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AN UNUSUAL SEQUENCE OF MOLTS AND PLUMAGES IN CASSIN'S AND BACHMAN'S SPARROWS[1]

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Abstract. An examination of feather replacement and plumage wear in study skins of *Aimophila cassinii* and *A. aestivalis* showed a sequence of molts and plumages for both as follows: Juvenal body plumage is replaced soon after fledging by a partial molt that produces plumage of adult-like body feathers combined with juvenal remiges, rectrices and greater primary and secondary coverts. This plumage has a spotted breast pattern intermediate between the streaked juvenal and spotless adult patterns, and is completely replaced in the bird's first autumn by a molt of all body, wing and tail feathers. A prolonged body molt of low intensity lasts through the spring-autumn breeding season, replacing feathers in all areas of the body. During autumn, adults have a complete molt coinciding with the second molt of the young birds.

The replacement of all pennaceous body plumage twice within a bird's first six months of age, and a molt of body feathers in adults throughout the breeding season have not been reported before for a North American passerine, nor was this pattern described in an earlier study of the molt of these species. It is suggested that these partial molts renew plumage that otherwise would become severely worn in the birds' abrasive habitats.

Key words: *molt; molting; plumage; plumages; sparrows;* Aimophila; *Emberizidae.*

INTRODUCTION

Wolf (1977) analyzed molting in the genus *Aimophila* using the post-juvenal molt of *A. cassinii* as a standard for comparing the members of the genus. He reported that a postjuvenal molt replaces the entire juvenal plumage, beginning on the body, then renewing the remiges and rectrices after the body molt is essentially complete. This plumage is retained until after the first breeding season, there being no prenuptial molt as in some other members of the genus. A postnuptial molt then replaces all body and flight feathers simultaneously. Wolf (1977) concluded that the closely-allied *A. botterii* and *A. aestivalis* follow this pattern too.

When I examined a series of specimens of *A. cassinii* (Cassin's sparrow) and *A. aestivalis* (Bachman's Sparrow) intending to evaluate the relationship between plumage wear, habitat and molt phenology, I discovered additional details of the molt not brought out in Wolf's (1977) study. In fact, I find these species to have a sequence of molts and plumages unlike any hitherto reported in North American passerines.

MATERIALS AND METHODS

I examined 249 skins of *A. cassinii* and 192 skins of *A. aestivalis* from the collections of the United States National Museum of Natural History (USNM), the Stovall Museum of Science and History of the University of Oklahoma (UO), the Bird Collection of the University of Arizona (UA), the Museum of Vertebrate Zoology, University of California (MVZ), the Carnegie Museum, Pittsburgh (CM), The Academy of Natural Sciences of Philadelphia (PANS), The American Museum of Natural History (AMNH), and The California Academy of Sciences, San Francisco (CAS). I assumed each specimen had been randomly selected from the population with respect to molting and degree of plumage wear when collected. In *A. aestivalis* I tried to limit variation owing to geographic differentiation by using specimens classified as *A. a. bachmani.*

Scoring each skin for relative degree of plumage wear helped me to discover instances of molting that might otherwise be overlooked, leading me to the discoveries on molting described below.

GENERAL PROCEDURE

To score a skin for wear and molting I used either a 10× or 7× binocular dissecting microscope and lifted feathers with a dissecting needle to inspect them for degree of wear and for evidence of active growth consisting of active follicles, pinfeathers, and sheaths adhering to the bases of newly grown feathers. Plumage areas scored were *crown,* including forehead; *throat,* including chin; *face,* including lores, superciliary line, eye ring, auriculars, and malar stripe; *breast*; *sides,* consisting of all feathers of the axillary and abdominal regions of the ventral tract, and therefore including feathers covering abdomen and flanks as well as the sides proper; *back,* including feathers of the rump; *rectrices*; *primaries*; and *secondaries.* These areas are readily accessible for detailed

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TABLE 1. Criteria used to assign wear scores to plumage.

