AN ANALYSIS OF PRAIRIE WARBLERS KILLED IN FLORIDA DURING NOCTURNAL MIGRATION

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This paper presents the results of an examination of 448 Prairie Warblers (*Dendroica discolor discolor*) killed during spring and fall migration as a consequence of nocturnal collisions with a television tower near Tallahassee, Leon County, Florida. The birds are separated into four classes, according to sex and age; and the measurements, weights, fat condition, migration schedules, and molt condition, are analyzed for each class. Also presented is information about plumage color, the bursa of Fabricius, and ectoparasites. When warranted, attention is given to the relationship between the time-advance of the season and the foregoing factors. Herbert L. Stoddard, Sr., who supplied us with the specimens, has described (1962) weather phenomena, details of construction of the 673-foot and 1010-foot towers (the latter replacing the former on April 15, 1960), and the methods and difficulties of collecting the dead birds. Although Nolan has data from other sources (field, museum, and literature) bearing on points considered herein, our discussion is largely confined to our sample, except where reference to other evidence is thought necessary to avoid confusion.

The specimens examined were killed in a period beginning with the fall migration in 1957 and ending with the fall migration of 1963. Extreme dates of spring kills were March 19 and May 13, and of fall kills, July 15 and October 19. These dates correspond to the normal migration periods of the species in northwestern Florida, although Stoddard (1962) has a record of a fatality on May 16, 1960. (Throughout this paper, dates refer to the day after the night on which a bird hit the tower.) All but a few Prairie Warblers picked up by Stoddard's daily searches were sent to us; the exceptions were specimens in such condition as to render them useless to us. The fact that not every bird identified as a Prairie Warbler could be used in our study accounts for the occasional discrepancy between Stoddard's report (1962) of numbers killed and our report herein. An additional unknown number of dead and injured birds may be assumed to have been removed by scavengers without leaving any trace behind, but it seems clear that we have had access to a very large proportion of the total of Prairie Warblers killed and that our material was a random sample of that total.

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METHODS AND LIMITATIONS

Birds were received by us approximately semiannually. These were frozen, labeled, and packaged in polyethylene bags in lots of various sizes. In almost all cases collection had taken place on the day after collision. Our examination of each lot followed within a few weeks to about three months after receipt. The effects these delays may have had on our data are considered beyond.

As the first step in processing, each bird was glanced at cursorily by Nolan as it lay thawing, and a tentative decision was made as to its sex and age. There were several reasons for this procedure; the one relevant to this study was to determine the extent to which we could rely on conspicuous plumage colors for ageing and sexing, if, in the case of some specimens, measurements and dissection should fail to be useful. Because results of this procedure are of importance in establishing the reliability of parts of the rest of the paper, they are discussed beyond in the section on plumage. All measurements were made by Nolan; weights were recorded on a triple beam balance. Mumford made the examination for molt and ectoparasites and proceeded with dissection. Fat condition was recorded on the scale of six described by McCabe (1943). The gonads, extent of skull ossification, stomach, and bursa of Fabricius, if any, were examined.

A number of factors prevented our taking exactly the same data from all specimens. These factors included mutilation of structures in the collisions and deterioration after death. We also decided to reject all bill measurements made early in the study because of doubts about our early procedure. Further, after the computer work had been completed and the manuscript prepared in supposed final draft, 40 more fall specimens were received. Age and sex were determined for these specimens and the sections on migration schedules and population structure were rewritten. The likelihood of learning other new facts of significance seemed too remote to justify a total revision of this paper. This was especially true in view of the fact that 35 of the new specimens were adults, an age class for which sufficient data had been obtained.

Special mention must be made of weights because all were subject to the possibility of change during the hours just following death and during storage. Weights of live birds taken by Nolan, as well as weights recorded in the Bahamas by L. H. Walkinshaw and summarized beyond, suggest that any changes in weight after death were small. However, we believe that the values obtained in this study only approximate absolute weights, although comparisons of average weights within subsamples should be reliable. It is very unlikely that the slightly longer periods of storage of specimens killed early in a season, as compared with those killed later, could substantially affect comparative analyses within our sample.

PLUMAGE

Male Prairie Warblers, especially adults, average considerably brighter than females in the yellow and black markings of the head and venter. A patch of chestnut-red on the back is often a conspicuous male character, although it is masked by olive in autumn. Immature birds of both sexes are identifiable by the presence of white and shades of gray on the head, a point described by earlier writers (for example, Dwight, 1900) and later apparently overlooked. This study showed that judgments, based on the foregoing plumage factors, of the ages of 246 autumn specimens, of which 72 were immature, were in all cases verified by examination of the skulls.

Nolan has found with both living birds and museum specimens that traces of immature plumage persist until the first postnuptial molt in all or nearly all females and in some males; details are to be described in another paper. In view of the reliability of ageing in fall by plumage and the fact that the same characters can be

TABLE 1

REDNESS OF BACK

	Male[1]		Female[1]	
	Adult	Immature	Adult	Immature
None	0	1	13	29
Slight	5	5	23	6
Conspicuous	13	6	2	0
Very marked	17	4	0	0
Totals	35	16	38	35

[1] All birds are fall specimens. Presence of masking olive tips on red feathers was disregarded in judging amount of red.

used in spring, we have felt that we could set up a category of "yearlings" for some of the spring studies herein, even though verification by skull-ageing is impossible at that season. The present study itself provides some objective evidence to support this decision: It reveals an average wing length in autumn immatures of both sexes that is significantly shorter than the average wing length in adults (table 3), and the average wing length of spring birds classed by us as yearlings is similar to the wing length of immatures. (Average wing length for 14 yearling males was 55.6 mm. and for 16 yearling females, 52.9 mm.) However, it must be emphasized that only with females is the yearling-older dichotomy probably fully reliable; with males the spring "old" class probably includes some year-old birds that had lost all their immature plumage characteristics as the result of prenuptial molt.

