

BREEDING BIOLOGY AND ECOLOGY OF THE HORNED LARK IN ALPINE TUNDRA

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ASPECTS of the breeding biology of the Horned Lark (*Eremophila alpestris*) are reported by Kelso (1931), Dubois (1935, 1936) and Bent (1942). DuBois' and Kelso's studies dealt with prairie-nesting populations. The study here reported was conducted in alpine tundra during the summers of 1963 and 1964. Data were collected incidental to a study of the Water Pipit (*Anthus spinoletta*) (Verbeek, MS). In the summer of 1963 little time was spent on the larks and only four nests were located. In 1964, larks were much more abundant and 12 nests were located, 11 of which were on the study area proper and one outside.

STUDY AREA

The study area (Fig. 1) consisted of about 116 hectares of alpine meadow about one km NE of Beartooth Pass on the Beartooth Plateau, Park County, Wyoming. A detailed description of the vegetation and geology of the Plateau is given by Johnson and Billings (1962). The average altitude was about 3,200 m. The Beartooth Highway bounded the study area on the south and the edge of the plateau above Rock Creek Canyon formed the western boundary. On the east, Pipit Hill, so named by us, formed part of the study area up to about 3,262 m. The face of Pipit Hill was a dry meadow, although in places, below pockets of snow, there were isolated areas of moist meadow. Scattered along the face of the hill were rock outcrops, rock polygons and solifluction terraces. On the north, the boundary ran about 100 m north of the main channel which drained the whole area. This main channel had a maze of narrow branches, many of which were dry toward the end of the season. Frost hummocks were characteristic of this wet area. The vegetation consisted of plants such as *Salix planifolia*, *Sedum rhodanthum*, and *Caltha leptosepala*. Besides the low wet area in the north and Pipit Hill, there was the Central Ridge running through the center of the area and West Hill in the southwest. The Central Ridge and West Hill both had areas with fellfield characteristics such as cushion plants and much exposed rock and gravel on the western exposure. Extensive snow accumulation areas between Pipit Hill and the Central Ridge and between the latter and West Hill were bare except for some sparse vegetation in late summer when the snow had melted from part of these areas.

TERRITORY AND HABITAT

The larks occupied the whole study area and their nests were located in all cover types except exposed snow accumulation, frost hummocks and wet meadow. The distribution of the nests is shown in Figure 1. For each of 11 nests in 1964, I noted the plants growing within a 30 cm radius of the nests (Table 1). The nests are placed in one of four categories: (a) Fellfield nests, characterized by cushion plants and exposed rock; (b) Dry Meadow nests, characterized by a general absence of cushion plants; (c) Moist

