Wilson Bull., 93(4), 1981, pp. 519–530

HORNED LARK BREEDING BIOLOGY AT CAPE ST. MARY'S, NEWFOUNDLAND

RICHARD J. CANNINGS AND WILLIAM THRELFALL

The Horned Lark (*Eremophila alpestris*) occupies a variety of barren habitats in Europe, North America (Vaurie 1959, Bent 1963) and Colombia. A number of studies have been made of this species in North America, mostly in the central part of the continent (Pickwell 1931; Garrett 1948; Beason 1970; Beason and Franks 1973, 1974; Boyd 1976). Little work has been done in the northern and eastern regions of the continent, however, other than that of Sutton and Parmelee (1955), who worked on Baffin Island, and Drury (1961) whose study area was Bylot Island.

STUDY AREA

We studied Horned Larks continuously during the 1976 breeding season (May–August) at Cape St. Mary's (46°47'N, 54°12'W), a headland at the southwestern tip of the Avalon Peninsula, Newfoundland and also made observations weekly in April and biweekly in February, March and September through November. In April 1977 a last visit was made.

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 common, and occurred 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 (13 June) to 23°C (12 July); daily maximums were usually between 10 and 15°C. Winds stronger than 20 km/h were common until late June and picked up again in late August. The severest storm of the summer (12–13 June) brought 70 mm of precipitation (rain and sleet) and winds up to 120 km/h.

The study area covered approximately 90 ha of headland heath extending back from the sea cliffs for 1–2 km. 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 patches of soft ground heath. The tract is flat to somewhat undulating and treeless, except for a few very stunted balsam firs (*Abies balsamea*) growing in places protected from the wind. Lark territories were mapped by repeatedly flushing individuals or pairs and recording their positions with regard to established grid-points (see Cannings 1977). Territorial interactions, such as threat displays with flight chases, were also considered in the mapping of territories.

METHODS

Observations, including those of larks at their nests, were made with 8 × 30 binoculars and a 15–60× spotting scope. No blind was used. One male and 15 female larks were captured, individually color-banded, aged, sexed, weighed to the nearest 2 g (300 g Pesola scale) and measured (wing, culmen, tarsus, tail, hallux plus claw, first and ninth primaries). Each adult is referred to by a letter prefix (F—female, M—male) followed by a numeral (e.g., F3 was the third female captured).

As most nests found already contained eggs, dates of nesting starts were determined (and hence defined) by back-dating from hatching. Nests with eggs were usually checked several times daily to discover precise hatching times; those with young were visited at least once daily to measure the nestlings, in the same manner as adults. For individual identification, birds were marked on the tarsi with indelible ink at hatching and banded when 7 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 in the nest, direct observation of nest-feeding behavior was difficult. After the young had left, the nests were measured, collected and frozen. They were examined later to determine nest composition, dried (at room temperature) and weighed.

RESULTS AND DISCUSSION

The first lark seen near the study area in 1976 was a male on 4 April. In succeeding weeks larks appeared in increasing numbers on the study area from 8 April (5 birds) to 30 April. Tuck (*in* Peters and Burleigh 1951) noted that "large flocks" arrived in Argentia, Newfoundland (50 km north of present study area) in spring, a phenomenon not seen during the present study. Other workers (Pickwell 1931, Bannerman 1953, Boyd 1976) indicated that male larks normally return shortly before the females. We also noted this in Newfoundland in 1977, but not 1976, when many presumed pairs arrived at the same time. The larks seen between 14–18 April 1976 showed no territorial behavior and were not singing, perhaps due to wind conditions (30–70 km/h), which inhibit singing (Beason 1970). Larks seen on 3 April 1977 were singing and chasing each other. On arrival, larks stayed almost exclusively on the dry headland heath. Larks later nested along the gravel road that ran through the bogs.