Sex determinations by the cursory examination of plumage, described previously, were slightly less reliable. In 267 adults (137 males) whose gonads could be found, three errors in sexing were made, or slightly over one per cent error. Among 58 immatures in fall (15 males), three errors were made, or about five per cent error. One of 31 spring yearlings was mistakenly sexed, or about three per cent error. As may be seen later, less conspicuous plumage characters, as well as measurements, can also be used to determine the sex of a bird; and we therefore believe that, in combination, external characters can be relied on for sexing with exceedingly small chance of error. For this reason, we have retained in our analyses the data derived from specimens whose gonads could not be found by us but about whose sex we were not in doubt.

The red or chestnut on the back, although a useful character for sexing most males, can be present in both sexes and at any age. Table 1 indicates the extent to

TABLE 2

WHITENESS OF FOURTH RECTRICES

	Male[1]		Female[1]	
	Adult	Immature	Adult	Immature
None	1	1	6	10
Little[2]	4	6	22	22
Much[2]	87	11	43	8
Totals	92	18	71	40

[1] All birds are fall specimens.
[2] "Little" indicates presence of one, occasionally two, spots not more than 5 mm. long, usually not extending to margin of feather; "much" is any greater amount of white.

TABLE 3

MEASUREMENTS OF FALL SPECIMENS

	Male		Female	
	Adult	Immature	Adult	Immature
Wing length[1]				
Number	97	20	76	49
Mean	57.16	55.74	54.70	52.70
Standard deviation	1.533	1.211	1.133	1.318
Standard error	0.15	0.26	0.13	0.19
Extremes	61.1–53.3	57.3–54.0	57.0–51.0	57.0–50.8
Tail length[1]				
Number	95	20	76	49
Mean	47.35	47.46	45.74	45.97
Standard deviation	1.863	2.684	1.755	1.712
Standard error	0.19	0.57	0.20	0.24
Extremes	54.0–43.0	50.0–44.0	49.0–41.5	50.0–40.2
Tarsus length[1]				
Number	97	20	76	49
Mean	18.82	19.03	18.32	18.55
Standard deviation	0.805	0.806	0.841	0.817
Standard error	0.08	0.18	0.10	0.12
Extremes	20.8–17.0	20.7–17.6	20.0–16.2	20.1–17.2
Bill length[1]				
Number	49	14	38	22
Mean	13.90	13.81	13.55	13.27
Standard deviation	0.505	0.770	0.658	0.534
Standard error	0.07	0.20	0.11	0.11
Extremes	15.2–12.8	15.3–12.0	14.7–11.9	14.3–12.2

[1] All measurements are in millimeters.

which the size and brightness of the patch vary in correlation with sex and age. In very brightly marked males, there is sometimes a large black spot along the rachis of several feathers, surrounded by, and at the proximal end of, the red spot. Dr. Pierce Brodkorb first called a specimen so marked to Nolan's attention. Two of our 17 very markedly red males exhibited such black spots.

White on the vanes of the outer two pairs of rectrices (numbers five and six) is a conspicuous fieldmark of all Prairie Warblers, and on some individuals the outer three or four pairs are marked in this way. Sharpe (1885) noted a relationship between age and the extent of this white, but he greatly underestimated how much variability there is, particularly in pair number four (table 2). This variability is expressed in amount, shape, and location of the white as well as in some asymmetry between the two feathers of the pair. Only the third pair of rectrices of our specimens can be made the subject of a generalization; if white was present on that pair, or in one feather of the pair, the bird was an adult male. Twelve of 92 adult males were marked in this way. There appeared to be little, if any, correlation between amounts of red in the back and of white in the tail, either for males or females.

The wing bars of birds of this species vary in color from yellow to dull shades of greenish, gray, and buffy, with the distal (or posterior) bar sometimes much less marked. Our notes are too subjective to present, but they lead us to believe that brightness and size of the wing bars vary much as does red in the back. However, birds with little red in the back may have bright wing bars, and vice versa.

We attempted to pluck all the plumage of a fresh-plumaged male and female, and after allowing the feathers to dry, we weighed them in midwinter under conditions of very low humidity. The male's feathers weighed 0.62 gm. and the female's 0.50 gm.

Two specimens each had one white body feather.

MEASUREMENTS

Measurements of four external structures are shown in table 3. Only birds killed in autumn and thus in fresh plumage are included. The wing measurement is of the flattened wing. The bill was measured as the length of the total culmen, the tail from its base between the central pair of rectrices to its longest point, and the tarsus from the heel to the last undivided scute.

It will be evident that the four sex and age classes differ significantly from each other in mean wing length ($P = < 0.001$). In tail length a similar difference obtains only as between the sexes; comparing the two adult sex classes, $P = < 0.001$; comparing the two immature sex classes, $P = < 0.01$. In average length of tarsus, the immature classes were larger, but there was a significant difference only as between the sexes; for example, for the difference between the means of the two adult sex classes, $P = < 0.001$. Bill length also differed significantly only as between the sexes; for the difference between the means of adult males and females, $P = < 0.010 > 0.005$. Our data show a small, nonsignificant difference in length of bill between adults and immatures.

