so long as every pair of beetles produce more than two beetles to join the next generation. If all the suitable corpses are utilised, and every corpse produces more than two beetles of either sex which enter the next generation, then the next year will see extremely vigorous competition for the available corpses. In years with fewer corpses, than normal e.g. 1964, competition will be very fierce, while in the following normal year (1965) there may be sufficient corpses for the beetles to reproduce with little competition. However, given a second normal year (1966) competition will again be fierce. Over-production of young is the rule in Necrophorus, and this allows the beetles to utilise unusually large amounts ofcarrion when these become available, e.g. during myxomatosis.

Competition within the genus Necrophorus is avoided by two mechanisms which have general applicability, separation of species in time, and in space. The Farne Islands Necrophorus demonstrate the separation of two populations in time; the two species breeding at different times of the year. N. humator finishes breeding before N. investigator, and the only time when these two species may be found on the same corpse is when N. humator is feeding prior to hibernation and N. investigator is feeding after reproduction.

Spatial separation of Necrophorus beetles was demonstrated by Pukowski who showed that in Germany the species reproducing at similar times tend to occupy different habitats, e.g. N. vespillo prefers open fields, N. humator damp deciduous woods and N. vespilloides coniferous woods. Spatial separation in this way is also shown by many birds, e.g. Tetraonidae (grouse, ptarmigan).

A different aspect of inter-specific competition of vital importance to Necrophorus breeding success is the way in which the mites Parasitus necrophori confer protection to the beetle by destroying dipteran eggs and larvae. This association points to a long-continued relationship between these two species. Under field conditions, where the beetles may not reach and bury the corpse until up to two days after death, the role of the mites may be even more important than in the laboratory situations studied during the present work.

The relationship with the mites is another facet of the social organisation of Necrophorus, for, as da Costa (1963) has pointed out, it is likely that social organisation and brood care by the host may be essential before successful associations between insects and mesostigmatid mites can evolve. Hughes (1959) has suggested that it is probable that associations where the immature stages of mites obtain food from the excretions of the beetle larvae, or from their dermal secretions, are more common than is generally supposed. The inability of P. necrophori to reproduce without the presence of Necrophorus seems to be a similar case, and the substance in question may well be the contents of the fore-gut with which the beetles baste the corpse. In this relationship, the mites might almost be described as an integral part of the social organisation of the beetles, taking the role of a defence system, and gaining advantages such as transport, shelter ~~and food from the beetle.~~

The study of the mortality of arctic terns provided little direct evidence of the ways in which tern populations are limited in numbers. As stated previously, population regulation can occur by the action of weather and other extrinsic factors (density independent), or by competition for food, space or other requisites (density dependent). Weather appears to be a major factor in killing chicks, for if heavy rain falls when the majority of the chicks are less than 48 hours old, mortality is high. Some arctic terns on Inner Farne nest in apparently unsuitable places amongst thick vegetation, and this factor increases the chick mortality considerably. The depressing effect of the weather on chick survival is shown by the numbers of chicks fledged per brood in 1963, a wet year, and 1964, a dry year. In 1963 the average number of chicks fledged from single broods was 0.7, and in broods of two 0.6, whereas in 1964 the equivalent figures were 0.9 and 1.6 chicks.

Food appears to play an unimportant part in determining chick or adult survival, although some of the evidence points to decreased fishing efficiency during certain weather conditions, and subsequent competition for food amongst nest siblings.

Space to breed appears to be the most important factor in regulating the numbers of arctic terns. Because there are apparently no more nest sites in the Cove, an ideal nesting area, arctic terns are nesting in the nearby tall vegetation, and this factor considerably increases the mortality. This occurs in spite of the fact that there are apparently suitable sandy areas on other islands away from the main colony, and seems to be similar to the situation found by Nelson (1966) in gannets *Sula bassana* L., and Patterson (pers. comm.) in black-headed gulls *Larus ridibundus* L., and Coulson and Hickling (1964) in the grey seal *Halichoerus grypus* L., where the animals choose to breed under crowded conditions. In the Cove there is much mortality caused by young chicks trespassing and being killed by adults, and a similar phenomenon has been described by Pettingill (1939), Sprunt (1948) and Paludan (1951). This pecking could be a density dependent check on numbers, the frequency of trespassing increasing as the density increases until so many chicks are killed in this way that recruitment ceases. It appears that in a colonial bird like the arctic tern, regulation of the breeding population is most easily achieved by competition for space, particularly if the tendency is for the birds and their chicks to be site tenacious, as in gannets (Nelson 1966), and if the most suitable breeding areas are limited in extent, as on the Farnes. In areas of high density, mortality by pecking is severe, and in more unsuitable areas mortality from other factors is apparently equally severe. It is significant that the arctic tern population on Inner Farne has remained static at between 1000 and 1250 nests for about 10 years, and that terns ringed as young chicks on Inner Farne are being recovered breeding on Coquet Island 25 miles further south, but not elsewhere. It could well be that the Inner Farne colony is at full capacity now, although there is still room for expansion, particularly in the Meadow, and on others of the Farne Islands group. Experimental evidence is lacking, but much could be done by artificially increasing the density of terns in the Cove on Inner Farne.