Plumage area	Degrees of wear, wear scores			
	No wear 0	Light wear 1	Moderate wear 2	Heavy wear 3
Throat and breast	All barbs intact, without loss of material, in 75% or more feathers.	More than 25% feathers have one or more barbs missing up to ⅓ of the original length.	More than 25% feathers have two or more barbs missing ⅓ to ⅔ of original length. Feather outline ragged or notched.	More than 25% feathers have two or more barbs missing more than ⅔ of original length. Feather outline truncated or scalloped.
Crown and back	As for throat and breast.	As for throat and breast.	As for throat and breast. Feather outline scalloped, truncated or jagged.	As for throat and breast. Marked loss of feather material. Fading or foxing near tips may be evident.
Inner secondaries (no. 6–9)	Pale edging intact, dark areas glossy.	Tips of some barbs are broken off, but light edging is not appreciably interrupted or narrowed anywhere.	Loss of tips of barbs so that pale edging is clearly narrowed or interrupted in places. Dark areas appreciably dulled and perhaps faded.	Pale edging gone from the distal ⅓ or more of the feather. Edges frayed or uneven. Color dull brown, much paler than when fresh.
Longest primaries (no. 5–8)	Pale edging intact; dark colors glossy.	Some barbs are missing their ends, so pale edging, though discernible, is notched in places. Dark colors somewhat dulled.	Most of the barbs of the distal ⅛ or more are lacking tips so pale edging is nearly gone. The tip retains a smoothly rounded contour. Dark colors dull and faded.	Barbs at tip of feather are of uneven length. Pale edging is gone from distal ⅛ or more. Contour of tip now pointed or truncated owing to loss of tips of barbs or rachis or both. Dark colors much faded.
Rectices, central pair	No appreciable loss of material at tip.	Distal ⅛ or less of the exposed part has uneven or slightly ragged edges from loss of tips of barbs.	More than the distal ⅛ of the exposed part has uneven or ragged edges. Up to half of the area of the vanes may be lost.	More than half the area of the vanes is lost.
Rectrices, pairs 2–5	As for central pair.	As for central pair.	The distal ⅛ to ¼ of feather has notched or frayed edges from loss of ends of some barbs.	More than the distal ¼ of feather has ragged edges, tip often truncated by loss of the end of the rachis.

examination without undue risk of damaging the study skin.

SCORING OF FEATHER WEAR

Plumage areas scored for relative degree of wear were crown, throat, breast, back, secondaries 6 through 9 (i.e., those most exposed and subject to wear), primaries 5 through 8 (also those most subject to wear), and all rectrices except the lateral pair (6–6, which is somewhat protected from wear by the longer medial pairs). Each area was scored as unworn, lightly worn, moderately worn, or heavily worn and assigned the corresponding numerical values of 0 through 3, respectively (Table 1). The wear score assigned a specimen is the sum of the numerical scores for all areas, and ranges from 0, indicating no wear in any area, to 21, indicating heavy wear in all areas.

Judging feather wear was simple in specimens where molting had replaced all the feathers of an area within a few weeks. However, I encountered specimens that had been molting slowly for a longer time, with a resultant mixture of feathers in various stages of wear from 0 through 2 or 3 in roughly equal proportions (Fig. 1). In these cases, I used the mean score of the various wear classes present in that plumage area.

When a specimen was in rapid molt, I used the wear score of the majority of feathers, or if feathers in two or more stages of wear were present in nearly equal proportions, I used the average score.

If the central pair of rectrices had a wear score different from the rest, as when they had been replaced in a partial molt, I assigned the average of the two scores.