Correlation coefficients were obtained between all pairs of measurements. Only in the correlation between wing and tail were the values significant (at the 99 per cent confidence level), except in young males where this value was not significant even at the 95 per cent level: adult male, 0.53 with 93 degrees of freedom; immature male, 0.41 with 18 degrees of freedom; adult female, 0.43 with 74 degrees of freedom; immature female, 0.41 with 47 degrees of freedom.

On a number of birds an effort was made to measure the areas of the wing by tracing the outline of that structure as it lay stretched and pinned in position on a card. We recognized that there were differences in the degree of pliability of the muscles of the specimens and that it was impossible to obtain an identical position for each wing measured. The further process of converting the tracings into values in square centimeters, which we performed by counting the squares on a transparent grid overlying the tracings, introduced additional slight inaccuracies and approximations. Table 4 shows the approximate area in square centimeters of the two wings combined of a series of birds with wings of various lengths. Each value was obtained by averaging the wing areas of three different birds of each wing length. Adult birds of both sexes were used; we observed no sex or age differences in the shape of the extended wing.

MIGRATION SCHEDULES AND POPULATION STRUCTURE

This section analyzes the composition of the samples of Prairie Warblers according to sex, age, and date of death. The principal object is to learn whether the sex-age classes migrate on the same or different schedules near Tallahassee. Secondarily, information about the structure of the nocturnal migrant population is developed. When this is compared with other information about the population structure of the race, it yields inferences about migration behavior.

TABLE 4

AVERAGE APPROXIMATE AREA OF BOTH WINGS COMBINED[1]

Wing length (mm.)	Area (sq. cm.)
50–51	43.2
51–52	46.1
52–53	47.7
53–54	47.3
54–55	49.9
55–56	53.1
56–57	55.8
57–58	57.1
58–59	57.2
59–60	60.4
60–61	63.4

[1] Three specimens of each wing length were used to obtain averages.

It should be emphasized that little attention is given to consideration of the absolute size of the flight of Prairie Warblers and that other sources have been relied on for the few instances in which absolute size enters into consideration. The impossibility of inferring the relative magnitude of the migration on two nights merely from the numbers of birds killed is obvious; the role of hazardous flying conditions, at least, must be considered. Less obvious is the unreliability of comparisons of the proportions that birds of one species comprise in the total mortality of all species on two nights, but data of Stoddard (pers. comm.) show the risks of too much reliance on changes in such proportions. For example, in middle September, Prairie Warblers are migrating southward near Tallahassee in large numbers, and weather conditions often contribute to high mortality. On September 15, 1961, 15 of an aggregate kill of 37 birds were Prairie Warblers, yet on the same date in 1958, there had been none of that species among 238 dead. Or, to take September nights from the same year, 1963, a kill of 21 Prairie Warblers among 122 birds on the 21st is to be contrasted with none among 168 dead on the 23rd. Various explanations are possible (see Brewer and Ellis, 1958), but without many more kills and knowledge of the circumstances surrounding them, only limited uses of numerical data on the extent of mortality at the television tower seem permissible.

In using the numbers of our specimens killed during the time-advance of the two migration seasons to compare the schedules of the movements of various elements within this one species, we have made the following assumptions: (1) that the samples were randomly drawn from the Prairie Warblers that migrated at night during each period at the location of and at or below the altitude of the two towers; and (2) that schedule relationships of the kind being considered did not vary annually to a degree that would prevent pooling of data from more than one year. We have compared the birds killed by the lower tower and its higher replacement and have found no reason to avoid pooling because of heterogeneity from that source.

Spring.—One hundred sixty-two specimens were examined, from a 56-day period from March 19 through May 13. Of these, 144 died in April, when nights on which at least five birds (without regard to species) died at the tower were nearly twice as numerous as in March and over four times as numerous as in May. Stoddard (1962) emphasizes the comparatively dangerous flying weather in April. Thus it is clear

TABLE 5

COMPOSITION OF SPRING SAMPLE BY PERIODS

	Old birds[1]				Young birds[2]		Totals
	Males		Females		Males	Females	
	Number	Per cent[3]	Number	Per cent[3]	Number	Number	
Mar. 15–31	11	91.6	1	8.4	1	1	14
Apr. 1–10	28	87.5	4	12.5	1	2	35
Apr. 11–19	19	44.2	24	55.8	5	5	53
Apr. 20–30	8	19.5	33	80.5	7	8	56
May 1–13	1	–	0	–	2	1	4
Totals	67		62		16	17	162

[1] Birds showing no trace of immature plumage. Some yearlings undoubtedly are included, at least among males.
[2] Birds showing traces of immature plumage.
[3] Per cents are of totals of old birds only, not young birds. The per cent of the total of all males was 51.2 and of all females 48.8.

that sampling of the spring migration of the Prairie Warbler was very unevenly distributed. Only April, with six well-spaced kills of from 11 to 19 birds, was adequately sampled; but the fact that it comprises the middle half of the period is advantageous. Almost nothing was learned about May.

