THE BREEDING BIOLOGY OF THE HORNED LARK (EREMOPHILA ALPESTRIS ALPESTRIS L.) AT CAPE ST. MARY'S, NEWFOUNDLAND

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THE BREEDING BIOLOGY OF THE HORNED LARK

(*EREMOPHILA ALPESTRIS ALPESTRIS* L.)

AT CAPE ST. MARY'S, NEWFOUNDLAND

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FRONTISPIECE

One-day old Horned Lark Nestlings.
Note the pattern of black dots in
the bright orange-yellow mouth.

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INTRODUCTION

The Horned Lark (*Eremophila alpestris* (L.)) is a Holarctic species, breeding throughout North America and northern Eurasia, with relict populations in the mountains of Colombia and Morocco (Godfrey, 1966). In Eurasia, the species is essentially restricted to arctic and alpine tundras (Vaurie, 1959). However, in North America, where it is the only native lark, it breeds in a variety of barren habitats from the deserts of Mexico to the high arctic tundra (Bent, 1963).

Throughout its range, the Horned Lark shows complex geographical variation, with 21 subspecies being recognized in North America alone (AOU Check list 1957). Due to this multiplicity of subspecies and the wide range of habitats in which it is found, the Horned Lark is an ideal subject for the study of how different environmental regimes affect breeding strategies.

This study deals with the nominate race, *E. a. alpestris* (L.), which breeds on the Gaspé peninsula, Newfoundland, Labrador, and southern Baffin Island, and winters on the Atlantic coast of the United States (AOU Check list 1957, Sutton and Parmelee 1955). To the north, its range merges with *E. a. hoyti* (Bishop), which breeds throughout the Canadian Arctic islands and western tundra (AOU Check list 1957). To the south, the range of *E. a. alpestris* meets *E. a. praticola* (Henshaw), which is found throughout the northeastern United States, southern Ontario and Québec, New Brunswick, Nova Scotia, and Prince Edward Island (Pickwell, 1931).

Although the breeding habits of *E. a. praticola* and *E. a. enthymia* (Oberholser) have been studied quite intensively (Pickwell, 1931; Garrett, 1948; Beason, 1970; Boyd, 1976), little detailed work has been done on the other subspecies of the Horned Lark. Sutton and Parmelee (1955) reported on seven nests of *E. a. alpestris* on Baffin Island, but this is one of the very few published articles dealing specifically with this race.

In central North America, *E. a. praticola* and *E. a. enthymia* lay an average of three eggs per nest, and usually raise two broods each season (Beason, 1970; Boyd, 1976). In the Arctic however, *E. a. hoyti* and *E. a. alpestris* have clutch sizes of four and five, and raise only one brood each season (Sutton and Parmelee, 1955; Drury, 1961). Populations of *E. a. alpestris* in Newfoundland, while breeding at a similar latitude to the previously studied populations of *E. a. praticola* and *E. a. enthymia*, have a much shorter breeding season than the latter races (Beason, 1970; Boyd, 1976; Peters and Burleigh, 1951). This study was therefore undertaken to determine how the breeding habits of the Horned Lark in Newfoundland compare with those reported elsewhere, and also to study the ways in which Horned Larks are adapted to breeding in typically exposed, barren habitats.

MATERIALS AND METHODS

Horned Larks were studied continuously during the 1976 breeding season at Cape St. Mary's (46°47'N, 54°12'W), a headland at the south-western tip of the Avalon peninsula, Newfoundland (Fig. 1). Further observations were made every week in April and every two weeks in February, March, September, October, and November. A single visit was made in April 1977.

Most observations, including those of larks at their nests, were made with the aid of 8 x 30 Bushnell binoculars and a 15-60x Bausch and Lomb spotting scope, without the use of a blind.

One male and fifteen female larks were captured during the summer in order to colour-band them and obtain morphometric data, using a variety of methods: mist-netting at various places on the study area (none caught), mist-netting at the nest (3 females caught), baited clap-nets and a two-celled Potter trap (2 females, 1 male caught), drop-net on nest (1 female caught), and netting females on the nest at night with a butterfly net and a flashlight (9 females caught).

Males could be distinguished from females by their clear pink-brown crown and nape--darker brown and streaked in the female (Beason, 1970)--and their clear-cut black and pale yellow facial markings (these appeared "smudged" in most females)(Plate 1).

Mist-netting was very difficult due to the constant winds on the study area and the high visibility of the nets on the flat barrens habitat. Many unsuccessful attempts were made to catch males in

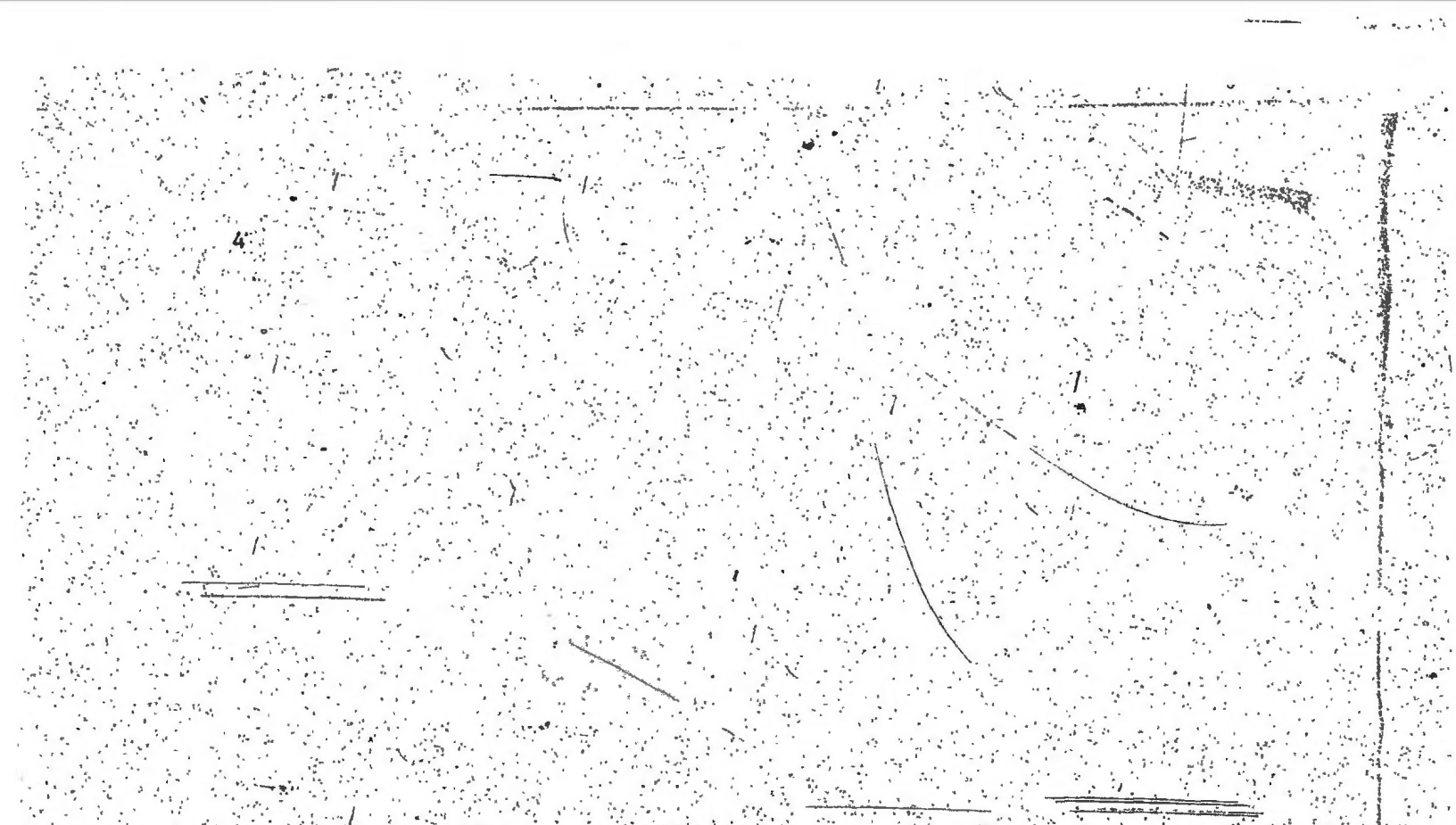


Figure 1

a) The Island of Newfoundland, showing the Avalon Peninsula in black.

b) The Avalon Peninsula; the star indicates the location of Cape St. Mary's.

c) Detail map of Cape St. Mary's; study area is outlined by the dotted line. Contours are in intervals of 50 ft. (15.4 m).

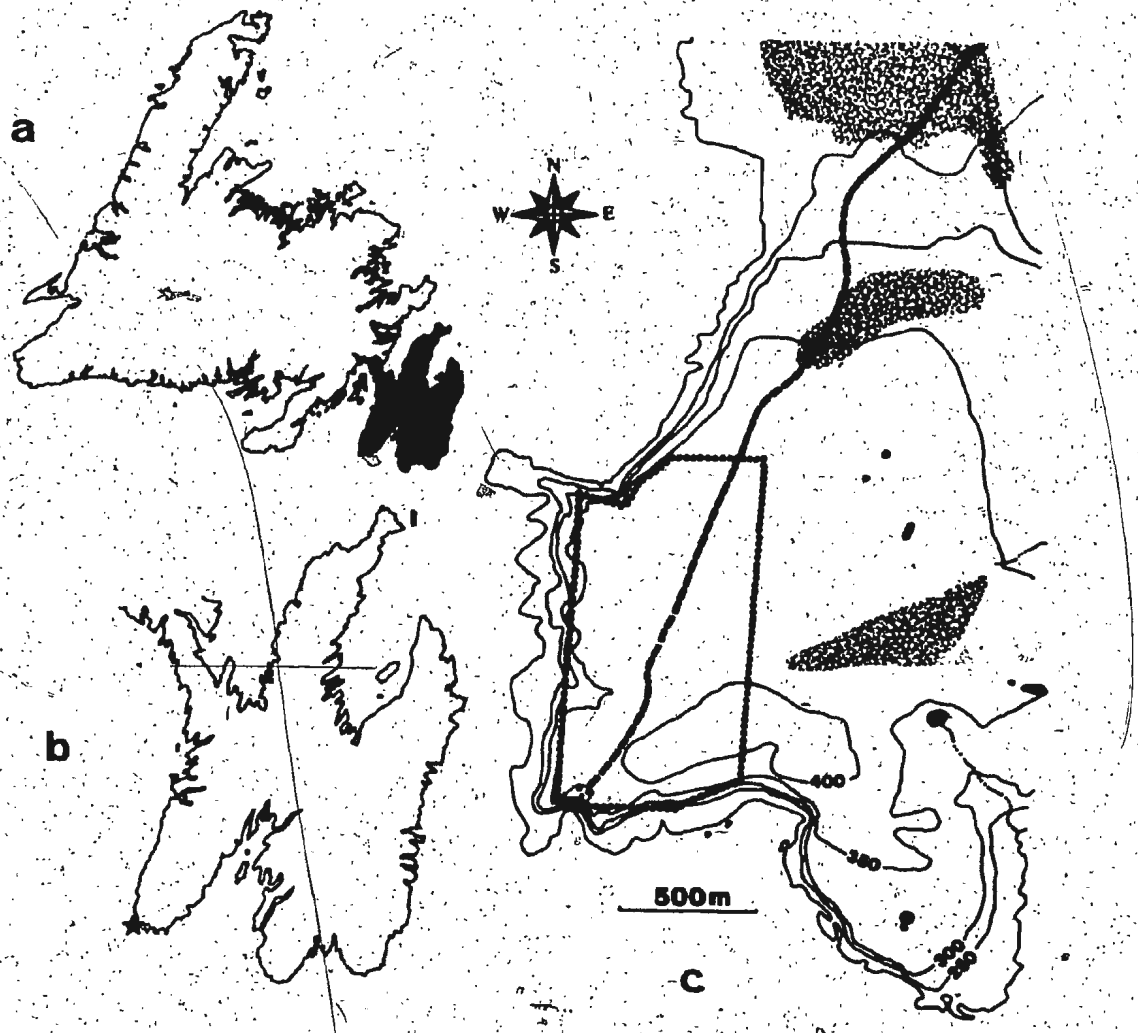

a
N
W
E
S
b
400
300
500m
c

Plate 1a

Female Horned Lark

Eremophila alpestris alpestris

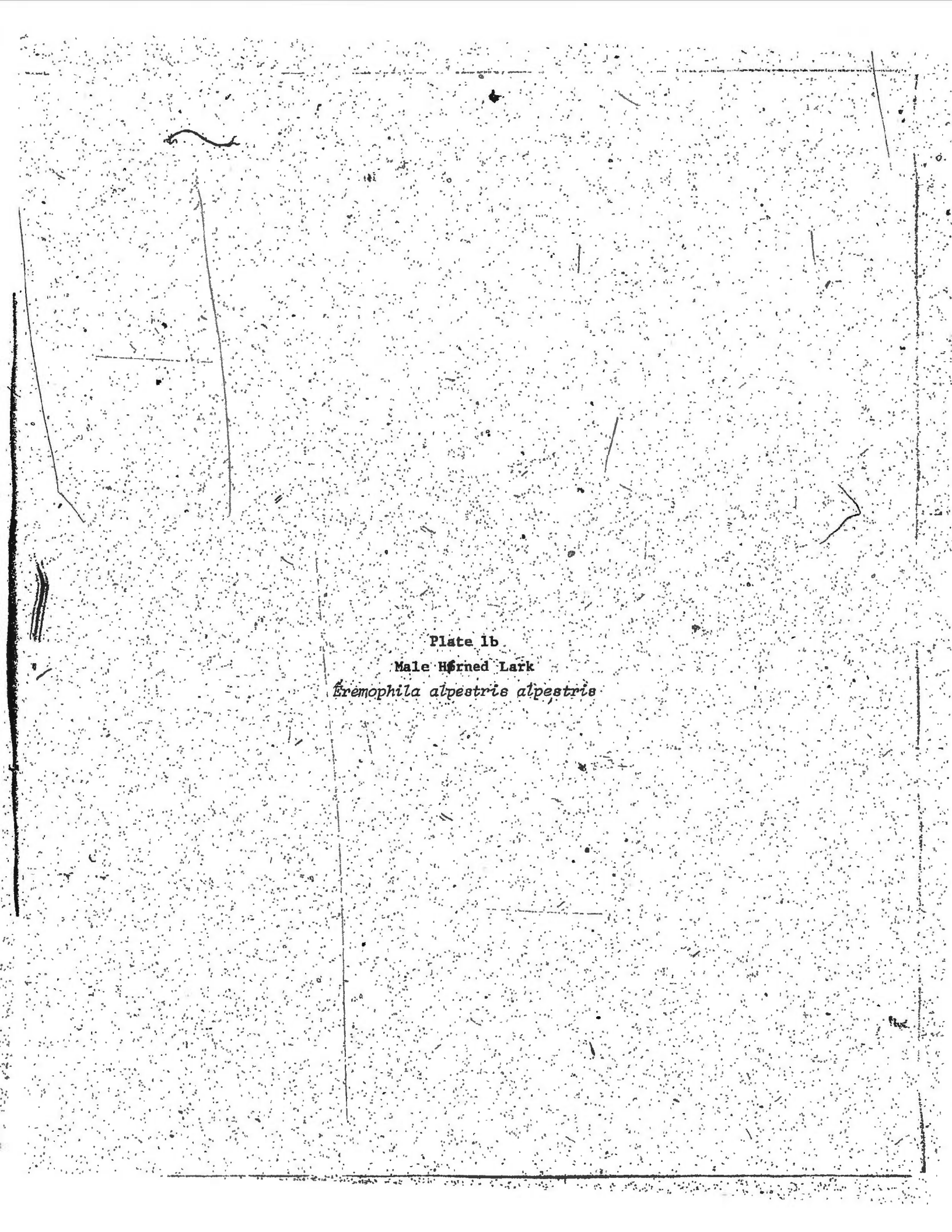


Plate 1b

Male Horned Lark

Eremophila alpestris alpestris

clap-nets set on boulders and knolls used as song posts. The one male caught was captured in a clap-net set on a boulder used as a perching site before feeding the young in the nest.

Both females that were caught on nests during incubation deserted the nests; none of the females with young did. Delius (1965) states that female skylarks (*Alauda arvensis* L.) will desert if trapped on the nest too early in incubation.

One interesting observation arising from this night-netting procedure was the ability of the females to find their nest at night, even in thick fog, after being displaced 30 m or so.

Each individual captured was banded with an aluminum Fish and Wildlife band and a unique combination of plastic colour bands. Two instances of birds pecking and pulling at their bands were noted; one two months after banding. Beason (1970), also reported this behaviour in Horned Larks.

In this thesis, individual adults will be referred to by a letter prefix (FM-female, M-male) followed by a numeral (e.g. FM3 was the third female captured).

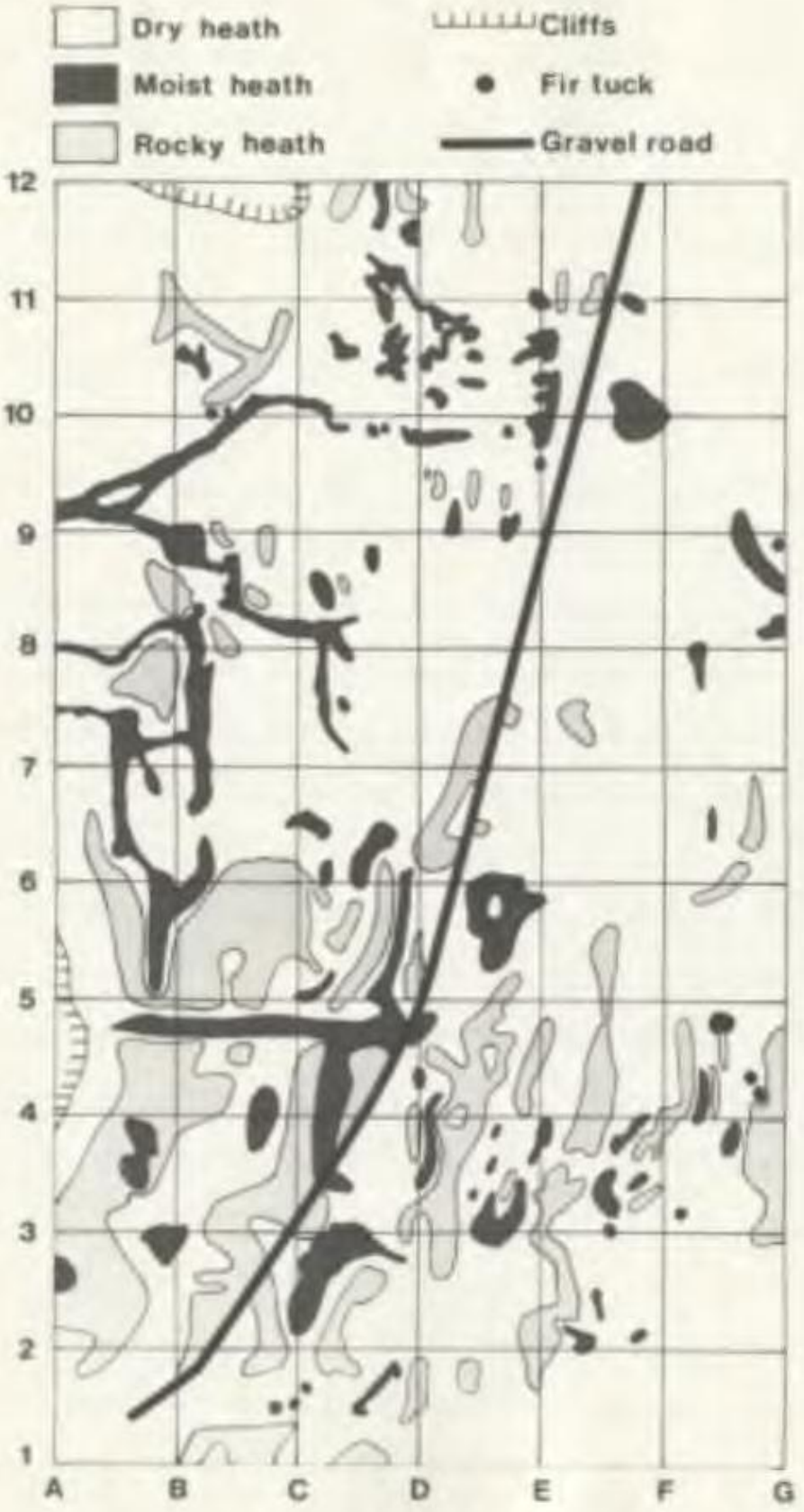
Individuals were weighed to the nearest gram in a cloth bag hung from a 300 g Pesola scale, and were measured with a millimeter ruler and dividers. Measurements taken were: culmen, tarsus, wing chord, and tail (as described in Godfrey (1966)), and hallux plus claw and first and ninth primaries (as described by Beason (1970)).

To aid the mapping of habitat and territories, a grid was set up covering an area 600 x 1000 m, with 5 x 5 x 100 cm marker posts every 100 m (Fig. 2). Each territory mapped was subsequently given a letter

Figure 2.

Map of study area showing the grid used for habitat analysis and territory mapping. Vegetation samples were taken at the intersection of Columns B, D, and F, and rows 2, 4, 6, 8, and 10, as well as grid point B12.

The "Rocky Heath" habitat is essentially the same as Meades' (1973) "*Diapensia* heath", the "Dry Heath" habitat the same as Meades' "*Rhacomitrium* barrens", and the "Moist Heath" corresponds to lush *Potentillum* heath and soft ground heath (Meades 1973).


Dry heath
Moist heath
Rocky heath
Cliffs
Fir tuck
Gravel road
12
11
10
9
8
7
6
5
4
3
2
1
A
B
C
D
E
F
G

designation (Fig. 3). Territories were mapped by repeatedly flushing individuals or pairs and recording their positions with regard to the gridpoints. Territorial hostilities, such as threat displays and flight chases, were also considered in the mapping of territories.

Vegetation cover was recorded in 1 m^2 plots at every other gridpoint.