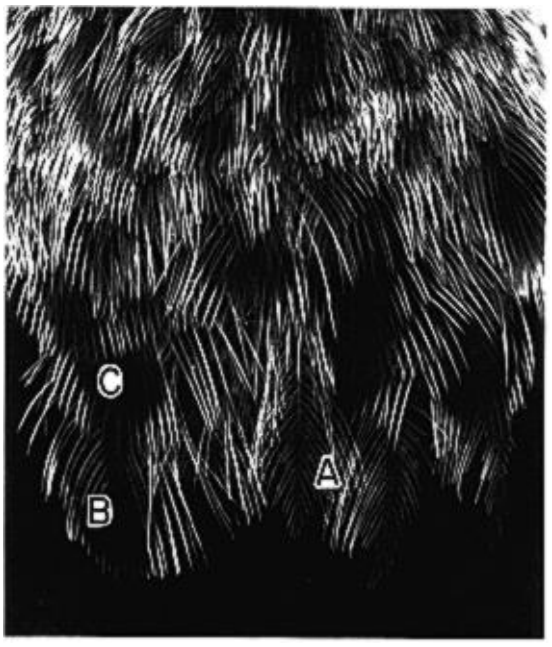

FIGURE 1. The back of a Cassin's sparrow (USNM 99676, 16 July) showing mixed wear. Feathers classed as heavily worn (A), moderately worn (B) and unworn (C) can be seen, some of which are set off by a dark background. The specimen received a wear value of 1.5 and a molt value of 0 on the back.

TABLE 2. Criteria used to assign molt scores.

Plumage areas	Condition	Score assigned
Throat and breast	No feathers growing.	0
	One or more feathers growing on one side only.	1
	One or two feathers growing on midline.	1
	One or more feathers growing on both sides of midline.	2
	Three or more feathers growing on midline.	2
Sides and face	No feathers growing.	0
	One or more growing on one side only.	1
	One or more growing on both sides.	2
Crown and back	No feathers growing.	0
	One or two feathers growing on midline, or one or more on one side only.	1
	Three or more growing on midline.	2
	One or more growing on both sides of midline.	2
Primaries and secondaries (including tertials)	None growing.	0
	One or more growing on one wing.	1
	One or more growing on both wings.	2
Rectrices	None growing.	0
	One or more growing on one side.	1
	One or both of central pair (1–1) only growing.	1
	One or more growing on both sides, including central pair in count (for example, both of central pair and one lateral rectrix, or both of pair 3–3 but no others, or left central and right 3).	2

SCORING FOR MOLT

I scored each plumage area for degree of molting according to the number of growing feathers present (Table 2). A bird that was replacing feathers lost by accident would receive a numerical score indicating some molting, but the criteria are intended to de-emphasize such replacement by yielding small numerical values. Thus, growth of feathers in an area on only one side of the body is given a score of 1 rather than 2 because it may have occurred by accidental feather loss. The higher the numerical score between 0 and 18, the more extensive is the molt indicated. This method of scoring does not account for growing feathers that slipped out during preparation and subsequent handling of the skin, so is likely to underestimate the extent of molting in some specimens.

AGE CLASSES

I have assigned each specimen to one of three age classes, *juvenile, immature* and *adult.* Specimens were classified as *juvenile* when juvenal feathers were present on all or most areas of the body, although these might be few and mixed with incoming adult-like feathers of the next plumage late in the postjuvenal molt. Juvenal body feathers have a characteristic fluffy quality with softer and more loosely adherent barbs (Dwight 1900), duller coloration, and thinner or more widely spaced barbules than corresponding adult feathers (Fig. 2). Specimens were classified as *immature* if they had replaced essentially all of their juvenal body plumage but retained juvenal primary coverts and sometimes greater secondary coverts, or were identified as immature by the collector although traces of juvenal plumage had practically disappeared.

Specimens having no sign of immaturity in the plumage or on the label are called *adult.*

RESULTS

MOLT OF ADULT CASSIN'S SPARROW

There is a partial molt involving the body feathers during spring and summer and a complete molt in autumn. Data are summarized in Figures 3 and 4 and Table 3. The body molt begins in some birds as early as the second week of February and continues at a low in-