This study emphasises the interdependence of factors which at first sight might appear quite separate. It is reasonable to assume that the tern population on Inner Farne is limited by space in which to breed, and the numbers of tern corpses available to <u>Necrophorus</u> have an ultimate limit. The fluctuations in <u>Necrophorus</u> numbers and also of the associated mites, are dependent on the numbers of dead tern chicks, which in turn are dependent on the degree of crowding within the colony, the weather and other factors. For instance, a period of rain can affect the <u>Necrophorus</u> population by killing more tern chicks than normal, and similarly a dry breeding season can depress <u>Necrophorus</u> numbers because the terns survive better than usual. Although the study is not the study of a food chain, it throws into sharp relief the interdependence of animals.

> "Strange combinations out of common things....
> Which meet from all the points of heaven,"

Percy Bysshe Shelley. Prometheus Unbound,
1820.

SUMMARY

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1. A study of the biology of Necrophorus (Col.) and the breeding mortality of arctic terns (Sterna paradisaea) is described. The work was carried out on the Inner Farne, one of the Farne Islands, Northumberland, U.K.

2. Two species of Necrophorus, N. investigator Zett., and N. humator Ol., occur on the Farne Islands, and their life histories were studied using a baited pit-fall trap technique. A branding method was used to mark beetles individually.

3. N. humator emerged in late April and was active until August. Callow individuals were caught in September and October, and these hibernated and emerged the following Spring.

4. N. investigator emerged in July and was active until October. The larvae hibernated as prepupae, and emerged the following July.

5. Dissection showed that in both species the fat body and gonads were undeveloped on emergence, but that over 70% of N. investigator and of N. humator had mature ovaries a month after initial emergence. Laboratory experiments showed that females could only develop mature eggs after laying down extensive fat body, and that gonad maturation took 14 days from emergence.

6. The post-reproductive life of N. investigator and N. humator was 10-11 days.

7. Estimates of the *Necrophorus* population of Inner Farne, using mark and recapture techniques, showed that *N. investigator* was more abundant (400 animals) than *N. humator* (100 animals).

8. Initial catches of both species of *Necrophorus* were not at random in relation to area, but were distributed according to the distribution of carrion the previous season.

9. A survey of the carrion available to *Necrophorus* showed that *N. investigator* utilised tern chicks and *N. humator* eider ducklings. Preference experiments in the field and laboratory suggested that small birds are preferred to rabbits for burial.

10. The mean number of eggs laid by *N. investigator* was 11.1, and by *N. humator* 12.5. In both species, over 80% of the eggs hatched.

11. The eggs hatch in 5 days from laying, and the larvae pass through 3 instars, being fed by the female during the first instar, and at the beginning of the second and third instar. The larvae died when the female was removed at these crucial times.

12. The survival of larvae, from first instar to emergence as an adult was 83% in *N. investigator*, and 86% in *N. humator*. The mean length of the pupal period in *N. investigator* was 26 days, and 29 days in *N. humator*.

13. Newly emerged individuals of N. humator survive for only 5 days without food.

14. The relationship between the mite Parasitus (Poecilochirus) necrophori and Necrophorus beetles was examined, and infestations of between 10 and 30 mites per beetle were common.

15. Infestations of mites were low on immature and mature individuals of N. investigator (16.2 mites/beetle) but high on spent beetles (31.8 mites/beetle). A similar situation was shown by N. humator.

16. High-density mite infestations (360-800/beetle) on spent females in culture were shown to be reduced to a more normal level (30-40) when the beetles were allowed to fly freely.

17. A series of choice experiments showed that Parasitus necrophori preferred Necrophorus to Carabus spp., and to Silpha carinata.

18. The role of the mites in the ecology of Necrophorus was investigated in experimental cultures, and it was found that the mites ate the eggs and small larvae of Calliphora on the corpse, which Necrophorus alone were unable to eradicate.