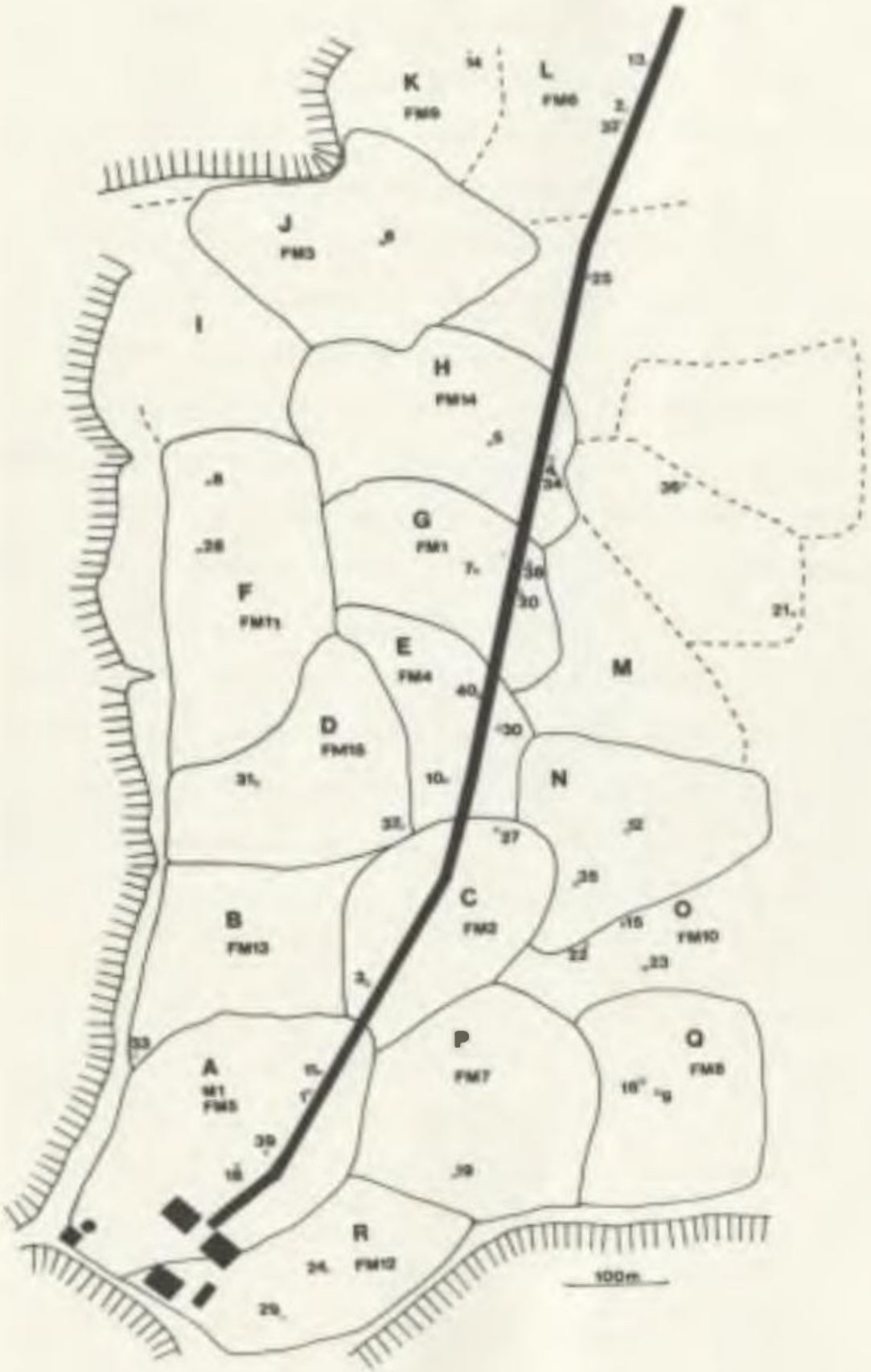
Song counts were made at various times of the day by counting the song bouts heard from one spot for one hour. Song bouts, which were initially quite short (about one minute) and constant in length, were used as the unit of measurement instead of individual songs because of the problem of quantitatively equating the intermittent and recitative song forms (Pickwell, 1931). As the season progressed, however, bout length increased drastically, and the song counts became quantitatively meaningless, although they did provide a good qualitative impression of singing rates through the day and season.

Nests were numbered in order of discovery. Those with eggs were usually checked several times daily to discover precise hatching times; those with young were visited at least once daily to take measurements of the nestlings. Measurements were obtained in the same manner as adults, except for the weight, where the nestlings were placed in small plastic bags suspended from a 50 g Pesola scale. To enable individual identification, they were individually marked on the tarsi with indelible ink and banded when seven days old. Young larks were named by their nest number followed by another numeral, indicating the order of hatching when known (e.g. 34-1 was the first young to hatch in Nest 34).

Owing to the extreme wariness of adult larks when feeding young

Figure 3.

Map of study area showing the boundaries of the mapped territories. The large single letter in each territory is the letter designating that territory, the letter-numeral groups (e.g. FM12) indicate the resident adult larks. Nest locations are shown by the small open squares with the nest number.


K
FM9
L
FM6
J
FM3
I
H
FM14
G
FM1
F
FM11
E
FM4
D
FM15
M
N
C
FM2
B
FM13
O
FM10
P
FM7
Q
FM8
A
M1
FM5
R
FM12
100m

in the nest, direct observations of nest-feeding behaviour were sparse.

After the young had left the nests, the nests were measured, collected, and frozen. They were examined later to determine nest composition, dried (at room temperature), and weighed.

To determine if larks placed their nests preferentially with regard to certain types of vegetation, the vegetation in a square meter plot around the nest was recorded to determine plant species composition.

Observations on the other bird species at Cape St. Mary's were made by casual observation and line transects through forest and bog habitats adjacent to the study area (Appendix 1). Measurements were taken of nestlings in four Savannah Sparrow (*Passerculus sandwichensis* Gmelin) nests found; the results are presented in Appendix 2.

Since Verbeek (1967, Delius (1965), and Boyd (1967) claimed that rodents and shrews may be an important source of nest-predation for larks, a grid of 50 Longworth traps covering an area 60 x 60 m was maintained and trapped on the study area in June.

STUDY AREA

The study area at Cape St. Mary's covered approximately 90 ha of headland heath which extends back from the sea cliffs for one to two kilometers (Plate 2, Fig. 2). Using Meades' (1973) classification, the habitat consists of rocky barrens (*Diapensia* heath, *Polygonum viviparum* variant), hard ground heath (*Rhacomitrium* barrens and *Potentilla* heath) and local areas of soft ground heath.

The area is essentially flat (though somewhat undulating in places) and treeless, although a few very stunted balsam firs (*Abies balsamea* (L.) Mills.) grow in locations protected from the wind. See Table 1 for vegetation details.

The habitat is thus very similar to those described by von Haartman (1969) as the breeding habitat of *E. a. flava* in Finland and by Harper (1958) as the breeding habitat of *E. a. alpestris* in Labrador.

CLIMATE AND WEATHER

Cape St. Mary's has a cool, temperate, maritime climate with long, relatively mild winters and short, cool summers (Meades, 1973). Annual precipitation averages 150 cm, spread fairly evenly throughout the year. Fog is extremely common, occurring on about 60% of the days from May to August, 1976, and on 24 days in July alone. Approximately 40% of the summer daylight hours in 1976 were foggy (visibility 25 - 100 m).

Temperatures from May to August varied from 0°C (June 13) to

Plate 2

West side of study area, looking north from near grid point B3

TABLE 1

Plant species recorded at six or more of the 16 grid points sampled, or which constituted more than 25% of the total plant cover at one or more of the points. Numbers following species names indicate the number of nest sites at which the species was recorded; numbers in parentheses indicate the number of nest-sites at which the species constituted more than 25% of the total plant cover.

Empetrum nigrum L.	12 (11)
Cladonia spp.	13 (8)
Empetrum eamesii Fern. & Wieg.	6 (6)
Rhacomitrium lanuginosum (Hedw.) Brid.	11 (11)
Vaccinium uliginosum L.	11 (1)
Foliose lichen spp.	2 (1)
Cornus canadensis L.	15
Vaccinium vitis-idaea L.	14
Betula pumila L.	9
Calamagrostis pickeringii Gray	9
Prenanthes trifoliata (Cass,) Fern.	8
Deschampsia flexuosa (L.) Trin.	8
Maianthemum canadense Desf.	7
Vaccinium oxycoccos L.	6
Myrica gale L.	6

Other plant species recorded at the grid points sampled were: *Dicranum scoparium* Hedw., *D. undulatum* Brid., *Drepanocladus uncinatus* (Hedw.) Warnst., *Hylocomium splendens* (Hedw.)B.S.G., *Hypnum* sp., *Pleurozium schreberi* (Brid.) Mitt., *Rhytidiadelphis triquetrus* (Hedw.) Warnst., *Osmunda cinnamomea* L., *Dryopteris spinulosa* (O. F. Muell.) Watt, *Juniperus communis* L., *Scirpus caespitosus* L., *Carex viridula* Michx., *Polygonum viviparum* L., *Salix ura-ursi* Pirsh, *Ledum groenlandicum* Rets., *Kalmia angustifolia* L., *K. polifolia* Wang., *Andromeda glaucophylla* Link, *Arctostaphylos alpina* (L.) Spreng., *Vaccinium angustifolium* Ait., *Diapensia lapponica* L., *Trientalis borealis* Raf., *Aronia prunifolia* (Marsh.) Rehder, *Fragaria virginiana* Duchesne, *Potentilla tridentata* Ait., *Sanguisorba canadensis* L., *Euphrasia oakesii* Wettst., *Lonicera villosa* (Michx.) R. & S., *Linnaea borealis* L., *Solidago uliginosa* Nutt., *Achillea millefolium* L., *Leontodon autumnalis* L.

23°C (July 12); daily maximums were usually between 10 and 15°C. Winds stronger than 30 kph were common until late June and picked up again in late August. The worst storm of the summer (June 11 - 13) brought 70 mm of precipitation (rain and sleet) and winds up to 120 kph.

Daily weather conditions are summarized in Appendix 3.

RESULTS AND DISCUSSION

ARRIVAL

In Newfoundland, Horned Larks usually arrive in late March or early April, although a few small flocks may overwinter (Peters and Burleigh, 1951; Tuck, 1948; and Tuck pers. comm.). No larks overwintered at Cape St. Mary's in 1975-1976, despite the fact that there was very little snow throughout the season. The only passerines seen on the study area from January to March were Snow Buntings (*Plectrophenax nivalis* L.) and Common Ravens (*Corvus corax* L.).

The first lark seen in 1976 was a male on April 4; that and other lark sightings on the April visits are summarized in Table 2. Although Peters and Burleigh (1951) stated that "large flocks" arrive in Newfoundland in spring, only small groups (1 - 12 individuals) were seen in early April at Cape St. Mary's.

Males certainly arrived first in 1977, but some of the early arrivals in 1976 seemed to be paired. Boyd (1976) stated that males of *E. a. enthymia* arrived on the breeding grounds in Colorado before the females because they are much less migratory; indeed, many males remained in that area all winter, while the females generally migrated to the south. Pickwell (1931) reported that the first larks to return to Illinois in mid-February are resident males, followed closely by a few mated pairs, then the resident females, and Bannerman (1953) stated that *E. a. flava* males arrive in southern Norway about five days before the females.

Although Pickwell (1931) and Dement'ev and Gladkov (1954) stated

TABLE 2

April visits to the study area.

Date	Number of larks seen (Numbers in parentheses indicate sizes of separate groups)	Comments
March 26	0	10 Snow Buntings seen
April 4	1 male	Male seen 3 miles N. of study area. Horned Larks seen on Fogo Is. (300 km N.) today (Maunder pers. comm.) 1 Snow Bunting
April 8	5 (1, 2, 2)	Along road from St. Bride's to Cape St. Mary's (15 km).
April 11	7 (2, 3, 1, 1)	Three near lighthouse, others along road.
April 18	16 (2, 2, 12)	Flock of twelve was of mixed sexes.
April 30	-	Pairs common, also flocks of 3's, 4's, and 5's. Singing and chases common.
April 3, 1977	10 (1, 1, 1, 2, 5)	All birds sexed were male; singing and chases observed, 8 Snow Buntings seen.

that singing begins shortly after arrival on the breeding grounds, no singing or territorial behaviour* was observed from April 4-18, even though the weather was fine (but windy) and females were definitely present on the latter date. Beason (1970) stated that wind inhibited Horned Lark singing, which would explain the differences between the April 1976 visits (wind 30 – 70 kph) and the April 3, 1977 visit (wind 10 kph), when several male larks were observed singing and chasing each other.

At Cape St. Mary's, larks were seen almost exclusively on the dry headland heath; only one lark was ever seen on the extensive barren bogs to the north and east, and that one was flying high overhead. Larks did, however, nest along the roadside through this boggy area, and were also seen in the grassy farm fields at St. Bride's (15 km north), utilizing much the same habitat as *E. a. praticola* does over the greater part of its range (Pickwell 1931).

VOCALIZATIONS

Horned Lark vocalizations can be separated, as can those of most passerines, into calls and songs. Songs referred to here are those described by Tinbergen (1939) as "advertising songs" : "those loud sounds that are given by birds of one sex especially at the beginning of the reproductive period." All other vocalizations are call-notes or calls.

Horned Lark ground songs function in territorial behaviour, song flights are primarily used in courtship, and call notes have a variety of uses (Beason and Franks, 1974).

Songs

Horned Larks have two basic song forms, the intermittent and the recitative (Pickwell, 1931). The commoner of these, the intermittent,

* e.g. threat displays or chases

is a high, tinkling song lasting 1.5 - 2 sec (Beason and Franks, 1974; Boyd, 1976), repeated every 6-10 sec, although the rate may increase at times to once every 3 sec.* A good verbal analogy to this song is Langille's (1892, *vide* Pickwell, 1931) "Quit quit quit you silly rig and get away." If this phrase is spoken rapidly and in high pitch, with the last syllable even higher, one gets a very good impression of the song.

The recitative song has much the same quality as the intermittent song, but is longer and more variable in length, lasting between 5 and 35 seconds. Pickwell (1931) describes this song as a "steady 'pit-wit, wee-pit, pit-wee, wee-pit'." They are usually interspersed in bouts of intermittent songs. However, especially after sunset, male larks are sometimes heard singing recitative songs almost exclusively, pausing briefly between each.

Verbeek (1967) stated that, in the alpine zone, Horned Larks are "the first birds to sing in the morning and the last to sing in the evening." Beason and Franks (1974) heard lark songs as early as 1.7 hours before sunrise. On clear mornings at Cape St. Mary's, a few Horned Larks and Savannah Sparrows were heard singing 1.25 hours before sunrise; 15 minutes later nearly all the male larks were singing in a general chorus. This stage lasted for about one half-hour, at which time there was usually an abrupt lull before the general chorus began again about ten minutes before sunrise. Water Pipits were first heard at this time. Singing continued at a moderate intensity for another four hours, when it would abruptly taper off to a much lower level for the rest of the day.

Singing rate increased abruptly at sunset and continued for about

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* Sonograms in Beason (1970, Fig. 12) and Boyd (1976, Fig. 8).

an hour afterwards. Savannah Sparrows sang for about as long as the larks; Common Snipe (*Capella gallinago L.*) kept bleating afterwards, perhaps continuing all night (Tuck 1972).

Although larks sang a certain amount in foggy weather, there was usually an abrupt increase in singing rate when morning fog cleared off.

Early in May, the mean lengths of individual song bouts during dawn chorus was 30-60 seconds, with a maximum of 90 seconds. On May 20, bout lengths of up to 8 and 9 minutes were recorded, on June 1, 14 minutes, and on June 27, 25 minutes. Beason (1970) stated that bout lengths of Horned Larks in Illinois varied from 2 sec (one song) to 45 minutes, but did not mention any seasonal change.

This increase in bout length over the season may be due to the fact that, during the dawn chorus early in the season, male Horned Larks moved around, perhaps defining the boundaries of their territory. Each of these moves created a pause in singing, thereby shortening bout length. Later, especially in the latter half of June, the males remained essentially stationary during dawn chorus, perhaps because the territorial boundaries needed no further definition. This allowed time for an increase in bout length; the early dawn chorus was usually uninterrupted at this time. Tinbergen (1939) noted this seasonal increase in song bout length in the Snow Bunting.

By July 20, the evening chorus had ended; on July 23 only one lark was heard singing after sunset. The last song of the year was heard on August 8, the same day that the young left the latest nest.

Ground songs can be given while the male is simply walking

along the ground, but are often sung from a raised perch such as a rock, small knoll, or fence post; some males have been observed singing from buildings (Beason 1970), small trees (Kelso 1931), or telephone poles (Sutton & Parmelee 1955). At no time were larks seen at Cape St. Mary's perching on anything higher than a boulder 1m in height, although there were a few buildings, telephone poles, and stunted trees in the study area.

Horned Lark song flights are not as common as ground songs. In this display, the male flies up in a wide helix to a height of about 100-200m (Pickwell (1931) mentions a maximum of 250m, most being delivered at 150 m). As the male nears his maximum height, he begins to sing both recitative and intermittent songs, but, as in ground singing, mostly the latter. Boyd (1976), however, reported that in his study larks seemed to sing mainly recitative songs during song flights.

The male maintains or gains altitude by climbing steadily for five or six seconds, then spreads his wings and tail and glides for about two seconds while delivering the song. When viewed from below, the blackish wings and tail edges are very conspicuous in this glide. While delivering a recitative song in song flight, the male does not glide, but uses a steady flapping flight to maintain altitude.

Pickwell (1931) stated that song flights last from one to five minutes, the average being 2.34 minutes. Verbeek (1967), on the other hand, gave a maximum duration of 11 minutes, and stated that all the song flights he witnessed were longer than five minutes. Beason and Franks (1974) gave minimum and maximum values of 25 sec and 8 min.

Song flights observed at Cape St. Mary's lasted from 25 sec to 14 min in length, with a mean of 3.67 min. (n=24).

At the height of the song flight, the performer generally remained fairly stationary, but often paused in singing to move 100m or more horizontally before resuming, eventually describing a large circle over its territory.

Beason (1970) mentioned one male which was carried by a strong wind well into a neighbouring territory during song flight, but for the most part, song flights took place more or less over the singer's territory.

At the end of a song flight, the lark usually folded its wings and plummeted downwards, opening its wings only 6 or 7m from the ground. This levelled off the dive into a long horizontal glide held for 30 or 40m before landing. Sometimes the descending lark checked its descent higher up, and slowed down in two quick swoops rather than one long one. Occasionally one or two "weet" calls were given during descent. The male often sang from the ground for a short while after a song flight.

Pickwell (1931) stated that only one male is ever in song flight at one time--"[the male] in flight song had exclusive privileges over a wide territory, undisputed, though another might go up as soon as the one in flight came down". Subsequent studies (Garrett (1948), Beason and Franks (1974)) have shown this not to be the case; at Cape St. Mary's eight cases were seen when two males were performing in simultaneous songflights. Three of these cases were seen within the space of one hour on July 17, all involving different males.

Whether the primary function of the song flights is in territorial or courtship behaviour is difficult to establish; as Tinbergen (1939) and as Armstrong (1973) pointed out, a song that attracts females will likely also deter rivals. Pickwell (1931) believed that they served to advertise an occupied territory, and "female ears [were] of little concern to the chorister". Beason and Franks (1974) found that song flights were commonest shortly after each brood left the neat or after the nests were destroyed, and are thus probably epigamic more so than territorial displays. Observations at Cape St. Mary's tended to agree with this; song flights became very common (10-12 seen per day compared with an average of about two) immediately after most of the first successful nests fledged on July 11. The last flight song was heard on August 7.

Calls

Horned Larks have at least four types of calls. The commonest is a clear "weet" or "su-weet", similar to but higher and purer than the Water Pipits (*Anthus spinoletta* L.) "jeet, je-jeet". The weet call can be used as a challenge call, a locating call, an alarm note, or a distress call (Beason and Franks 1974). In juveniles observed in this study this call is more of a "breet" or "djeed".

Two other calls can be considered variations on the weet call. In flight, the weet call is often extended to a clear "weet-it-it", which DuBois (1936) correctly compares to "the travelling calls of the goldfinch". Pickwell (1931) describes it as "zeet-it-it" or "zeet-it-a-weet".

When alarmed, larks began to call much louder, and sometimes changed from "weet" to "weet-it-it" and finally to a loud, rapid "ti-ti-ti-ti".

The fourth call given by Horned Larks in a rich, warbling "sirilip", described in Witherby *et al.* (1965) as "a rich . . . tsee-tsurrp", and probably the same as Beason's (1970) "chittering note". If one imitates the intermittent song as "Quit quit quit you silly rig and get away", the "sirilip" call is very similar to the "silly-rig" section. It is thus quite different from the "weet" or "su-weet" calls.

At Cape St. Mary's, the sirilip call was commonly given by males during pauses between song bouts. For example, in the dawn chorus, most males stopped singing about one-half hour before sunrise and began sirilipping at a rate of about 10-11/min. before resuming singing about 15 min. later. This call was also given by both males and females while feeding, and was given, very loudly, as a challenge call by males to opponents during threat displays. The call was often so quickly repeated in these displays that it built up into a "a perfunctory song", as Sutton and Parmelee (1955) noted.

GENERAL BEHAVIOR

Dust Bathing and Roosting

Horned Larks were commonly seen dust bathing on the gravel roads and on the steep gravel slopes above the sea cliffs. This behaviour was observed from late morning until after sunset, but was commonest in mid-afternoon and around sunset.

When dust bathing, the larks settled down into small hollows

dug in the gravel, fluffed their feathers, vibrated their wings, moved their tail from side to side, and occasionally flicked sand over their backs with the bill. Grit was often picked up and eaten during dust-bathing.

These small dust bathing hollows are likely used as roost holes at night, as they are identical to the roost holes described by Trost (1972) for Horned Larks in the Mojave Desert. When driving along the road at night, larks were commonly seen flushing in front of the car, so they obviously roosted on it. The increase in dust bathing just before dark may be a preparation for roosting. Trost (1972) found that the small hollows used for roosting created a more favourable micro-climate for the larks during the cold nights.

Storms

In windy, stormy weather, larks usually huddled in the lee of grass clumps, and always faced into the wind when not running from place to place. The wind was often strong enough to blow the larks off their feet when they ran. Drury (1961) stated that the elongated hind claw of larks and other ground dwelling passerines (e.g. Water Pipits and Longspurs (*Calcarius* sp.) was an adaptation for firm footing in high winds.

Two or three pairs of larks usually fed together, with minimal aggression, in the lee of the few buildings at the Cape during storms.

TERRITORIES

During the breeding season, Horned Larks maintain territories for courtship, nesting, and feeding (Beason, 1970).

Twelve territories at Cape St. Mary's were mapped accurately enough to calculate the territory sizes; these ranged from 2.313 ha (Territory E) to 5.125 ha (Territory A), averaging 3.542 ha (Fig. 3). Six territories measured at Argentia, Nfld. in June 1973 averaged 3.089 ha (Ryder, pers. comm.).

These areas are comparable to the sizes of early season territories of *E. a. praticola* studied by Pickwell (1931), but are larger than the 0.6 - 3.1 ha values reported by Beason and Franks (1974), also for *E. a. praticola*. Even small territories were recorded by Boyd (1976) for *E. a. enthymia* (0.29 - 1.35 ha) and Lobachev and Kapitonov (1968) for *E. a. albigula* Bonaparte (0.15 - 0.25 ha).

Horned Lark territories at Cape St. Mary's filled all the available suitable habitat, but seemed to be smaller away from the sea cliffs.

Since the gravel road was favoured by male larks for dust-bathing, roosting, and singing, territories along it (e.g. A, C, E, G, and H) invariably took in land on either side of it; the road was never used as a natural territorial boundary. This created a chain of territories along the road, a phenomenon also reported and discussed by Boyd (1976).

Territorial Behavior

Singing and territorial hostilities were evident shortly after the larks arrived in early April and were maintained until the last young left the nest in early August.

Beason divides Horned Lark territorial hostilities into three

types: threat displays (Boyd's (1976) "forage displays"), fights, and chases. These events can occur separately, nut more often occur in conjunction with one another.

In the threat displays observed, one male approached the other by running 30 or 40 cm with head low to the ground, tail fanned and wings drooping, then stopped abruptly and gave a loud "sorilp", standing very erect with neck stretched. This process was repeated until the two larks were 1 or 2 m apart, when they began alternating bowing and standing very erect. The fanned tail was held high when bowing, and there was much displacement feeding at this stage, both males vigorously pecking the ground.

Both Pickwell (1931) and Boyd (1976) noted this apparent displacement behaviour; it was also reported by Tinbergen (1939) in the threat displays of male Snow Buntings.

The tail-fan and bow displays the black borders of the tail over the lowered head, and standing erect while giving the "sirilip" call may serve to display the black chest patch. The rapid bowing may be a ritualization of the displacement feeding, but more field observations would be needed to confirm this.

Beason and Franks (1974) stated: that the challenge calls resembled the "su-weet" calls given in other situations, but were louder. The challenge calls heard at Cape St. Mary's were loud, usually three-syllabled "sirilip" calls.

Threat displays almost invariably ended in a fight, chase, or both. Fights usually began on the ground, but quickly moved to the air, the two birds struggling violently a few metres above the ground.

Most aerial fights ended with the birds separating and landing a few metres apart, the process beginning again with more threat displays.

