BREEDING BEHAVIOR OF THE HORNED LARK

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THE Horned Lark (*Eremophila alpestris praticola*) is the only midwestern alaudid. Its population in Illinois has increased in this century more than that of any other native bird (Graber and Graber 1963), perhaps because of its acceptance of farm fields as nesting sites. We studied its breeding behavior from September 1968 through April 1970 on a university campus and on farmland at Macomb, Illinois. The farm study area (Figure 1) consisted of a 25-acre hayfield and a 63-acre cornfield.

VOCALIZATIONS

Calls of the Horned Lark consist of one or two notes, while songs are much longer and more complex.

Calls.—Most calls resemble "su-weet" and are louder during the breeding season than in winter. Four different meanings are apparently conveyed by varying intensities and associated postures.

The loudest call, given by a male with the body stretched and head held high, is a challenge note to an intruding male.

The locating note is somewhat softer, given by parents when bringing food to fledglings. It is a call of one of two syllables, "weet" or "su-weet." When the vegetative cover is over 20 cm tall, effectively hiding the young, the adults call while flying or hovering. Fledged young use a loud "weet" note to answer and call for the adults.

An alarm note is given by either sex. It is more abrupt but softer than the challenge note, and is given from a crouched posture, usually just before the bird flees.

The distress note is softest. This was given by birds in banding traps and by one female when an observer was near her nest.

Song.—The male has two songs, with the intermittent being shorter and less variable than the recitative (Pickwell 1931). We found that the intermittent song is the more frequent of the two and lasts only 1.5 to 2.0 seconds. It usually consists of three (sometimes two or four) introductory notes followed by a rapid series of chittered notes (beginning at 0.8 seconds on the spectrogram in Figure 2) that first decreases, then increases in pitch.

The recitative song is used less frequently and consists of an apparently random series of notes followed by the same chittering that ends the intermittent song. It may last from a few seconds to more than a minute. Pickwell (1931) thought that it was frequently the prelude to

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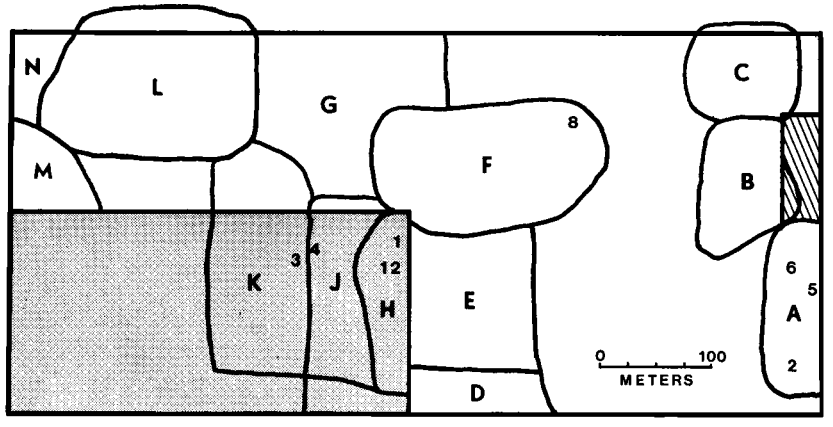

Figure 1. The farm study area. Shading indicates hay field, the hatched sector was a cattle feedlot, and the remainder was planted with corn. Territories are lettered. Territories G, M, and N are not shown completely. Numbers denote the nest number and location.

the intermittent song, but we found that the two songs were often interspersed.

Each song can be delivered either as a ground song given while standing or as a flight song. Ground songs were heard from the middle of January until early July, but were most frequent in March and April. Singing sessions ranged from 1.5 seconds to 45 minutes. Ground songs consisted only of intermittent songs in January and February, but included recitative songs by mid-March. The earliest ground songs of the morning were intermittent. The ratio between the intermittent and recitative ground songs varied among individuals, and among singing sessions of the same individual.

Although Wright (1912) and Pickwell (1931) found that the lark was one of the last species to begin morning singing, we found that they were the earliest to sing on the farm study area in spring. On six

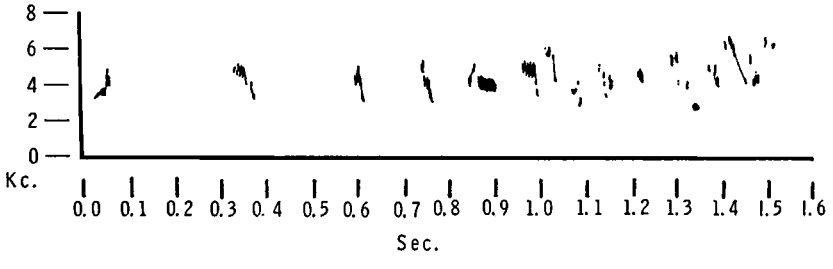

Figure 2. The intermittent song of the Horned Lark.

mornings in May ground songs started 1.6 to 1.9 hours before sunrise and reached a peak intensity about 15 minutes later. By sunrise songs are heard only occasionally, perhaps because feeding begins with the increased light. Singing reaches a minor peak about 2 hours after sunrise and again 1 to 2 hours before sunset. Ground song is inhibited by wind and by cloud cover, but not by temperatures as low as −25°C. Ground song appears to function in the maintenance of territories as described on the next page.

