Despite the wide distribution, large size, and bold coloration of the American Avocet (*Recurvirostra americana*), it has received little ecological or behavioral study. Fragmentary information has been collected by Rockwell (1912), Pearson (1916), Mitchell (1917), Wetmore (1925), and Bent (1927), among others. Hamilton (MS) has added more complete data in a comparative study of the avocet and the Black-necked Stilt (*Himantopus mexicanus*) in California. Here I present information on aspects of avocet breeding biology gathered incidental to behavioral studies which will be reported more extensively elsewhere (Gibson, MS). Data were collected during the springs and summers of 1967 (2 June–10 August), 1968 (7 April–13 July), and 1969 (1 April–10 July).

THE STUDY AREA

The study was conducted on the Summer Lake Management Area, Lake County, Oregon (T. 30 S., R. 16 E.), a game refuge operated by the Oregon State Game Commission. The area is an alkaline marsh bisected by a series of dikes topped by service roads (fig. 1). The terrain is flat and much of the marsh is covered with shallow ponds and waterways 2–15 cm deep, although some canals are much deeper. Water is supplied by a river and canal system, both of which are fed by artesian wells, assuring rather constant water levels throughout the season. The investigation was performed primarily in the area of Windbreak Dike (fig. 1) which is 3.2 km long, approximately 35 m wide, and covered with salt grass (*Distichlis stricta*) plus a few unidentified weedy species. Around the dike, in wet soils and shallow water, three-square tule (*S. americanus*) and marsh bullrush (*S. robustus*) are common. Great bulrush (*S. validus*) and cattail (*Typha latifolia*) have a patchy distribution in deeper water. Rabbit brush (*Chrysothamnus nauseosus*) and willows (*Salix sp.*) occur along the dikes. Some sections of the marsh, particularly on the eastern edge, are characterized by large alkali flats.

METHODS

To obtain an index of the seasonal flux of breeding activities in the population, a 3.75 km census route was established through the marsh (fig. 1), along which avocets were counted and their activities at first sighting were recorded. The route was traveled between 08:00 and 10:00 daily 1 April–17 May and on alternate days through 10 July during the 1969 season.

Behavioral observations were made from an automobile or blind or from 10-ft observation towers. Time budget data were obtained by recording the activity of a pair of avocets at 10-sec intervals for 30-min observation periods. The time base was kept with a periodic metronome timing device (Wiens et al. 1970). Observations were concentrated on several pairs, which were followed throughout their breeding cycle. I located all avocet nests on Windbreak Dike in 1967 and 1969, but studied only selected nests during 1968. Eggs were individually marked with fingernail polish and their fate followed by twice-daily visits during egg laying and hatching, and by daily or alternate-day checks during incubation.

To determine the position, boundaries, and patterns of utilization of avocet territories, I recorded, at 10-sec intervals, the positions of both members of a pair within a grid system. Observations were collected and mapped to provide information on flux in territory size and utilization.

RESULTS

THE BREEDING SEQUENCE

Avocet breeding activities extended over a four-month period from late March until late July. Figure 2A summarizes the breeding chronology for avocets at Summer Lake during the 1969 season. For any single pair, territory establishment, courtship, nest site selection, and nest building activities occurred during the same time period, and are considered one stage (fig. 2B). The length of this stage is probably closely related to the time of arrival and the hormonal state of the pair (Marler and Hamilton 1966:102).

ARRIVAL

Avocets began arriving at Summer Lake around 20–25 March and most had arrived by the end of April (fig. 3). The greatest influx of birds occurred between 1–15 April. In early April single birds and small flocks of four to ten birds were frequently observed. Whether the birds migrate in flocks or as individuals, at night or during the day, is unclear. Hamilton (pers. comm.) suggests that they migrate at night since he found that in certain wintering areas in south San Francisco Bay there were

fewer and fewer birds each day until all birds had gone.

At the peak of migration in mid-April, large flocks of 50–200 avocets were present in the larger bodies of water within the marsh. The number of birds varied from 103 to 296 on a day-to-day basis during April, suggesting that Summer Lake was a stopping-over spot and many avocets continued to other areas.