Sometimes, however, one male would separate from the other and fly away. The second male followed immediately, chasing the other lark low to the ground at high speed matching move for move until one lark landed and the other continued on. If they landed close to one another, the whole process often began again with more threat displays.

It was common to see as many as four males involved in a chase, especially early in the season. Later, chases and fights were only directed at trespassers, and the chases were usually the "tit-for-tat" type described by Pickwell (1931) and Tinbergen (1939) in which chaser became chased each time the territorial boundary was crossed. These chases usually ended with both birds alighting in their respective territories, one or both of them singing.

Males in flight or song flight were not always immune from such attacks (as Pickwell (1931) claims) - on July 11 M1 was attached while in song flight over the southern edge of Territory B by the male from that territory.

The great majority of agonistic behaviour in Horned Larks is restricted to male versus male territorial hostilities. Beason and Franks (1974) stated that "territories are defended only by males, and only against males", although Pickwell (1931) reported a female with a young bird just out of the nest attacking an intruding male. Boyd (1976) observed a female whose mate had disappeared giving threat displays to neighbouring males.

At Cape St. Mary's, several instances were recorded in which

female larks were definitely involved in agonistic behaviour.

On May 6. two pairs were seen feeding together near the lighthouse. The two males occasionally engaged in short fights and chases, and the females ran and pecked at each other several times.

On June 25, two females and one male were observed feeding together near the conjunction of Territories B, C, D, and E. The females showed much agonistic behaviour towards each other: one ran quickly at the other, body and head held low to the ground, and the second female gave a loud challenge call, standing erect. This process went on in much the same manner as in male threat displays, and ended in a minor aerial fight. The male took no part in these displays, and eventually all three larks flew south into the thick fog. Unfortunately, all three were unbanded, so their territories or breeding conditions could not be ascertained, but they were probably from Territories B and D, as the females in C and E had been banded.

On July 20, FM2 was seen on the northwest corner of her territory (C), "weeting" loudly. The female from Territory D flew in, also calling. FM2 ran at her, "sirilipping" loudly and flicking her wings rapidly; then flew back to her territory. FM2 had 18-day old juveniles in the vicinity, and may have been acting to protect them.

A female lark was seen on July 27 60 m ESE of grid-point E7. She then flew to a point 25 m ESE of E7, where another lark flew at her and drove her away to 30 m NW of F7. Neither lark was identified as to individual.

On August 4, FM4 chased FM15 out of Territory E, and on the same day an unbanded juvenile (more than six weeks old) ran at and chased FM1 in Territory G.

Female hostilities thus seem to be directed primarily at other females, in a similar, though not so frequent, manner to that described by Tinbergen (1939) in Snow Buntings.

Territorial fights and chases were common in late April, May, June, and July, becoming rare by the end of the latter month. Hostilities thus seemed to be more spread out through the season at Cape St. Mary's than other studies (Pickwell, 1931 and Beason, 1970) on Horned Larks have indicated.

Some of the later hostilities may have involved new or non-territorial, non-breeding males in the population. It was impossible to determine if and when any males disappeared or if any new males replaced them, since all except one of the males on the study area were unbanded. Beason (1970) stated that territorial fights occurred for about two weeks after a new male replaced a male which had disappeared.

With the large territories and very foggy weather found at Cape St. Mary's, it may have been more difficult for male larks to police their boundaries, leading to a greater prevalence of unchallenged trespasses and thus prolonging territorial disputes.

Territorial trespassing was fairly common at Cape St. Mary's. FM13 was once observed gathering food for her nestlings in the immediate area of Nest 18, 150 m from her territory. She was completely ignored by FM5 and M1, who were feeding young in Nest 18 at the time.

Larks from territories which did not take in the gravel road (e.g. Territory N) were sometimes seen dust-bathing on the road. More often than not, these larks were not attacked, although some clashes did take place in similar situations.

Individual territories broke down as soon as breeding ended, that is, when the last brood left the nest. Independent juveniles are not challenged on foreign territories, although young larks out of the nest still being fed by their parents seemed to be guided by their parents to remain within the territory.

On July 27, 13 unbanded larks (five males, two females, and six juveniles) were seen feeding in the northeast part of Territory A. Although M1 (from Territory A) still had young in Nest 39, and was only 30 m away, he did not challenge this flock.

From that time on, small flocks of unbanded larks were a common sight on the study area, and little or no agonistic behaviour was noted between them and the resident larks.

COURTSHIP DISPLAYS

Courtship displays were seen nine times at Cape St. Mary's. These displays contained the following elements in common with the territorial threat displays: wing-drooping, stretching, bowing, and tail-fanning.

The male would approach the female with body held low to the ground, wings drooping and quivering (wing-quivering was never seen in threat displays), then bow and fan the tail. When the male stretched and held his head high, the black breast feathers were usually raised, enlargening the breast patch.

Copulation never followed any of the coutship displays observed. Males attempted to mount several times, but each time the female side-stepped or fended him off with a kick of the foot. Often the female ran at the male as he approached. Boyd (1976) observed copulation after a

male approached a female in a similar manner, but with something in his bill. In this case, too, the female ran at him twice, but on the third approach squatted with wings drooped and quivering, and copulation followed. Beason and Franks (1974) observed copulation following an invitatory display by the female with no accompanying male display. They also reported an instance of courtship feeding followed by copulation. Pickwell (1931) mentioned seeing one female "flutter and crouch before him as one observes the female House Sparrow do so frequently."

The similarity of this invitatory display to the dust-bathing behaviour described previously was demonstrated in three instances where males attempted to mount dust-bathing females.

In the first incident, two females and a male were seen dust-bathing on the gravel road near Territory L. After a few seconds, the male approached one of the dust-bathing females, fluttering his wings rapidly, and attempted to mount her, but the female sidestepped quickly. This process was repeated three times, whereupon the male flew at the female and chased her for about 40 m.

On July 6, a pair of larks flew to the gravel road, and the female began dust-bathing. The male immediately approached the female, wings drooped and fluttering. The female ran at him and drove him away; the male approached once again, but with similar results. At this the male began dust-bathing himself.

An incident almost identical to this one, although involving a different pair, was witnessed on July 23.

No male-female chases were seen which could definitely be called

"sexual chases" as described by Beason and Franks (1974).

NESTING

In Newfoundland, Horned Larks usually begin nesting in mid-May to early June; second broods, if any, occur in July and early August. The earliest known nesting date for the island can be extrapolated from a three-week old juvenile collected in St. John's on May 26, 1968; this bird must have come from a nest begun around April 24. The latest date is Tuck's report of almost flightless young at Argentia on September 11, 1947 (Peters and Burleigh, 1951).

At Cape St. Mary's, nesting behaviour was observed from May 13 (nest-building) until August 8, when the young left the last nest.

Since most nests found already contained eggs, dates of nesting starts were determined (and hence defined) by calculating when the first egg was laid (assuming an 11-day incubation period).

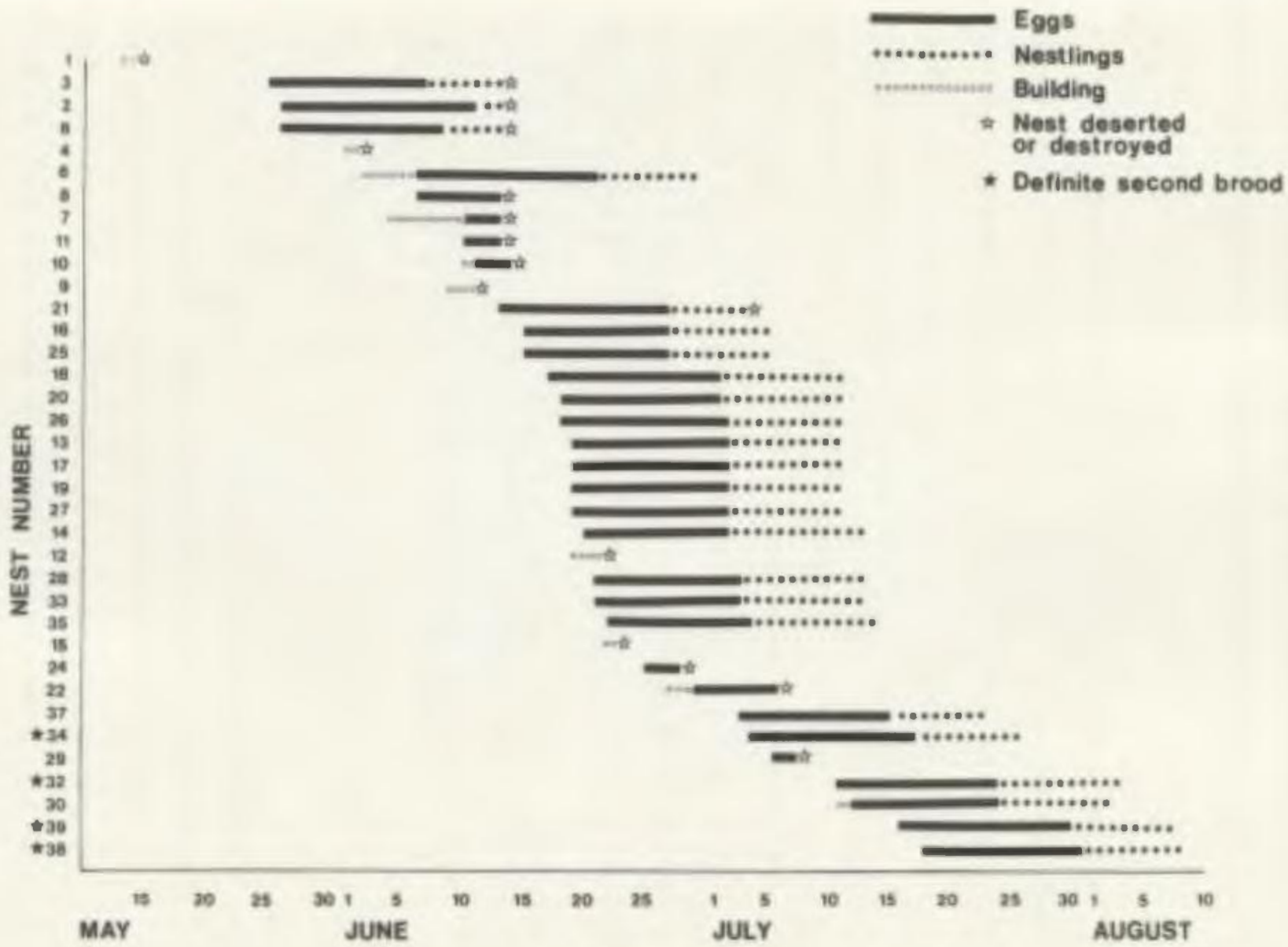
Nesting starts were initially spread over a two-week period from about May 25 until June 11. A heavy storm on June 12 - 13, however, destroyed all nests with young, and caused desertion of all but one known nest (Nest 5) with eggs. Three nests found after the storm (Nests 16, 21, and 25) were probably built before June 12, and may have survived the storm due to the fact that incubation had not begun.

Ten nests were found which had been started between June 15 and June 21, with no subsequent starts until July 3. The June 12 storm thus had a very noticeable synchronizing effect on nesting times (Fig. 4).

The earliest known second brood was started on July 4 (Nest 34), in Territory H, where one of the few nests to survive the storm was

Figure 4

Nesting phenology of Horned Larks in 1976
at Cape St. Mary's


Eggs
Nestlings
Building
Nest deserted or destroyed
Definite second brood
NEST NUMBER
1
3
2
8
4
6
5
7
11
10
9
21
16
25
18
20
26
13
17
19
27
14
12
28
33
35
15
24
22
37
★34
29
★32
30
★39
★38
15 20 25 30 1 5 10 15 20 25 1 5 10 15 20 25 30 1 5 10
MAY
JUNE
JULY
AUGUST

located. Three of the later nests (Nests 32, 38, and 39) were second broods in territories whose nests had not survived the storm.

Nest-finding

One of the major tasks on a study of passerine breeding biology is finding the nests of the breeding birds. Without this knowledge, little can be deduced as to breeding success, breeding strategies, or other problems associated with the eggs or nestlings of the species. In a study of larks--small, ground-nesting birds with large territories--nest finding can be a difficult and time-consuming problem.

In the present study seven nests, in all stages of development, were found by luck, nine nests were found by watching the female bring nesting material to them, 18 nests with eggs were found by watching the female return to them, and six were found by watching the adults bring food to the young.

Two of the nests found by luck had been destroyed, the scattered grass and feathers making their position obvious; two others were empty and never did contain eggs.

Five nests were found on June 22 alone (two by luck); Pickwell's record of seven nests found in one day was never reached.

The most reliable way to find nests is by patient observation, from a distance, of a "broody" female. When a lark nest containing eggs or newly-hatched young was approached, the female will usually fly off at a distance of 50 - 100 m--the "casual abandonment" described by Pickwell (1931). This distance generally decreased in bad weather and towards nightfall, and varied between individuals. For example, at

0430 on June 1, FM2 left Nest 3 at a distance of 5 m; this distance increased to 15 m by 0600 and to 50 m by 1030. FM6, however, would usually allow approach to within 1 or 2 m of Nest 13 before flushing.

After leaving the nest, the female usually ran back and forth some distance from the nest, constantly displacement-feeding. She then gradually approached the nest and, if the observer was far enough away (usually more than 30 m), finally returned to it, generally in 5 - 15 minutes.

In bad weather, when the females stayed on the nests until the intruder was only a few metres away, several nests were found by methodically traversing suspected nesting areas until the female flushed.

Nests with young, although blatantly advertised by adult birds carrying food, were, for two reasons, often more difficult to find than nests with eggs. Firstly, at this stage, the adults were very hesitant to return to the nest while humans were within even 100 m of it. Therefore, one had to watch their activity from a great distance, usually for an hour or more, and then try to find the nest from the general area where the adults seemed to be feeding their young. Secondly, older young (five days old or more) blended in so well with the ground it was almost impossible to see them in the nest. Two nests were very nearly stepped on at this stage before being found.

Nests

Horned Lark nests are invariably built on the ground, and those at Cape St. Mary's were no exception. The nest was constructed in a depression in the ground hollowed out by the female, and consisted of a

grassy cup which was usually lined by a softer material. Most had a small area of pebbles or dried mud pavings, next to them.

Vegetation cover associated with nest-sites at Cape St. Mary's is shown in Table 3. Nine of 31 nests sampled were located within 50 cm of bare ground, compared with only two out of the 16 grid points sampled. In the territories which contained the gravel road, 15 of 18 nests found were within 10 m of the road. A similar situation was reported by Pickwell (1931) for a new subdivision in Evanston, Ill., where 15 of 20 lark nests found were in a thin strip of grass between the sidewalks and the bare earth of the new streets.

No nests at Cape St. Mary's were found in a moist habitat, as Verbeek (1967) reported in Wyoming. Three nests, however, were located in the lusher *Osmunda cinnamomea – Sanguisorba canadensis* habitat, more typical of Savannah Sparrow nest-sites.

Table 4 indicates the sizes and weights of the nests examined in this study, as well as the direction the nest faced. The direction faced was directly opposite the most protected side of the nest, and was usually the side on which the pavings were placed.

The mean dry weight of 30 nests was 16.0 g, and there was no significant variation in nest size or construction throughout the summer, as sometimes observed in *E. a. praticola* (Pickwell, 1931). This constancy of structure is probably due to the relatively static nature of the barrens habitat as compared to the farm fields where *E. a. praticola* breeds. Thus, nest materials available at the beginning of the season are just as common in mid-July, when the last nests are built.

Most nests faced west to northeast, the mean direction being 13°

TABLE 3

Plant species recorded at 11 or more of the 31 nest sites sampled, or which constituted more than 25% of the total plant cover at one or more of the points. Numbers following species names indicate the number of nest sites at which the species was recorded; numbers in parentheses indicate the number of nest sites at which the species constituted more than 25% of the total plant cover.

Empetrum nigrum L.	21	(15)
Cladonia spp.	22	(7)
Deschampsia flexuosa (L.) Trin.	23	(4)
Rhacomitrium lanuginosum (Hedw.) Brid.	17	(4)
Empetrum eamesii Fern. & Wieg.	8	(4)
Salix uva-ursi Pursh	5	(1)
Festuca rubra L.	4	(1)
Poa palustris L.	1	(1)
Agrostis tenuis Sibth.	1	(1)
Potentilla tridentata Ait.	27	
Cornus canadensis L.	23	
Vaccinium uliginosum L.	23	
V. vitis-idaea L.	20	
Betula pumila L.	19	
Polygonum viviparum	15	
Kalmia angustifolia	14	
Aronia prunifolia (Marsh.) Rehder	13	
Maianthemum canadense Desf.	12	
Vaccinium angustifolium Ait.	12	
Calamagrostis pickeringii Gray	11	

Other plant species recorded at the nest sites were: Lichens spp., *Dicranum scoparium* Hedw., *D. undulatum* Brid., *Drepanocladus uncinatus* (Hedw.) Warnst., *Hylocomium splendens* (Hedw.) B.S.G., *Hypnum* sp., *Pleurozium schreberi* (Brid.) Mitt., *Pogonotum urnigerum* (Hedw.) P.-Beauv., *Ptilidium ciliare* (L.) Nees, *Osmunda cinnamomea* L., *Dryopteris spinulosa* (O. F. Muell.) Watt, *Juniperus communis* L., *Agrostis scabra* Willd., *Scirpus caespitosus* L., *Carex viridula* Michx., *Juncus trifidus* L., *Luzula confusa* Lindeb., *Myrica gale* L., *Cerastium beeringianum* C. & S., *Coptis groenlandica* (Oeder) Fernald, *Ranunculus* sp., *Thalictricum polygamum* Muhl., *Dedum groenlandicum* Retz., *Andromeda glaucophylla* Link, *Arctostaphylos alpina* (L.) Spreng., *Vaccinium oxycoccos* L., *Diapensia lapponica* L., *Trientalis borealis* Rat., *Rubus pubescens* Rat.,

TABLE 3 (CONTINUED)

Sanguisorba canadensis L., *Trifolium repens* L., *Cornus suecica* L., *Plantago maritima* L., *Campanula rotundifolia* L., *Lonicera villosa* Michx., *Linnaea borealis* L., *Aster nemoralis* Ait., *Solidago uliginosa* Nutt., *Achillea millefolium* L., *Leontodon autumnalis* L., *Prenanthes trifoliata* (Cass.) Fern.

TABLE 4

Nest Structure

Nest	Dry Weight (g)	Inner Width (mm)	Outer Width (mm)	Height of Protection (mm)	Direction Faced
1	17		-	-	NW
2	13	70–80	-	75	N
3	15	85	120	-	N
5	19	75	110	-	-
6	16	65	85	-	N
7	15.5	70	90	100	NNE
8		-	-	-	W
10	7.5	55–70	-	-	W
11	24	65	100–125	-	NE and SW
12	33	55	65	-	E
13	12	65–75	100	130	NE
14	-	-	-	-	-
16	16	70	95	100	NNW
17	-	-	-	-	-
18	23	70	95	-	N
19	14	75	90	-	NW
20	11.5	70–80	80–90	110	ESE
21	18	-	-	-	-
22	10	-	-	-	-
24	15	70	100	-	-
25	16	65	100	110	NNW
26	18	70	95	-	N
27	12.5	70–80	115	80	W
28	7	70–80	80	100	-
29	22	70	100	-	NW
30	8	70	75	110	NNW
31	9	65–75	110	80	WSW
32	19	75–80	95–105	110	NNW

TABLE 4 (CONTINUED)

Nest	Dry Weight (g)	Inner Width (mm)	Outer Width (mm)	Height of Protection (mm)	Direction Faced
33	24	70	110–135	-	ENE
34	18	80	115	70	NNW
35	14	70–75	95–100	100	ENE
37	16	65–70	105	50	W
38	22	70	95–105	60	W
39	17	70–75	100–110	-	-

west of north (Fig. 5). The distribution of the directions is non-random, based on the Rayleigh test for randomness around a circle ($r = .4142$, $p < .05$). This bias in nest placement direction is probably due to the fact that the prevailing winds are from the southwest, and stronger winds are most often from the south to east. DuBois (1935) reported that all of 35 nests he found in Montana, where the prevailing winds are from the west, faced northeast to south-southeast. He adds: "No doubt the bird chooses a spot to the leeward of a tuft of grass and stands facing the wind while scratching the excavation."

As found in other Horned Lark breeding biology studies (e.g. Pickwell, 1931; Verbeek, 1967; Beason and Franks, 1974), the bulk of every nest consisted of grass stems and leaves (primarily *Deschampsia flexuosa* in this study); also included in the main nest structure were small amounts of lichens, rootlets, moss, leaves, feathers, small twigs, and paper (Table 5). Most of the lichens (primarily *Cladonia* spp.) and mosses were on the outside of the grass cup, and were perhaps used to even out the nest cup dug in the ground before the main grass structure was woven in.

The linings found in lark nests at Cape St. Mary's reflected the abundance of certain soft materials (Table 6). Thousands of feathers, mainly from Black-legged Kittiwakes (*Rissa tridactyla* L.) and Gannets (*Morus bassanus* L.) are blown on to the study area every day from the huge seabird colonies on the cliffs immediately to the south; these were found in the lining of every nest examined. Wool originating from the approximately 300 head of sheep on the study area, was found in over half the nests. The only soft plant material found in nest linings

Figure 5

Vectors indicating the number of nests facing each direction.