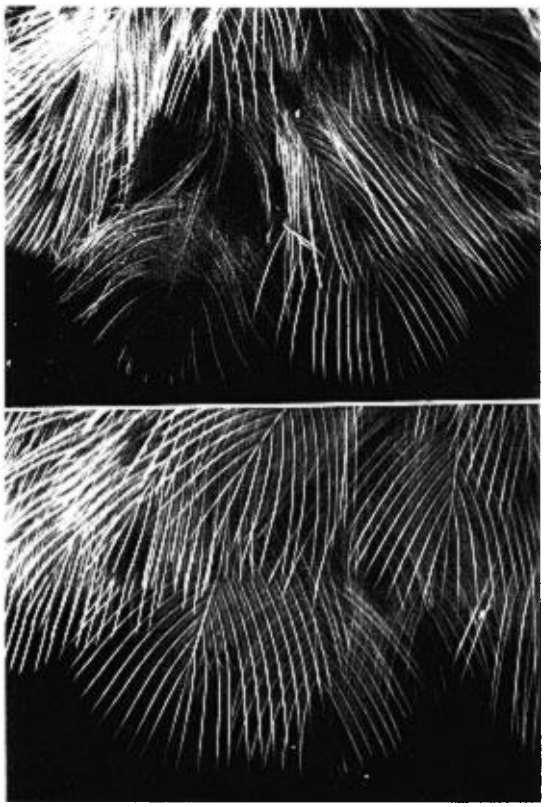

FIGURE 2. Molting juvenile (upper) and immature (lower) Bachman's Sparrows, showing replacement of breast feathers in two successive molts. The upper specimen, USNM 240126, shows a lightly worn juvenal feather on the left, set off by the darkened background, and an unworn replacement feather beside it. Note the distinctive appearance of the juvenal feather and its large central dark area. The new feathers coming in have the denser character of adult feathers, but have a small subterminal dark spot typical of this plumage. The lower specimen, USNM 363295, shows set off by the dark background a lightly worn feather of the second generation with the subterminal dark spot to the right of, and partly under, a newer, unworn, unmarked adult feather of the third generation of pennaceous feathers.

tensity until the middle of July. During this period, molt scores averaged between 2 and 3 (range 0 to 12), with 73% of specimens having molt scores of 2 or higher and 56% having molt scores of 3 or higher. In July and August, the body molt intensifies to produce average scores of 6.4 and 6.6, respectively (Table 3). During the earlier part of this molt (March to June), the plumage areas most likely to be scored as molting are throat and face, but all other areas of the body are involved to a varying degree, with the crown being scored in molt least frequently (Fig. 3). Although only two birds in the period March through July were actually growing new tertials (secondaries 7–9), it is safe to say that these feathers are frequently involved as another 19 of the 111 specimens have at least a few newer unworn or lightly worn tertials mixed with older more worn ones. A few birds had also recently renewed the central pair of rectrices.

The body molt coincides with the breeding season which lasts from early April through early September (Ligon 1961, Ohmart 1966, Webster 1968, Williams and LeSassier 1968). The early phase of this molt (March to June) is clearly of low intensity, and is perhaps interrupted at intervals in an individual when it is actively engaged in a breeding effort. This possibility is suggested by the occurrence of occasional individuals with molt scores of 0 or 1. The gradual and prolonged nature of this molt is shown also in the appearance on the back of mixtures of feathers in various stages of wear, always with a few unworn feathers (Fig. 1). Specimens having such mixtures occur in increasing frequencies each month (Table 3). The January specimen (UA 10188, 28 January) showing mixed wear on its back (Table 3) has three moderately worn (stage 2) feathers on the back, evidently left from the previous plumage.

The complete molt begins in some individuals as early as 24 August (one specimen) and is completed by about the end of November. Judging from the time between median starting and stopping dates (Fig. 4) this molt lasts on average 1½ months. In this molt all the body feathers are renewed along with the remiges and rectrices, so that by December wear scores are near a minimum (Table 3), and a fresh plumage has been acquired.