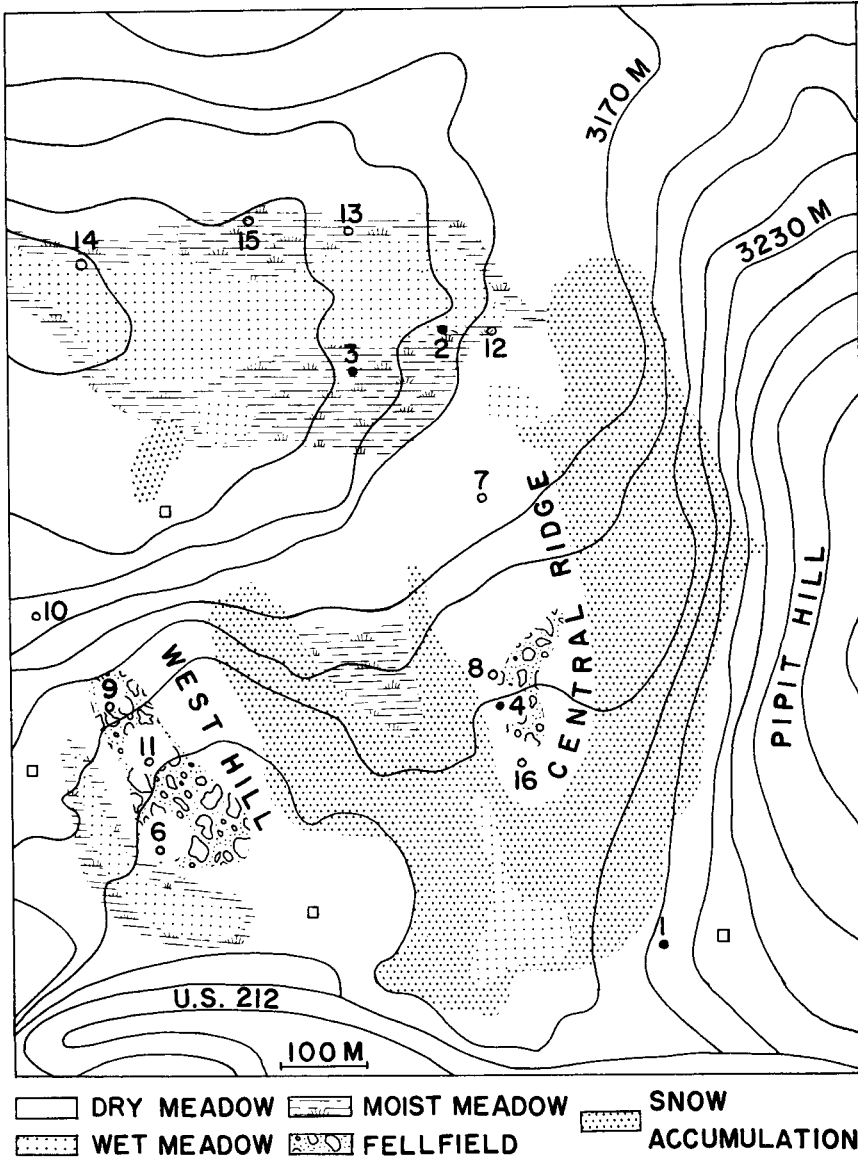


FIG. 1. Distribution of nests of the Horned Lark found in 1963 (dots) and in 1964 (open circles). The squares are suspected locations of nests in 1964. Contour lines are 12.2 m apart.

Meadow nests, characterized by moisture loving plants such as *Carex scopulorum*; and (d) an intermediate type between Dry and Moist Meadow.

Of all the nests, including those of 1963, nine were located in a dry habitat, five in a moist habitat and one in an intermediate type. The presence of five nests in a moist habitat is unusual since heretofore lark nests have been associated only with dry and gravelly sites. Two nest territories and the areas occupied by 22 pairs reported by Drury (1961) were all located in the most exposed places "where most of the surface was tan angular rock." Pickwell (1931) writes: "The Prairie Horned Lark selects the bleakest barrens available" and he feels that bare ground is the most essential condition required. The fact that nests were found in moist habitat in both years eliminates the possibility of increased population pressure in 1964 forcing the birds to occupy less favorable habitat. It seems that in an alpine population of this species, a wider range of habitat is utilized.

Horned Larks have very large territories. Besides the 11 nests found in 1964 there were at least four more known territories the nests of which were not located. Because large areas on the study plot were not suitable lark habitat, it is not possible to calculate the average size of each territory by simple division. The average distance between two nests in the same continuous habitat type, for instance between N16 (Nest 16) and N8, and between N8 and N7, etc., was about 142 m. If we take the nest as the center of the territory, then each territory occupied about 1.5 hectares.

Larks defend their territory with great persistence throughout the breeding cycle from the moment the territory is established till the time the young leave the nest. Males chase each other with great speed, often close to the ground. Sometimes several birds participate in these chases. On 5 July 1964, two males fought by standing close together and beating one another by suddenly extending one wing. After each blow they would walk away from each other for about 30 cm and then walk back again to repeat the performance. Two males can often be seen to start a fight on the ground and then continue it in the air, climbing higher and higher up to about 20 m at times. This behavior was noted also by DuBois (1935).