Inspection of table 5 reveals that the old males migrate earlier than do the old females and probably earlier than does either sex among the yearling birds. Further information about March and May might magnify the differences. Several statistics express the dissimilar schedules shown in table 5: (1) The average date of death for old males was April 9, and for old females and first-year males and females the average date of death was April 19. (2) The median date of death of old males was April 6, a date on which only 8 per cent of the old females had died. By the median date for old females, April 21, 88 per cent of the old males had died. The median date for young males was April 21 and for young females, April 23. (3) A four-by-two contingency table distributing old males and old females in time, duplicating the data for those classes in table 5 except that the May period is omitted, can be tested for independence by chi-square, with hypothetical frequencies based on border totals. The sum of chi-squares is 41.88; with 3 degrees of freedom, $P = < 0.001$.

With different migration schedules thus having been established, sampling shown to have been unevenly distributed, and only a fraction of the yearling males identifiable, there is little to be learned about the population structure of the Prairie Warbler from the data in table 5. On the other hand, information that Nolan has about population leads to a further inference about migration: The 4 : 1 ratio, shown in table 5, of old females to yearling females understates the true proportion of first-year females in the breeding population of Prairie Warblers. These yearling females "missing" from our data might have shown up if there had been greater mortality in May; that is, it seems more likely that they have a later migration schedule than old females rather than that they follow different routes or migrate at different altitudes or hours of the day.

Fall.—There were 286 birds killed and sent to us from the 97-day period from July 15 through October 19. The first third of this interval yielded only 11 specimens. Relatively safe weather at this time and low numbers of migrants probably contributed to this result. The remainder of the migration was well sampled. Whatever decreases in the volume of migrants there may have been, at some point as the flight drew to

TABLE 6

COMPOSITION OF FALL SAMPLE BY PERIODS

	Adults				Immatures				Totals
	Males		Females		Males		Females		
	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent	
July 15–31	0		0		1		4		5
Aug. 1–15	2		1		0		3		6
Aug. 16–31	46	42.2	38	34.8	10	9.2	15	13.8	109
Sept. 1–15	21	47.7	13	29.5	4	9.1	6	13.6	44
Sept. 16–30	31	40.8	25	32.9	4	5.3	16	21.0	76
Oct. 1–19	21	45.7	11	23.9	4	8.7	10	21.7	46
Totals	121	42.3	88	30.8	23	8.0	54	18.9	286

an end, were masked by the fact that flying conditions become progressively more dangerous until after the end of the migration of Prairie Warblers (Stoddard, 1962). More than half of our birds died on one of five occasions; four of these were on single nights and one was an interval spanning three nights. As table 7 shows, these five large fatalities were fairly well distributed between August 20 and October 5 and contributed from 19 to 69 Prairie Warblers each.

In table 6 the total numbers of dead of each sex-age class are allocated among six periods of approximately equal, half-month lengths, beginning on July 15. The numbers during the last four periods are also translated into percentages. The average date of death of adult males was September 10; of adult females, September 7; of immature males, September 3; and of immature females, September 5. Median dates of these classes, in the same order, were September 15, September 12, September 3, and September 12. Discussion of the fall data follows in numbered paragraphs:

1.—The earliest seven birds to die, all before August 12, were young of the year. [While this paper was in press, we received birds killed in 1964. Data from these specimens are not included in this paper. Six of these birds had struck the tower in July and five others had done so in August, prior to the 12th. All were immature. Thus, the 18 birds that died on the earliest dates in fall were, without exception, immature.] Individuals of this age continued to be killed until the end of the migration of the species, and their numbers in proportion to adults migrating did not change after mid-August. The bird killed July 15 could scarcely have been older than 70 days, in view of the fact that the very earliest nest-leaving does not occur before the middle of May (Burleigh, 1958; Sprunt and Chamberlain, 1949). The latest nest-leaving takes place in the middle of August (Nolan, 1963*a*), and the protracted

TABLE 7

COMPOSITION OF FIVE LARGE AUTUMN KILLS

	Adult		Immature		Totals
	Males	Females	Males	Females	
Aug. 20, 1957	28	26	5	10	69
Sept. 12–15, 1961	14	9	1	2	26
Sept. 19, 1962	12	14	3	7	36
Sept. 21, 1963	13	5	0	1	19
Oct. 5, 1957	14	5	2	5	26
Totals	81	59	11	25	176

passage of young in fall corresponds in length with the duration of the period of production.

2.—From the middle of August onward, the relationships between the proportions represented by the four sex-age classes remained remarkably consistent. In a series of chi-square tests, data from table 6 were inserted in contingency tables in an effort to detect significant differences in the distribution of the sex-age classes as time advanced. Expected numbers were calculated from marginal totals; when necessary because of the low numbers of immature males, data for the two classes of immatures were pooled. None of the tests yielded significant values, as the following summary shows. In each instance the data distributed, the sum of chi-squares, the degrees of freedom, and probability are stated in that order: (1) The two adult sex classes and immatures without regard to sex, distributed among the four periods beginning with the second half of August: chi-square = 2.59; d.f. = 6; $P = < 0.90 > 0.75$. (2) The two adult sex classes, distributed among the four periods: chi-square = 0.95; d.f. = 3; $P = < 0.995 > 0.990$. (3) Adults and immatures without regard to sex, distributed among the four periods: chi-square = 1.16; d.f. = 3; $P = < 0.90 > 0.75$. (4) The two sexes without regard to age, distributed among the four periods: chi-square = 1.54; d.f. = 3; $P = < 0.75 > 0.50$. (5) Adult males and the pooled totals for the other three classes, distributed among the four periods: chi-square = 0.70; d.f. = 3; $P = < 0.90 > 0.75$. (6) Adult females and the pooled totals of the other three classes, distributed among the four periods: chi-square = 1.93; d.f. = 3; $P = < 0.75 > 0.50$. (7) Each of the four periods was compared with the other three periods pooled. The greatest differences found to exist were between the August period and the others (chi-square = 2.09; d.f. = 3; $P = < 0.75 > 0.50$) and October and the others (chi-square = 1.74; d.f. = 2; $P = < 0.50 > 0.25$).