General behavior: territories and courtship.—Twelve lark territories mapped in the study area (Fig. 1) ranged from 2.3 ha (E) –5.1 ha (A), with a mean of 3.5 ha. The territories were comparable in size to those found by Ryder (3.1 ha, at Argentia, Newfoundland, pers. comm.) and Pickwell (1931), but were larger than those of Beason and Franks (1974, 0.6–3.1 ha), Boyd (1976, 0.29–1.35 ha) and Lobachev and Kapitonov (1968, 0.15–0.25 ha), who worked with other subspecies. Territories were distributed in a linear fashion along the road, as male larks favored this area for dust-bathing, roosting and singing. Such an arrangement was also reported by Boyd (1976).

Territorial behavior (singing and the three types of hostile behavior described by Beason [1970]) was evident shortly after the larks arrived in April and was maintained until the last young left the nest in early August.

Territorial fights and chases were common from late April into July, becoming rare by the end of July. Aggressive behavior seemed to be more evenly distributed over the nesting season at Cape St. Mary's than pre-

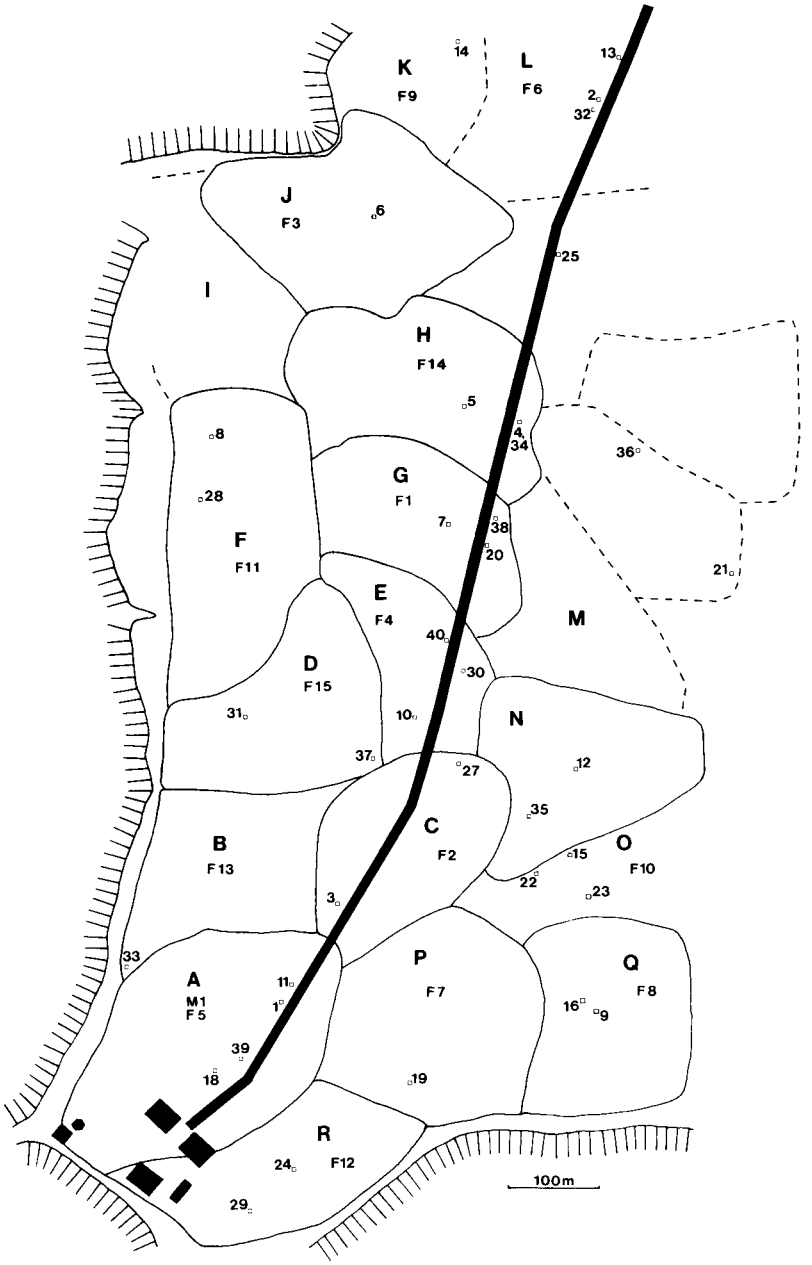

FIG. 1. Map of study area showing the boundaries of the mapped territories. The large single letter in each territory designates the territory, the letter-numeral groups (e.g., F12) indicate the resident adult larks. Nest locations are shown by the small open squares with the nest number. (Lighthouse complex located lower left.)

viously reported by Pickwell (1931) and other workers. With the large territories and very foggy weather at Cape St. Mary's, it may have been more difficult for male larks to patrol their boundaries, leading to many unchallenged trespasses and thus prolonging territorial disputes.

Trespassing was fairly common, as illustrated by the following: F13, observed gathering food for her nestlings in the immediate area of nest 18, 150 m from her territory, was completely ignored by F5 and M1, who were feeding young in nest 18 at the time. Larks from territories that did not take in the road sometimes dust-bathed on the road without being attacked.