SONG

In the alpine zone larks are the first birds to sing in the morning and the last to cease in the evening. The flight song is given from the ground as well as from the air. On the ground, males sing while perched on some projection, usually a rock. In the air, the bird sings while his wings and tail are spread wide open and in between bursts of song he hovers to maintain altitude. The duration of the only flight song timed was 11 minutes, twice as long as that given by Pickwell for *E. a. praticola* and my impression is

TABLE 1
SPECIES OF PLANTS RECORDED WITHIN 30 CM RADIUS OF 11 NESTS OF THE HORNED LARK

Species	Fellfield nests				Dry meadow nests			Moist meadow nests			Intermediate meadow nest
	5	6	9	11	7	8	10	13	14	15	16
Rock	1	1	1	1							
<i>Geum rossii</i>	1	1		1	1	1	1		1	1	1
<i>Smelowskia calycina</i>	1	1	1		1		1				
<i>Potentilla diversifolia</i>	1	1		1	1	1	1				
<i>Antennaria</i> sp.	1										
<i>Mertensia alpina</i>	1		1		1		1		1		
<i>Silene acaulis</i>	1	1					1				
<i>Polygonum bistortoides</i>		1	1		1	1		1		1	1
<i>Douglasia montana</i>		1									
<i>Eritrichium alpinum</i>		1									
<i>Castilleja</i> sp.		1		1						1	
<i>Carex</i> sp.		1	1		1	1					1
<i>Myosotis alpestris</i>					1		1				
<i>Pedicularis oederi</i>					1		1				
<i>Lloydia serotina</i>			1		1		1				
<i>Phlox caespitosa</i>			1	1	1	1					
<i>Erigeron caespitosa</i>					1						
<i>Stellaria crassifolia</i>					1						
<i>Claytonia lanceolata</i>						1	1	1		1	
<i>Senecio fuscatus</i>			1			1					
<i>Draba</i> sp.						1		1			
<i>Lupinus monticola</i>			1				1				
<i>Cerastium</i> sp.			1								
<i>Aster alpigenus</i>				1							
<i>Carex scopulorum</i>								1		1	
<i>Caltha leptosepala</i>								1	1	1	
<i>Artemisia scopulorum</i>								1	1	1	1
<i>Gentian algida</i>									1	1	
<i>Dodecatheon pauciflorum</i>									1		
<i>Sedum stenopetalum</i>											1
<i>Trifolium parryi</i>											1

that all of the flight songs were longer than the five minutes reported as a maximum by Pickwell.

NESTS

Before the actual nest is built, a nest cavity is scratched out in the ground. The depth of this cavity varies with the substrate. In some cases a rock prevented any deeper excavation. The average depth of seven nest cavities was 5.0 cm (4.3 to 6.2). The nest is made of dead forbs and grasses. No

hair or feathers are used to line the inside. One nest was lined with an unidentified felt-like plant material. Drury (1961) reports the use of feathers in *E. a. alpestris*.

All nests found were constructed so that there was some protective feature such as a projecting rock or a tuft of grass on the windward side. The nest entrance of 12 nests in 1964 all faced between NNW and E; one faced NNW, three N, one NNE, four NE, two ENE, and one E. The predominant winds were from the S and SW. A similar orientation with respect to the wind was reported by DuBois (1935), who found nests facing between NE and SSE under prevailing W winds. I did not notice any evidence of a "pavement" of stones or mud as reported by DuBois (1935) and Pickwell (1931).

Eleven finished nests had an average width of 7.0 cm (6.5 to 7.6) and ten nests had an average depth of 3.8 cm (3.2 to 4.7). The average thickness of seven nests of which both the depth of the scooped-out nest cavity and the completed nest were known was 1.0 cm (0.3 to 1.7). These measurements were taken after the young had left the nest.

EGGS AND INCUBATION

Eggs were laid early in the morning, some time before 0730 hours. The clutch size varied from two to four eggs (one with two eggs, ten with three eggs and three with four eggs).

Only two of the 16 nests were found before the clutch was completed. In N5, the third and last egg was laid in the morning of 29 June. All three eggs had hatched before 0530 hours on 10 July. In N8, the last of three eggs was laid in the morning of 2 July and the first egg hatched 13 July before 0930 hours. The other two eggs in this nest never hatched. The incubation period is taken to be about 11 days. DuBois (1935) gives an incubation period of 10 to 11 days and MacDonald (1916) states 11 days.

Silloway (1903) states that both male and female incubate the eggs. My own observations make me believe that only the female incubates. There is only one clutch per season in contrast to the two clutches reported by DuBois (1935) at lower altitudes. In 1964, all eggs were laid between 25 June and 10 July.