The only serious challenge to the hypothesis that there is no change in the proportions of the total migrants contributed by the sex-age classes is the change in the composition of the two large kills in 1957. In table 7 it may be seen that adult females became less numerous in relation to adult males in the late flight. However a chi-square test of independence of these two samples gives no evidence of heterogeneity in the numbers of adults; chi-square adjusted for continuity is 1.92; with 1 d.f., $P = < 0.25 > 0.10$. Similarly, introduction of the pooled numbers of immatures makes no significant change. Therefore, even after giving special force to any suggestion from two kills within a single year, we see no reason to believe that males tend to migrate later into the autumn. The latest kill of as many as five Prairie Warblers in one night occurred on October 14, 1961, and consisted of one immature male, three adult females, and one immature female.

3.—It follows from the conclusion that adult males and females migrated on the same schedule (that is, at night near Tallahassee, at or below tower level) after August 15, that the pooled totals of specimens of those two classes should reflect the sex ratio of the adult migrants, unless better sampling between July 15 and August 15 would have altered the result. All our information indicates both that few adults could be expected to be migrating before August 15 and that the sex ratio among early migrants would not vary from those obtained later. The sex ratio in our sample, in per cent, is 57.8 adult males to 42.2 adult females. Chi-square, adjusted for continuity, of the pooled totals is 4.66; with one degree of freedom, $P = < 0.050 > 0.025$. Whether this indicates a difference in the sex ratio of the race *D. d. discolor* as a whole or a difference, for example, in the routes, times, or heights of flight is not clear. Museum studies would suggest a preponderance of males; but the probability of random sampling by collectors is very low. A field investigation by Nolan (1963*b*) in Indiana found no difference in the ratio and concluded that if either sex is more numerous, it is probably the female.

4.—The sex ratio of the sample of immature birds is 29.9 per cent males to 70.1 per cent females. Adjusted chi-square is 11.69; with one degree of freedom, $P = < 0.001$. The possibility that our sample is representative of the race has no support from any other evidence, requiring, as it would, greatly different sex ratios at hatching or nest-leaving and at least as large differences in mortality in the first winter and spring of life. An alternative possibility, that better sampling in July and early August would have made up the deficit in young males, is equally unacceptable for this would require the assumption that early nests produce predominantly male individuals, or that young females migrate at an older age than young males. We conclude that fewer immature males were exposed to the risk of death at the tower and that explanations involving differences in routes, times of day or heights of flight, and behavior in adverse weather are more likely than those suggested in the preceding sentence.

5.—Age ratios representative of the total population passing the tower cannot be expected, in view of the poor sampling in the early period of migration. It is improbable, based on the conclusion in the foregoing paragraph, that more early kills would have produced a sample reflecting the age ratio in males of the race. But the 3 : 2 proportion of old females to immature females among our birds may be not far from the ratio in the population of the race as a whole.

MOLT

Spring.—Prenuptial molt in the Prairie Warbler usually involves only some of the feathers of the head, chin, and throat. Seventeen out of 77 males and four out of 66 females were still molting in one or more of these areas. One of the seventeen molting males also had a few sheathed feathers on the ventral tract. Only on this last bird was any large number of feathers still in the process of renewal. Of the total of 77 males, 12 still retained traces of immature plumage; three of those 12 were molting. Sixteen of the 66 females were entering the first adult year, and one of these 16 yearlings was molting.

Dates of death of the molting birds tended either to be early, or, if late, molt was associated with the fact that the individual was a yearling. The latest date on which molt was found on a male that lacked traces of immature plumage was April 11, and on a male that showed such traces, May 3. Two of the three old females in molt died in the first third of April; or, to change the emphasis, of the five old females that died as early as April 10, two were molting.

In view of the average ten-day difference in the dates of death in spring of old males and old females, the fact that molt was more common in the former sex may be a function only of date. Yearling birds were not numerous enough to throw light on this point. It is also possible that molt in males is more extensive or that more males molt in spring. If this is true, it might explain why, in this species, fewer males can be recognized as yearlings than can females. The explanation may be that the molt has replaced the recognizably immature plumage in some yearling males.

About 66 per cent of the birds showing immature plumage also had noticeably worn to exceedingly worn and ragged flight feathers, especially the rectrices. The central pair of rectrices was most heavily worn; the three outer pairs of primaries always showed the least wear among the primaries. Only about ten per cent of old

TABLE 8

INCIDENCE AND LOCATION OF MOLT ON 199 FALL SPECIMENS

	Adults		Immatures	
	Males	Females	Males	Females
None	17	8	8	20
Head[1] only	36	26	4	5
Head[1] and body[2]	18	18	1	4[3]
Body[2] only	11	7	5	11
Totals	82	59	18	40

[1] Includes chin; evidence of molt on one or more areas of head and chin.
[2] Evidence of molt on dorsum, venter, or both.
[3] Two of these were molting also on the upper wing coverts, more specifically, one on the greater primary coverts and the other on the lesser coverts.

males and females had heavily worn plumage, but an additional approximately 20 per cent exhibited a noticeable degree of wear.