MOLT OF JUVENILE AND IMMATURE CASSIN'S SPARROWS

The series of 54 young birds collected between 1 June and 21 November indicates that a body molt usually begins within two months of fledging, but sometimes within days, while primaries and rectrices are still sheathed proximally. This molt is gradual and lasts about two months (Fig. 4), involving all areas of the body and the tertials, sometimes the rectrices, but not the primaries and outer secondaries (Fig. 5). During this molt the heavily streaked juvenal breast pattern changes to spotting that can vary individually from heavy to nearly or entirely unmarked (Fig. 6). At the end of this molt, the only sign of immaturity in the 23% (9 of 39) birds, that attain an essentially unspotted breast in this molt, may be the juvenal primary coverts combined with moderately to heavily worn primaries and rectrices. Usually, however, other signs of immaturity can be found by careful inspection, including a few juvenal feathers scattered on other areas of the body, particularly the neck, occiput and nape, and greater secondary coverts, At this time,

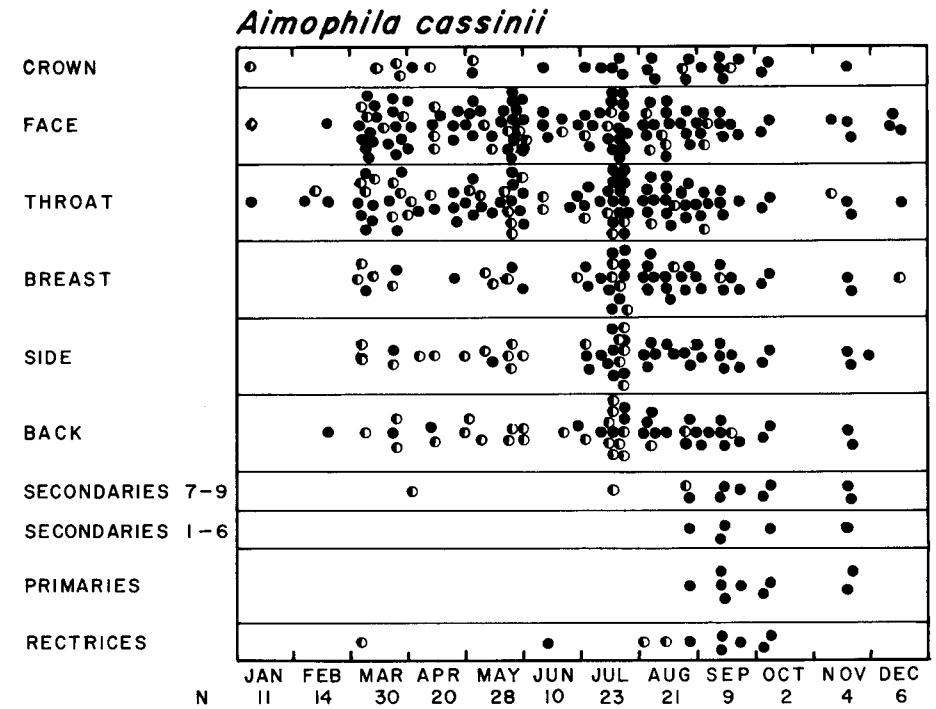

FIGURE 3. Occurrence of molting in adult Cassin's Sparrows in each plumage area. A specimen was scored as molting if any active feather growth was detected. The half-darkened circles indicate a molt score of 1, the fully-darkened circles a molt score of 2. Specimen dates are plotted on two-day intervals. Only specimens showing active feather growth in a plumage area are plotted. N is the number of specimens examined for each month.

molt scores are as low as 0 (six specimens) or 1 (three specimens) and most of the wear score is attributable to the retained juvenal remiges and rectrices. These birds now are classed as immature.