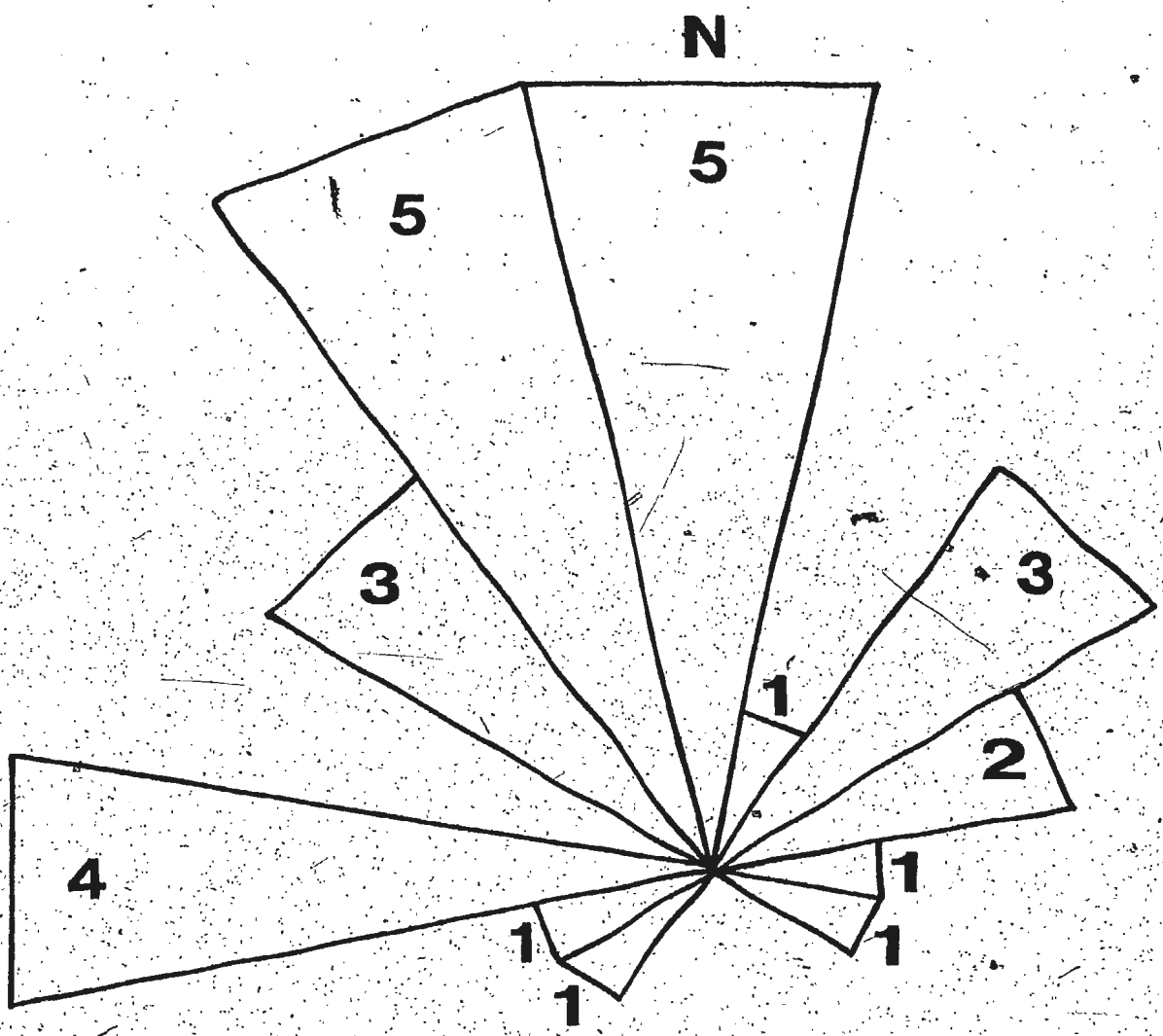

N
5
5
3
3
1
2
4
1
1
1
1

TABLE 5

Materials in the body of Horned Lark nests
xxx = abundant, xx = common, x = scarce

Nest	Grass	Lichens	Moss	Rootlets	Feathers	Leaves	Twigs	Paper
1	xxx	x	x					
2	xxx		x	xx				
3	xxx		x	x		xx		
5	xxx	xx	x		xx			
6	xxx		x	xx				
7	xxx			x	x			
8	xxx						x	
10	xxx	x	x					
11	xxx	xx	x	x				
12	xxx	x	x		xx		x	x
13	xxx							
16	xxx		x			xx		
18	xxx	xx		x				
19	xxx	x	x	x				
20	xxx							
21	xxx	x						
22	xxx	x	x	x		x		x
24	xxx			xx				
25	xxx	x		x				
26	xxx				xx			
27	xxx	x	x			x		
28	xxx		x			x		
29	xxx	x	x	x				
30	xxx				x			
31	xxx							
32	xxx	xx						
33	xxx	xx			xx			
35	xxx				xx			
37	xxx	x	x			x	x	
38	xxx	x		xx				
39	xxx	xx				x		

TABLE 6

Materials in the lining of Horned Lark nests
xxx = abundant, xx = common, x = scarce

Nest	Feathers	Wool	*Lonicera* leaves	Willow down
1	x	x		
2	xxx			
3	x		xx	
5	xxx	x		
6	xx			
7	xx			
8	xx			
10	xxx			
11	xxx	x	xx	
12	xxx			
13	xxx			
16	xx	xx	x	
18	x	xx	x	
19	xx	xxx		
20	xxx			
21	xxx			
22	xx	xxx		
24	xx	xxx		xx
25	xx		xx	
26	xxx		x	
27	xx	xx		
28	xx	xx		
29	xx	xxx		
30	xxx	x		xx
31	x	x		
32	xxx			
33	xxx			
35	xxx			
37	xx	xx		
38	xx	xx		
39	xxx	xxx		

were leaves of the Northern Honeysuckle (*Lonicera villosus*) and down from willow (*Salix uva-ursi*) catkins. Mousely (1916) reported that the nests of *E. a. praticola* he found were lined with plant down and Pearly Everlasting (*Anaphilis margaritacea* (L.) Gray) flower heads. Beason (1970) stated that the nests he found were lined primarily with grasses and shredded cornstalks.

Certainly the most interesting aspect of Horned Lark nest construction is the area of pavings usually placed on one side of the nest. This structure consists of a group of small flat objects such as pebbles, clods of mud, or twigs (Table 7). The function of this pavement is unknown, although several suggestions have been put forward. Since lark nests are usually built against a protective structure which slopes away on the opposite side, Pickwell (1931), and Lobachev and Kapitonov (1968) suggested that the pavings leveled the nest to the downhill slope (Fig. 6a). Pickwell also stated that the pavings may simply provide a bare surface on which the larks could approach the nest. DuBois (1935) believed that the pavings served to cover and camouflage the dirt excavated from the nest cup and placed opposite the protective structure. Beason and Franks (1974) and Lloyd (1976) agreed with this view, and observations at Cape St. Mary's seem to support it also. At Cape St. Mary's, nest cups excavated in *Empetrum* often did not reach ground level, since the nests were simply built in the tight mat of vegetation (Fig. 6b). Therefore, no dirt was thrown out beside the nest. Seven of fifteen nests built in this habitat had no trace of paving, and four more had only one or two pieces present. On the other hand, only one of 15 nests built in short grass on the roadside or in gravelly habitat had no trace

TABLE 7

Pavings at Horned Lark nests

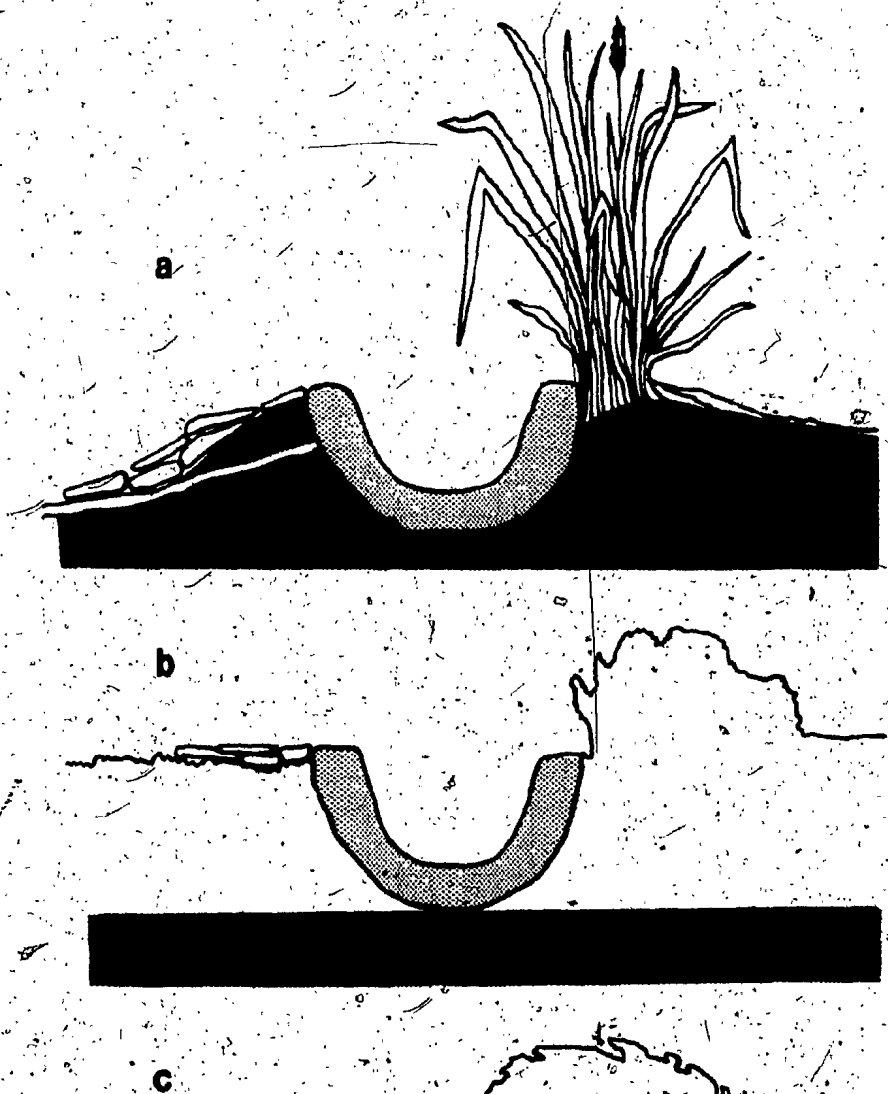
Nest	Total Weight of Pavings (g)	Extent (mm)	Materials (quantity, or: x = uncommon, xx = common, xxx = abundant)				
			Pebbles	Lichens	Moss	Mud	Sticks
1	-	-		xx			
2	11	40 x 60	4				
3	30	100 x 10		x	x	xx	
5	0	none					
6	8	100 x 50			x	x	
7	-	200 x 120			xx	x	
8	-	-		x			
10	-	-			1		
11	16	90x90;60x65	4	x		x	6
12	-	80 x 55		x			
13	1	-	1				
16	0	none					
18	-	65 x 70		xx			
19	-	100 x 150					
20	-	-	1				
24	0	0					
25	70	145 x 75	xxx				
26	0	0					
27	-	-	1				1
28	0	none					
29	-	80 x 80					
30	0	none					
31	37	160 x 95					
32	69	140 x 80	38		3		
33	51	100 x 100	23	1			3
34	-	85 x 105					
35	3	-	1				1
37	0	none					
38	0	none					
39	-	-		2			

Figure 6

a) Horned Lark nest built in thin vegetation. Note pile of earth covered by pavings to the left of the nest cup.

b) Horned Lark nest built in thick *Empetrum* mat. The nest cup barely reaches the soil, and no pile of earth is present; a few pavings are placed directly on the vegetation to the left of the nest.

c) Loosely constructed Horned Lark nest, broadly overhung by clump of *Empetrum nigrom* and *Cladonia* sp. (e.g. Nests 30, 38). No pavings are present.


a
b
c

of paving, and four more had only one or two pieces present. This difference (7/15 vs. 1/15) is significant ($X^2 = 6.136$, $p<.05$). This may, however, simply reflect a closer supply of paving material at the roadside nests.

Verbeek (1967) stated that none of his 15 nests had any sort of paving.

Nest-building

Horned Lark nests are built solely by the female. At first, the nest cup is dug into the ground, or, as in many cases at Cape St. Mary's, into the tight mat of vegetation (*Empetrum* spp., *Cladonia* spp. and/or *Rhacomitrium lanuginosum*). Then the grass is added, along with the paving material and feathers or wool for the lining.

No larks were actually observed digging the nest cup, although one nest (15) was found in this stage. Presumably it is dug primarily with the bill, in much the same manner as the larks search for food, as Beason (1970) and Boyd (1976) observed.

On May 13 and 14, FM5 was observed building Nest 1. After collecting dried grass for a minute or so, usually within 30 m of the nest, she flew to the nest with steady, rapid wing beats, landed within 2 m of the nest, then walked to it and deposited the grass. Sometimes, when collecting close by, she walked directly to the nest without flying. Occasionally, she would fly farther to gather nest material, or perhaps to feed; these trips would take five or six minutes.

The time spent at the nest was very short, usually only 4-6 sec, although every five or ten trips the female would spend about a minute

at the nest, presumably arranging the material into a tighter structure.

Other females seen building nests used much the same technique. Lining material (e.g. feathers) was usually added last, as would be expected, although FM14 added paving, grass, and a feather to Nest 5 on successive visits.

Most of the nest-building behaviour observed took place in the morning, as Boyd (1976) also noted.

Beason (1970) stated that it took 1-2 days to dig the nest cup and 2-3 days to build the nest. It took FM1 three days to build Nest 7 after digging the nest cup; she laid the first egg in it three days later.

Nest 30 was the most rapidly built of those observed at Cape St. Mary's. When discovered, it was a simple cup dug in the *Empetrum nigrum* mat with a few grass stems, feathers, and bits of willow down in it; the next morning it contained the first of three eggs. Upon examination, this nest was found to be very loosely constructed (Fig. 6c); Nest 37 was made in a similar manner.

Lining material was often added to nests after the first egg had been laid. FM1 was seen adding a feather to Nest 7 after laying her first egg, and Nest 32 was found, containing two eggs, after FM6 was seen carrying willow down to it.

Horned Larks may build two or more nests before laying eggs in one (Pickwell, 1931). Several nests were found at Cape St. Mary's while under construction that were never used for actual breeding purposes (Nests, 1, 9, 12, 15, and 40). These could be examples of desertion after minor disturbances while the commitment to continue with a particular nest was very low. Beason (1970) however, reported

a female building two nests at the same time, a phenomenon that was also seen during the present study. On June 1, FM14 was seen adding bits of paving and *Cladonia* to a nest cup near the eastern boundary of her territory. The next day I saw the same female building another nest about 60 m to the west. This second nest contained grass and feathers, and four days later contained one egg. But after successfully raising three young in the nest, FM14 returned to the original nest cup, finished it, and raised her second brood.

While the female built the nest, the male was usually close at hand, feeding, singing, and chasing trespassers. Once, while watching FM5 building Nest 1, her mate (M1) chased a Savannah Sparrow from the immediate nest area, then walked to the nest and stayed there for one minute. This was the only time a male was observed going to a nest before the eggs hatched.

Egg-laying

Eggs were laid early in the morning, usually before 0500, at a rate of one per day until full clutch size was reached. Boyd (1976) stated that eggs are often laid every other day in very early nests, but no evidence of this was found in the present study.

Clutch size

Clutch sizes of 26 nests varied from two to four (1(2), 16(3), and 9(4)) with a mean of 3.31. This value is slightly lower than the mean of 3.5 for 11 nests on Newfoundland Nest Record Cards. The combined mean (nest records plus this study) is 3.36, somewhat, though not significantly, lower than the mean clutch size of 3.42 for *E. a.*

praticola in the American midwest, calculated from the data of Pickwell (1931), Garrett (1948) and Beason and Franks (1974). Clutch sizes found in other Horned Lark populations are summarized in Table 8. There seems to be a line of increasing clutch size from the west coast to central North America and from south to north, in agreement with Cody's (1966) general theory of clutch size.

There was a significant increase in clutch size over the breeding season at Cape St. Mary's. The mean clutch size of 10 nests begun before June 15 was 3.0, while that of 16 nests begun after June 15 was 3.5 ($t = 2.48$, $p<.05$).

Of the eight females for which two or more nesting attempts were recorded (in which full clutches were laid), four had two clutches of three and four had first a clutch of three and then a clutch of four. Only one possible first brood (Nest 21) had a clutch size of four, and it was one of the latest first broods.

Pickwell (1931) reported that March nests of *E. a. praticola* had smaller clutches, and clutches of five were found only in later nests. Bowles (1900) stated that "sets [of *E. a. strigata*] found early in the season almost invariably are of two eggs, while three eggs to the set may be expected with almost equal certainty in the latter half of the season." This trend to increase clutch size over the breeding season is well known in birds, especially those which raise two broods (Hussell, 1972), and was well-documented in Skylarks (*Alavda arvensis* L.) by Delius (1965).

TABLE 8

Incubation Periods, Nestling Periods, and Clutch Sizes of Horned Larks

Source	Location	Incubation Period (days)	Nestling Period (days)	Mean Clutch Size (n)
Tyler (1913) in Bent (1963)				3.23 (35)
Bowles (1900)	Tacoma, Wash.	-	-	2.5[1] (25)
Kelso (1931)	Aurora, Colo.	-	7 - 10	3.0 (4)
Boyd (1976)	Weld Co., Colo.	11 - 14	9 - 10	2.85(262)
DuBois (1935)	Teton Co., Mont.	11	9 - 12	3.30 (47)
Verbeek (1967)	Park Co., Wyo.	11	9 - 12	3.25 (15)
Pickwell (1931) Garrett (1948) Beason (1970)	Ohio; Illinois	11 - 14	10 - 14	3.37 (44)
Mousely (1916)	Hatley, Qué.	-	-	3.75 (4)
This study	Cape St. Mary's, Nfld.	11 - 14	8 - 10	3.31 (24)
Lobachev and Kapitonov (1968)	Karzhantau Mtns., USSR.	10	10 - 11	3[1] (23)
Sutton and Parmelee (1955)	Frobisher Bay, NWT.	-	8 - 10	4.0 (7)
Drury (1961)	Bylot Is., NWT.	-	8 - 9	4.85 (6)

[1]Approximate.

Eggs

Eggs collected from deserted nests, and in several cases half-shells were found in nests shortly after the young had hatched. Most of the eggs taken from deserted nests were already broken or were opened to check for developmental stages of the embryos, but three were kept intact for measurement. These measured 23.7 x 16.6 mm, 24.7 x 17.5 mm, and 22.8 x 15.9 mm, averaging 23.7 x 17.3 mm; slightly larger than that given by Bowles (1900) for *E. a. strigata* (21.0 x 15.7 mm), by Pickwell (1931) and Beason and Franks (1974) for *E. a. praticola* (21.6 x 15.7 mm and 21.1 x 15.2 mm respectively) and by Boyd (1976) for *E. a. enthymia* (22.0 x 15.9 mm).

Fourteen eggs were examined for colour and pattern. Although some eggs were evenly spotted over their entire surface, most are wreathed by a concentration of spots around the large end. Sometimes this wreath almost covers the end to form a dark cap (Plate 3).

There was quite a variation in background colour, spot concentration, and spot size. The background colour varied from a light cream (Munsell notation 7.5Y 9/2) to a greyish green-yellow (10GY / 9/1); most backgrounds had a Munsell notation of 10Y 9/1 - 5GY 9/1.

The spots were essentially of two colours - light brown (Munsell notation 2.5Y 5-6/4) and grey-blue (10B 6-8/1). Brownish spots were commoner than grey-blue ones; the latter were usually concentrated in the wreathed area. Spots averaged less than a millimetre in diameter, although some eggs had spots larger than 2 mm in diameter. One egg had a dark brown (10YR 3/2) hairline streak on the large end.

Eggs with few spots appeared light in colour; conversely, a

Plate 3

Nest 3 with two eggs and one newly-hatched nestling.

high concentration of spots gave an egg a darker overall appearance.

Incubation

Incubation usually began after the last egg was laid, although in eight nests (four each of clutch sizes three and four) it apparently began when the penultimate egg was laid. This early incubation resulted in asynchronous hatching in some of the nests. In Nest 18, for example, one egg hatched on the evening of July 1, by 0930 on July 2, there were three young in the nest, and the fourth egg hatched early on July 3. FM6 was observed sitting on Nest 2 early in the afternoon while it contained one egg, but all three eggs in this nest hatched in the same morning.

The usual incubation period of the Horned Lark is 11 days (Pickwell, 1931). Only four of the nests found at Cape St. Mary's could be used to calculate incubation period, since the nests must be found before all eggs are laid (Pickwell calls this "the rarest kind of accident") and the eggs must successfully hatch. These four nests had incubation periods of 13, 14, 11, and 11 days, for an average of 12.25 days. The longer incubation periods are probably due to adverse weather conditions which caused temporary desertions. Several times when Nest 2 (incubation period 14 days) was visited, the eggs were cold, and Nest 5 (incubation period 13 days) was one of the few which made it through the severe storm of June 11 - 13. Pickwell (1931) mentioned a case where incubation was delayed because of a two-day desertion after incubation had begun, and Boyd (1976) stated that longer incubation periods were caused by inclement weather.

Only females were observed incubating; at no time was a male seen to approach a nest at this stage. Sutton and Parmelee (1955) observed a male bringing food to an incubating female, but usually the female makes short trips off the nest to feed. Lovell (1944) reported that these trips are longer but less frequent in warmer weather.

Hatching

Eggs hatched at all times of the day. The first sign of hatching is a small hole which appears several hours before hatching. The chick initiates the actual hatching by cutting the eggshell in two around its widest point, by apparently turning slowly as it pokes its bill rhythmically outward. One chick (19-4), observed while hatching made bill-pokes about every 17 seconds (range 15 - 22 sec.), and had cut one-third of the way around the egg in five minutes.

Once the shell has been cut in two, the chick pushes rhythmically upward with its head until the two shell halves are sufficiently far apart that the chick can emerge. One chick (6-3) made two of these upward pushes at precise 15-second intervals for six repetitions, then paused for 25 seconds and began again. DuBois (1936) mentioned a chick that, immediately after hatching, lifted its head and opened its mouth every 24 seconds.

The broken shells were usually removed very shortly after hatching; Boyd (1976) stated that the female removes them immediately, carrying them 20 - 30 m away, although in this study half-shells were found in or very near the nests on four occasions some time after the young had hatched.

Nestlings

On hatching, the young are covered in a long, buff down, which is damp and twisted for an hour or so after emergence (Plate 3). DuBois (1936) reported that the down is fully dry 10 hours after hatching. Table 9 gives the down lengths of newly-hatched larks.

The skin of a day-old nestling is light orange-yellow ventrally, and blackish on the eyelids, crown, and back (Frontispiece). As the nestlings grow, this black area spreads over the dorsal surface of the wings as well. The mouth lining is a bright yellow-orange, with three conspicuous black spots on the tongue.

Shortly after hatching, the nestlings gave a higher-pitched "weeh-weeh-weeh" which could be heard only if the bird was held close to one's ear. Other, louder, peeping sounds were not heard until the nestlings were several days old. The eyes opened at two to three days of age, and the instinctive gaping to any stimulus (e.g. whistle or jarring the nest) disappeared a day or so later. At six to seven days of age, the young crouched down in the nest when disturbed, their buff-speckled backs blending in perfectly with the ground (Plates 4 and 5). At this age, and especially when eight or nine days old, the nestlings often squealed and struggled violently when picked up. They often left the nest, at least temporarily, when handled at this stage.

The young were brooded by the female for the first few days after hatching, and every night until they left the nest. When brooding her newly-hatched young in Nest 3, FM2 left every 20 - 30 min to feed herself or bring back food for the young.

TABLE 9

Down Lengths[1]

Mean Length[2] (mm)

Source	Cor.[3]	Occ.	Spi.	Fem.	Cru.	M2°C	G°C	Sca.
This Study	7 (6)	7.8 (5)	10.8 (8)	9.5 (4)	2 (2)	10 (1)	9.8 (4)	9 (1)
Wetherbee (1957)	5	9	10	11	-	8	8	4
Beason[4] (1970)	-	6 (13)	8 (13)	7 (13)	2 (13)	5.2 (13)	6.9 (13)	10 (13)

[1]Not all tracts were measured in this study.

[2]Numbers in parentheses are sample sizes.

[3]Abbreviations are for coronal, occipital, spinal, femoral, crural, median secondary covert, greater secondary covert, and scapular down tracts.

[4]It should be noted that, in his table, Beason (1970) has misinterpreted Wetherbee's (1958) and Verbeek's (1967) "down distribution" (i.e. numbers of feathers in each tract) for down lengths.

Plate 4

Nest 37 with two six-day old young.

Plate 5

Nestling 19-2 shortly before nest-leaving.

Both parents generally feed the young, although FM2 apparently had no help from her mate in feeding the young in both her nests. This lack of help did not seem to affect the growth rates of the nestlings involved, although 27-4, a late-hatcher, was apparently not fed and eventually died at 5 days of age. Pickwell (1931) cited "one or two" cases in which the male did not share in his feeding duties.

At Nest 39, in the mid-afternoon, M1 and FM5 fed the nestlings an average of once every three minutes. Pickwell (1931) gave an average of once every 5.5 minutes, and Levy (1920) reported an extraordinary case in which two larks fed eight young in one nest once every minute. FM5 took a fecal sac from Nest 39 twice in a 20-minute period, flying to the road (20 m away) each time to discard it. Usually, both parents walked or ran from the nest after feeding the young.

Forty-seven nestlings of known age were measured, usually daily, for a total of 302 nestling-days of measurement. The results are shown in Figures 7 to 13 and compiled in Appendix 4. Measurements of juveniles and adults are summarized in Table 10.

Growth rate (weight increase) was analyzed using Ricklefs' (1967) graphical method. As Ricklefs (1968) reported for all passerine growth data he examined, nestling growth in this study followed a logistic curve (Fig. 7). In contrast, Boyd (1976) stated that the growth curve for his *E. a. enthymia* nestlings resembled a Gompertz curve.