NESTLINGS

The nestling period varied from 9 to 12 days with an average of 10.2 days. This is a very short period but it agrees well with the results obtained by DuBois (1935). The young leave the nest when they have hardly any tail and when the primaries and secondaries are only one-third to one-half grown. The young are incapable of flight at first but walk readily. I caught

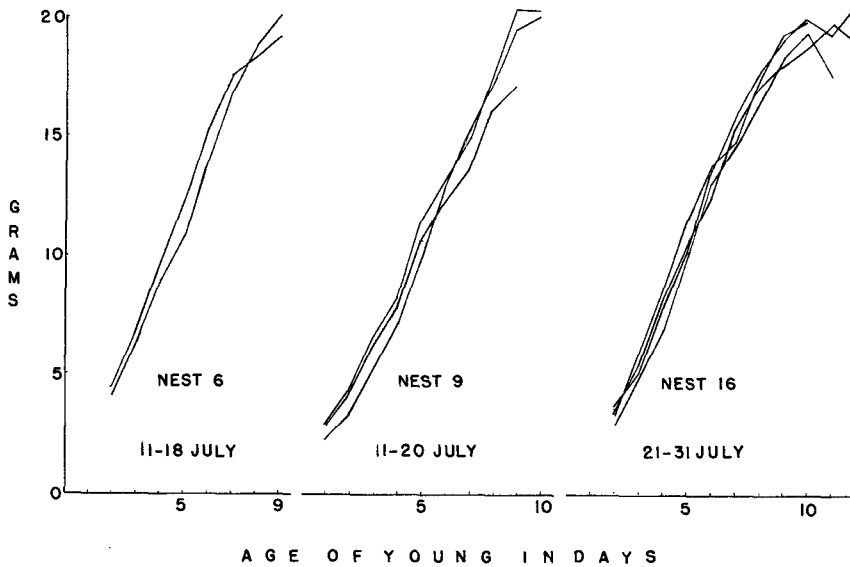


FIG. 2. Growth curves of two, three and four young in three nests of the Horned Lark.

one color-marked young five days after it had left the nest. It could only fly a few meters at the time and was soon exhausted.

Nestling development is very rapid. The average gain in weight of nine young was 1.9 g per day (0.52 to 3.45). When the young reach a weight of about 20 g, they seem to have developed sufficiently to leave the nest. Growth curves for the young of three nests are shown in Figure 2. Earlier departures (Fig. 2) are due to disturbance caused by handling the young. One young of N9, which left when it weighed 17.6 g was recaptured 5 days later when it weighed 20.2 g. The average weight of 15 adult males in the University of Montana Zoological Museum, taken on the study area in June, July, and August, was 32.3 g and the average weight of 7 adult females of the same period was 30.6 g. The young then leave the nest when they are about two-thirds the adult weight. Sexual difference in weight in adult larks has been shown by Behle (1943) and Montagna (1943).

The eyes open when the young are 3.6 days old (average of 10 nests). The primaries and secondaries break the sheaths when the young are 6 days old (average of 2 nests).

During 128 minutes of observation from a blind when the young were one day old, the female brooded them for 78 minutes or about 61 per cent of the time. The average length of the brooding period was 11 minutes (6 to 17). When the female was not brooding she was off gathering food for the young

and presumably for herself. If the male came to the nest while the female brooded, she would step off the nest till the male was finished feeding the young, after which she would resume brooding. When the young were four days old, no brooding occurred during one hour of observation, but the female provided shade by standing over the young in the nest. No shading or brooding occurred when the young were 8 days old. Both parents fed the young and both removed feces.

When approaching the nest to feed the young both male and female land at some distance, about 3 to 5 m, from the nest and then walk toward it. The female approaches without any vocalization, while the male makes a soft *tjreeh* call which seems to be a call used around the nest. After feeding is finished the female tends to walk away from the nest but sometimes she flies away from within about 30 cm of the nest. The male flies from the nest more often than he walks.

The food of six nestlings in July consisted of 100 per cent insects, while 12 adults taken between 14 June and 1 September had stomach contents of 78 per cent insects and 22 per cent seeds. The 12 adults had an average of 0.15 (0.03 to 0.26) grams of grit in their stomachs and the nestlings had an average of 0.10 (0.01 to 0.17) grams of grit.