Territoriality broke down as soon as the last brood left the nest and independent juveniles were not challenged on foreign territories. Young larks that had left their nest, but were still being fed, seemed to be kept within territorial limits by their parents. After 27 July small flocks of unbanded larks were common on the study area, and little or no agonistic behavior was noted between them and the resident larks.

Most agonistic behavior observed in the larks was restricted to male vs male confrontations. On only five occasions were females involved in this type of behavior, with hostilities being directed at other females, in a manner similar to—though not so frequent—as that described by Tinbergen (1939) for Snow Buntings (*Plectrophenax nivalis*).

Courtship displays were seen nine times, but copulation never followed any of those seen. The male approached the female with body held low to the ground, wings drooping and quivering, then bowed and fanned the tail. When the male stretched and held his head high, the black breast feathers were usually raised, enlarging the breast patch. Males attempted to mount females several times, but each time she side-stepped or fended him off with a kick. Often the female ran at the male as he approached. The similarity of the invitatory display (see Beason and Franks 1974) to dust-bathing was demonstrated in instances where males attempted to mount dust-bathing females. No male-female chases were seen that were definitely referable to the "sexual chase" as described by Beason and Franks (1974).

Nesting, eggs, incubation and hatching.—In Newfoundland, Horned Larks usually begin nesting between mid-May and early June; second broods, if any, occur in July and early August (Fig. 2). Nesting behavior was noted from 13 May (nest building) until 8 August, when the young left the last nest. The earliest known nesting date for the island can be extrapolated from a 3-week-old juvenile collected in St. John's 26 May 1968; this bird must have come from a nest begun around 24 April. The latest nesting date is Tuck's report of essentially flightless young at Argentia on 11 September 1947 (Peters and Burleigh 1951).