TERRITORY
Avocets at Summer Lake established and maintained territories which were defended by both members of a pair. Observations made during early April 1970 indicated that the transition from flocking to territorial behavior is probably gradual, at least for birds arriving early in the season. The behavior of a flock of 26 avocets observed almost con-
FIGURE 2A. A breeding chronology for the avocet population at Summer Lake during the 1969 breeding season. B. A breeding chronology for a single pair. The beginning and end of each stage are based on dates when various breeding activities were first and last observed.

Continually for two days oscillated between complete non-aggression in flocks to intensely aggressive interactions characteristic of territorial establishment. The aggressive interactions seemed to spread the pairs over the marsh, where they usually engaged in nest selection activities and copulations, but within 15-30 min most of the birds would come together again to form a flock. This flock-pair-flock sequence continued until the pairs finally stayed separated on territories.

Avocet territories assumed three different
The situation was slightly different at sites where the nest was located well away from the feeding area (fig. 4B). Here only one foraging site was maintained, and there seemed to be only a small territory associated with the nest site, but this point was difficult to establish since avocets seldom approached another's nest. The feeding territory was more exclusive in this case because one member of the pair was usually in attendance.

Once the eggs hatched, the territory became chick-centered and somewhat mobile. The adults usually moved the chicks to a suitable foraging site, maintaining a strict territory of roughly 20–100 m in diameter around them at all times. Defense was interspecific as well as intraspecific. Nearly all avian species were excluded, with attacks being most frequent on blackbirds (Icteridae) and ducks (Anatidae).

COURTSHIP AND PAIR BOND

Avocet courtship was rather simple. Either the male or the female elicited precopulatory activity with a breast preening ceremony. Makkink (1936) and Hamilton (MS) give complete descriptions of courtship and copulation ceremonies for R. avocetta and R. americana, respectively. At Summer Lake, copulation displays were initiated as soon as the birds arrived; many individual pairs continued to copulate until after incubation began.

Avocets seem to be paired when they arrive on the breeding grounds at Summer Lake, for pairs were evident in the flocks. Wolfe (1931) and Brown (1948) believed that avocets pair during migration. Hamilton (MS) reports that pairing occurs in late winter. He states that pairing involves the selection of a male by a female; she associates herself with him despite initial rebuffing by the male.

Armstrong (1942) has generalized that birds in which there is no marked sexual dimorphism have an extended courtship. This seems to apply to the avocet. Pairs copulated frequently (several times a day) from arrival until after incubation had started, nearly a month in some cases. Mates formed a close association prior to egg laying. They fed side by side, drove intruders from the territory as a unit, and selected a nest site together. Each of these activities may contribute to strengthening the pair bond.

Lack (1965) considers members of the family Recurvirostridae to be monogamous. However, there was not complete fidelity between members of a pair at Summer Lake. In 1969 I observed three males and one female (all individually marked) copulate with unmarked birds which were not their mates. These op-
portunistic copulations always occurred during the incubation period on the territory of the marked birds. The breeding condition of the unmarked avocets could not be determined with accuracy, but in one case a female was followed for several minutes after a copulation. She intruded other territories and was driven off, indicating that she might have been unpaired. Perhaps the avocet resembles the oystercatcher (Haematopus ostralegus) in its tendency to mate with birds outside the pair bond (Makkink 1942).

Observations on a pair of color-banded birds in 1967 suggest that pair bonds may last for more than one season. This pair was seen with young in 1968 but was absent from the study area in 1969. They were observed together again in May 1970. Whether they remained together for the entire year is unknown.