Newly hatched larks are richly covered with a creamy-white natal down. The distribution of natal down of a young just hatched is shown in Table 2. Wetherbee (1957, 1958) has summarized the information regarding natal pterylosis of the Horned Lark. To his list of tracts present can be added: crural, rectrices, and upper tail coverts. My specimen did not have the ocular tract reported by Wetherbee (1958).

The young made begging sounds on my approach to the nest, at about 4.5 days. They directed their beaks to human sounds when 3 days old and before their eyes had opened. When about 5 days old, they followed the movement of my hand over the nest without the accompaniment of human sound. After about 6.5 days, the young no longer react to human sound and movement. After this time, when one approached they remained silent and immobile or tended to crouch deeper in the nest.

Sutton and Parmelee (1955) report finding one instance of nestling larks out of the nest and they suggest that the unprotected and poorly lined nature of this particular nest could have been the cause of this. Observations from my blind, however, showed that the two 8-day old young of N13 left the nest whenever a parent came to the nest with food. They went as far as 30 to 40 cm from the nest and then crawled back again. At this age they do not leave the nest until the parent is about 100 cm from the nest. In N2, one of the four young appeared to be smaller and weaker. This bird died on 20 July when two large nestlings were outside of the nest while a third weak

TABLE 2
TRACT DISTRIBUTION OF NATAL DOWN FEATHERS OF A HORNED LARK
NESTLING (JUST HATCHED)

Tract	Left	Right
Coronal	14	13
Occipital	12	11
Dorsal	22	22
Spinal		7
Rectrices	6	6
Upper tail covert	2	3
Humeral	12	14
Greater secondary covert	9	10
Middle secondary covert	8	6
Carpal remex covert	1	1
Femoral	15	13
Crural	2	2
Abdominal	2	2

nestling was in the nest. The latter nestling died the next day. In N14, on 12 July, three of the four young were out of the nest, the smallest one farthest away, about 30 cm. The next day this one had died, while the other three were back in the nest. It seems that nestling larks leave the nest in competition for food.

When the young were about 4 days old, they panted when the sun shone in the nest. Panting could have started at an earlier age but was not observed.

FLEDGLINGS

Newly fledged young are more often heard than seen after they leave the nest. They call their parents with a single loud *peep* which sounds as if it comes from far away, although the young in actuality may only be a few meters away. The young are very well concealed and crouch when approached. One young of N6 left the nest when it was 9 days old and I saw it fly about 75 m when it was 15 days old. Young larks fly in an undulating manner, more so than the adults do. When they alight they face the intruder and they have a habit of bowing their heads, as if looking at their feet. This bowing is repeated about once every four seconds.

BREEDING SUCCESS

There was a great difference in breeding success between 1963 and 1964. In 1963, of 13 eggs laid in 4 nests, 10 young hatched, only four of which fledged, a success of 31 per cent. In 1964, out of 34 eggs in 11 nests, 31

TABLE 3
SUMMARY OF BREEDING DATA OF THE HORNED LARK

	1963		1964	
	Number	Percent	Number	Percent
Nests	4		11	
Eggs laid	13	100.00	34	100.00
Eggs per nest	3.25		3.09	
Eggs hatched	10	76.92	31	91.18
Eggs hatched per nest	2.50		2.82	
Eggs not hatched	0	0.00	2	5.88
Eggs lost before hatching	3	23.08	1	2.94
Young fledged of eggs hatched	4	40.00	21	67.74
Young fledged per nest	1.00		1.82	
Young lost before fledging	6	60.00	10	32.26
Young fledged of eggs laid	4	30.77	21	61.76

hatched, 21 of which fledged for a breeding success of 62 per cent. Details are shown in Table 3.

Causes of mortality were twofold. In 1963, 3 eggs and 6 of the 10 young that hatched were eaten by mammalian predators, probably the deer mouse (*Peromyscus maniculatus*), which was abundant that summer (Pattie, MS). No nestlings were lost to mammalian predators in 1964.