Two males and one female had lost or were renewing from one to three primaries or rectrices, but the absence of symmetrical patterns indicated accident rather than molt.

Fall.—The postnuptial molt of Prairie Warblers is complete. Most adults were in the late stages of this molt; fewer immatures were molting. Live immature birds examined closely with binoculars in the field cease to show observable molt at an age of about 40 days. We do not know how long thereafter partly sheathed feathers may be found; but the speed with which the observable phase of molt goes on suggests that at 60 to 70 days of age the process might be complete.

Table 8 shows the numerical incidence and the locations of molt on birds of the four sex and age classes. Before discussing these classes, the following general points may be noted: Few birds were undergoing extensive molt, either in the distribution of sheathed feathers over wide areas of the body or in numbers of feathers being renewed; no sheathed remiges or tail feathers were found except for five cases of asymmetrical renewal of from one to three rectrices (and one case of simultaneous renewal of all rectrices), suggestive of accidental loss. Five specimens with one or more newly lost rectrices may have lost them in striking the tower. In most birds, of all sex and age classes, the molt of the head (often the auriculars) was completed last. As table 8 indicates, a higher proportion of molting immatures was molting on the body than was true of adults. No pattern emerged of any sequence in the completion of plumage renewal as between the dorsal and ventral surfaces of body or head, and the last traces of body molt could not be expected to be found in any particular tract or region. Adult females on the average appeared to finish the molt at a later date than adult males. In immatures, in which age is clearly a factor in the onset and completion of molt, no sexual difference in schedule was apparent.

ADULT MALES.—Progress of molt was closely correlated with date of death. Thirty-seven of 39 birds killed in August were molting, but only nine of 19 males killed in October were molting. Thus, of the 17 individuals no longer molting, ten died in October. Renewal of the body plumage was still going on in 29 adult males, but only two of these were killed after August 31. In all but five cases we regarded the molt as light; it was visible only if the plumage was parted, and involved at the most a small proportion of the feathers in the tract. The five adult males considered to be molting heavily had numerous quills on the head and body; four of these died in August and one in September.

Adult females.—Only eight individuals in this class had completed molt, with less correlation between completion and date than was apparent in males. Of nine October specimens, eight were molting. However, of the 25 instances involving molt on the body, only two occurred after August 31. Seven birds, all from August, were replacing many feathers, distributed extensively on the head and body. All other females were in light molt.

Immature males.—Seven of ten August birds were in molt, compared to one of four killed in October. No body molt occurred after August 31. Only light molt was noted.

Immature females.—Nine of the ten October kills were birds that had finished molting; as compared with this, only three of the 13 killed in the second half of August had finished molting. Molt on the body was not found in immature females after September 15. Only two birds (one in July and the other in late August) were molting heavily; the others had only a few sheathed feathers.

If the presence of a few quills can be interpreted to mean that the postjuvenal molt is just concluding, and if completion of the postjuvenal molt is a function of age, then it appears that some young birds may migrate at an age of not much more than two months. Indeed, no other conclusion is possible when the earliest date of nest-leaving, mid-May, and the earliest date of tower collision, mid-July, are compared. When it is further noted that fledgling Prairie Warblers remain with their parents until they are 40 to 45 days old, then a reasonable speculative probability would be that the very early migrants as well as all the molting immatures were not likely to have had time to come from the northern part of the range of the species. If the proportion of molting immatures had risen in late fall, one might have been tempted to suspect that birds hatching late are under pressure to migrate at an earlier stage of development. Instead, the numbers of molting birds declined sharply as the season advanced. It may be relevant that we noted wear of the flight feathers of five autumn immatures, four killed in October and one on August 31; none of the five was molting.

WEIGHT AND FAT

Spring.—The statistics of the weights of spring migrants (table 8) indicate a slightly but significantly ($P = < 0.001$) higher mean weight for males than for females, with no differences according to age. It must be remembered that the "old" class among males probably contains some yearling birds; but the work of Odum, Rogers, and Hicks (1964) indicates that age would be relevant to weight only as it affected amounts of fat deposition or general body size.

Our weights in table 9 can be compared with ten weights obtained from live Prairie Warblers caught between March 18 and March 25, 1960, on Andros Island, Bahamas, by L. H. Walkinshaw, who kindly gave us his data. Walkinshaw's birds, which were in the winter range, must have been near the point of migrating and some may actually have been migrating. Six males ranged between 8.2 and 6.9 gm. and averaged 7.5 gm. Four females ranged between 7.5 and 5.9 gm. and averaged 6.6 gm.