THE NEST
Numerous accounts of avocet nest construction have been published (Wetmore 1925; Bent 1927; Wolfe 1931; Wheeler 1955; Hamilton, MS). Briefly, the nest is a simple scrape 15–25 cm in diameter, 0.5–3 cm deep, and lined with a variety of materials from grass to mud chips. The amount of lining is variable; some nests contain none while others are built up to a height of 38 cm (Wetmore 1925) in areas subjected to flooding. The largest nest I found was 7.5 cm high. I sampled 56 nests in order to determine the materials most commonly used in nest construction and the vegetation predominating

FIGURE 4A. Territories of three pairs of avocets during the incubation period along Windbreak Dike. Each pair defended two territories, one which included the nest and the other in a large pond nearby. B. Territories of three pairs located on the eastern edge of the Summer Lake Management Area. The nests were located in an alkali flat some distance from the defended feeding area, resulting in only one foraging site being defended.
nests in loose colonies usually do not defend. Lack (1968) states that the recurvirostrids makes a similar statement specifically for

nest in loose colonies and Hamilton (MS) stated like mo're colonial birds such as gulls, species more colonial species, but the nests within the colony are dispersed to aid concealment, Un-

NEST DISPERSION

Brown (1949), investigating R. avocettu, and Hamilton (MS), studying R. americana, state that the scrape is made by the bird rotating its breast on the ground. My observations indicated that the scrape was made with the feet rather than the breast. A scraping avocet rested on its breast and scratched with its feet; it then stood and turned to a new position and repeated the action until a scrape was made. Scratch marks made with the feet were quite obvious in newly formed scrapes. I did not see avocets rotating or rocking on their breast to form a scrape, and I often found nest scrapes on substrate types much too hard to be hollowed out with the breast.

Before the lining was added a scrape was made. Both birds took part in this activity. Bent (1927) and Hamilton (MS) state that avocets normally have a clutch of four eggs. I found a mean clutch size of 3.7 (2-4) for 111 nests. Nests containing six or more eggs (see table 4) were not included in the clutch size calculations, as they probably did not represent the clutch of a single female. Length and width measurements of eggs in 50 clutches revealed that the eggs of a single female were uniform in size. Nests containing six or more eggs had two distinct size classes, suggesting that two females laid the eggs. Dump nesting in this species requires a violation of territory; unfortunately the mechanism by which this was accomplished was not observed.

In 1967 and 1968 the first clutch was found on 7 May and in 1969 on 24 April. Egg laying reached its peak between 11 and 20 May in 1968 and 1969 (fig. 6). The laying period for a clutch of four eggs was usually five days. The exact laying interval was not precisely determined but it probably ranged from 24 to 36 hr, with four eggs being laid in five days.

Data from three nests deserted as a result of human disturbance showed that avocets can renest a short time after losing a clutch. One pair copulated and initiated nest construction
FIGURE 5. Avocet nest dispersion in different habitats at Summer Lake. A-B. At a salt grass habitat located along Windbreak Dike in 1969 and 1970, respectively (mean distance between nests in A, 47.3 m, and in B, 29.8 m). C. In a large salt grass field (mean distance between nests, 80.0 m). D. In an alkali flat (mean distance between nests, 50 m). E. On and near Windbreak Dike in 1967 and 1969.

one day after desertion. Two pairs completed second clutches of four eggs in eight days and a third pair took six days (three eggs) after desertion of a previous clutch. In each case fewer than four days remained in the incubation period when they deserted, so the effect of the stage of incubation on the rapidity of renesting could not be determined.

INCUBATION

Both sexes develop incubation patches and incubate, relieving each other at the nest rather often. From 480 min of observation at each of three nests, I found that the female’s incubation intervals averaged 52.2 min (3–255), and the male’s 38.0 min (3–75). Hamilton (MS) reported that males incubated 87.6 min (n = 26 intervals) and females 64.3 (n = 18 intervals). Both estimates are based on small samples and the large ranges involved indicate that there is considerable variation.

Time budgets of four pairs were analyzed to determine the amount of time each sex spent on the nest throughout the incubation period (table 2). During the first eight days the male spent nearly twice as much time on the nest as the female. However, these first eight days were characterized by a high degree of nest inattentiveness. The female predominated during the last 16 days of incubation. Hamilton (MS) found that the male incubated
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FIGURE 6. Time of nest initiation (laying of the first egg) at Summer Lake in 1968 and 1969.

about twice as much as the female but he gives no indication at which stage of the incubation period he collected his data.