The loss of 8 nestlings in 1964 was due to blowfly larvae. The average age at death in infested nests was 8.6 days. In each of two nests one young survived. These young showed evidence of having suffered from the larvae. Their development was slowed down and the nestling period extended to 11 and 12 days. In one nest the larvae did not seem to have harmed the nestlings at all, although there were 29 larvae in the nest. Early fledging could be advantageous in escaping blowfly predation. Dead young are removed by the adults.

POST-NESTING PERIOD

Toward the middle of August when the young are independent of the adults, flocks begin to form. These flocks are very loose in nature with 10 to 20 birds scattered out in ones and twos over about 30 to 40 sq m. Whereas earlier in the season larks are found in many habitats, toward the end of the summer they are found almost exclusively in Fellfield and Dry Meadow, in this order.

SUMMARY

An account is given of the breeding biology of the Horned Lark in alpine meadows at an altitude of 3,200 m on the Beartooth Plateau, Park County, Wyoming. Of a total

of 15 nests, 9 were located in a dry habitat, 5 in a moist habitat and one in an intermediate type. Lark territories were large and in 1964 each occupied about 1.5 hectares. All nests faced between NNW and E, away from the predominant S and SW winds. Each nest had some protective feature in the form of a rock or vegetation on the windward side. The average clutch size was 3.1. The incubation period was about 11 days in two nests. Only the female incubates and there is only one clutch per season. The average nestling period was 10.2 days. Young develop rapidly and gain on the average 1.9 g per day. Young leave the nest when they weigh about 20 g. The eyes open on the average when the young are 3.6 days old and the primaries and secondaries break their sheaths when the young are 6 days old. Nestling mortality in 1963 was believed due to the deer mouse, while in 1964, nestlings were lost due to predation by blowfly larvae. Young leave the nest before they are able to fly and they become independent of the adults by the middle of August at which time flocks begin to form.

ACKNOWLEDGMENTS

This study was made possible by a grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History and a Louis Agassiz Fuertes Research Grant of the Wilson Ornithological Society. I also wish to acknowledge funds from National Science Foundation Grant No B14098 directed by Drs. R. D. Taber and R. S. Hoffmann.

Special thanks are due to Mr. D. L. Pattie and Mr. C. I. Fudge for their companionship in the field and the latter for some lark data for the 1963 season. Drs. R. S. Hoffmann and F. A. Pitelka read and criticized the manuscript for which I extend my sincere thanks.

LITERATURE CITED

- BEHLE, W. H.
1943 Weights of some western subspecies of Horned Larks. *Auk*, 60:216-221.
- BENT, A. C.
1942 Life histories of North American flycatchers, larks, swallows, and allies. *U.S. Natl. Mus. Bull.*, 179.
- 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.
- JOHNSON, P. L., AND W. D. BILLINGS
1962 The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. *Ecol. Monog.*, 32:105-135.
- KELSO, L. H.
1931 Some notes on young Desert Horned Larks. *Condor* 33:60-65.
- MACDONALD, H.
1916 Incubation period of the Horned Lark. *Auk*, 33:435.
- MONTAGNA, W.
1943 Weights and plumages of the Horned Larks of Central New York. *Auk*, 60:210-215.

PICKWELL, G. B.

1931 The Prairie Horned Lark *Trans. Acad. Sci. St. Louis*, 27:1-160.

SILLOWAY, P. M.

1903 Birds of Fergus County, Montana. Press of the Argus, Lewiston, Montana.
Fergus Co. Free High School Bull., 1:1-77.

SUTTON, G. M., AND D. F. PARMELEE

1955 Nesting of the Horned Lark on Baffin Island. *Bird-Banding*, 26:1-18.

WETHERBEE, D. K.

1957 Natal plumages and downy pterylosis 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.

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NEW LIFE MEMBER



Dr. Glen E. Woolfenden has recently become a Life Member of The Wilson Ornithological Society. Dr. Woolfenden is Associate Professor of Zoology at The University of South Florida, Tampa, and holds degrees from Cornell University, University of Kansas, and University of Florida. His ornithological interests include anatomy, ecology, systematics, and paleontology, and he has published 25 papers in these fields. He is a member of the Cooper Society, Bird Banding Association, BOU, Sigma Xi, Florida Academy of Sciences, and an Elective member of the AOU. Dr. Woolfenden is married and has three children.