19. The experimental cultures also showed that the mites reproduce at the same time as Necrophorus and up to a dozen mites may attach themselves to the beetle larvae and pupate with them in the soil.

20. Arctic terns return to the Farne Islands in late April, and occupy pairing territories prior to egg laying. The eggs were laid in territories often different from the pairing territories.

21. Egg laying is highly synchronised, 65.2% of the eggs were laid within a week of the first egg. Arctic terns normally lay 2 eggs, the laying interval between 1st and 2nd egg is 44 hours.

22. Replacement clutches were laid if the first clutch was lost, but in cases where the first egg was lost before the second was laid, a third egg was not normally laid.

23. Incubation was intermittent until the second egg was laid, and the mean incubation period from the laying of the first egg was 21.6 days.

24. The mean hatching success was 52%, and predation by starlings (<u>Sturnus vulgaris</u> L.) was the major cause of egg loss, accounting for up to 35% of the eggs laid. Other causes of egg loss were infertility, failure to hatch, puncturing by adult terns, and mammalian disturbance.

25. Chicks fledged between 21 and 26 days after hatching and fledging success varied between 60% in 1963, and 88% in 1964.

26. Most chick mortality occurred during the first week of life, when 20-30% of those at risk died. Four categories of chick mortality were important, killed by adults, exposure, starvation and desertion. Chicks in the Cove

area were more liable to die from adult attacks, but survived heavy showers and prolonged rain better than chicks in the Gut Garden. Early mortality was heaviest in the Gut Garden, where thick vegetation chilled chicks after rain.

27. Over 18% of the chicks in the study areas starved to death in 1963, but only 3% starved in 1964. Most birds dying of starvation were free flying juveniles.

28. The second chicks in broods of two survived less well than their siblings, particularly under adverse conditions. During the first week of life, second chicks suffer double the mortality of first-hatched chicks.

29. The curve of daily weight increase in chicks is sigmoid and between the third and thirteenth day after hatching, the mean daily weight increase was approximately linear at 7.2 gm/day.

30. The mean weight of 90 adults was 104.3 ± 7.75 g.

31. The mean daily weight increase of single chicks was 6.83 ± 1.33 g, of first chicks in broods of two 6.21 ± 1.79 g and of second chicks in broods of two, 5.80 ± 1.39 g. These differences were significant at the 0.05 level.

32. Single chicks and first hatched chicks in broods of two gain weight at a similar rate between 3-13 days, but second hatched chicks in broods of two gain weight more slowly during the first half than during the second half of the period.

33. The mean daily weight increase of each chick category did not vary according to the date of hatching.

34. Calm weather decreased the daily weight increase of all chicks, and second hatched chicks in broods of two gained significantly less weight on calm days than on other days. Rain and temperature had no effect on the daily weight gain of chicks.

35. Second hatched chicks in broods of two never gained significantly more weight than their elder siblings. It was concluded that in years of good weather and adequate food supply adult terns may rear two chicks successfully, but that in adverse conditions only the first hatched survive.

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APPENDIX: THE ANALYSIS OF THE MARK AND RECAPTURE DATA FOR *NECROPHORUS*

Appendix

This appendix includes the methods and data used to calculate the population estimates, expectancy of further life and the mortality estimates of Necrophorus.

1. Population estimates

Initially the method of Leslie et al (1953) was used to give population estimates, and for this purpose the recaptures of marked and unmarked animals were tabulated according to the date of their last previous capture. The recaptures arranged in this way are shown in Table 75 to Table 78 for both sexes and both species of beetle.

The following estimates were obtained from the tables of recaptures:

$\hat{\psi}\ t$ - the total number of animals captured at least once, which were alive in the population as a whole at time t. (The maximum-likelihood estimate).

$\check{N}_t$ - The total number of animals alive at the time of trapping $_t$, incorporating a correction for small number (Bailey, 1952).