During 8320 min of observation on 18 pairs extending over the entire incubation period, the female spent 46.0 per cent of her time on the nest and the male, 40.0 per cent, during the daylight hours. The apportionment of incubation time between the sexes showed little variation throughout the day (table 3).

The incubation period, defined as the interval from laying of the last egg until that egg hatches, was 24.2 (22-29) days for 28 nests. Effective incubation probably did not begin until the last egg was laid as all the eggs generally hatched within a day or two. However, avocets often covered incomplete clutches during especially cold or hot weather. As the season progressed, the length of the incubation period tended to decrease. Nests started in late April averaged 27 days of incubation; by early May the average period had dropped to 25, by mid-May to 24, and finally to 23 in early June. The increase in daytime temperatures as the season progressed may have allowed development to continue even when the eggs were unattended.

Avocets will incubate long past the normal incubation period if the eggs do not hatch. One pair attended a nest for 39 days before I accidently destroyed it.

Avocets turned their eggs after each nest relief. Upon settling on the nest the eggs were rotated with the feet. If an egg was removed from the nest an avocet replaced it by straddling the egg and rolling it back to the nest with its bill.

HATCHING

Hatching usually occurred over a one- or two-day period. The chicks began to pip the eggs four or five days before hatching; they could be heard calling in the eggs at this time. Shortly before hatching, a 4-15-mm hole was pipped in the egg. As soon as a chick freed itself from the egg, a parent removed the shell, dropping it 5-50 m from the nest. The nidifugous young were usually dry and able

<table>
<thead>
<tr>
<th>Time of day</th>
<th>% incubation</th>
<th>No. min</th>
<th>% incubation</th>
<th>No. min</th>
</tr>
</thead>
<tbody>
<tr>
<td>06:00-08:00</td>
<td>31.2</td>
<td>1740</td>
<td>50.3</td>
<td>1439</td>
</tr>
<tr>
<td>08:00-10:00</td>
<td>40.9</td>
<td>1320</td>
<td>46.0</td>
<td>1320</td>
</tr>
<tr>
<td>10:00-12:00</td>
<td>43.8</td>
<td>1620</td>
<td>43.4</td>
<td>1620</td>
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<tr>
<td>12:00-14:00</td>
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<td>1050</td>
<td>49.2</td>
<td>1050</td>
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<td>900</td>
<td>48.1</td>
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</tr>
<tr>
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<td></td>
<td>7618</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>39.6</td>
<td></td>
<td>45.7</td>
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</table>

TABLE 3. Diurnal incubation pattern for both sexes of avocets during the 1969 season.

<table>
<thead>
<tr>
<th>Incubation period: Early (days 1-8)</th>
<th>Middle (days 9-16)</th>
<th>Late (days 17-24)</th>
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<tbody>
<tr>
<td>Nest no.:</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1       2     3     4</td>
<td>1       2     3     4</td>
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<tr>
<td>% incubation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>δ</td>
<td>37.8</td>
<td>63.3</td>
</tr>
<tr>
<td>mean</td>
<td>52.3</td>
<td></td>
</tr>
<tr>
<td>θ</td>
<td>62.2</td>
<td>22.2</td>
</tr>
<tr>
<td>mean</td>
<td>21.8</td>
<td></td>
</tr>
<tr>
<td>Inattentive (δ and θ)</td>
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<td>14.4</td>
</tr>
<tr>
<td>mean</td>
<td>25.8</td>
<td></td>
</tr>
<tr>
<td>No. min. observ.</td>
<td>90</td>
<td>180</td>
</tr>
<tr>
<td>total</td>
<td>1200</td>
<td></td>
</tr>
</tbody>
</table>

TABLE 2. Role of the sexes during the incubation period at four avocet nests during the 1969 season.
TABLE 4. Summary of avocet hatching data for the 1969 breeding season.