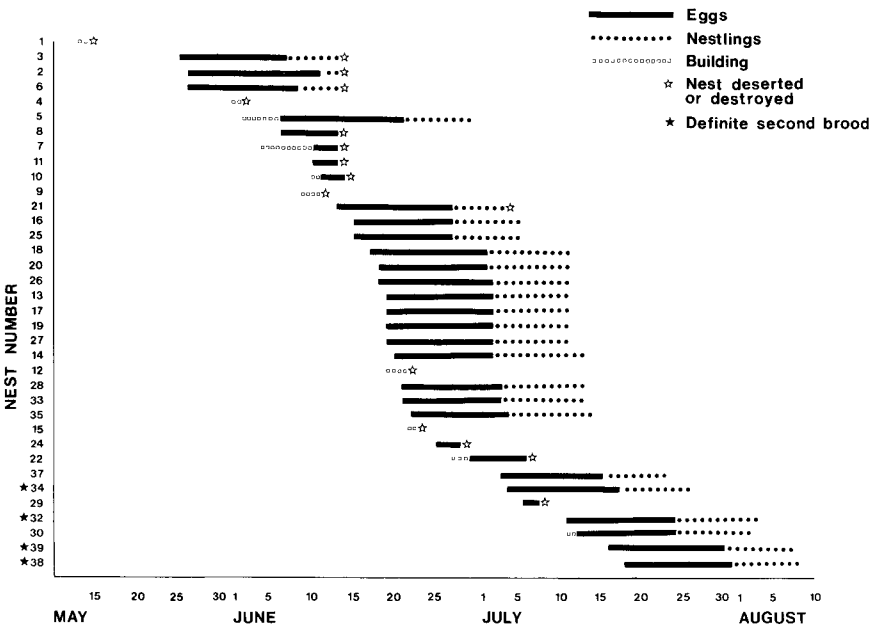

FIG. 2. Nesting phenology of Horned Larks in 1976 at Cape St. Mary's.

Nesting starts occurred from about 25 May until 11 June. A severe storm on 12–13 June, however, destroyed all three nests with young, and caused desertion of 4 of 5 nests with eggs. Three nests found after the storm (nests 16, 21, 25) were probably built before 12 June, and may have survived the storm because incubation had not begun. The earliest known second brood was started on 4 July (nest 34), in territory H, where one of the few nests to survive the storm was located. Three of the later nests (32, 38, 39) were second broods in territories where nests had not survived the storm.

Only the female built the nest, usually in the morning. The site was located in a depression dug in the ground, or in a tight mat of vegetation—crowberry (*Empetrum* sp.), lichen (*Cladonia* spp.) and/or moss (*Rhacomitrium lanuginosum*). Nests consisted of a grassy cup which was usually lined with a softer material (feathers or wool). Most had a small area of pebbles, or dried mud (paving) next to them. Vegetation cover associated with nest-sites is given in Cannings (1977). Nine of 31 nests examined were located within 50 cm of bare ground, and in the territories which contained the road, 15 of 18 nests were found within 10 m of the road, recalling Pickwell's (1931) earlier observations. Three nests were

located in cinnamon fern (*Osmonda cinnamommea*)—American burnet (*Sanguisorba canadensis*) habitat, but none were found in moist habitat, as they were by Verbeek (1967). While the female built the nest, the male was usually nearby, feeding, singing and chasing trespassers.

The mean dry weight of 31 nests was 16 g (range = 7–33 g), with the nests having a mean outer diameter of 99 mm (N = 26, range = 65–135 mm, some nests being asymetrical) and a mean inner diameter of 71 mm (N = 28, range = 55–85 mm). There was no significant variation in nest size or composition throughout the summer, contra Pickwell (1931).

Most nests were protected by vegetation on the windward side (N = 15, mean height of protection = 92 mm, range = 5–130 mm), with the open side facing west to northeast. The distribution of the directions was non-random, based on the Rayleigh test for randomness around a circle (r = 0.4142, $P < 0.05$). This bias in nest placement was probably due to the fact that the prevailing winds were from the southwest, and strong winds were most often from the quadrant south to east.

Nests were constructed primarily of grass, mostly *Deschampsia flexuosa*, with some lichens, rootlets, moss, leaves, feathers, small twigs and paper. Most of the lichens (predominantly *Cladonia* spp.) and mosses were on the outside of the grass cup, and were perhaps used to level the nest cup dug in the ground before the main grass structure was built. Seabird feathers were present in all nests examined, and wool in more than 50% of them. The only soft plant materials used in nest linings were leaves of the northern honeysuckle (*Lonicera villosus*) and down from willow (*Salix Uva-ursi*) catkins.