Flight songs may include both intermittent and, especially from April through June, recitative songs. The male climbs silently at about a 60° angle into a strong wind, or ascends in a wide helix if winds are light, to reach a singing altitude of 80 to 250 m (Pickwell 1931). He glides while delivering intermittent songs, or uses wide, slow wingbeats while delivering recitative songs. He then regains altitude and repeats the process. During the delivery, the male usually faces into the wind and may remain almost stationary. If he is blown backwards, he occasionally stops singing long enough to fly forward to near his original position. If he moves forward as he sings, he pauses and circles back to his starting position. His altitude usually increases slightly after the first few songs, then decreases throughout the remainder of the flight. At the end of his flight, he closes his wings and plunges directly toward the ground. Males in this study did not land on a song post near the nest (cf. Arlton 1949).

Song flights varied from 25 seconds to 8 minutes ($N = 17$, mean = 2.46 minutes) for the entire flight, in contrast to a range of 1 to 5 minutes Pickwell (1931) measured and shorter than the 11 minutes Verbeek (1967) reported in another subspecies. Though Pickwell (1931) reported seeing only one lark in song flight at a time, we saw two larks in song flight simultaneously only 100 m apart; they could probably see and hear each other easily.

Song flights were most common in March and April, especially after each brood left the nest or when a nest was destroyed. After losing his mate one male performed frequent song flights for 2 weeks. As song flights occur at these times, they are probably a part of courtship rather than related to territorial defense.

Territoriality

The larks begin defending territories in January and February concurrently with the initiation of pairing. Territories were more congested on stubble fields (from hay or corn) than on plowed ground. They are defended only by males, and only against males. If both larks of a pair crossed the boundary, only the male was chased. If the males flew over

the female during the chase, she followed them back to her own territory. A juvenile we displaced into another territory was not challenged.

Territorial hostilities can be divided into three types: threat display, fight, and chase. In the territorial threat display, the male gives a challenge call and runs toward the other male. He stops every 30 or 40 cm and repeats the call. This display usually precedes a territorial fight.

Most territorial fights occur in the air, although Verbeek (1967) reported two males fighting on the ground. The birds fly at each other and struggle as they rise straight up for 10 to 15 m. The fight may last from a few seconds to more than a minute. Finally one male may fly away, or both may land and repeat the fight. Territorial fights are most common in February and March and become rare by mid-April. When a territorial male disappeared from the study area and was replaced by another, some fighting occurred in the week required for the newcomer to establish the territorial limits. The new territory roughly coincided with the former one.

The territorial chase may follow or substitute for the territorial fight, and may be preceded by a threat display. In the chase the victor may pursue the loser to the territorial limits and then circle back to a song post and sing. Or the chase may be for only a meter, after which both males land and feed or simulate feeding. The most common chase observed was called by Pickwell (1931) a "tit-for-tat" chase. One male chases another across a territorial boundary, then the second male chases the first one back across the boundary. This back and forth chase may be repeated several times. The frequency of chases reached a peak in April about the time territorial fights ceased, but a few occurred throughout the breeding season.

Following a territorial fight or chase, one or both contestants may give a ground song. Ground songs are heard only when the territories exist.

The territories in the study area ranged from 0.6 to 3.1 ha (mean = 1.6) (Figure 1) compared to the 0.4 to 5 ha Pickwell (1931) observed. The boundaries remained fairly stable during the breeding season.

COURTSHIP AND NESTING

Courtship.—Courtship occurs after territory establishment and periodically throughout the nesting season. It consists of song flights (discussed earlier), courtship displays, sexual chases, and courtship feeding.

Courtship displays were given by males whose mates had nests with eggs. The male holds his body more horizontal than usual, droops his wings, and spreads his tail. While making chittering sounds with an

open bill, he struts around for up to a minute in front of the female, quivering his wings and spreading his black chest patch (also reported by Sutton and Parmelee 1955). The female appears to feed and ignore her mate. Copulation did not follow any of the displays.