This body molt is followed by a complete molt in September through November, in which all the body feathers are replaced again along with the remiges and rectrices (Figs. 4, 5). During this second molt, all traces of juvenal plumage disappear so that first-winter birds are indistinguishable in appearance from

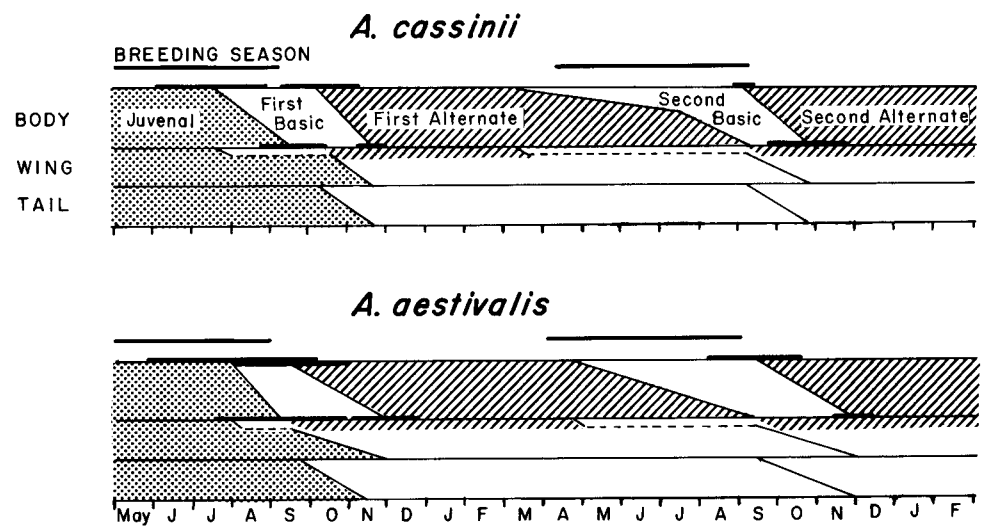

FIGURE 4. Plumage cycles of Cassin's and Bachman's Sparrows. Terminology for the plumages follows the system of Humphrey and Parkes (1959). See text for discussion of this and of alternate terminology. A diagonal line indicates molt with its upper end the start, lower end the finish. Starting and ending dates with bars are the medians and the bars connect the extreme dates for the specimens examined. For the prebasic molt the starting date is the day after which at least half the specimens had molt scores of 3 or higher. The ending date for the prebasic molt coincides with the start of the second prealternate molt.

TABLE 3. Wear and molt scores of adult Cassin's and Bachman's Sparrows by month.

Month	*A. cassinii*				*A. bachmani*			
	Number of specimens (*n*)	Molt score, mean (range)	Wear score, mean (range)	Percentage showing mixed wear on back	*n*	Molt score, mean (range)	Wear score, mean (range)	Percentage showing mixed wear on back
Jan.	11	0.4 (0–4)	3.7 (1–10)	9[1]	19	0.4 (0–3)	3.7 (0–8)	0
Feb.	14	0.6 (0–6)	4.8 (1–14)	0	10	0.1 (0–1)	6.1 (2–9.5)	0
Mar.	37	3.2 (0–8)	8.5 (2–14.5)	0	39	1.3 (0–5)	8.4 (3.5–16)	3
Apr.	20	2.2 (0–6)	10.2 (3–16)	10	25	1.4 (0–9)	11.4 (3–18)	12
May	28	3.2 (0–7)	13.1 (8.5–20)	11	19	6.1 (0–12)	13.7 (11–17)	11
June	10	2.6 (0–7)	16.4 (13–19)	50	14	6.2 (0–12)	14.5 (8–18.3)	57
July	23	6.4 (0–12)	17.1 (9–20.5)	70	7	7.0 (1–12)	12.5 (8.8–16)	86
Aug.	22	6.6 (0–18)	17.2 (8–21)	82	5	6.0 (0–13)	14.5 (12.5–16)	100
Sept.	9	10.9 (3–18)	11.4 (3–18.7)	78	1	16	6	100
Oct.	2	18	8.3 (6.5–10)	0	5	12.2 (3–18)	6.3 (2–9)	60
Nov.	4	8.3 (2–15)	1.0 (0–2.5)	0	6	8 (0–15)	0.8 (0–2)	0
Dec.	6	1.5 (0–5)	4.8 (2–8)	0	8	4.0 (0–16)	1.7 (0–4)	0

[1] A single specimen with a few worn feathers among the new, see text.