Assuming an asymptote weight of 34 g, nestling growth rate was 0.543; the equation for nestling growth in this study is thus

$$W = \frac{34}{1+e^{-.543(t-3.8)}}$$

TABLE 10

Measurements of adults and juveniles

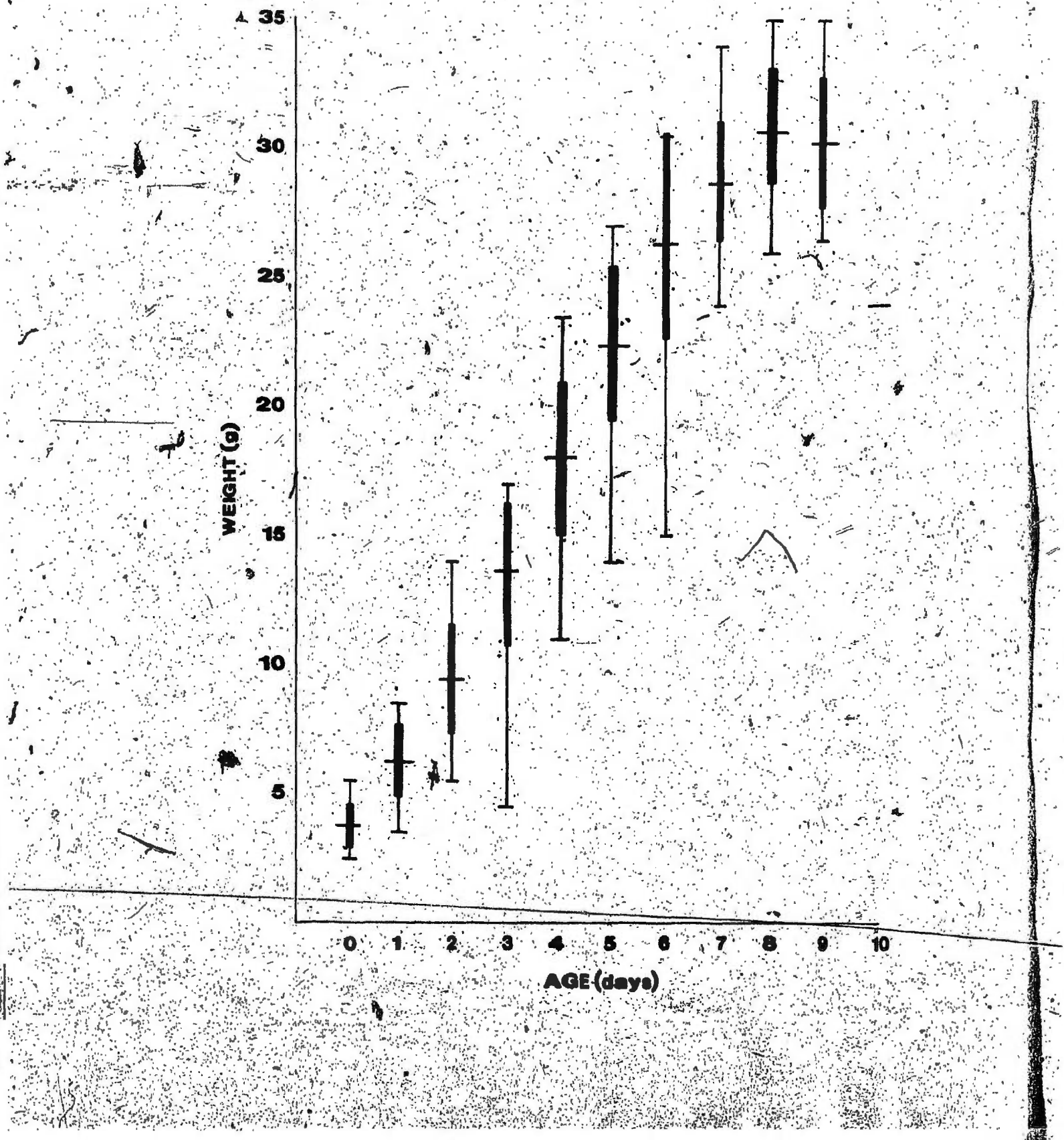
		14 days of age	28–29 days of age	Adult Males	Adult Females
Weight (g)	n	1	-	3	17
	$\bar{x}$	34	-	44.37	41.87
	Sx	-	-	1.10	2.09
	$S\bar{x}$	-	-	0.63	0.51
	R	34	-	43-45	38-45
Culmen (mm)	n	1	-	49	48
	$\bar{x}$	10	-	12.79	12.16
	Sx	-	-	1.17	0.99
	$S\bar{x}$	-	-	.17	0.14
	R	10	-	9-15	9-14
Tarsus	n	1	1	6	17
	$\bar{x}$	24	25	24.58	23.91
	Sx	-	-	0.92	1.63
	$S\bar{x}$	-	-	0.37	0.40
	R	24	25	23-25.5	22-28
Hallux and Claw	n	1	1	6	15
	$\bar{x}$	17	17	18.0	19.47
	Sx	-	-	1.87	1.92
	$S\bar{x}$	-	-	0.76	0.50
	R	17	17	16-21	16-23
Claw	n	1	1	6	17
	$\bar{x}$	8	8.5	11.17	11.65
	Sx	-	-	1.21	1.72
	$S\bar{x}$	-	-	0.49	0.42
	R	8	8.5	9-12.5	9-16

TABLE 10 (CONTINUED)

		14 days of age	28-29 days of age	Adult Males	Adult Females
Rectrix	n	1	1	50	47
	$\bar{x}$	32	58	63.64	59.73
	Sx	-	-	6.03	4.02
	$S\bar{x}$	-	-	0.85	0.59
	R	32	58	61-74	52-70
Wing	n	1	2	50	48
	$\bar{x}$	78	100.5	110.57	102.82
	Sx	-	-	9.57	3.67
	$S\bar{x}$	-	-	1.35	0.53
	R	78	97-104	104-121	95-111
First Primary	n	1	-	1	9
	$\bar{x}$	42	-	55	53.44
	Sx	-	-	-	2.96
	$S\bar{x}$	-	-	-	0.99
	R	42	-	55	48-58
Ninth Primary	n	1	2	3	10
	$\bar{x}$	49	72.75	83.67	77.05
	Sx	-	-	2.08	1.82
	$S\bar{x}$	-	-	1.20	0.57
	R	49	71.5-74	82-82	74-80

Figure 7

Weights of nestlings of various ages. Long horizontal lines are means, thin vertical lines are ranges, and thick vertical bars are standard deviations.


35
30
25
20
15
10
5
WEIGHT (g)
0
1
2
3
4
5
6
7
8
9
10
AGE (days)

where W is the nestling's weight in grams, and t is its age in days.

This growth rate is slightly higher than the 0.464 calculated from Pickwell's (1931) data reported by Ricklefs (1968), but very near the mean values given for ground-nesting passerine species by Ricklefs (1968).

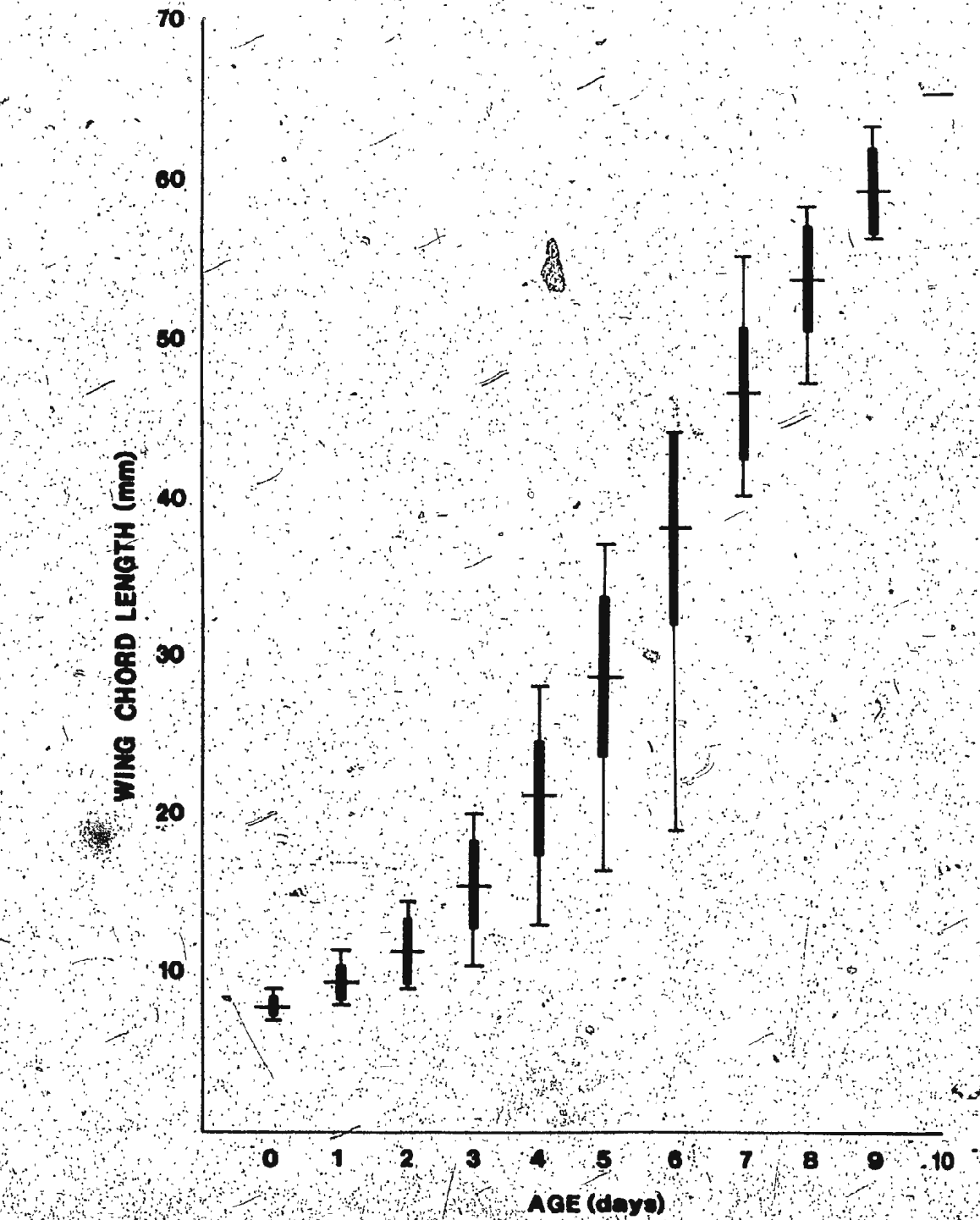
The largest mean daily weight increments occurred on the fourth and fifth days (4.4 g/day); nestling 19-4 gained 9 g in 28 hours in this period. After the sixth day, daily weight gain decreased to the point where 9-day old nestlings were on the average, lighter than 8-day old nestlings. This weight loss was probably due to increased energy losses through activity, feather production, and homiothermy associated with the latter part of the nestling period (Pickwell, 1931; Banks, 1959). Also, larger young tended to leave the nest after 8 days thus biasing the data for nine-day olds towards smaller nestlings. At nest-leaving, the young larks weighed about 30 g, or 75% adult weight, slightly higher than the 66% reported by Verbeek (1967), Beason and Franks (1973), and Boyd (1976).

Increase in wing chord length (Fig. 8) was slow until the nestlings were three days old, at which time the primaries began to grow rapidly. From then until nest-leaving, wing-growth is linear, increasing by 7-8 mm per day. Wing chord length at nest-leaving (8 - 10 days of age) was about 60% of the adult length, and about 80% of the adult length at 14 days of age, when the young larks had begun to fly. Two 28-day old larks that were measured had adult-sized wings.

Pin feather tracts were clearly visible by the third day. At four days of age, the first primary began to grow about 6 mm per

Figure 8

Wing chord lengths of nestlings of various ages.
Symbols as in Fugure 7.


70
60
50
40
30
20
10
WING CHORD LENGTH (mm)
0
1
2
3
4
5
6
7
8
9
10
AGE (days)

day, until its growth slowed abruptly at eight days of age. It was about 60% of the adult length at nest-leaving (Fig. 9). The ninth primary, the longest primary in the adult, grew slower than the first (Fig. 10), and was only about 35% of the adult length at nest-leaving, but continued to grow, fairly rapidly, and was equal in length to the first primary at about twelve days of age.

Primaries began to unsheath at about 6 days of age, and are 60% unsheathed by nest-leaving.

Rectrices appeared at the same time as remiges but grew much more slowly, and were only one-quarter to one-third adult length at nest-leaving (Fig. 11).

The tarsus (Fig. 12) increased rapidly in length over the first five days, and was usually adult-sized by seven days of age. Hallux growth (Fig. 13) closely paralleled that of the tarsus. The hallux claw (Fig. 13) grew much more slowly, and was only about one-half adult size at nest-leaving.

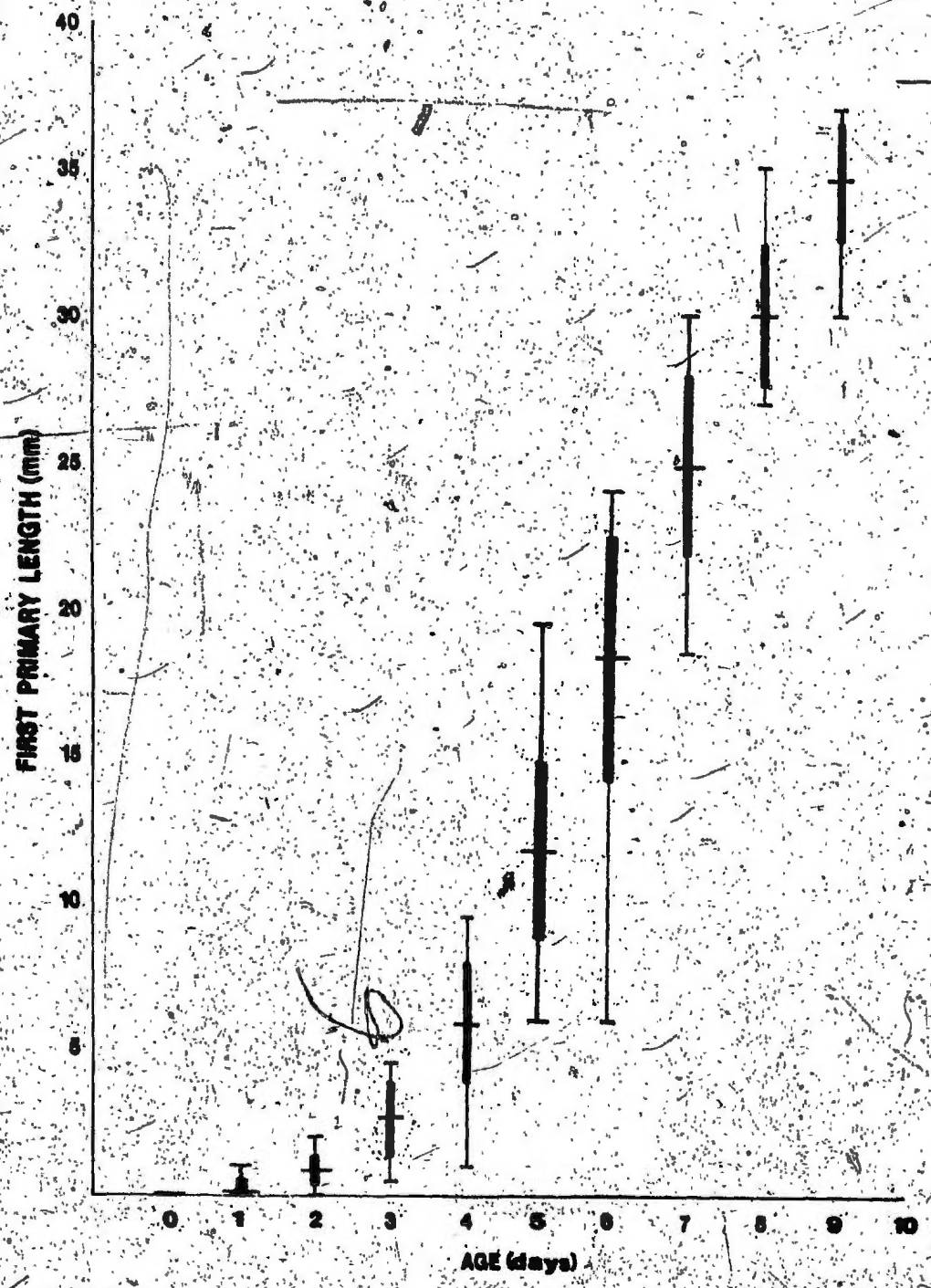
This rapid development of the legs and feet is closely tied in with the ground-nesting habit of Horned Larks, which makes early nest-leaving to avoid nest predation highly advantageous (Burns, 1921). The Savannah Sparrow nestlings measured at Cape St. Mary's also showed this rapid development of the tarsus (Appendix 2).

Culmen growth is shown in Figure 14.

The nestlings in the early nests found at Cape St. Mary's (those which hatched before June 13) grew much more slowly than those from later nests. This slower growth can be attributed to the shortage of food and the poor weather during this period. All these nestlings eventually died of hypothermia in the heavy storm of June 12-13. The

Figure 9

First primary lengths of nestlings of various ages.
Symbols as in Figure 7.


FIRST PRIMARY LENGTH (mm)
40
35
30
25
20
15
10
5
0
1
2
3
4
5
6
7
8
9
10
AGE (days)

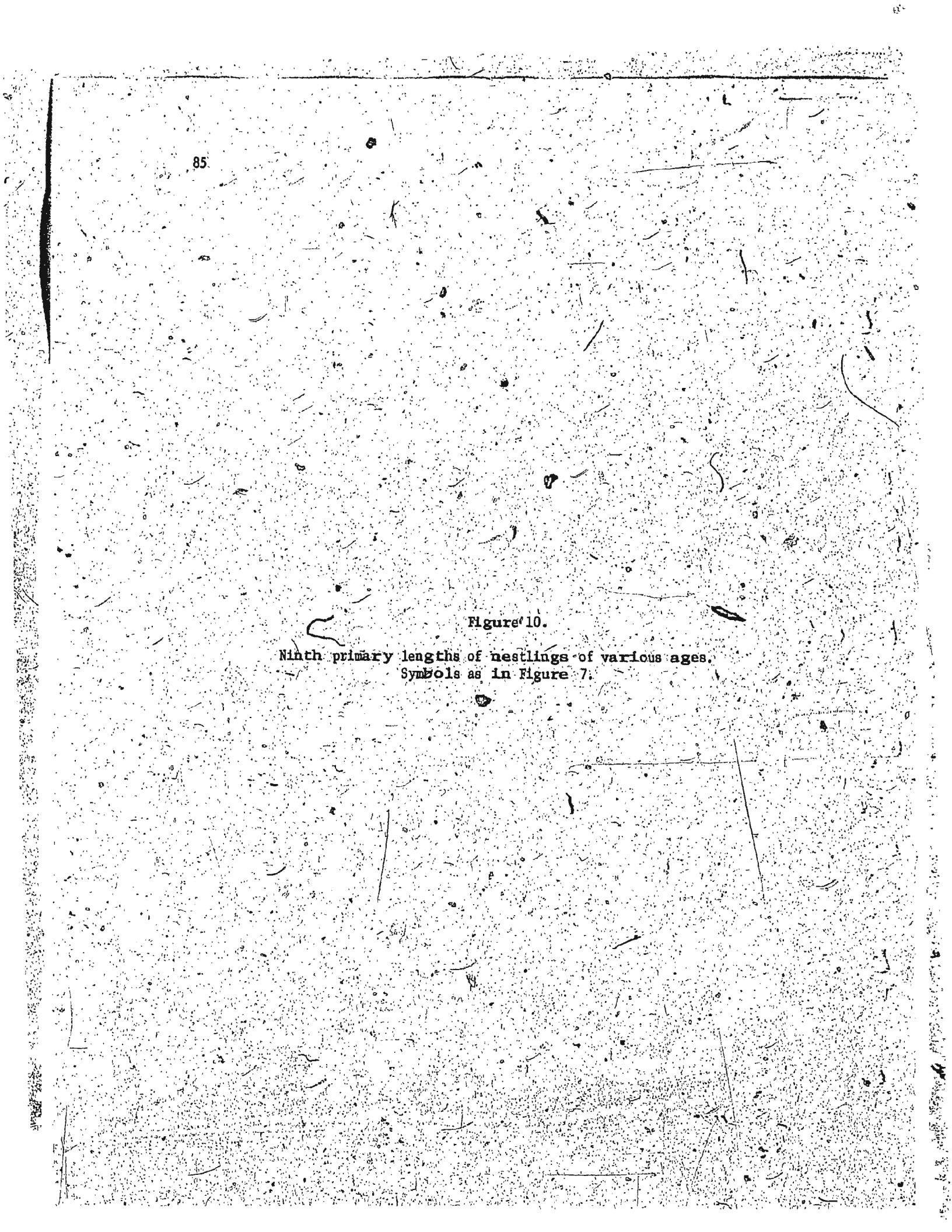


Figure 10.

Ninth primary lengths of nestlings of various ages. Symbols as in Figure 7.