Dubois (1935), Beason and Franks (1974) and Boyd (1976) all noted that during Horned Lark nest construction an area of "pavings" (small pebbles and mud) was usually placed on one side of the nest. Dubois (1935) believed that the pavings served to cover and camouflage the dirt excavated from the nest cup, a view with which Beason and Franks (1974) and Boyd (1976) concurred and which is supported by our observations. In nest cups made in the mat of *Empetrum* no dirt was thrown out beside the nest. Seven of 15 nests built in this habitat had no trace of paving, while only 1 of 15 nests built in short grass on the roadside, or in gravelly habitat, had no trace of paving. This difference (7/15 vs 1/15) is significant (χ^2 = 6.136, $P < 0.05$). This may, however, simply reflect a closer supply of paving material at the roadside nests. The nest building time noted in this study approximates that noted by Beason (1970). The most rapidly built and loosely constructed nest of those observed in the present study was a simple cup dug in the *Empetrum nigrum* mat, with a few grass stems, feathers and bits of willow down. It contained an egg the day after discovery. Nests 1, 9, 12, 15 and 40 found in the study area were incomplete

and apparently deserted early. Beason (1970) reported a female building two nests simultaneously, a phenomenon that we also found once; the female used one nest, later finishing the second nest in which she raised a second brood.

Renesting after nest destruction or desertion was recorded nine times. The time interval between nest abandonment and renesting (measured to the day the first egg was laid) averaged 5.8 days (N = 5, range = 4–8). The interval between the time the young left a successful nest and the initiation of a second brood averaged 4.0 days (N = 4, range = 0–7). The zero value came from territory L, where F6 laid the first egg in nest 32 on the same day the young left her nest 13. The second nest must have been built while she was feeding the young in the first. Four of 16 pairs of larks raised two successful broods.

Eggs were usually laid before 05:00, at a rate of one per day until completion of the clutch. In contrast, Boyd (1976) found eggs were often laid every other day in very early nests. Clutch-sizes of 26 nests varied from 2–4 (1 [2], 16 [3], 9 [4]), with a mean of 3.3 ± 0.6. A significant increase in clutch-size over the breeding season was noted, with a mean clutch-size of 3.0 in 10 nests begun before 15 June. That of 16 nests begun after 15 June was 3.5 ($t = 2.48$, $P < 0.05$). Of eight females for which two or more nesting attempts were recorded, four had two clutches of three, and four contained a first clutch of three and then a clutch of four. Only one first nest contained a clutch-size of four, and it was one of the latest first nests. This trend to increased clutch-size in passerines, over the breeding season, is well documented (e.g., Delius 1965).

Incubation, by the female only, usually began after the last egg was laid, although in eight nests it began with the penultimate egg. The latter led to asynchronous hatching, with chicks emerging over a 3-day period in one instance. In only four nests was the incubation period determined, averaging 12.3 days (11, 11, 13, 14 days, respectively). Pickwell (1931) reported an 11-day incubation in this species, although it may be longer in inclement weather (Boyd 1976).

Posthatching behavior.—The chicks, on hatching, were covered with a long buff down, as noted by Dubois (1935), Wetherbee (1957) and Beason (1970), which enabled them to blend into the background when they crouched on being disturbed. The young were brooded by the female for the first few days after hatching, and every night until they left the nest.

Both parents normally fed the chicks, although in one case a female raised two broods alone. The lack of help in the latter case (whereabouts of the male was unknown) did not appear to affect nestling growth, although one late-hatcher probably was not fed and died 5 days after hatching. The mid-afternoon mean feeding rate of nestlings, in one nest, was

once every 3.0 min vs a mean of 5.5 min noted by Pickwell (1931), and the extraordinary case noted by Levy (1920) where two adult larks fed eight young in one nest once every minute.

Forty-seven nestlings of known age were measured, usually daily, for a total of 302 nestling-days of measurement. The results are shown in Fig. 3. Growth rate (weight increase) was analyzed using the graphical method of Ricklefs (1967). Assuming an asymptote weight of 34 g, nestling overall growth rate was 0.543, which 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 (1967). As noted in other ground-nesting passerines the legs and feet developed rapidly, this being highly advantageous in allowing early nest-leaving and thus avoidance of nest predation (Burns 1921).