<table>
<thead>
<tr>
<th>Eggs/clutch</th>
<th>No. nests</th>
<th>No. eggs</th>
<th>Eggs hatch</th>
<th>% eggs hatch</th>
<th>% eggs hatch/nest</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>7</td>
<td>14</td>
<td>6</td>
<td>43</td>
<td>1.1</td>
</tr>
<tr>
<td>3</td>
<td>6</td>
<td>18</td>
<td>16</td>
<td>89</td>
<td>2.6</td>
</tr>
<tr>
<td>4</td>
<td>59</td>
<td>236</td>
<td>212</td>
<td>90</td>
<td>3.6</td>
</tr>
<tr>
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<td>2</td>
<td>14</td>
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<td>—</td>
<td>—</td>
</tr>
<tr>
<td>8</td>
<td>4</td>
<td>32</td>
<td>3</td>
<td>9</td>
<td>0.75</td>
</tr>
<tr>
<td>Totals</td>
<td>78</td>
<td>314</td>
<td>237</td>
<td>79</td>
<td>3.0</td>
</tr>
</tbody>
</table>

to leave the nest within an hour or two. However, the chicks tended to stay in the nest or near to it for at least a day if not disturbed.

Hatching data for 78 nests followed during the 1968 and 1969 seasons are summarized in table 4. Hatching success was similar to that of other Charadrii (66-96 per cent; Boyd 1962). Nest losses due to predation were low; two nests were destroyed by a badger (Taxidea taxus) and I found no evidence of other nest predation. Predation on nests may be unusually low at Summer Lake because all types of terrestrial predators were rigorously controlled.

There was a correlation between clutch size and hatching success. Nests containing three or four eggs hatched a greater percentage of eggs than two- or eight-egg nests. Possibly, clutches of fewer than three eggs did not elicit a strong enough brooding drive for a pair to complete incubation. Eight-egg clutches probably had too many eggs to be effectively covered by the incubation patch, causing egg mortality. Eggs in multiple-clutch nests were also not turned properly, compounding egg mortality.

The hatching success was so low for eight-egg nests that it is difficult to appreciate the advantage gained by dump nesting. Perhaps the four nests I studied were atypical since Black-necked Stilts frequently have eight-egg clutches (pers. obser.; Hamilton, MS). One would suspect that there is a selective advantage or dump nesting would not continue in either species. Apparently an egg-dumping female has a better chance of hatching some eggs in a foster nest.

CARE OF THE YOUNG

Avocets were attentive parents even though they did not feed their young. Once the chicks hatched, the parents became aggressive toward all other species including other avocets. They allowed no other animal close to the young. I have seen a Canada Goose (Branta canadensis) successfully driven away by an avocet. At least one parent was always in attendance of the chicks. The parents relieved each other at intervals, similar to incubating birds.

Hamilton (MS) describes broods containing two age classes of chicks. He explains the occurrence of mixed broods by suggesting that avocets are unable to recognize their own young and lack territoriality during the parental stage. I observed no mixed broods at Summer Lake. The mixing of broods would require an intrusion of territorial boundaries. However, in certain situations when cover is lacking, a disturbance such as an approaching human creates chaos, with chicks running in all directions. It seems possible that under such conditions broods could become mixed.

The young spent most of their time feeding and resting. They exhibited preening and bathing behavior when less than a week old. Chicks usually ran for cover and lay flat when approached, making them very difficult to find. Hiding behavior lasted until at least the third week, after which they just ran. Chicks attempted to dive if chased in the water.

When young avocets became separated from their parents they were often attacked by other avocets. In one instance in an open expanse of shallow water, a lone chick was attacked numerous times by four different adults. The young bird was either struck by the attacker’s feet or picked up in the bill and violently shaken. Hamilton (MS) also reports this activity, as does Makkink (1936) for R. avocetta.

Parental care continued until after the chicks could fly (4-5 weeks). The members of one brood were able to fly in 27 days. Parental attentiveness waned as the young matured and the parents spent less time defending the area around them. The actual duration of the family group is unknown.

In order to determine how successful avocets were in raising young once they left the nest, I made three weekly counts during peak hatching and rearing periods of the number of young per brood for two age classes (n = 111 in downy plumage, 1-2 weeks of age; n = 110 in juvenal plumage, 3-4 weeks old). There was no difference in the number of chicks per brood for the two age classes (mean = 3.08 and 3.05, respectively) which indicates that those pairs which hatch young and do not lose the entire brood are quite successful in raising young, at least through the first month following hatching.