The formulae from which these estimates were derived are as follows:

$$\hat{\psi}\ t = \frac{n_{t+1}\,C_t}{m_{t_1\ t+1}} + S_t \qquad (A)$$

$$\text{with variance} = V(\hat{\psi}_t) = (\hat{\psi}_t + u_t)^2\ \frac{n_{t+1}}{S_{t+1}\ m_{t_1\ t+1}} \qquad (B)$$

$$\overset{v}{N}_t = \frac{t\ (C_t + 1)}{(S_t + 1)}$$ (The correction for small numbers involves adding 1 to the total catch C_t and 1 to the total of marks S_t) (C)

with variance $$V(\overset{v}{N}_t) = \overset{v}{N}_t^{\,2} \left(\frac{u_t}{(S_t + 2)\ (C_t + 1)} + \frac{V(\hat{\psi}_t)}{\hat{\psi}_t^{\,2}} \right) \quad (D)$$

where S_t is the sum of the numbers of animals recaptured at time $_t$, which were last captured at time x (x = 0, 1, 2, 3, ... t-1), and is composed of two observed values n_t and $m_t - 1$,

where $$n_t = \sum_{x = o}^{t-2} m_{x_t};$$

C_t is the number of animals captured at time $_t$; u_t is the number of unmarked animals captured at time $_t$.

As mentioned previously the population estimates obtained by this method had large variances. To gain the death rate (μ_t) the successive survival factors ($\hat{P}_t$) from time $_t$ to $_{t+1}$ were calculated, and $$\hat{P}_t = \frac{\hat{\psi}_t + 1}{(\hat{\psi}_t + \gamma_t)} \quad (t = o, 1, 2, \ldots\ldots, T - 2),$$

where $\gamma_t = R_t - S_t$.

The death rate μ_t = the force of mortality between $_t$ and $_t + d_t$, then $P_t = e^{-w\mu_t}$, and it follows that $\mu_t = \dfrac{-\log_e \hat{P}_t}{w}$

where w is the time interval (= 1 in this study).

Many of the estimates of the death rate gained by using this method were innaccurate, negative death rates appearing on several occasions. It was concluded that the biology of

Table 75 The distribution of ♂ N. investigator recaptures according to the interval since the last previous capture (M_{xt}), arranged after Leslie et al (1953).

Date when last previously captured (x)	Date of capture (t) (week ending)										
	July			August				Sept			Oct
	14	21	28	5	12	19	26	2	9	23	6
14 July			2	1	1						
28 July				17	3	7	8				
5 August					3	10	9	1	1		
12 August						5	3		3		
19 August							29		9		
26 August								6	40	2	
2 September									3	1	1
9 September										4	2
23 September											1
6 October											
Total marks (S_t)	0	0	2	18	7	22	49	7	56	7	4
Total unmarked (u_t)	4	0	65	32	8	50	105	1	9	1	0
Total catch (C_t)	4	0	67	50	15	72	154	8	65	8	4
Total release (R_t)	4	0	67	50	15	72	154	8	65	8	4

Table 76 The distribution of ♀ *N. investigator* recaptures according to the interval since the last previous capture (M_{xt}), arranged after Leslie et al (1953)

Date when last previously captured (x)	Date of capture (t) (Week ending) July 14	21	28	August 5	12	19	26	Sept 2	9	23	Oct 6
14 July		1	1								
21 July			1								
28 July				22	2	3	16				
5 August					2	5	18	1	1		
12 August						1	2		1		
19 August							13	2	2	1	
26 August								5	53	3	1
2 September									5	1	0
9 September										4	4
23 September											1
6 October											
Total marked (S_t)	0	1	2	22	4	9	49	8	62	9	6
Total unmarked (u_t)	2	0	69	18	2	20	33	1	11	0	0
Total catch (C_t)	2	1	71	40	6	29	82	9	73	9	6
Total release (R_t)	2	1	71	40	6	29	82	9	73	9	6

Table 77 Distribution of ♀ N. humator recaptures according to the interval since the last previous capture (M_{xt}), arranged after Leslie et al (1953)

Date of capture (t) (Week ending)

Date when last previously captured (x)	Apr	May				June					July				Aug
	28	5	12	19	26	2	9	16	23	30	7	14	21	28	5
28 April		3	2	1						1	6	1			
5 May			2			2									
12 May				2	1	1		No recaptures	1	2	11	2	1		
19 May											1		1		
26 May						1									
2 June													1		
9 June											1				
16 June															
23 June															
30 June											2				
7 July								No recaptures				3		1	
14 July													1		
21 July															1
28 July															
5 August															
Total marked (S_t)	0	3	4	3	1	4	0	0	1	3	21	6	4	1	1
Total unmarked (u_t)	14	1	25	3	1	1	1	0	0	0	3	2	0	0	0
Total catch (C_t)	14	4	29	6	2	5	1	0	1	3	24	8	4	1	1
Total release (R_t)	14	4	29	6	2	5	1	0	1	3	24	8	4	1	1

Table 78 Distribution of ♂ *N. humator* recaptures, according to the interval since the last previous capture (M_{xt}), arranged after Leslie et al (1953)