The nestlings in the early nests (those which perished in the storm of 12–13 June) grew much more slowly than those from later nests, probably due to a scarcity of food and the poor weather during this period. Nestlings in the majority of nests were fed equally, despite competition for food from conspecifics. However, in at least four nests the last hatched chick grew more slowly than its nest-mates. In one case a female was seen to feed two chicks in a nest while at the same time the male fed a third chick and a juvenile from the previous brood.

The nestling period (time between hatching and fledging) averaged 9 days (5 nests, 8 days; 26 nests, 9 days; 5 nests, 10 days). The chicks left during the daylight hours, often over a period of 2–3 days. One or 2 days after leaving the nest the young could not fly, but hopped clumsily, using their wings for balance. Their main predator-avoidance behavior was crouch-concealment (Pickwell 1931). As their locomotory ability increased, the young larks began to run along behind their parents, giving a distinctive *breet* call, which was used for several weeks after nest-leaving and which was easily distinguishable from the adult *weet* call. After 3 or 4 days out of the nest, the young could fly a few meters, and by 14 days of age they could fly distances of 50 m repeatedly without any noticeable tiring. If a juvenile of this age was forced to fly several times consecutively, its parents accompanied it, giving loud alarm calls, and near territorial boundaries the adults seemed to try to herd the young bird back into the home territory. Young larks began to be independent of their parents when they were about 3 weeks old, at which time they were able to fly strongly. Although juveniles as old as 26 days were seen with their parents, an equal number of birds this age were observed feeding by themselves in the territory of another pair of adults. Young larks fed primarily on pink crowberries (*E. eamesii*) after reaching independence.