To determine whether there was any change in the weights of Prairie Warblers as spring advanced we divided our old males into subsamples of 39 and 28, depending on whether they were killed on or before April 10 or after that date. Old females were similarly divided, but the date used to obtain approximately equal (29 and 33)

TABLE 9

WEIGHTS

	Male		Female	
	Old[1]	Young[2]	Old[1]	Young[2]
SPRING				
Number	65	15	61	15
Mean in grams	6.99	7.03	6.63	6.51
Standard deviation	0.542	0.470	0.525	0.479
Standard error	0.07	0.12	0.07	0.12
Extremes	8.3–5.6	8.0–6.6	7.7–5.7	7.3–5.8

	Male				Female			
	Adult		Immature		Adult		Immature	
	July–Aug.	Sept.–Oct.	July–Aug.	Sept.–Oct.	July–Aug.	Sept.–Oct.	July–Aug.	Sept.–Oct.
FALL								
Number	41	56	10	10	36	40	18	30
Mean in grams	7.55	8.73	8.04	8.48	6.83	7.66	6.97	8.10
Standard deviation	0.778	0.841	1.183	1.173	0.516	0.941	0.795	1.025
Standard error	0.12	0.11	0.37	0.37	0.09	0.15	0.19	0.19
Extremes	9.9–6.3	10.1–6.6	10.0–6.5	10.5–7.2	8.4–5.7	10.8–6.2	9.2–6.0	10.6–6.3

[1] Applied to birds in spring, "old" means that no vestiges of immature plumage were recognizable.
[2] Applied to birds in spring, "young" means that vestiges of immature plumage were recognizable.

subsamples was April 20. There was no indication of a weight change; the early and late males averaged, respectively, 6.9 and 7.0 gm., and the female subgroups averaged 6.7 and 6.6 gm.

Visual inspection of birds for fat condition led to the conclusion that there were no differences among sex and age classes and also no variations correlated with date. Lumping all males to produce a total of 67 specimens, 8 had no fat, 43 had little fat, and 16 moderate fat (average index 1.1). Of the total of 52 females, 6 had no fat, 34 little fat, and 12 moderate fat (average index 1.0).

Fall.—Unlike the condition of birds in the spring, the weights of all sex-age classes increased significantly as autumn advanced (see table 9). For the differences between the mean weights of adult females, for example, killed in the two halves of fall, $P = < 0.001$. Immatures of both sexes averaged greater in weight than adults.

To explore the assumption that the increase in weight corresponding to time-advance was attributable to an increase in fat condition and not to the possibility that late migrants were birds larger in general linear dimensions (conceivably from a different population), we calculated wing length for all classes in early autumn and late autumn, using the same specimens as those whose weights appear in table 9. Changes in average wing length were minute and nonsignificant; three averages increased, the largest increase being 0.2 mm., and one average decreased 0.4 mm. The weight increase thus appears not to be attributable to a general increase in dimensions of late migrants.

As would be expected, a frequency distribution of birds in various fat classes, segregated into subgroups from July to August and September to October, shows a sharp increase in the amounts of fat on the later migrants. There appeared to be no adult sexual difference in this pattern of higher fat classification, which in adult males changed from an average index of 4.0 to 5.2 and in adult females from 3.8 to 5.4. The change in average fat index of adult sex classes combined was from 3.9 to 5.3, whereas the comparable figures for 29 immature birds of both sexes in the first half of autumn and 28 in the last half showed a rise only from 4.2 to 4.9. For 19 early fall immature females and 20 late fall birds of the same class, the respective indexes were 4.0 and 4.7. Immature males were not numerous enough for separate analysis.

Connell, Odum, and Kale (1960:8) have found that "fat-free weight . . . is relatively constant for birds of the same size (as indicated by wing length) and species in marked contrast to the total live weight which, in migratory species, fluctuates greatly because of the large variations in fat deposits." Unfortunately, we do not have fat-free weights for Prairie Warblers, but coefficients of correlation of wing length and total weight (table 10) emphasize the lack of constancy in the relation when weight includes fat. Fourteen of 20 coefficient values were nonsignificant at the five per cent level, six were significant at that level, and four of the latter were also significant at the one per cent level. As table 10 shows, correlations were higher in the spring, when birds were less fat. However, there was no higher correlation for fall birds in the early, low-fat period than there was later in the season, except in immature males. Similarly the change in the coefficient for old males between early and late spring cannot be equated with change in fat condition. Graber and Graber (1962) have shown that in several species substantial weight change occurs during the hours of nocturnal migration. Presumably our weights, and therefore correlations, were affected to some extent by the times of death, but we have no idea of the hours at night when our specimens died. As expected, the stomachs of all birds were empty.

Tordoff and Mengel (1956) have suggested that wing-loading, that is, the relative weight carried by the flying surface of the wing, might affect the rates of migration of sex and age classes of a species. They illustrate this point with a hypothetical species in which immatures, weighing about the same as adults, have shorter wings and thus would require more energy to fly the same distance. In the Prairie Warblers in our sample, if the average fall weights derived from table 9 are divided by the average wing areas (table 4) of birds having wings comparable to the average wing lengths (table 3) of the four autumn sex-age classes, the average wing-loading of adult males is 0.141, of immature males, 0.155, of adult females, 0.147, and of immature females, 0.161 gm. per square cm. of carrying surface.

Odum, Rogers, and Hicks (1964:1038) have studied the tissues of three species of parulids and report, as regards fat and nonfat tissue, that "age and sex proved to have a negligible effect on body composition." If this is also true of Prairie Warblers, young birds weigh more than adults, on the average, probably only because young birds are fatter. Thus, while it is true that for aerodynamic reasons immature Prairie Warblers will require more energy to migrate the same distance as adults, as suggested by Tordoff and Mengel (1956), the very factor that produces the additional wing-loading is itself the source of the energy. To elaborate on the simile used by Odum, Rogers, and Hicks (1964), we can compare the two age classes of Prairie Warblers with two airplanes of identical model except for a slight difference in size. The smaller airplane takes on more fuel and is more heavily wing-loaded. With its added fuel, it may have as great as, or greater, net flying range as the larger plane. Its size and load may, however, reduce its flight speed.