Date of capture (t) Week ending

Date when last previously captured (x)	Apr	May				June					July				Aug
	28	5	12	19	26	2	9	16	23	30	7	14	21	28	5
28 April		2	2	2	1	3		1		1					
5 May			2			1									
12 May				1	2	3		1		1	1				
19 May					1	2					2				
26 May						1		1	1		2				
2 June							1	1			6		1		
9 June															
16 June									1	1	1			1	
23 June										1	1				
30 June											2	2			
7 July												4	1		
14 July															
21 July															
28 July															
5 August															
Total marked (S_t)	0	2	4	3	4	10	1	4	2	4	15	6	2	1	0
Total unmarked (u_t)	15	0	8	2	1	4	0	1	0	1	5	1	1	0	0
Total catch (C_t)	15	2	12	5	5	14	1	5	2	5	20	7	3	1	0
Total release (R_t)	15	2	12	5	5	14	1	5	2	5	20	7	3	1	0

Necrophorus, in particular the disappearance of marked animals underground for long periods and then their reappearance, prevented the use of this method for estimating death rates.

A more recent method of analysis, using the last previous captures but tabulated in a slightly different way to Leslie's, has been developed by Jolly (1965). In this method, the probability of an animal surviving from one sample to the next sample is derived, and this is different (and probably more realistic) than Leslie's method where it is assumed that any group in the population has an exact survival rate per unit of time.

The following estimates were derived from the tables of recaptures according to Jolly (1965).

$\hat{P}_i$ = the estimate of population on day i

$\hat{M}_i$ = the estimate of the total number of marked animals at risk in the population on the sampling day α_i = the proportion of marked animals in the population at the moment of capture on day i.

The formulae from which these estimates were derived are as follows:

$$\hat{P}_i = \frac{\hat{M}_i \ n_i}{r_i} \tag{1}$$

$$\hat{M}_i = \frac{a_i \ Z_i}{R_i} + r_i \tag{2}$$

$$\alpha_i = \frac{r_i}{n_i} \tag{3}$$

where in (1) and (2) a_i is the total number of animals released on day $_i$ and subsequently recaptured (R_i); Z_i is the number marked before time $_i$ which are not caught in the i th sample, but are caught subsequently; r_i is the total number of marked animals recaptured on day i, and n_i is the total number captured on day i.

The total population for each day is then estimated as:

$$\hat{P}_i = \frac{\hat{M}_i}{\alpha_i} \qquad (4)$$

The probability that an animal alive at the moment of release of the i th sample will survive until captured in the i th + 1 sample is given by

$$\hat{\phi}_i = \frac{\hat{M}_{i+1}}{\hat{M}_i - r_i + a_i} \qquad (5)$$

which is converted to a loss effect (death or emigration) by

$$Y_i = 1 - \hat{\phi}_i \qquad (6)$$

The approximate variance of $\hat{P}_i$, the population estimate, was obtained by:

$$\operatorname{var}(\hat{P}_i/P_i) = P_i(P_i - n_i)\left(\frac{M_i - r_i + a_i}{M_i}\left(\frac{1}{R_i} - \frac{1}{a_i}\right) + \frac{1 - \alpha_i}{r_i}\right) \qquad (7)$$

The tabulation of the recaptures according to Jolly's method are set out in Tables 79 a, b to 82 a, b, for both species and each sex.

Both methods were expected to show large standard errors attached to the population estimates, principally because of

Table 79a The distribution of recaptures of ♂ *N. humator* tabulated according to Jolly (1965)

	Total (n_i) captured	Total (a_i) released	Week when last captured ( )													
			Apr	May				June					July			
			28	5	12	19	26	2	9	16	23	30	7	14	21	28
28 April	15	15														
5 May	2	2	2													
12 May	12	12	2	2												
19 May	5	5	2	0	1											
26 May	5	5	1	0	2	1										
2 June	14	14	3	1	3	2	1									
9 June	1	1	0	0	0	0	0	0								
16 June	5	5	1	0	1	0	1	1	0							
23 June	2	2	0	0	0	0	1	0	0	1						
30 June	5	5	1	0	1	0	0	0	0	1	1					
7 July	20	20	0	0	1	2	2	6	0	1	1	2				
14 July	7	7	0	0	0	0	0	0	0	0	0	2	4			
21 July	3	3	0	0	0	0	0	1	0	0	0	0	1	0		
28 July	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	
	R_i	=		3	9	5	5	9	0	4	2	4	5	-		