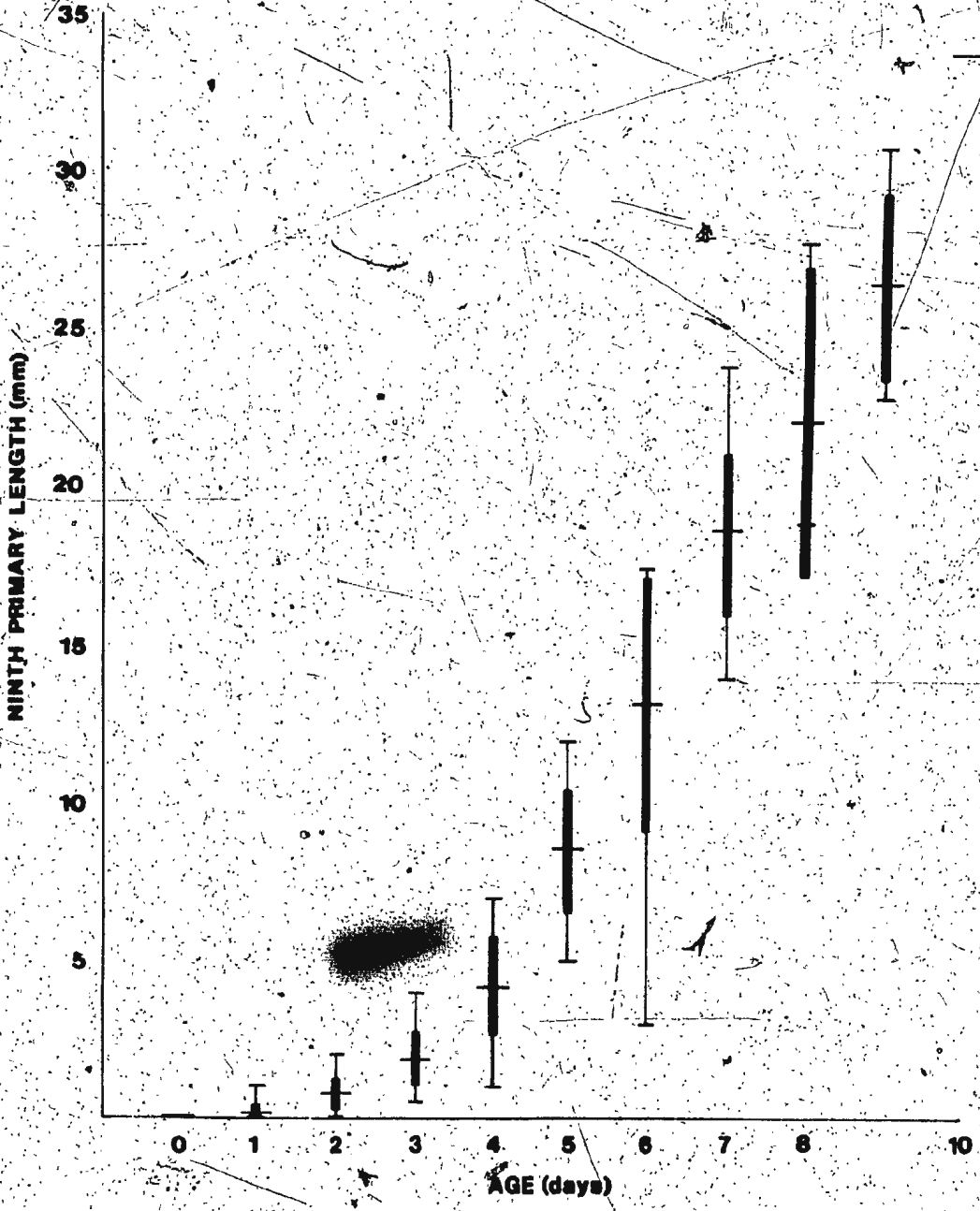
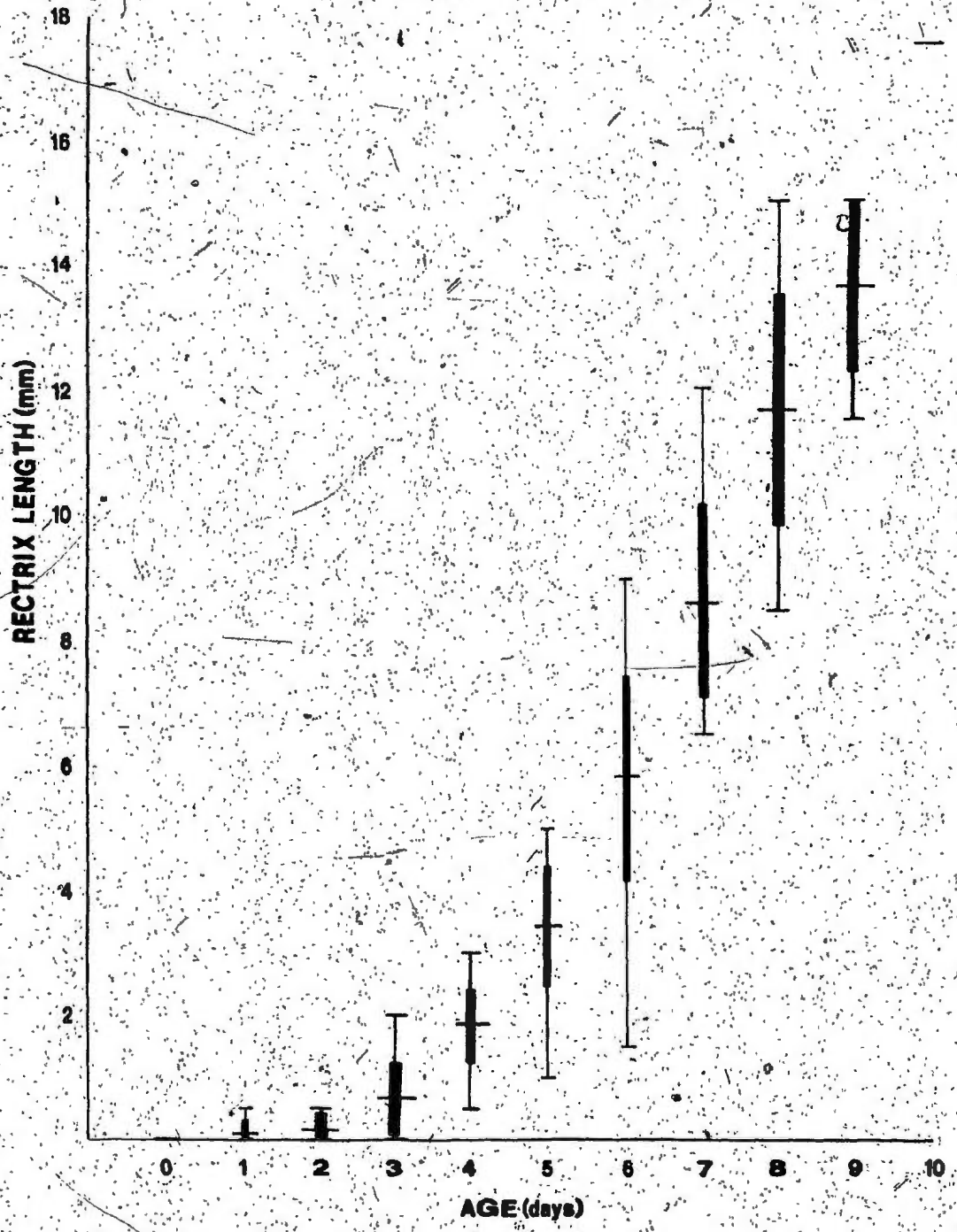

35
30
25
20
15
10
5
NINTH PRIMARY LENGTH (mm)
0
1
2
3
4
5
6
7
8
10
AGE (days)

Figure 11.

Rectrix length of nestlings of various ages.
Symbols as in Figure 7.


RECTRIX LENGTH (mm)
18
16
14
12
10
8
6
4
2
0
1
2
3
4
5
6
7
8
9
10
AGE (days)

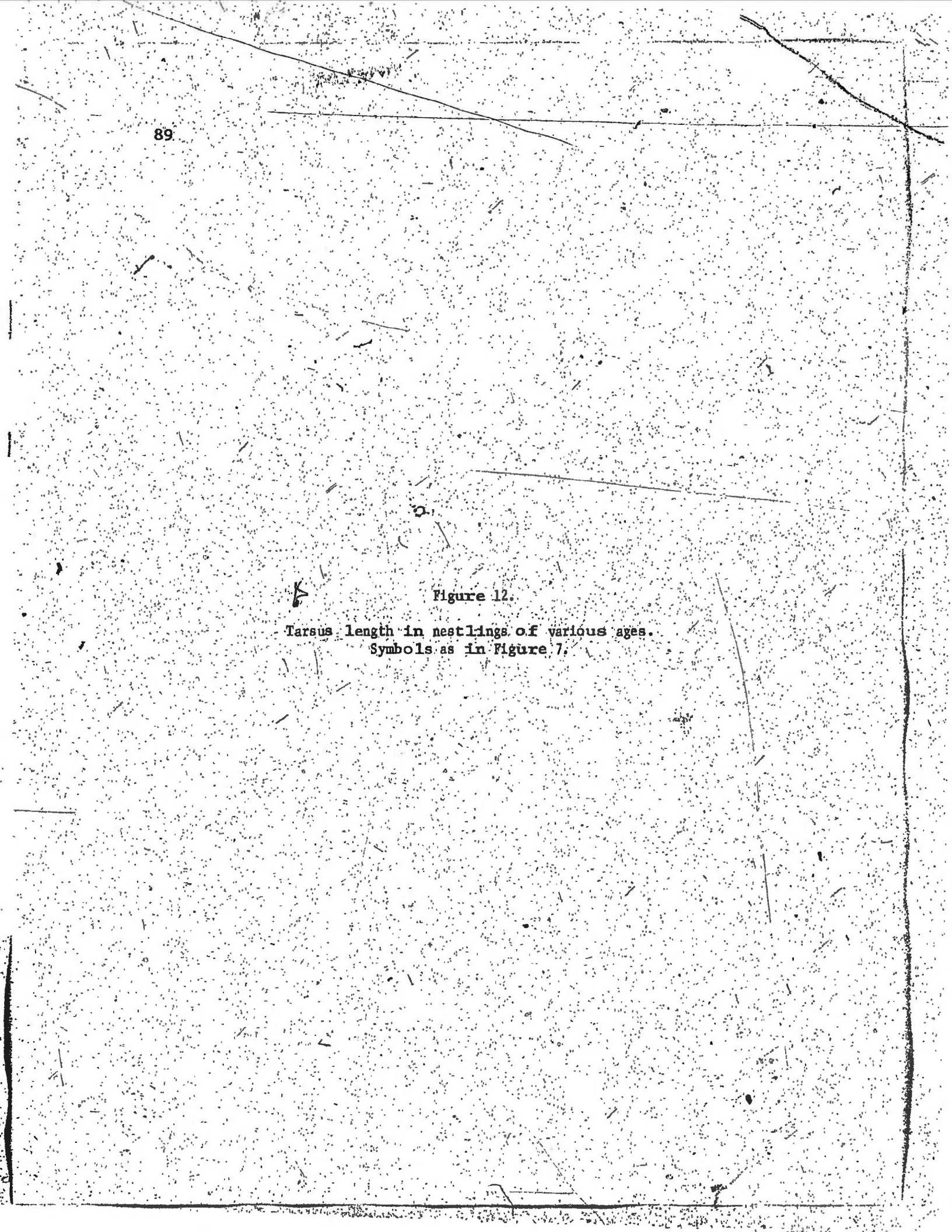


Figure 12.

Tarsus length in nestlings of various ages.
Symbols as in Figure 7.

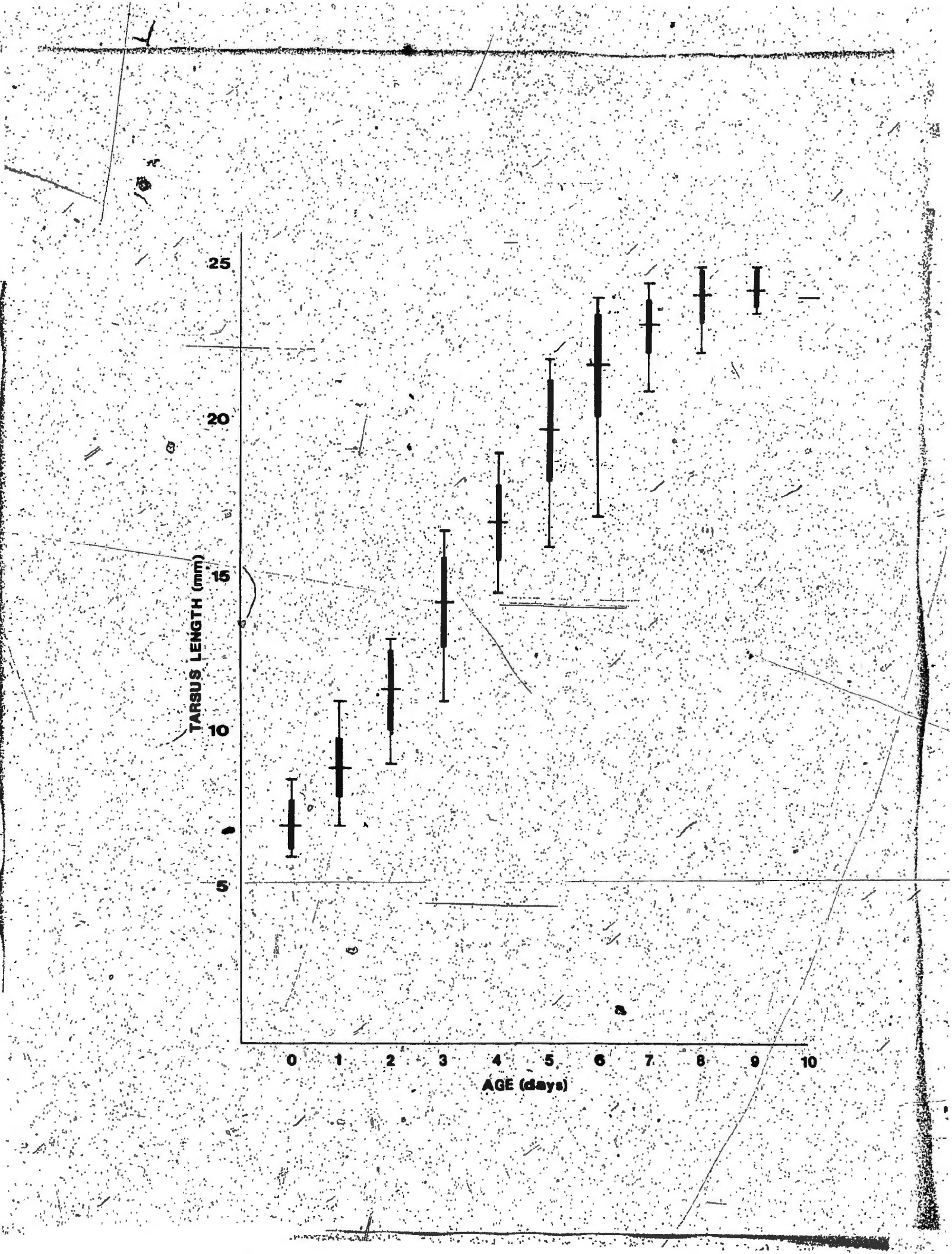

25
20
15
10
5
TARSUS LENGTH (mm)
0
1
2
3
4
5
6
7
8
9
10
AGE (days)

Figure 13.

Hallux plus claw and claw length in Horned Lark nestlings of various ages.
Symbols as in Figure 7.

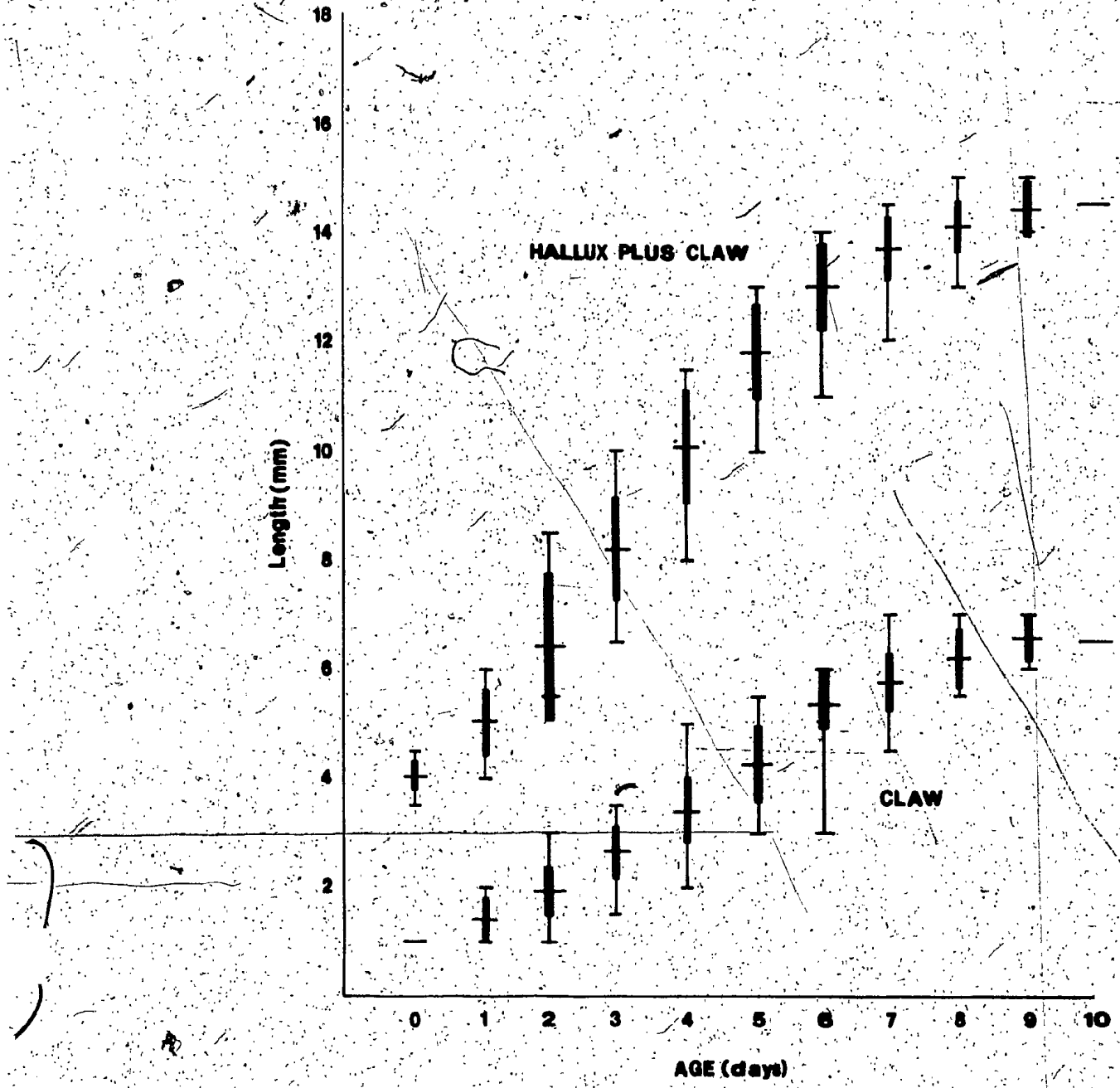
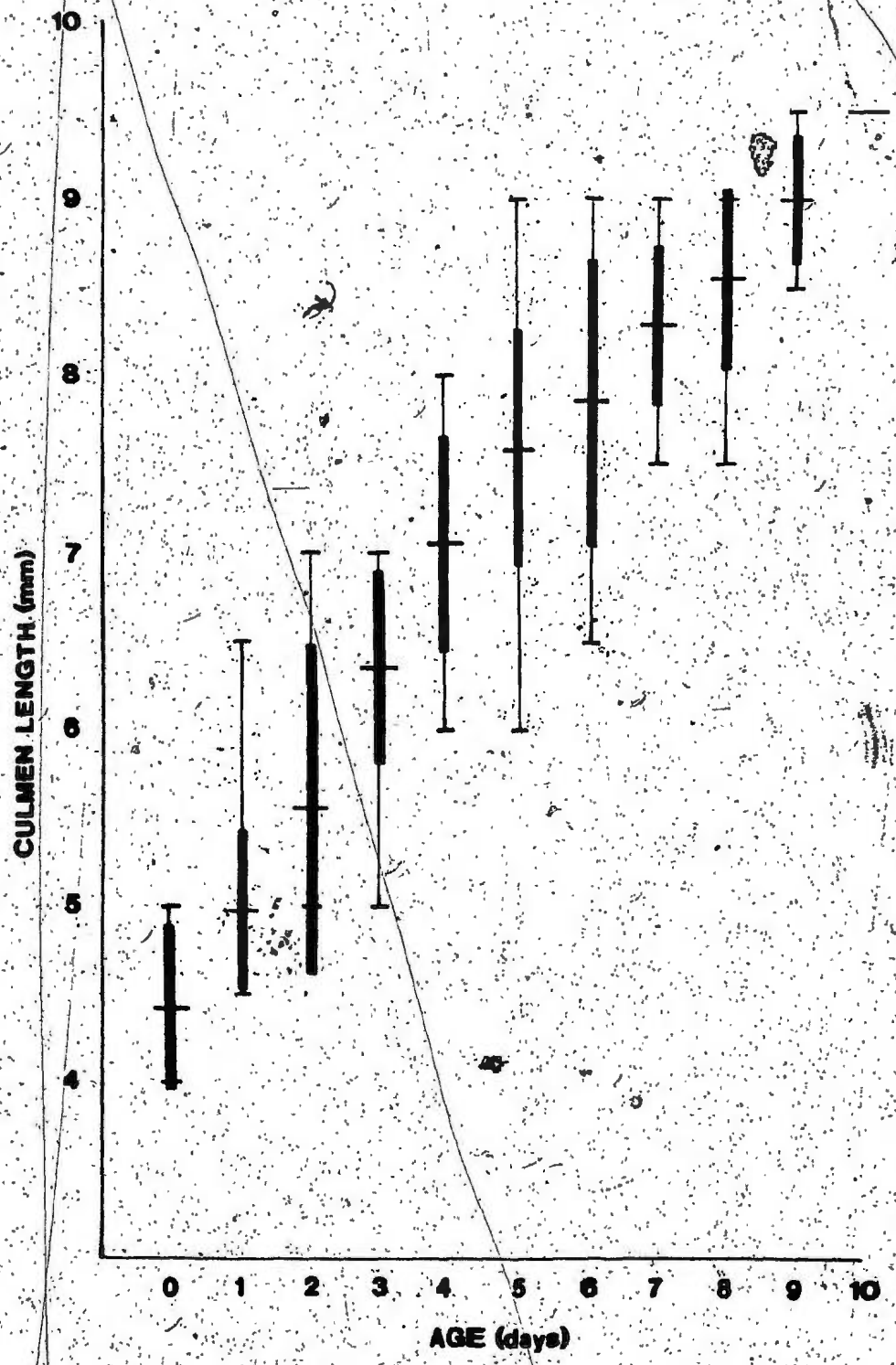

HALLUX PLUS CLAW
CLAW
Length (mm)
AGE (days)
18
16
14
12
10
8
6
4
2
0
1
2
3
4
5
6
7
8
9
10

FIGURE 14

Culmen length in nestlings of various ages. Symbols as in Figure 7.


CULMEN LENGTH (mm)
10
9
8
7
6
5
4
0
1
2
3
4
5
6
7
8
9
10
AGE (days)

effect that these young had on the mean growth curves can be seen in the large ranges up to six days of age (Figs. 7 - 13).

In at least eight nests, one young hatched a day after its siblings, probably due to incubation beginning after the penultimate egg was laid. This younger nestling was possibly outcompeted for food and thus grew at a slower rate than its siblings.

Pickwell (1931) remarked that "a slight difference in age gave the older larks a great advantage in securing food from the parents." He gives several examples, particularly from early nests, where late-hatching nestlings died before leaving the nest.

In four nests (14, 18, 30, and 32) the youngest nestling grew at a slightly slower rate than its nest-mates, and remained in the nest an extra day before leaving.

Nestling 27-4 showed no weight gain after reaching 6 g, showed negligible body growth, and was dead at five days of age. Nestling 34-4 gained only 1.5 g in the first two days, then lost a gram on the third. Its growth was minimal, and it still resembled a newly-hatched or day-old young when it died at four days of age. Its flattened body was found in the bottom of the nest under its three large siblings.

Nestling 39-4 fied at two or three days of age, but the cause of death was not determined and its growth rate was not monitored.

Although no observations were made of adults feeding the young at these nests, it was apparent that the youngest nestlings received little, if any, food during their lives. Even at four days of age they gaped constantly at any stimulus, while their nest-mates generally gaped for a very short time, if at all, before settling down in the nest.

Because of this high mortality rate in late-hatching young, asynchronous hatching has been suggested as a mechanism to reduce brood size in the event of food shortages (Ricklefs, 1965; Boyd, 1976). Hussell (1972) however, discounts this theory and suggests that asynchronous hatching is an adaptation to shorten the time between the laying of the first egg and the nest-leaving of the first young, thus reducing mortality due to nest predation.

Although there seems to be a great deal of competition for food among the nestlings in each nest, most seem to be fed equally. From observations on Nest 39, it was apparent that FM5 was feeding two of the three young, while M1 fed the third and a juvenile from their previous nest.

Verbeek (1967) reported that, near the nest-leaving time (i.e. 8 - 9 days old), the nestlings will leave the nest and approach the adult as the adult comes with food, hopping back into the nest after being fed. This behaviour was seen at Nest 33, where, the day before nest-leaving, one of the nestlings scrambled out and hopped to the female when she brought food. Pickwell (1931) and Verbeek (1967) suggested that this action may be the primary stimulus for the young to leave the nest, and Boyd's (1976) observations support this.

The nestling periods (time period between hatching and permanent nest-leaving) of 36 nestlings, when rounded off to the nearest day, averaged 9.0 days (5 (8), 26 (9), 5 (10)).

Nest-leaving

The young usually left the nests during the daylight hours, since

the females brood them during the night. The young in Nest 33, however, left the nest at midnight when the brooding female was captured for banding; and were not in the nest early the next morning.