The first small flocks, indicative of post-breeding activity, were seen in

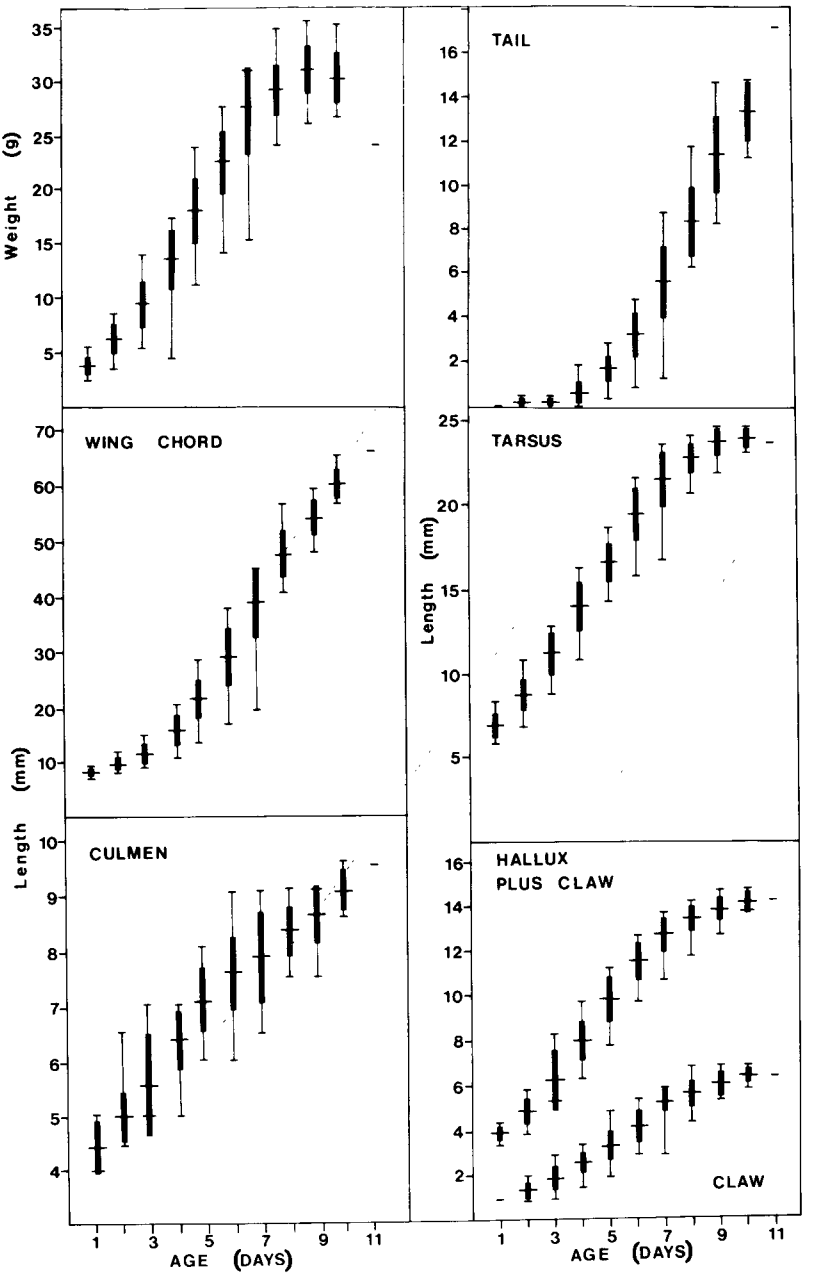

FIG. 3. Growth rates of nestling Horned Lark chicks. Day 1 represents the day the chicks hatched. Each bar shows the mean, standard deviation and range of measurements.

late July. On 27 July, 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 birds were banded. By early August, when most local juveniles were about 1 month old, several small mixed flocks of local young and female larks were seen feeding together.

Horned Larks leave their breeding grounds in Newfoundland in late September and October, with a few remaining until early November (Peters and Burleigh 1951). We saw small flocks of larks (3–35 individuals) on the study area through September in 1976, and had seen larks until mid-November in 1975 (during a seabird census).

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 figure being high when compared to others in the literature. The mean number of fledglings produced by each breeding pair during this study was 4.0 (N = 12, range = 0–7). The birth rate (fledgling/adult/season) was 2.0, with a replacement rate of approximately 67%.

Predation probably accounted for 43% of all egg and nestling loss, with ermines (*Mustela erminea*), mink (*M. vison*), red fox (*Vulpes vulpes*), meadow voles (*Microtus pennsylvanicus*), shrews (*Sorex cinereus*) and a domestic cat (*Felis domestica*) being regularly present in the study area. Ravens (*Corvus corax*) were also present, but seemed to confine their nest-robbing activities to adjacent seabird colonies.

Inclement weather (the storm of 12–13 June) accounted for 28% of egg and nestling losses. All nestlings known to be present died at this time and nest 7, which contained three eggs, was deserted. Three other nests (8, 10 and 11) suffered predation during or shortly after the storm. Nest desertion occurred at two nests after the incubating female had been captured on the nest for banding. Only 1 of 86 eggs observed through the normal hatching period proved to be infertile, and one egg (containing a well-developed embryo) in nest 16 failed to hatch after it was pushed up onto the nest lip, apparently by the incubating female. An egg was also found just outside the cup of nest 8. It was marked and returned to the nest, but a predator destroyed the nest before the eggs hatched. 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.

Food and feeding.—Horned Larks usually fed by 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 5 August, F3 was seen repeatedly flying after moths in the manner of a flycatcher. Larks also ate bog cranberries (*Vaccinium oxycoccos*), pink crowberries, large black ants, moth caterpillars

and adults, beetles, craneflies (Tipulidae) and spiders. Nestlings were fed arthropods almost entirely, whereas adults, especially early in the season, ate more seeds, berries and small leaves. This is consistent with the findings of McAtee (1905 *fide* Beason 1970) and Boyd (1976). All birds examined, except the nestlings from nest 2 (which were only 1 day old at death), had some grit in their gizzards. Almost half (8/18) of the gizzards from birds collected at Cape St. Mary's contained small bits of mollusc shell.