Table 79b The distribution of recaptures of ♂ N. humator tabulated according to Jolly (1965)

The total number of marked animals recaptured on a given day (i) bearing marks of day   or earlier

	Apr		May			June					July			
	28	5	12	19	26	2	9	16	23	30	7	14	21	28
28 April														
5 May	2													
12 May	2	4												
19 May	2	2	3											
26 May	1	1	3	4										
2 June	3	4	7	9	10									
9 June	0	0	0	0	0	1								
16 June	1	1	2	2	3	4	4							
23 June	0	0	0	0	1	1	1	2						
30 June	1	1	2	2	2	2	2	3	4					
7 July	0	0	1	3	5	11	11	12	13	15				
14 July	0	0	0	0	0	0	0	0	0	2	6			
21 July	0	0	0	0	0	1	1	1	1	1	2	2		
28 July	0	0	0	0	0	0	0	1	1	1	1	1	1	
	10	9	15	16	11	19	15	17	15	4	3	1	-	
	Z_2	Z_3	Z_4	Z_5	Z_6	Z_7	Z_8	Z_9	Z_{10}	Z_{11}	Z_{12}	Z_{13}		

Table 80a The distribution of recaptures of ♀ <u>N.</u> <u>humator</u>

tabulated according to the method of Jolly (1965)

		Week when last captured													
		Apr	May				June					July			
	$n_i = a_i$	28	5	12	19	26	2	9	16	23	30	7	14	21	28
28 April	14														
5 May	4	3													
12 May	29	2	2												
19 May	6	1	0	2											
26 May	2	0	0	1	0										
2 June	5	0	2	1	0	1									
9 June	1	0	0	0	0	0	0								
16 June	0	0	0	0	0	0	0	0							
23 June	1	0	0	1	0	0	0	0	0						
30 June	3	1	0	2	0	0	0	0	0	0					
7 July	24	6	0	11	1	0	0	1	0	2	0				
14 July	8	1	0	2	0	0	0	0	0	0	0	3			
21 July	4	0	0	1	1	0	1	0	0	0	1	0	0		
28 July	1	0	0	0	0	0	0	0	0	0	0	0	1	0	
	R_i =		4	21	2	1	1	1	0	2	1	3	1	-	

Table 80b The distribution of recaptures of ♀ *N. humator*, tabulated according to the method of Jolly (1965)

The total number of marked animals recaptured on a given day (i) bearing marks of day j or earlier

	Apr			May				June				July		
	28	5	12	19	16	2	9	16	23	30	7	14	21	28
28 April														
5 May	3													
12 May	2	4												
19 May	1	1	3											
26 May	0	0	1	1										
2 June	0	2	3	3	4									
9 June	0	0	0	0	0	0								
16 June	0	0	0	0	0	0	0							
23 June	0	0	1	1	1	1	1	1						
30 June	1	1	3	3	3	3	3	3	3					
7 July	6	6	17	18	18	18	19	19	21	21				
14 July	1	1	3	3	3	3	3	3	3	3	6			
21 July	0	0	1	2	2	3	3	3	3	4	4	4		
28 July	0	0	0	0	0	0	0	0	0	0	0	1	1	
	11	11	29	30	27	28	29	28	27	7	4	1	-	
$Z_{(i-1)+1}$	Z_2	Z_3	Z_4	Z_5	Z_6	Z_7	Z_8	Z_9	Z_{10}	Z_{11}	Z_{12}	Z_{13}	. . .	

Table 81a The distribution of recaptures of ♂ *N. investigator* tabulated according to the method of Jolly (1965)

		Week when last captured									
		July		August				Sept			Oct
	$n_i = a_i$	14	28	5	12	19	26	2	9	23	6
14 July	4										
28 July	67	2									
5 August	50	1	17								
12 August	15	1	3	3							
19 August	72	0	7	10	5						
26 August	154	0	8	9	3	29					
2 September	8	0	0	1	0	0	6				
9 September	65	0	0	1	3	9	40	3			
23 September	8	0	0	0	0	0	2	1	4		
6 October	4	0	0	0	0	0	0	1	2	1	
	R_i =		35	24	11	38	48	5	6	1	-

Table 81b The distribution of recaptures of ♂ N. *investigator* tabulated according to the method of Jolly (1965)

The total number of marked animals recaptured on a given day (i) bearing marks of day j or earlier