Boyd (1976) observed that nestlings leaving the nest to be fed by an adult will stay out and follow the adult if the adult does not fly away after the feeding. He also found that, after leaving the nest, the young are fed only by the adult they left with.

Although Beason (1970) stated that young Horned Larks leave the nest within a few hours of their nest-mates, in eight out of fourteen nests at Cape St. Mary's, nest-leaving was spread over two or perhaps three days. The three young in Nest 28 apparently left the nest on three consecutive days, although the first may have left the nest very early in the morning, in which case the nest-leaving was spread over two days.

For the first one or two days after nest-leaving, the young generally stay within 30 m of the nest (Sutton and Parmelee, 1955; Beason, 1970). Young at this stage observed at Cape St. Mary's could not fly, but hopped clumsily, using their outstretched wings for balance. Their main predator-avoidance behaviour was crouch-concealment, making them hard to find at this stage. When approached, the young larks remained motionless until touched, when they squealed and struggled violently. Only five young larks were found at this stage of development, even though the areas surrounding nests were thoroughly searched after the young had left the nests.

As their locomotory ability increased, the young larks began to run along behind their parents, calling for attention with a distinctive "breet", easily separable from the "weet" call of the adults, and which

was retained for several weeks after nest-leaving. After three or four days out of the nest, the young could fly a few metres, and by 14 days of age they could fly 50 m again and again without any noticeable tiring.

If a juvenile bird of this age was forced to fly repeatedly, its parents accompanied it, giving loud alarm calls. This was especially true near territorial boundaries, where the adults actually seemed to try to herd the young bird back into the home territory.

At three weeks of age, the juveniles had a strong, direct flight in comparison with the slow, very undulating flight characteristic of the two-week old birds.

The young larks usually retained some down, especially on the superciliaries, for 5 - 12 days after leaving the nest. In the juvenal plumage (Plates 6 and 7), the feathers on the dorsum are a very dark brown, edged with golden-buff. The white outer edges of the outermost rectrices are very prominent in flight, much more so than those of the adults. There is a light yellow superciliary stripe, a faint yellow eye-ring, dark grey auriculars and sides of throat, and a light yellow band across the lower throat to the sides of the neck. The breast is yellow, but heavily spotted with grey, and the belly is yellow fading to off-white at the vent. The tarsi are greyish-yellow, remaining so for at least one month, then changing to black before the immature plumage is obtained.

The young larks began to be independent of their parents when they were about three weeks old. Although juveniles as old as 26 days were seen with their parents, just as many of this age were observed

Plate 6

Juvenile 5-1 at 20 days of age,
in alert stance.

Plate 7

Juvenile 5-1 at 20 days of age,
in a semi-crouch stance.

feeding by themselves in a foreign territory. Young 14-2 was seen catching a large ant (though he didn't swallow it) at 20 days of age, while in the company and territory of a neighbouring male. The latter was feeding one of its own young, the same age as 14-2. Boyd (1976) stated that juvenile *E. a. enthymia* were independent of adult females and males at 25 and 30 days of age respectively. The females apparently left their juveniles sooner in order to build the second nest.

In this study, the young larks ate primarily berries after reaching independence. Pink crowberries (*Empetrum eamesii*) were especially abundant, and seemed to form the main part of the juveniles' diet. Judging from its gizzard contents (Table 13), juvenile 5-3 was eating mainly bog cranberries (*Vaccinium oxycoccos*) at two weeks of age.

On August 11, a deformed juvenile lark approximately one month old was captured on the study area. Its left wing was a mere stump about 20 mm long; the left tarsus was flattened and bent under the body, and had only two toes, both deformed.

The first small flocks indicative of post-breeding activity were seen in late July. On July 27, a flock of 13 Horned Larks (five males, two females, and six juveniles) was seen on the study area. These were probably not local larks, since none of the females or juveniles were banded. By early August, when most local juveniles were about one month old, several small mixed flocks of local young and female larks were seen feeding together.

Breeding Success

The overall breeding success (number of young leaving nest per

eggs laid) of Horned Larks at Cape St. Mary's in 1976 was 58.8% (n = 24 nests, 80 eggs). This is a fairly high success rate for Horned Larks, considering other values given in the literature. Table 11 summarizes breeding success statistics for the Horned Lark in this and other similar studies.

The mean number of fledglings produced by each breeding pair during this study was 4.0 (n = 12); these values ranged from zero (Territory R and perhaps Territory O; since the nests on these territories were deserted as a result of trapping disturbance, they were not considered in calculating the mean) to seven fledglings per pair (Territories A and L). The birth rate (fledglings/adult/season) was therefore 2.0. Assuming a stable population, the replacement rate can be calculated from the equation

$$g = \frac{b}{1+b} = 0.667 \quad \text{(Fretwell, 1972).}$$

Thus, the Horned Lark population at Cape St. Mary's must suffer about 65% annual mortality to remain stable. High death rates of first year birds, especially newly-fledged juveniles, probably accounts for most of this mortality.

Egg and nestling loss (Table 12)

The most important cause of egg and nestling loss was predation, which accounted for 42.9% of all nest losses. Animals seen regularly on the study area which could have been nest predators were: ermines (*Mustela erminea* L.), mink (*Mustela vison* Schreber), red fox (*Vulpes*

TABLE 11

Horned Lark Breeding Statistics

	Pickwell (1931)	Sutton and Parmelee (1955)	Verbeek (1967)		Beason (1970)	Giezentanner and Ryder (1969)	from Boyd (1976)			Boyd		Cape St. Mary's 1976
			1963	1964			Strong (1971)		Porter and Ryder (1972)	1974	1975	
							1970	1971				
Nests	24	6	4	11	8	15	28	46	46	65	62	24
Clutch Size	3.42	4.00	3.25	3.09	3.2	2.8	2.79	3.04	2.65	3.11	2.66	3.31
Total Eggs	82	24	13	34	26	39	78	140	122	202	165	80
Eggs Hatched	65	23	10	31	13	23	40	84	67	140	28	63
% Hatched	79.2	95.8	76.9	91.2	50.0	58.9	51.0	60.0	54.9	69.3	35.2	78.8
Young Fledged	39	15	4	21	6	16	24	47	46	103	38	47
% Fledged	47.6	62.5	30.8	61.8	23	41	31.0	34.0	37.7	51.0	23.0	58.8
% Fledged of Eggs Hatched	60	65.2	40	67.7	46.2	69.6	60.0	56.0	68.7	73.6	65.5	74.6
Brood Size Fledged	1.63	2.50	1.00	1.91	0.74	1.15	0.86	1.03	1.00	1.59	0.61	1.95
No. of Broods	2	1	1	1	2	-	2?	2?	-	2	1-2	1-2

TABLE 12

Sources of Egg and Nestling Loss

	Weather	Predation	Desertion	Infertility	Malnutrition	Miscellaneous
Eggs Lost	3	12	6	1	-	2[1]
% of Eggs Lost	12.5	50.2	25.0	4.2	-	8.3
% of Eggs Laid	3.5	13.5	6.7	1.1	-	2.3
Nestlings Lost	9	6	0	-	3	0
% of Nestlings Lost	50.0	33.3	0	-	16.7	0
% of Eggs Hatched	13.6	9.1	0	-	4.5	0
Total Loss	12	18	6	1	3	2
% of Total Loss	28.6	42.9	14.3	2.4	7.1	4.8
% of Eggs Laid	13.5	20.2	6.7	1.1	3.4	2.3

[1]These eggs were accidentally knocked out of the nest, presumably by the incubating female.

vulpes L.), meadow voles (*Microtus pennsylvanicus* (Ord)), shrews (*Sorex cinereus* Kerr) and a domestic cat (*Felis domestica* L.). Ravens were also present, but seemed to confine their nest-robbing activities to the adjacent sea-bird colonies.

Ermines and larks were seen together twice. On May 15, a female lark was seen approaching an ermine in short flights. The lark made no attack on the ermine, which eventually ran off. On July 11 an ermine was observed carrying off a nestling between Nests 26 and 17. Since no young were lost from these nests, and several Savannah Sparrows, along with one or two larks, were scolding the ermine, it was assumed that a sparrow nestling had been taken.

When Nest 25 was discovered on July 1, two dead nestlings, about five days of age, were lying about 50 cm from the nest, and the one young bird in the nest had been bitten on the left wing, losing a secondary and several covert pinfeathers. Both of the dead young had open wounds in their sides.

It is doubtful that Meadow Voles were an important source of nest predation for larks; trapping indicated a population density of about 25 voles/ha in the voles' favoured habitat of *Empetrum nigrum* earth hummocks (Meades, 1973), where very few lark nests were found.

On August 3, one of the lightkeeper's sons reported seeing a sheep pick a young lark up out of Nest 39 and carry it for 10 m in its mouth before dropping it. The boy returned the lark to its nest; it was unhurt when examined a few minutes later. The sheep probably accidentally grazed the nest, which at that stage was very difficult to differentiate from the surrounding vegetation.

Trampling of nests by sheep was a hazard on the study area, although it was never positively observed.

Bad weather accounted for 28% of egg and nestling losses; all of this occurred during the June 12 – 13 storm. All known nestlings died at this time, and Nest 7, which contained three eggs, was deserted shortly afterwards by FM1. Three other nests (8, 10, and 11) suffered predation during or shortly after the storm. At 0855 on June 14, FM5 was observed sitting on Nest 11, but after she flushed, the nest was seen to be empty (there had been three eggs in it).

Nest desertion occurred in two nests after the incubating female had been captured on the nest for banding.

One egg in Nest 17 proved to be infertile, and one egg in Nest 16 failed to hatch after it was pushed up onto the nest lip, apparently by the incubating female. It contained a well-developed embryo when opened a few days later. An egg in Nest 8 was also found just outside the nest cup. It was marked and returned to the nest, but a predator destroyed the nest before the eggs hatched, so the effects of this treatment on the egg's viability could not be determined. Beason and Franks (1974) also reported that females took no notice of eggs outside the nest cup.

Starvation caused the death of at least three late-hatching nestlings at Cape St. Mary's.

Renestings

Nine instances of renesting after nest destruction or desertion were recorded. The time interval between nest abandonment and renesting

(measured to the day the first egg was laid) averaged 5.8 days (range 4-8, n = 5). The interval between the time the young left a successful nest and the initiation of a second brood averaged 4.0 days (range 0-7, n = 4). The zero value came from Territory L, where FM6 laid the first egg in Nest 32 on the same day the young left her Nest 13. The second nest must therefore have been built while feeding the young in the first.

Four out of 16 pairs of larks studied at Cape St. Mary's raised two successful broods.

FOOD AND FEEDING

Horned Larks usually fed by vigorously probing the ground vegetation with their bills, searching for arthropods, berries, and seeds. They sometimes interrupted this ground-probing to run quickly after a low-flying wasp or moth. On August 5, FM3 was seen repeatedly flying after moths in the manner of a flycatcher.

At Cape St. Mary's larks were observed eating bog cranberries (*Vaccinium oxycoccos*), Pink Crowberries (*Empetrum eamesii*), large black ants, moth caterpillars and adults, beetles, craneflies (Tipulidae), and spiders.

Table 13 shows the gizzard contents of nine adult, 13 nestling, and one juvenile Horned Larks collected in Newfoundland. The nine adults and two of the nestlings were collected in April and May 1973 (Ryder, pers. comm.), the remainder being obtained from the study area in 1976.

It is apparent that the nestlings receive almost entirely

TABLE 13

Gizzard Contents of Horned Larks[1]

	Grit	Shell Bits	Caterpillars	Beetles	Ants	Spiders	Seeds	Miscellaneous
Nestlings								
6-1	1	3		2	1	10	1 *Vaccinium uliginosum*	
-2	1	6		2		3	1 unident.	
-3		200		10	2			
3-1	2			1				
-2		1		2			01 unident.	
-3	1			1				1 small twig
2-1			4		20			
-2			1			2		
-3			5			3		
25-2	9	10	6	3				1 moth, 2 sowbugs
-3	20	4	6	2				
1045[2]	28	1	2	8				
1046	33	4						
Juvenile								
5-3[3]	20						75 *Vaccinium oxycoccos* 45 *Juncus (?)*	

TABLE 13 (Continued)

	Grit	Shell Bits	Caterpillars	Beetles	Ants	Spiders	Seeds	Miscellaneous
Adults								
1035	40			4			40 *Empetrum* sp.	1 small feather, 7 small leaves.
1036	51			3	6	1		1 small feather, 2 leaves.
1037	65			3	3			1 small feather, 20 leaves.
1038	108				3			8 small leaves.
1039	35			2		1	40 *Empetrum* sp.	
1040	25		2		32	20	13 *Juncus(?)*	2 leaves.
1041	58		2		35	8		
1042	36		1			6		
1043	23	35	2		19	6	1 *Empetrum* sp.	

[1]Figures given indicate number of items found.

[2]Four-digit numbers indicate specimens collected by Dr. R. A. Ryder in 1973. 1035-1039 were collected on April 16 at Argentia, Nfld., 1039-1043 on May 8 at Cape St. Mary's. The nestlings 1045-1046 were killed by a predator at St. John's, Nfld., on May 27.

[3]Fourteen days of age.

arthropods, while the adults, especially early in the season, eat more seeds, berries, and small leaves. This is consistent with the findings of McAtee (1905 *vide* Beason 1970) and Boyd (1976). All birds examined, except the nestlings from Nest 2 (which were only one day old at death), had some grit in their gizzards, and almost half (8/18) of the gizzards from birds collected at Cape St. Mary's contained small bits of mollusc shell. Hågvar and Østbye (1976) reported finding mollusc shells and small rodent bones in gizzards of the Meadow Pipit (*Anthus pratensis* (L.)) and speculated that these may be ingested as a source of calcium, as well as functioning as an abrasive.

PREDATION

Although Merlins (*Falco columbarius* L.) were seen regularly on or near the study area, and American Kestrels (*Falco sparverius* L.) and Sharp-shinned Hawks (*Accipiter striatus* Vieillot) were common during spring and fall migration, no instances of predation on adult or juvenile larks were observed.

On September 24 a Peregrine Falcon (*Falco peregrinus* Tunstall) was seen over the study area. As it soared overhead, five larks feeding on the ground crouched motionless until the falcon disappeared over the cliffs.

The Red Foxes and domestic cat present on the area could have taken a few incubating females, but no evidence of this was observed.

The major source of mortality to larks seemed to be cars, which killed at least one adult and two juveniles over the course of the season.

POST-BREEDING PERIOD

Peters and Burleigh (1951) stated that Horned Larks leave their breeding grounds in Newfoundland in late September and October, with a few remaining until early November. Small flocks of larks (3 - 35 individuals) were seen on the study area throughout September and October; adverse weather conditions (heavy rain and 120 kph winds) on the November 14 visit prevented a search for larks. In 1975, during several trips to Cape St. Mary's to census marine birds, flocks of Horned Larks were observed throughout September and October, and a few as late as November 18.

An adult in molt (outer rectrices only half grown) was seen on September 16, 1976.

Banded Larks were last seen on September 24, when 35-1 was observed in a small flock of unbanded ones.

GENERAL DISCUSSION

The Horned Lark is a species adapted for life in barren, often inhospitable environments. It meets with little competition in these habitats (Drury, 1961), indeed *Eremophila* means "solitude-loving". The only bird species sharing the Cape St. Mary's barrens with the larks during the breeding season were Savannah Sparrows and Water Pipits. The Savannah Sparrows were more or less restricted to the soft ground heaths and the lusher hard ground heaths characterized by *Osmunda cinnamomea*, *Sanguisorba canadensis*, and *Iris setosa* Pall., but occasionally foraged on the dry hard ground heaths and rocky barrens. Water Pipits were observed only on the very steep grassy slopes above the sea cliffs until the young pipits left the nests, after which time pipit families foraged extensively across the hard ground heaths running back from the cliffs.

Later in the season, flocks of migrant Whimbrels (*Numenius phaeopus* (L.)) and Golden Plovers (*Pluvialis dominica* (Müller)) were commonly seen on the study area, feeding primarily on crowberries (*Empetrum* sp.).

In such extreme environments, the low level of competition led Drury (1961) to state "We should not look, then, for the reasons why the species has an advantage in living [there], but look for the features which allow it to live there." The Horned Lark, in several ways, exemplifies these features.

Although Horned Lark nests provide little protection from storms,

their inconspicuousness reduces losses to predators. The inconspicuousness of the actual nest is further enhanced by the "casual-abandonment" behaviour (Pickwell, 1931) of incubating females, noted in this and other Horned Lark studies, and the wariness of the adults while feeding nestlings, that was evident at Cape St. Mary's

Another possible strategy to reduce egg and nestling losses in vulnerable nests is to shorten the nesting periods. Boyd (1976) calculated that the normal incubation period for an egg the size of a Horned Lark's would be 15.6 days; the actual period of 11 days found in this and other studies, is therefore a substantial reduction.

Lark nestlings hatch in an altricial state, but develop rapidly, especially their legs. This allows them to leave the nest only eight days after hatching, four or five days before they can fly. The minimum period between the laying of the first egg and the nest-leaving of the first young is therefore about 21 days. This period can be further reduced by starting incubation before the final egg is laid, a relatively common strategy in ground-nesting birds and particularly longspurs (Drury, 1961; Hussell, 1972). Asynchronous hatching may be adaptive in shortening the nest period for at least some of the nestlings. It can also function as a method of reducing brood size during food shortages (Ricklefs, 1965; Boyd, 1976), as some of the younger nestlings observed in this study were never fed, and died a few days after hatching.

The ability of Horned Larks to renest after storms, predation, or other disturbances have blocked the initial nesting attempt is also important when considering the overall effects of these disturbances. Despite predation and a devastating storm, all but one of the

twelve most closely studied pairs at Cape St. Mary's managed to successfully fledge at least one young.

The mean clutch size of 3.31 in lark nests at Cape St. Mary's is very similar to those found in studies of *E. a. praticola*, although the incidence of second broods seems to be lower in the Newfoundland population. The number of second broods might have been much larger were it not for the storm of June 12 – 13, which set back the first broods by about three weeks. Boyd (1976) found that the number of second broods in *E. a. enthymia* declined markedly during years of bad weather.

Arctic populations of Horned Larks are restricted to only one brood per season, as are those breeding in alpine tundra in the Rocky Mountains (Sutton and Parmelee, 1955; Verbeek, 1967). Clutch sizes in the Arctic, however, are much larger (mean 4.8 on Bylot Island (Drury, 1961) than those in alpine tundra, which are essentially the same as those in populations in the surrounding valleys (Verbeek, 1967; Kapitonov and Lobachev, 1968; Boyd, 1976).

The number of nestlings produced by a given pair of Horned Larks in one season is therefore the result of complex interactions among clutch size, brood size, number of successful broods, and fledging success. All of these are affected in turn by factors such as the length of the breeding season, food availability, predation, weather, and overwinter mortality. It became apparent during this study that much more field work would be needed to determine which factors are important in the various environments.

LITERATURE CITED

American Ornithologists' Union. 1957. Checklist of North American birds. Am. Ornithol. Union, Baltimore, 691 pp.

Armstrong, E. A. 1973. A Study of Bird Song. 2nd enl. ed. Dover, N.Y. 343 pp.

Banks, R. C. 1959. Development of nestling White-crowned Sparrows in central coastal California. Condor 61: 96-109.

Bannerman, D. A. 1953. The Birds of the British Isles. Vol. 2. Oliver and Boyd, London. 301 pp.

Beason, R. C. 1970. The annual cycle of the Prairie Horned Lark in west central Illinois: Unpubl. M.Sc. Thesis, Western Illinois Univ., Macomb, Ill. 162 pp.

_____ and E. C. Franks. 1973. Development of young Horned Larks. Auk. 90: 359-363.

_____. 1974. Breeding behaviour of the Horned Lark. Auk 91: 65-74.

Bent, A. C. 1963. Life Histories of North American Flycatchers, Larks, Swallows, and their Allies. Reprint, Dover Publ., N.Y. 555 pp.

Bowles, J. H. 1900. Nesting of the Streaked Horned Lark. Condor 2: 30-31.

Boyd, R. L. 1976. Behavioural biology and energy expenditure in a Horned Lark population. Unpubl. Ph.D. Thesis, Colorado State Univ., Fort Collins, Colorado. 194 pp.

Burns, F. L. 1921. Comparative periods of nestling life of some North American nidicolae. Wilson Bull. 33: 4-15.

Cody, M. L. 1966. A general theory of clutch size. Evolution 20: 174-184.

Delius, J. D. 1965. A population study of Skylarks, *Alauda arvensis*. Ibis 107: 466-492.

Dement'ev, G. P., and N. A. Gladkov (Eds.) 1954. Birds of the Soviet Union. Vol. 5. Translated from Russian by the Israel Program for Scientific Translation. Jerusalem 1970 957 pp.

Drury, W. H. 1961. Studies of the breeding biology of Horned Lark, Water Pipit, Lapland Longspur, and Snow Bunting on Bylot Island, Northwest Territories, Canada. Bird-Banding 32: 1-46.

Dubois, A. D. 1935. Nests of Horned Larks and Longspurs on a Montana prairie. Condor 37: 56-72.

_____. 1936. Habits and nest life of the Desert Horned Lark. Condor 38: 49-56.

Fretwell, S. D. 1972. Populations in a Seasonal Environment. Princeton University Press, Princeton, N.J. 217 pp.

Garrett, M. L. 1948. The life history of the Prairie Horned Lark. Unpubl. M.Sc. Thesis, Ohio State University, Columbus, Ohio.

Godfrey, W. E. 1966. The Birds of Canada. National Museum of Canada Bull. 203. Queen's Printer, Ottawa, 428 pp.

Hågvar, S. and E. Østbye. 1976. Food habits of the Meadow Pipit, *Anthus pratensis* (L.), in alpine habitats at Hardangervidda, south Norway. Norw. J. Zool. 24: 53-64.

Harper, F. 1958. Birds of the Ungava Peninsula. Univ. of Kansas Publs., Mus. Nat. Hist. 17: 1-171.

Hussell, D. J. T. 1972. Factors affecting clutch size in arctic passerines. Ecol. Monogr. 42: 317-364.

Kelso, L. 1931. Some notes on young Desert Horned Larks. Condor 33: 60-65.

Levy, F. 1920. An unusual Horned Lark family. Bird-Lore 22: 85-86.

Lobachev, Yu. S. and V. I. Kapitonov. 1968. Ecology of the Horned Lark (*Eremophila alpestris albigula* Bp.) in the Karzhantau Mountains (Western Tien-Shan). (In Russ, with Engl. summary). Byull. Mosk. O-va. Ispyt. Prir. Otd. Biol. 73: 17-25.

Lovell, H. B. 1944. Breeding records of the Prairie Horned Lark in Kentucky. Auk. 61: 648-650.

Meades, W. 1973. A phytosociological classification of the Avalon Peninsula heath, Newfoundland. Unpubl. M.Sc. Thesis, Memorial University of Newfoundland, St. John's, Newfoundland, 249 pp.

Mousely, H. 1916. The breeding of the Prairie Horned Lark at Hatley, Stanstead County, Quebec. Auk. 33: 281-286.

Peters, H. S. and T. D. Burleigh. 1951. The Birds of Newfoundland. Houghton Mifflin Co., Boston. 431 pp.

Pickwell, G. B. 1931. The Prairie Horned Lark. St. Louis Acad. Sci. Trans. 27: 1-153.

Ricklefs, R. E. 1965. Brood reduction in the Curve-billed Thrasher. Condor 67: 505-510.

_____. 1967. A graphical method of fitting equations to growth curves. Ecology 48: 978-983.

_____. 1968. Patterns of growth in birds. Ibis 110: 419-451.

Sutton, G. M. and D. F. Parmelee. 1955. Nesting of the Horned Lark on Baffin Island. Bird-Banding 26: 1-18.

Tinbergen, N. 1939. The behaviour of the Snow Bunting in spring. Trans. Linn. Soc. N.Y. 5: 1-91.