SUMMARY

The breeding biology of the Horned Lark (*Eremophila alpestris*) was studied during the 1976 breeding season at Cape St. Mary's, Newfoundland. Territorial behavior was investigated, and territories were subsequently mapped to determine their size (2.3–5.1 ha, $\bar{x}$ = 3.5 ha).

Nesting phenology was studied in detail. Nests were weighed, measured and their composition determined; they were so placed as to be protected on the windward side. Clutch-sizes of early and late nests were compared (early 3.0 eggs, late 3.5 eggs, overall mean 3.31 eggs). Forty-seven nestlings were measured to calculate growth curves for weight and other body variables. Breeding success (58.8%), incidence of renesting, and the mean number of fledglings (4.0) produced by each pair were calculated. Causes of egg and nestling loss were analyzed, and predation determined to be the most important factor. About 25% of the breeding pairs raised two successful broods.

ACKNOWLEDGMENTS

We wish to thank O. L. Austin, Jr., G. Brassard, S. Cannings, J. Rice, R. A. Ryder, P. Scott and the late L. M. Tuck for their help and advice during the course of this study. This manuscript was written while the junior author was a Visiting Professor in the College of Veterinary Medicine, University of Florida, Gainesville. This work would not have been possible without generous support from the National Research Council of Canada.

LITERATURE CITED

BANNERMAN, D. A. 1953. The birds of the British Isles, Vol. 2. Oliver and Boyd, London, England.

BEASON, R. C. 1970. The annual cycle of the Prairie Horned Lark in west central Illinois. M.Sc. thesis, Western Illinois Univ., Macomb, Illinois.

——— AND E. C. FRANKS. 1973. Development of young Horned Larks. Auk 90:359–363.

——— AND ———. 1974. Breeding behavior of the Horned Lark. Auk 91:65–74.

BENT, A. C. 1963. Life histories of North American flycatchers, larks, swallows, and their allies. U.S. Natl. Mus. Bull. 179.

BOYD, R. L. 1976. Behavioral biology and energy expenditure in a Horned Lark population. Ph.D. thesis, Colorado State Univ., Fort Collins, Colorado.

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

CANNINGS, R. J. 1977. The breeding biology of the Horned Lark (*Eremophila alpestris* L.) at Cape St. Mary's, Newfoundland. M.Sc. thesis, Memorial Univ., St. John's, Newfoundland.

DELIUS, J. D. 1965. A population study of skylarks, *Alauda arvensis*. Ibis 107:466–492.

DRURY, W. H. 1961. Studies on 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 27:56–72.

GARRETT, M. L. 1948. The life history of the Prairie Horned Lark. M.Sc. thesis, Ohio State Univ., Columbus, Ohio.

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

LOBACHEV, Y. S. AND V. I. KAPITONOV. 1968. Ecology of the Horned Lark (*Eremophila alpestris albigula* Bp.) in the Karzhantau Mountains (Western Tien-Shan). Byull. Mosk. O-va. Ispyt. Prir. Otd. 73:17–25.

MEADES, W. 1973. A phytosociological classification of the Avalon Peninsula heath, Newfoundland. M.Sc. thesis, Memorial Univ., St. John's, Newfoundland.

PETERS, H. S. AND T. D. BURLEIGH. 1951. The birds of Newfoundland. Dept. Nat. Resour., St. John's, Newfoundland.

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

RICKLEFS, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48:978–988.

———. 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 behavior of the Snow Bunting in spring. Trans. Linn. Soc. N.Y. 5:1–91.

VAURIE, C. 1959. The birds of the Palearctic fauna. H.F. and G. Witherby, London, England.

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

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

DEPT. BIOLOGY, MEMORIAL UNIV. OF NEWFOUNDLAND, ST. JOHN'S, NEWFOUNDLAND A1B 3X9 CANADA. ACCEPTED 17 FEB. 1981.