An invitatory display by a female occurred the same day her young fledged. Without any display by the male, the female held her body horizontal, drooped her wings slightly, and moved her tail from side to side. The male ran to her and copulated. A few seconds later the male gave a courtship display, but his mate moved away.

Sexual chases occurred from March to June. The chase usually starts on the ground, and may involve flight. The male apparently tries to grasp the head or tail feathers of the female. If he succeeds while the birds are flying, they drop to the ground. Copulation was not observed after any chase.

One instance of courtship feeding was seen. A female begged for food from an approaching male that had a worm in his bill. He mounted her momentarily, dismounted and walked around a few seconds, then repeated the process. The female then took the worm from him.

One banded pair remained mated for the entire breeding season. No marked birds were known to change mates during the nesting season except when their former mate died or disappeared.

Nesting.—Although larks may nest on marshy ground (Mousley 1916, Verbeek 1967), the preferred habitats in Illinois are stubble fields, plowed ground, and fall-planted fields (Graber and Graber 1963, Beason 1970). Crop growth may force the larks off by June, but this does not affect their choice of nest sites in early spring.

The female selects the nest site with no apparent aid from the male and with no regard for the center of the territory (Figure 1). Apparently seeking a nest site a day after her former nest was destroyed by rain, a female approached tufts of grass and appeared to inspect them. She made short flights, each less than 1 m in length, from place to place while the male walked after her; sometimes she flew back and forth between two places.

Nest building is by the female alone. She usually digs the nest cavity, although Bowles (1900) and Sutton (1927) found that a natural depression was sometimes used. Two females in this study used only the bill to loosen the soil and to flip it from the hole; larks Sutton (1927) studied also kicked dirt from the hole with their feet. Digging requires 1 or 2 days depending on the time of day it starts. Most nests have some protective object such as a tuft of grass or a rock on the windward side, so the bird digs in relative shelter (DuBois 1935). Table 1 lists the cavity diameters.

TABLE 1
MEASUREMENTS OF THE NESTS AND NEST CAVITIES OF THE HORNED LARK

Date nest completed	Nest number	Cavity diameter (mm)	Nest inside diameter (mm)	Nest inside depth (mm)	Nest weight (g)
29 March	4	87	75	37	15.0
2 April	1	90	63	40	19.0
5 April	2	91	65	40	25.0
5 April	3	79	58	41	—
23 April	6	76	64	42	26.5
ca. 1 May	7	95	64	50	23.5
ca. 10 June	9	75	60	40	22.6
29 June	8	95	65	45	13.2
Average		86.0	64.3	41.9	20.7
SD		8.2	5.0	3.7	5.1

Two to four days after digging the cavity, the female builds a nest in it from fine plant parts available nearby. Grass was the most common element of nests on the campus, and cornstalk shreds of those in the fields. Grass heads, lint, fur, feathers, string, cloth, and paper were also used in the body of the nests, and some linings contained cellulose fibers as well.

Hess (1910), Sutton (1927), and Pickwell (1931) found that early nests were more solidly woven than later ones, possibly because fine roots and stems are less available when the vegetation becomes tall late in the spring. In this study, nest dimensions and weights (Table 1) and materials used showed no consistent change as the season progressed.

An unusual feature of the lark nests is a collection of "pavings" the female places beside the nest. They included pieces of clod, corncob, cornstalk, and cow dung. The overall size of the paved area varied between successive nests by the same female, for example at nests 2, 5, and 6 (Table 2).

Pickwell (1931) felt that pavings function to provide a bare approach to the nest. Yet one pair of larks did not approach the nest over the pavings when bringing food to their young. If a nest was built beside a protecting object, the pavings were on the opposite side of the nest, covering most of the dirt thrown out during the excavation. Thus our data, like those of DuBois (1935), suggest that the pavings serve to cover the fresh dirt from the nest cavity.

The female lays the paving while building the nest (cf. Mousley 1916). When she picked up a piece of paving, she immediately carried it back to the nest, but when gathering nest materials she waited until her bill was full before returning. She often simply dropped pieces of

TABLE 2
PAVINGS

Habitat and nest number	Paved area Length (mm)	Paved area Width (mm)	Largest piece Length (mm)	Largest piece Width (mm)	Smallest piece Length (mm)	Smallest piece Width (mm)	Location from nest	Substance
Hayfield								
1	200	76	53	17	15	12	S and SW	Cornstalk, clod
3	100	35	27	19	19	11	S	Corncob, clod
4	—	—	64	11	38	13	SW and E	Cornstalk, cow dung
Plowed field								
2	140	72	50	15	15	10	S	Corncob, clod
5	190	135	50	33	20	8	WSW	Cornstalk
6	125	60	30	20	13	6	NE	Clod
7	150	80	28	20	4	3	WNW	Clod
Lawn								
9	50	20	30	15	10	10	ESE	Clod
10	220	70	25	20	4	3	E	Clod
Average	146.9	62.5	39.7	18.9	15.3	8.4		
SD	56.4	34.9	14.5	6.1	10.3	3.7		

paving or nesting material into the excavation and walked away. The pavings in the cavity may help keep the grass from blowing away until she has enough to begin forming the nest.