	July		August				Sept			Oct
	14	28	5	12	19	26	2	9	23	6
14 July										
28 July	2									
5 August	1	18								
12 August	1	4	7							
19 August	0	7	17	22						
26 August	0	8	17	20	49					
2 September	0	0	1	1	1	7				
9 September	0	0	1	4	13	53	56			
23 September	0	0	0	0	0	2	3	7		
6 October	0	0	0	0	0	0	1	3	4	
	2	19	36	25	14	55	4	3	-	
	Z_2	Z_3	Z_4	Z_5	Z_6	Z_7	Z_8	Z_9		

Table 82a The distribution of recaptures of ♀ *N. investigator*, tabulated according to the method of Jolly (1965)

		Week when last captured										
		July			August				Sept			Oct
	$n_i = a_i$	14	21	28	5	12	19	26	2	9	23	6
14 July	2											
21 July	1	1										
28 July	71	1	1									
5 August	40	0	0	22								
12 August	6	0	0	2	2							
19 August	29	0	0	3	5	1						
26 August	82	0	0	16	18	2	13					
2 September	9	0	0	0	1	0	2	5				
9 September	73	0	0	0	1	1	2	53	5			
23 September	9	0	0	0	0	0	1	3	1	4		
6 October	6	0	0	0	0	0	0	1	0	4	1	
	R_i =		1	43	27	4	18	62	6	8	1	

Table 82b The distribution of recaptures of ♀ N. **investigator** tabulated according to the method of Jolly (1965)

Total number of marked animals recaptured on a given day (i) bearing marks of day j or earlier

	July			August				Sept			Oct
	14	21	28	5	12	19	26	2	9	23	6
14 July											
21 July	1										
28 July	1	2									
5 August	0	0	22								
12 August	0	0	2	4							
19 August	0	0	3	8	9						
26 August	0	0	16	34	36	49					
2 September	0	0	0	1	1	3	8				
9 September	0	0	0	1	2	4	57	62			
23 September	0	0	0	0	0	1	4	5	9		
6 October	0	0	0	0	0	0	1	1	5	6	
	1	0	21	44	39	8	62	6	5	-	
	Z_2	Z_3	Z_4	Z_5	Z_6	Z_7	Z_8	Z_9	Z_{10}	Z_{11}	

the relatively low incidence of recaptures. This was particularly the case with N. humator, where the population estimates must be regarded as giving only a rough guide to the numbers present. Similarly, both methods gave unreliable estimates for the death rate of both species, and the derivation of death rate estimates by these methods for Necrophorus populations is regarded as being valueless.

The weekly mortality was finally derived from the recapture data by arranging the data in a simple trellis diagram according to the date when the beetles were first marked (Tables 83 to 86). The average weekly mortality was then found using the formula:

$$M_w = \frac{D_1 + D_2 + D_3 \text{.........}}{D_1 + 2D_2 + 3D_3 \text{.........}}$$

where D_1, D_2, D_3..... represents the number of deaths in the 1st, 2nd and 3rd weeks after marking. The number of deaths was determined by subtracting the number of marks captured on week D_2 from the number of marks released on week D_1, then subtracting the number of marks recaptured on D_3 from those recaptured on D_2 and so on. A worked example clarifies this procedure: Take the 15 males of N. humator marked on 28 April, and the numbers recaptured out of these 15 animals from 29 April- 25 June. Then taking approximately weekly intervals:

	Initial	May				June					July	
	no. marks	5	12	19	26	2	9	16	23	30	7	14
No recaptured	15	2	2	2	1	3	0	1	0	0	1	0
No. dying (D_1,D_2...)	13	0	0	1	-2	3	-1	1	0	-1	1	
No. dying x length of life (D_1+2D_2 +3D_3)	13	+ 0	+0	+ 4	+(-10)	+18	+(-7)	+8	+ 0	+(-10)	+11	

Table 83. The number of captures and recaptures of female N. investigator, arranged according to the date of first marking.

	July												August																		September				October	
	7		12		16		25		25		30		5		12		16		18		20		23		25		31		3		6		19		6	
-		-		1						20		-		-						1		3		1				1		1						12
	2		-		1				1		-		2		-				3		1		4		1		1						1		17	
		1		-		1		1		-		4		1		-				2				2				3		1				119		
			2		-		1		-				2		4		-		1		6		2				4		1				22			
				69		-		-						2		4		-		2				1		20						17				
					40		-								3		4		-		1				13		2				57					
						-		-								4		5		-				9		3		1		47						
							6		-						1		3				-						2		28							
		Captures						8		-		1				1		2		3		-				2		27					Marks Released			
									21		-								4		3		-				11									
										16		-								5		1		-		12										
											31		-								1				-											
												35		-										63												
													9		-								68													
														12		-						3														
															61		-				2															
																8		-		2																
																	6		-																	

Table 84. The number of captures and recaptures of male N. *investigator*, arranged according to the date of first marking.