BURSA OF FABRICIUS

A bursa of Fabricius was found in 12 of 18 immature males and in 26 of 38 immature females killed in autumn. No adults, of 140 examined in fall and 95 in spring, had a bursa of Fabricius. Size of the bursa ranged from about 1.5 to 3.0 mm. in

TABLE 10

COEFFICIENTS OF CORRELATION OF WING LENGTH TO WEIGHT

Class	Degrees of freedom	Coefficient (r)
Fall adult male	95	0.16
Early[1] fall adult male	39	0.16
Late[1] fall adult male	54	0.14
Fall adult female	74	0.18
Early[1] fall adult female	34	0.10
Late[1] fall adult female	38	0.19
Fall immature male	18	0.68**
Early[1] fall immature male	8	0.87**
Late[1] fall immature male	8	0.56
Fall immature female	46	0.25
Early[1] fall immature female	16	0.14
Late[1] fall immature female	28	0.31
Spring old male	63	0.18
Early[2] spring old male	37	0.04
Late[2] spring old male	24	0.38*
Spring old female	59	0.39**
Early[3] spring old female	27	0.38*
Late[3] spring old female	30	0.49**
Spring yearling male	13	–0.42
Spring yearling female	13	0.48

* and ** indicate, respectively, values at the 5 per cent and 1 per cent levels of significance.

[1] "Early" and "late" as applied to fall refer, respectively, to the periods before September 1 and beginning with September 1.

[2] "Early" and "late" as applied to males in spring refer, respectively, to the periods before April 11 and beginning with April 11.

[3] "Early" and "late" as applied to females in spring refer, respectively, to the periods before April 21 and beginning with April 21.

length and 1.0 to 2.0 mm. in diameter. Six of 10 immature males killed prior to September 1 and 6 of 8 killed after September 1 had bursas. In females, 16 of 18 killed before September 1 and 10 of 19 killed after that date had bursas.

PARASITES

The following parasites were collected in our examination of the plumage of our specimens. These examinations were sometimes superficial in character.

Mites: Acarina, *Proctophyllodes* sp., seven specimens, determined by E. W. Baker; *Neocheyletiella* sp. probably new, near *chanayi*, nine specimens, determined by E. W. Baker.

Ticks: Acarina, *Haemaphysalis leporis-palustris*, one larva, determined by Nixon Wilson.

Lice: Mallophaga, *Ricinus* sp., 21 specimens, determined by Nixon Wilson; *Philopterus* sp., tentatively *citrinellae*, nine specimens, determined to genus by Nixon Wilson and tentatively to species by K. C. Emerson. In a later lot of two specimens sent to K. C. Emerson, the determination was *Philopterus* sp. *Myrsidea* sp., tentatively *ridulosa*, seven specimens, determined to genus by Nixon Wilson and tentatively to species by K. C. Emerson.

Rarely were more than two or three parasites collected from a single host warbler.

Nixon Wilson took from the heads of several of our birds 40 specimens of a nasal mite, *Ptilonyssus* sp.

SUMMARY

Four hundred forty-eight Prairie Warblers, *Dendroica d. discolor*, killed in nocturnal collisions with television towers near Tallahassee, Florida, during spring and fall migration, yielded measurements and weights as well as information about fat, molt, color of plumage, parasites, the bursa of Fabricius, migration, and composition of the sampled population.

Consideration is given to the differences among the age-sex classes (adults and immatures, males and females). Significant differences existed in average measurements and weights; in some instances the differences were related both to sex and age, in some to only one of these variables. Similar patterns of variation in plumage occurred. Autumn immatures were without exception recognized as such by plumage, and sex of adults and immatures was determinable before dissection in 95 per cent or more of the samples.

There was little fat or molt on spring birds; fat condition did not change as the date advanced. Autumn birds were quite fat, becoming more so as the season progressed; immatures were fatter than adults and were more heavily wing-loaded. Wing length and weight, including fat, showed only limited correlation, with the greater number of significant correlations in spring birds.

Traces of molt were present on various tracts of most autumn adults, but only about half the immatures were molting. Because molt in birds-of-the-year seems to be correlated with age, it is suggested that molting immature specimens probably cannot have come from more distant parts of the breeding range. This inference is reinforced by the fact that traces of molt were found more frequently in young birds killed in July and August than in birds that died later.

The migration of males in spring is earlier than that of females, although the two overlap. There were indications that first-year adults, some of which are recognizable as such, may migrate later, on the average, than older birds of the same sex. The dates of mortality in spring, which ranged from March 19 to May 13, did not permit any inferences about the ratios of age or sex classes in the migrant population.

In fall, the few July migrants were immatures, not over about 70 days old. By mid-August the migration of adults had begun, and thereafter the composition of the night-migrant population did not vary in the proportions contributed by the four sex-age classes. Extreme dates were July 15 and October 19. The percentages of the total fall kill by sex-age class were: adult males, 42.3; adult females, 30.8; immature females, 18.9; and immature males, 8.0. Differences in the sex ratio in each age class were significant. In immatures this indicates differential migration behavior between the sexes; this is probably true in adults as well, but females may be less numerous in this race of the species.

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