Because of their habituation to humans, the females nesting on campus were less easily frightened from their nests than those in the fields. One could be approached as near as 40 cm before she flew. The reaction of any given female to intruders was variable. Birds showed more concern if we were at the nest a long time or if eggs or young were present, and were less inclined to leave the nest near sunset.

Females showed two types of nest-protective behavior when we approached a nest. In casual abandonment the female flew directly from the nest, silently and near the ground, while the intruder was up to 100 m away. Often she flew directly to a feeding ground, where both mates appeared unconcerned while the intruder was present. In the distraction display, a female who was flushed from her nest several times in a short period fluttered up and landed 30 cm from the nest in a crouched posture with her wings spread as if feigning injury. She then flew about 2 m from the nest in a normal manner. Another type of distraction display consisted of soft distress calls and simulated foraging within 5 m of the nest. If followed, the female walked rapidly from the vicinity of the nest before flying. Although some nest desertion occurred, none resulted from the females being flushed from their nests to measure their eggs or young.

Renesting after nest destruction or desertion was initiated generally within 2 days. Renesting after successful fledging (one datum) occurred about a week after the young left the nest, or about 30 days after the start of the previous nest.

Eggs.—One egg is laid each day until the clutch is completed. We found one clutch with 2 eggs, six with 3, one with 4, and one with 5, the average being 3.2. The consecutive clutches of one color-banded female contained 3, 3, and 4 eggs respectively.

Egg color varied from a dark "pearl gray" to "pale gray," with "brownish olive" spots (colors from Palmer 1962). The spots were evenly distributed over some eggs; others had the blunt end ringed or capped with brownish olive.

The mean dimensions of 26 eggs were 2.17 × 1.57 cm, similar to the values found by Reed (1904), Bent (1942), and Preston (1969). The length was more variable than the width. Egg weights varied considerably (2.0 to 3.3 g, N = 25, mean = 2.8) partly because not all the eggs were weighed the day they were laid.

Incubation.—The 11 days of incubation by the female usually begin when all eggs are laid, but in early nests it may start sooner and cause

the hatching to spread over 2 days. Although Sutton and Parmelee (1955) noted a male taking food to an incubating female, she normally leaves the nest briefly to feed. Contrary to the egg recovery behavior of incubating Herring Gulls (*Larus argentatus*) (Tinbergen 1960), one female lark did not respond to one of her eggs placed in full view 8 cm outside the nest.

The brood patch of one female was 20 × 35 mm. The abdominal skin in both sexes was thin enough to be seen through, but it was without any feathers and was redder in the female.

Nest success.—The major cause of nest destruction on the farm study area was agricultural activities. Heavy rain destroyed some nests, and a predator raided one. Of 8 clutches studied in detail, 26 eggs produced 13 nestlings, and the 6 young that fledged were from two nests (23% fledgling success). Pickwell's (1931) 24 nests at Evanston, Illinois, contained 82 eggs, 65 of which hatched, and the 39 young that fledged were from 15 nests (48% fledgling success).

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SUMMARY

Horned Larks frequently nested in farm fields where farming operations destroyed many of the nests. Only 23% of the eggs laid produced fledglings.

The Horned Lark has two songs, each delivered either on the ground or in flight. Intermittent songs last 1.5 to 2.0 seconds; recitative songs vary from a few seconds to more than a minute. Songs given on the ground are associated with territoriality; flight songs function in courtship.

Territories are established in January and February and are held until July.

Courtship involves displays and song flights by the male, invitatory displays by the female, sexual chases, and courtship feeding. The pair apparently remains together the entire breeding season if both survive.

The female builds the nest alone. She picks the location and digs a shallow hole, in which she builds the nest from materials at hand. She paves the dirt scratched from the nest hole with small pieces of clod, cow dung, and corncob.

When disturbed the female usually flies directly from the nest, low to the ground, while the intruder is some distance away. If she is flushed too often or from too close, she may use a distraction display.

The eggs are grayish, sprinkled with brownish spots, and are laid at the rate of one per day. Clutch sizes ranged from 2 to 5 eggs, with 3 the commonest. Incubation by the female alone usually begins when the final egg is laid, and lasts 11 days.

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