Trost, C. H. 1972. Adaptation of Horned Larks (*Eremophila alpestris*) to hot environments. Auk. 89: 506-527.

Tuck, L. M. 1948. Recent observations on Newfoundland birds in the Argentia-Dunville area. Can. Field. Nat. 62: 103-112.

_____. 1972. The Snipes: a study of the genus *Capella*. Canadian Wildlife Service Monograph Series No. 5. Queen's Printer, Ottawa. 429 pp.

Vaurie, C. 1959. The Birds of the Palearctic Fauna. H. F. and G. Witherby, London. 762 pp.

Verbeek, N. A. M. 1967. Breeding biology and ecology of the Horned Lark in alpine tundra. Wilson Bull. 79: 208-218.

von Hartman, L. 1969. The Nesting Habits of Finnish Birds I. Passeriformes. Societas Scientiarum Fennica, Helsinki. 187 pp.

Wetherbee, D. K. 1957. Natal plumages and downy pteryloses of passerine birds of North America. Am. Mus. Nat. Hist. Bull. 113: 343-436.

_____. 1958. New descriptions of natal pterylosis of various bird species. Bird-Banding 29: 232-236.

Witherby, H. F., F. C. R. Jourdain, N. E. Ticehurst, and B. W. Tucker. 1965. The Handbook of British Birds. Vol. 1, H. F. and G. Witherby Ltd., London. 348 pp.

APPENDIX 1

Birds seen on or near the study area[1]

CANADA GOOSE (*Branta canadensis* (L.)). Small groups (3 - 10 birds) seen flying over the study area throughout May and early June. Nested on ponds 8 km to north.

BLACK DUCK (*Anas rubripes* Brewster). August 29 - 1, September 16 - 1.

PINTAIL (*Anas acuta* L.). May 27 - 3 males, July 2 - 2 pairs, September 16 - 3 females.

GREEN-WINGED TEAL (*Anas crecca* L.). May 27 - 2 males on bogs to north, August 29 - 2.

SHARP-SHINNED HAWK (*Accipiter striatus* Vieillot). September 14, 1975 - 1, September 16 - 1, October 1 - 1.

ROUGH-LEGGED HAWK (*Buteo lagopus* (Pontoppidan)). May 19 - 2, May 27 - 3.

BALD EAGLE (*Haliaeetus leucocephalus* (L.)). May 14 - 1 adult, May 26 - 1 adult and 1 immature.

MARSH HAWK (*Circus cyaneus* (L.)). September 14, 1975 - 1, October 15, 1975 - 1, June 7 - 1, September 16 - 3.

OSPREY (*Pandion haliaetus* (L.)). Inidividuals on June 5, July 6, September 24, and October 1.

PEREGRINE FALCON (*Falco peregrinus* Tunstall). September 24 - 1.

MERLIN (*Falco columbarius* L.). Individuals seen seven times in May and June; September 16 - 4, September 24 - 3, October 1 - 1.

AMERICAN KESTREL (*Falco sparverius* L.). September 14, 1975 - 2, May 20 - 1, September 24 - 2, October 1 - 3.

WILLOW PTARMIGAN (*Lagopus lagopus* (L.)). Common resident on the soft ground heaths to the north and east of the study area.

[1]All records are from the study area in 1976 unless otherwise noted; "forest" refers to small forest 5 km north of study area. Marine birds and Horned Larks are not included.

AMERICAN GOLDEN PLOVER (*Pluvialis dominica* (Müller)). September 14, 1975 - 70, dwindled to two by October 30, 1975. August 4 - 3, high numbers on August 30 - 40 and September 24 - 30; last seen October 21 - 15.

COMMON SNIPE (*Capella gallinago* (L.)). Common summer resident on bogs to north and east. Last seen October 15, 1975, September 24, 1976.

WHIMBREL (*Numenius phaeopus* (L.)). September 14, 1975 - 2. First seen on July 2 - 1, numbers built up to July 23 - 50, last seen August 30 - 20.

GREATER YELLOWLEGS (*Tringa melanoleucus* (Gmelin)). July 11 - 1, August 15 - 1.

SPOTTED SANDPIPER *Actitis macularia* (L.)). One pair nested on small pond just east of study area.

RUFF (*Philomachus pugnax* (L.)). May 20 - 1 female.

LEAST SANDPIPER (*Calidris minutilla* (Vieillot)). June 9 - 1, July 2 - 1, July 30 - 1, August 8 - 1.

MOURNING DOVE (*Zenaida macroura* (L.)). September 24 - 1.

SNOWY OWL (*Nyctea scandiaca* (L.)). May 19 - 1, on bogs 8 km north

SHORT-EARED OWL (*Asio flammeus* (Pontoppidan)). One seen regularly hunting for voles on study area in May and June.

COMMON FLICKER (*Colaptes auratus* (L.)). October 6, 1975 - 1, May 25 - 2.

HAIRY WOODPECKER (*Picoides villosus* (L.)). April 30 - 1 male in forest.

EASTERN KINGBIRD (*Tyrannus tyrannus* (L.)). June 6 - 1, June 23 - 1.

TREE SWALLOW (*Iridoprocne bicolor* (Vieillot)). Common visitant in late May and June (e.g. June 7 - 20) and early August (August 9 - 31).

BARN SWALLOW (*Hirundo rustica* L.). May 31 - 1, June 7 - 1, July 11 - 1.

GRAY JAY (*Perisoreus canadensis* (L.)). Common resident in forest.

COMMON RAVEN (*Corvus corax* L.). Common resident; one pair nested on cliffs west of A6.

COMMON CROW (*Corvus brachyrynchos* Brehm). Common resident in forest.

BLACK-CAPPED CHICKADEE (*Parus atricapillus* L.). November 18, 1975 - 1 in forest.

BOREAL CHICKADEE (*Parus hudsonicus* Forster). Common resident in forest.

AMERICAN ROBIN (*Turdus migratorius* L.). Common summer resident in forest and fir tuck. Earliest date - April 3, 1977. Large southward migration on October 21.

GRAY-CHEEKED THRUSH (*Catharus minimus* (Lafresnaye)). June 3 - 1, June 9 - 1.

HERMIT THRUSH (*Catharus guttatus* (Pallas)). Common summer resident in forest. Migrants on May 14 - 1, June 14 - 1.

SWAINSON'S THRUSH (*Catharus ustulatus* (Nuttall)). May 31 - 1, June 2 - 1, June 3 - 1, June 10 - 1.

GOLDEN-CROWNED KINGLET (*Regulus satrapa* Lichtenstein). Resident in forest.

RUBY-CROWNED KINGLET (*Regulus calendula* (L.)). Common summer resident in forest. Individual migrants on May 1, 5, 6, and 7.

WATER PIPIT (*Anthus spinoletta* (L.)). Common summer resident on steep slopes above sea cliffs. First seen May 14 - 5 males singing, May 19 - small groups (females?) feeding on barrens, June 7 - gathering nest material, June 23 - gathering food for nestlings, July 17 - last song heard, September 24 - flock of 75 on barrens.

STARLING (*Sturnus vulgaris* L.). May 14 - 3, June 4 - 2, July 19 - 1.

YELLOW-RUMPED WARBLER (*Dendroica coronata* (L.)). Common summer resident in forest. Migrants - October 15, 1975 - 1, May 12 - 1, September 24 - 2, October 1 - 1.

BAY-BREASTED WARBLER (*Dendroica castanea* (Wilson)). May 24 - 1 male killed at lighthouse.

BLACKPOLL WARBLER (*Dendroica striata* (Forster)). Common summer resident in forest. Migrants - May 25 - 1, May 26 - 1, June 7 - 1; all males.

NORTHERN WATERTHRUSH (*Seiurus novaboracensis* (Gmelin)). Common summer resident in forest; migrant on barrens June 1.

COMMON YELLOWTHROAT (*Geothlypis trichas* (L.)). Summer resident in bogs to north.

WILSON'S WARBLER (*Wilsonia pusilla* (Wilson)). June 9 - 1 male in forest.

RUSTY BLACKBIRD (*Euphagus carolinus* (Müller)). Common summer resident in forest.

PINE GROSBEAK (*Pinicola enucleator* (L.)). February 12 - 1 pair in forest.

PINE SISKIN (*Carduelis pinus* (Wilson)). October 15, 1975 - 2, November 18, 1975 - 1 in forest.

WHITE-WINGED CROSSBILL (*Loxia leucoptera* Gmelin). October 30, 1975 - 6, November 18, 1975 - 1 in forest.

SAVANNAH SPARROW (*Passerculus sandwichensis* (Gmelin)). Common summer resident on study area, very common on soft ground heaths to north and east. Nests with eggs found June 23 - 28. Last seen September 24 - 2.

DARK-EYED JUNCO (*Junco hyemalis* (L.)). October 15, 1975 - 1, April 30 - 1, May 5 - 2, May 25 - 2.

CHIPPING SPARROW (*Spizella passerina* (Bechstein)). May 25 - 1.

WHITE-THROATED SPARROW (*Zonotrichia albicollis* (Gmelin)). Common migrant - May 5 - May 31 (1 - 6 birds/day).

FOX SPARROW (*Passerella iliaca* (Merrem)). Very common summer resident in forest and fir tuck. Migrants on sea cliffs south of study area - April 18 - 10, April 3, 1977 - 4. Fledglings in forest June 9, latest date October 15, 1975 - 2 in forest.

LINCOLN'S SPARROW (*Melospiza lincolnii* (Audubon)). May 19 - 1 in forest.

SWAMP SPARROW (*Melospiza georgiana* (Latham)). Very common summer resident in fir tuck. First seen May 19, migrant at lighthouse May 31.

LAPLAND LONGSPUR (*Calcarius lapponicus* (L.)). 1 male changing to breeding plumage with a pair of Horned Larks on barrens June 15.

SNOW BUNTING (*Plectrophenax nivalis* (L.)). Common winter resident on study area; flocks of up to fifty birds seen from mid-October to early April.

APPENDIX 2

Measurements of Savannah Sparrow Nestlings

Age (days)		0	1	2	3	4	5	6	7	8	9
Weight	$\bar{x}$	2.50	3.63	5.83	7.50	10.13	[illegible]45	14.75	18	17.5	17.7
(g)	Sx	0.46	0.83	1.15	1.32	1.49	1.17	0.65	-	1.00	0.67
	$S\bar{x}$	0.16	0.30	0.67	0.76	0.75	0.35	0.32	-	0.45	0.30
	R	1.5-3	2.5-5	4.5-6.5	6-8.5	8.5-12	10.5-14.5	14-15.5	18	16.5-19	17-18.5
	n	8	8	3	3	4	11	4	1	5	5
Tarsus	$\bar{x}$	7.2	8.63	10.0	12.0	15.33	17.36	21.0	20	21.1	21.9
(mm)	Sx	0.76	1.27	1.73	1.00	0.58	1.00	0.82	-	1.24	0.55
	$S\bar{x}$	0.34	0.45	1.00	0.58	0.33	0.30	0.41	-	0.56	0.24
	R	6.5-8	7-11	9-12	11-13	15-16	16-19	20-22	20	20-23	21-22.5
	n	5	8	3	3	3	11	4	1	5	5
Wing	$\bar{x}$	7.2	8.14	9.17	11.67	16.0	21.05	27.0	35	36.0	39.0
(mm)	Sx	0.27	0.56	1.15	1.53	1.78	1.47	1.63	-	2.57	1.54
	$S\bar{x}$	0.12	0.21	0.67	0.88	0.89	0.44	0.82	-	1.15	0.69
	R	7-7.5	7-8.5	8.5-10.5	10-13	13.5-17.5	20-25	25-29	35	33-40	36.5-40
	n	5	8	3	3	4	11	4	1	5	5

APPENDIX 2 (Continued)

Age (days)		0	1	2	3	4	5	6	7	8	9
Rectrix	$\bar{x}$	-	-	-	-	-	-	-	8.5	8.63	10.33
(mm)	Sx	-	-	-	-	-	-	-	-	1.49	1.86
	$S\bar{x}$	-	-	-	-	-	-	-	-	0.75	0.76
	R	-	-	-	-	-	-	-	8.5	7-10.5	8-13
	n	-	-	-	-	-	-	-	1	4	6
Culmen	$\bar{x}$	5	-	-	-	-	-	-	8	8.5	8.8
(mm)	Sx	-	-	-	-	-	-	-	-	0.41	0.45
	$S\bar{x}$	-	-	-	-	-	-	-	-	0.20	0.20
	R	5	-	-	-	-	-	-	8	8-9	8-9
	n	1	-	-	-	-	-	-	1	4	5

[1]R = Range.

APPENDIX 3

Daily Weather Conditions

Date	Sky	Wind (kph)	Precipitation	Fog (dayl. hrs.)	Approx. Temp.[1]
April 30	Clear	SW 15-35	none	6	
May 1	Clear	S 0-10	none	0	
2	Clear	N 0-10	none	9	warm
3	Fog	S 45	rain all day	17	cold
4	Fog	S 25-30	none	17	cold
5	Overc./Clear	SW 15-30	none	0	cool
6	Clear	S 50-60	none	0	cool
7	Overcast	WNW 10-30	none	0	cool
12	Clear	Calm	none	0	warm
13	Overcast	SE 25-30	rain in PM	3	cool
14	Clear/Overc.	NW 10-SW 10	none	4	warm
15	Overcast	SW 10	rain all day	8	cool
16	Overcast	NE 60	rain all day	0	cool
17	Cloudy	NE 45	none	0	warm
18	Fog	SE 5	none	17	cool
19	Clear	Calm	none	7	warm
20	Clear/Fog	SE 15-30	none	4	warm
21	Overcast	-	intermittent	8	cool
22	Overcast	-	intermittent	8	cool

APPENDIX 3 (Continued)

Date	Sky	Wind (kph)	Precipitation	Fog (dayl. hrs.)	Approx. Temp.[1]
May 23	Overcast	-	intermittent	8	cool
24	Fog	calm	none	17	cool
25	Overcast	N 30-NW 10	none	0	cold
26	Overcast	NE 10	none	0	
27	Overcast	E 10	none	0	cool
31	Clear	-	none	3	cool
June 1	Clear/Overc.	NE 2-E 30	none	0	cool
2	Clear	NW 30	none	0	warm
3	Fog	S 10	none	13	cool
4	Clear	0 -W 30	none	0	
5	Clear/Overc.	SW 20-45	none	0	cool
6	Clear	SSE 15-SW 40	none	0	warm
7	Overcast	ESE 5-E 45	none	0	cold
8	Overcast	SE 45-NW 15	none	15	cool
9	Overcast	SE 25	rain in AM	13	cool
10	Clear/Overc.	NW 30	none	0	warm
11	Overcast	SW 45	intermittent	9	cold
12	Overcast	NE 45-SE 70	rain all day	0	cold

APPENDIX 3 (Continued)

Date	Sky	Wind (kph)	Precipitation	Fog (dayl. hrs.)	Approx. Temp.[1]
June 13	Overcast	SW 120	rain and sleet	0	cold (0°C)
14	Clear	SW 40	none	0	cool
15	Fog	W 10	none	17	-
16	Fog/Overc.	-	heavy rain-AM	17	cool
17	Fog	-	-	17	-
18	Fog/Clear	-	none	8	warm
19	Clear	-	none	0	warm
20	Fog	SW 10	none	17	-
21	Fog	SW 10	none	17	-
22	Clear	NW 15	none	0	-
23	Overcast	SW 10	none	0	-
24	Fog	S 10-NW 10	none	17	-
25	Overcast	E 20-NE 30	none	13	-
26	Overc./Clear	NE 30	rain in AM	0	-
27	Clear	calm	none	4	warm
28	Overcast	SE 20	none	5	-
July 1	Overcast	calm	none	0	warm
2	Overcast	E 30	rain in PM	0	-

APPENDIX 3 (Continued)

Date	Sky	Wind (kph)	Precipitation	Fog (dayl. hrs.)	Approx. Temp.[1]
July 3	Overcast	calm	none	4	warm
4	Clear	calm	none	7	warm
5	Overc./Clear	calm	none	7	warm
6	Clear	E 20	none	0	warm
7	Fog	SSW 10-20	none	17	warm
8	Fog/Clear	SW 20	none	13	warm
9	Fog	SW 20	intermittent	17	cool
10	Fog	SW 20	none	17	-
11	Clear	WNW 5	none	0	warm
12	Clear	SSE 15	none	2	hot (23°C)
13	Overcast	ESE 30	none	9	-
14	Fog	-	rain in AM	17	-
15	Fog	-	-	17	-
16	Overcast	-	-	8	-
17	Overcast	NNW 5	none	0	-
18	Overcast	SE 30	none	8	-
19	Fog	SSW 15	none	17	-
20	Overc./clear	S 30	-	8	-

APPENDIX 3 (Continued)

Date	Sky	Wind (kph)	Precipitation	Fog (dayl. hrs.)	Approx. Temp.[1]
July 21	Fog/Clear	SE 20-SSW 20	none	10	-
22	Overcast	W 15	intermittent	8	-
23	Clear	N 10	none	0	-
24	Fog/Clear	SW - SE 15	none	9	-
25	Fog	SE 40	rain in PM	17	-
26	Fog	SE 25	rain in AM	14	warm
27	Overcast	NNW 10	none	0	-
28	Clear	-	none	0	-
29	Fog	-	-	17	-
30	Fog	-	none	15	-
31	Clear	-	none	8	-
Aug. 1	Fog	SE 60	intermittent	17	cool
2	Fog	SW 30	none	17	cool
3	Clear	WSW 10	none	2	-
4	Clear	SSW 10	none	0	warm
5	Overcast	SW 10	none	9	-
6	Fog	SSW 30	none	17	-
7	Clear	WNW 10	none	6	-

APPENDIX 3 (Continued)

Date	Sky	Wind (kph)	Precipitation	Fog (dayl. hrs.)	Approx. Temp.[1]
Aug. 8	Overcast	SW 5	none	0	-
9	Fog/Overc.	W 5	none	8	-
10	Fog	-	none	17	-
14	Fog/Overc.	NNE 10	none	8	-
15	Overcast	NE 25	light rain	0	cool
30	Clear	E 30	none	0	cool
31	Overcast	-	intermittent	0	cool

[1]cold = approx. 0-10°C; cool = approx. 10-15°C; warm = approx. 15-20°C; hot = approx. 20+°C.

APPENDIX 4

Horned Lark Nestling Growth Data

Age in Days

(sample sizes in parentheses)

		0 (40)	1 (40)	2 (36)	3 (36)	4 (34)	5 (38)	6 (29)	7 (33)	8 (18)	9 (9)	10 (1)
Weight	$\bar{x}$	3.76	6.24	9.47	13.58	18.01	22.43	26.41	28.71	30.72	30.33	24
(g)	Sx	0.76	1.35	2.05	2.74	2.95	3.00	3.73	2.65	2.43	2.49	-
	$S\bar{x}$	0.12	0.21	0.34	0.46	0.51	0.49	0.69	0.46	0.57	0.83	-
	R	2.5-5.5	3.5-8.5	5.5-14	4.5-17	11-23.5	14-27	15-30.5	24-34	26-35	26.5-35	24
Culmen	$\bar{x}$	4.43	4.98	5.56	6.35	7.06	7.59	7.86	8.29	8.56	9.00	9.5
(mm)	Sx	0.45	0.44	0.92	0.53	0.59	0.66	0.82	0.43	0.51	0.35	-
	$S\bar{x}$	0.07	0.07	0.17	0.09	0.10	0.11	0.15	0.08	0.12	0.12	-
	R	4-5	4.5-6.5	5-7	5-7	6-8	6-9	6.5-9	7.5-9	7.5-9	8.5-9.5	9.5
Tarsus	$\bar{x}$	7.00	8.83	11.38	14.19	16.81	19.74	21.86	23.14	24.11	24.28	24
(mm)	Sx	0.71	0.88	1.23	1.43	1.16	1.59	1.66	0.82	0.80	0.57	-
	$S\bar{x}$	0.11	0.14	0.21	0.24	0.20	0.29	0.31	0.14	0.19	0.19	-
	R	6-8.5	7-11	9-13	11-16.5	14.5-19	16-22	17-24	21-24.5	22.5-25	23.5-25	24
Hallux	$\bar{x}$	4.04	5.04	6.39	8.19	10.08	11.79	13.00	13.69	14.08	14.39	14.5
plus	Sx	0.26	0.60	1.35	0.93	1.04	0.85	0.78	0.56	0.46	0.49	-
Claw	$S\bar{x}$	0.04	0.10	0.24	0.16	0.19	0.14	0.16	0.10	0.11	0.16	-
(mm)	R	3.5-4.5	4-6	5.5-8.5	6.5-10	8-11.5	10-13	11-14	12-14.5	13-15	14-15	14.5

APPENDIX 4 (Continued)

		0 (40)	1 (40)	2 (36)	3 (36)	4 (34)	5 (38)	6 (29)	7 (33)	8 (18)	9 (9)	10 (1)
Claw	$\bar{x}$	1	1.43	1.92	2.68	3.40	4.28	5.32	5.75	6.17	6.56	6.5
(mm)	Sx	0	0.36	0.42	0.48	0.62	0.69	0.67	0.52	0.54	0.42	-
	$S\bar{x}$	0	0.06	0.07	0.08	0.10	0.11	0.13	0.09	0.13	0.15	-
	R	1	1-2	1-3	1.5-3.5	2-5	3-5.5	3-6	4.5-7	5.5-7	6-7	6.5
Wing	$\bar{x}$	7.9	9.4	11.35	15.56	21.08	28.76	38.05	46.42	53.58	59	65
(mm)	Sx	0.48	1.00	1.99	2.58	3.57	4.93	5.96	3.99	3.29	2.66	-
	$S\bar{x}$	0.08	0.16	0.33	0.43	0.59	0.80	1.11	0.69	0.78	0.89	-
	R	7-9	8-11.5	9-14.5	10.5-20	13-28	16.5-37	19-44	40-55	47-58	54.5-63	65
First	$\bar{x}$	0	0.18	0.84	2.64	5.91	11.81	18.34	24.88	30.0	34.56	38
Primary	Sx	0	0.32	0.47	1.18	2.00	2.96	4.09	2.92	2.45	2.01	-
(mm)	$S\bar{x}$	0	0.05	0.08	0.20	0.35	0.49	0.76	0.51	0.58	0.67	-
	R	0	0-1	0-2	0.5-4.5	1-9.5	6-19.5	6-24	18.5-32	26-34	30-37	38
Ninth	$\bar{x}$	0	0.15	0.77	1.90	4.21	8.56	13.21	18.64	22.26	26.6	34
Primary	Sx	0	0.28	0.46	0.80	1.53	1.92	4.03	2.55	4.92	2.95	-
(mm)	$S\bar{x}$	0	0.04	0.08	0.14	0.27	0.33	0.75	0.45	1.19	0.93	-
	R	0	0-1	0-2	0.5-4	1-7	5-12	3-18	14-24	19-28	23-31	34

ABSTRACT

The breeding biology of the Horned Lark (*Eremophila alpestris alpestris* (L.)) was studied during the 1976 breeding season at Cape St. Mary's, Newfoundland.

The timing and function of ground singing, song-flights, and other vocalizations was discussed. Territorial behaviour was investigated, and territories were subsequently mapped to determine their size (2.313 - 5.125 ha, mean 3.542 ha). Male territorial hostilities and courtship behaviour were discussed.

Nesting phenology was studied in detail. Nests were analyzed for position and structure; they tended to be protected on the windward side. Clutch sizes of early and late nests were compared (early 3.0, late 3.5, overall mean 3.31). Forty-seven nestlings were measured to calculate growth curves for weight and other body parameters. Breeding success, incidence of renesting, and the mean number of fledglings produced by each pair were calculated. Causes of egg and nestling loss were analyzed. About one-quarter of the breeding pairs raised two successful broods.