PREPARATION FOR MIGRATION

Once the young could fly, the birds joined a postbreeding flock. This usually involved
moving to some of the larger bodies of water within the marsh or to the lake. Flocks began forming in late June and by mid-July thousands of avocets were congregated along the west shore of the main lake. The large numbers of birds observed could not all have come from the marsh. Summer Lake thus seemed to be a stopping place for migrating avocets, as large numbers could be seen there in September and even into October (A. B. Claggett, pers. comm.). The postnuptial molt took place while the birds were in these flocks.

DISCUSSION OF AVOCET TERRITORIALITY

Avocets exhibited three different territorial arrangements throughout the breeding season. The prenesting territory consisted mainly of a feeding area on which mates spent nearly all their time. When not on the territory the pair was from a few to several hundred meters away searching for a nest site or building a nest. When interpreting the functions of such a territory, both ecological and social factors must be considered. Ecologically, food supply may be an important function of the avocet's territory. Unfortunately, the importance of food supply as a territorial function is difficult to substantiate. Indeed, food is not generally considered an important function of territories, even when all foraging is done on the territory (Hinde 1956). A more feasible function may be to facilitate maintenance of the pair bond. Avocets spent extended periods of time in close association on the territory while feeding, preening, courting, and defending it. This "togetherness" may also function to reduce the possibility of copulations outside the pair bond.

During incubation the territory still encompassed a foraging area but in addition a nest site was defended. This situation resulted in two spatial locations being defended simultaneously. Lind (1965) found a similar paired territorial system in oystercatchers (Haematopus ostralegus). In this paired territorial system it is difficult to determine just why the avocets or oystercatchers defend a site solely for feeding unless it functioned at least in part to assure an adequate food supply. Lind (1965) feels that the paired territories of the oystercatcher are closely related to features of the habitat and the oystercatcher's unique parental feeding system. I suspect that the paired arrangement in avocets is correlated with habitat and their semi-colonial type of nest dispersion. Nests situated in colonies cannot always be located in close proximity to foraging sites. The paired arrangement allows avocets to place their nests in association with other avocets and still maintain the advantages of both colonial and solitary nesting. Nests are spaced far enough apart for concealment, yet close enough together for group predator defense. They also enjoy solitary feeding and courting areas which offer the advantages of familiarity, undisturbed foraging and mating, plus, possibly, assurance of an adequate food supply.

Perhaps an extension of the function of the feeding territory is its potential to regulate population numbers. In habitats where there is a finite amount of feeding space, only those pairs holding a feeding territory can breed, thus limits are placed on the breeding population. Unfortunately exceptional conditions, in which feeding space is limited, are not available to test the possibility of density regulation as a territorial function.

SUMMARY

A study of the breeding biology of the American Avocet (Recurvirostra americana) was carried out in an alkaline marsh at Summer Lake, Oregon, during the breeding seasons of 1967-1969. Avocets arrived at Summer Lake in early April and usually spent a few days in flocks before dispersing to set up territories. Both sexes helped maintain a territory which was centered around a food source. The territorial system changed at each stage of the season, with the most important probable function being preservation of a food supply, although this cannot be conclusively shown. Courtship usually began soon after arrival and continued until after incubation had begun. Pairing probably occurred before the birds arrived at Summer Lake.

Nest building involved making a simple scrape and lining it with materials immediately available. Nests were distributed in a semi-colonial manner, generally near suitable feeding areas.

A clutch of four eggs was normally laid over a five-day period and egg laying reached its peak in the middle of May. Both sexes incubated the eggs, with the female tending to incubate slightly more that the male during the day. The incubation period was 24.2 (22-29) days.

The entire clutch usually hatched on the same day and the young could leave the nest within an hour. Hatching success was 79 per cent for the 1968 and 1969 seasons.

Avocets were attentive parents, keeping all species away from the chicks. Parental care
lasted four or five weeks. Pairs which did not lose the entire brood at hatching raised about three chicks. Once the young could fly, the family unit moved to flocking areas in preparation for migration.

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LITERATURE CITED


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