	July												August																September						October	
	7		12		16		25		28		30		5		12		16		18		20		23		25		31		3		6		19		6	
1				-		-		1		15		-		-						1		7		2						2		1				8
	3		-				-		1		-		3		-				2		2		4		1		2		1						14	
		-				1		-		-		3		1		-				2		2		1		1		1						91		
			2				1		-		1		4		11		-		1		2		2		4		4						25			
				65				-		-				6		4		-		1				1		1		1				15				
					50		-				-				3		3		-						17						78					
						-						-				4		4		-				4		2				72						
							15						-		1		4		1		-		1				2		53							
		Captures						23						-				2		2		-				1		66					Marks Released			
									49						-				3		4		-				28									
										43						-				4				-		22										
											52						-				1				-											
												59						-				1		68												
													8						-				69													
														13						-		2														
															52						-															
																9				3																
																	4		1																	

Table 85. The number of captures and recaptures of male *N. humator*, arranged according to the date of first marking.

		April				May																June										July											
		28		29		4		7		11		14		17		18		24		29		2		8		14		18		25		1		7		12		16		25			
			1				1												1										1		1				3								
15				1		1												1				1		1				1		1		1		1		1							
	1				2														1										1				2										2
		1				-								1								1																			5	
			11				1				1		2										1																	13		
				1										2												3														20			
					1				1				1		1												3						1						15				
						1				1										1						2												9					
							3				1						1								2				1								4						
								5				2																								9							
Captures																																							Marks Released			
									8				-						1																2								
										6				1						1														10									
											1				-																		14										
												5				1																24											
													2				-														5												
														5				-												1													
															8				-										2														
																12				-								1															
																	7				-						7																
																		3				-				2																	
																			1						2																		
																								15																			

Table 86. The number of captures and recaptures of female N. *humator*, arranged according to the date of first marking.

		April				May																				June												July												
		28		29		4		7		9		11		14		17		18		24		29		2		8		14		18		25		1		7		12		16		25		30		
	14		2		1					1				1		-		-											-		-				1		2		2		1						2	
		2		1		2				1				-				-				1						-				-				1		1						1		2		
			2		2									-					-						-						-										1				3				
				26										-								-				-										-										13				
					1							-		1		1							-		-										1		-											28				
						2				-														-												-								13					
							2		-								1							-		-														-						5							
								-														-				-																-		2							
									4				1		1						-						-		1				1								-									
										2										-								-										1									
Captures											3						-		1										-								4										Marks Released
											2				-				2				1				-						5											
												1		-						4						1		-				3													
													-								6								-		5															
														1								2								-															
															3								1						3															
																8												3																	
																	16										2																			
																		8						30																					
																			4				4																							
																				1				4																							
																					1		14																							

$$M_w = \frac{\text{Total } D_1,\ D_2 \text{ etc}}{\text{Total } D_1,\ 2D_2 \text{ etc}} = \frac{15}{27} = 0.555 \text{ Or } 55.5\%$$

This method gives the weekly average mortality of beetles marked on a particular date and in the example the males of N. humator marked on 25 April (the beginning of the flight season) had a weekly mortality of 55%. The method has the advantage that standard errors may be attached to each value, and the formula by which the S.E. is derived is:

$S.E. = M_w\sqrt{\frac{S}{N}}$ when S is survival (which is $1 - M_w$) and N is the number dying x length of life ($D_1 + 2D_2 + 3D_3$etc).

The average expectancy of further life, in weeks, was calculated on the assumption that each beetle lived for half the week in which it died or disappeared, ie: animals dying in their second week (present at week 1, absent at week 2) were assumed to have lived for $1\frac{1}{2}$ weeks. For example, if 20 animals were alive at the start and the number of survivors per week is as shown below:

	No. of survivors	No. dying	Average length of life	
	20			
end of week 1	15	5	$5 \times \frac{1}{2}$	2.5
end of week 2	10	5	$5 \times 1\frac{1}{2}$	7.5
end of week 3	5	5	$5 \times 2\frac{1}{2}$	12.5
end of week 4	0	5	$5 \times 3\frac{1}{2}$	17.5
			Total	40.0

Then the average expectation of further life is gained by dividing the total average length of life (40.0), by the original number of animals (20); in this example the average expectation of further life is 2.0 weeks.