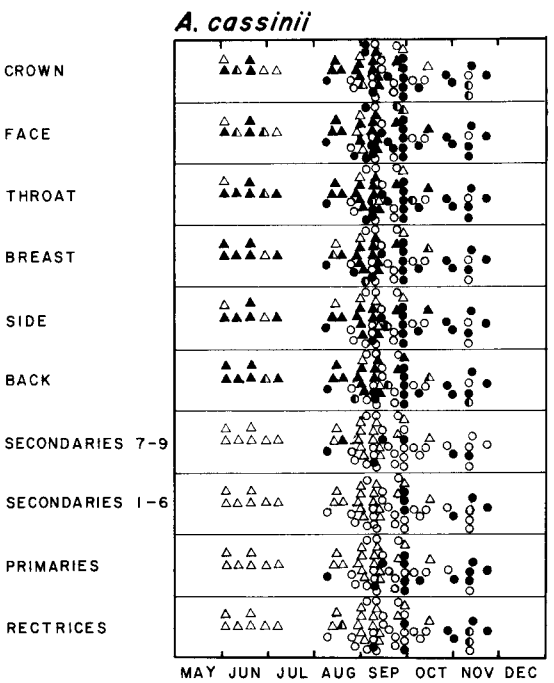

FIGURE 5. Occurrence of molting in juvenile and immature Cassin's Sparrows. Triangles represent juveniles, circles immatures. (See text for definition of age groups.) Open symbols indicate no molting, half-darkened and fully-darkened symbols indicate molt scores of 1 and 2, respectively. Specimen dates are plotted on two-day intervals. Every specimen is represented in each plumage area.

older birds, and have to be classified as *adults*. Although the breast of adults is typically unmarked, occasional individuals retain some spotting or faint streaking. Among 58 skins from January through March which I scored for breast pattern, there are 11 that show some marking, but only one of these is as heavily spotted as a typical immature bird.

Seven specimens show signs that this second molt was interrupted at an early stage, perhaps during migration. Noteworthy of these is CAS 68475, collected 23 September, 1969 on South Farallon Island by Henry Robert. It shows molting only on the face (molt score of 1) but it had recently replaced primaries 1 and 2 on the left and 1 on the right. The tail had been partly renewed also, as the central pair (1-1) and right 2 through 6 are moderately worn, but left 2 through 6 are heavily worn and considerably more faded than the rest. The body plumage shows light to moderate wear, the breast is spotted but has no juvenal feathers, and the skull is not fully ossified. The fact that this bird was over 1,120 km outside its normal range suggests it was in a migratory condition. The other six specimens show signs of having replaced one to four inner primaries before interrupting wing molt for a time. Two of these, both from southeastern Arizona, clearly show

FIGURE 6. Breast patterns of juvenile, immature and adult Cassin's Sparrows (above) and Bachman's Sparrows (below). The specimens of Cassin's Sparrow illustrate from left to right: a juvenile before replacement of streaked juvenal breast plumage (AMNH 83994); three immature birds after replacement of the juvenal breast plumage showing individual variability of spotting in this species, from faint to heavy (USNM 567703, 575432 and 184136, respectively); an immature bird undergoing its second molt in which spotted breast feathers have nearly all been replaced by unspotted adult feathers (USNM 130911); and an adult bird in typical fresh plumage without breast spots (AMNH 763571). The Bachman's sparrows illustrate from left to right the sequence of change of breast pattern from the juvenal to the adult. Specimens are from left to right: a fledgling (AMNH 401751); a juvenile that has just started to replace the streaked juvenal plumage with spotted immature plumage (AMNH 401757); a juvenile with its first molt nearly completed (USNM 363312); an immature bird in its second molt beginning to replace feathers with large spots by feathers with small spots and no spots (USNM 362890); an immature bird replacing spotted feathers with entirely unspotted ones (USNM 477961); and an adult in typical fresh plumage (USNM 341028).

a mixture of wear stages on the body that is also consistent with an interruption of the second molt. These are CAS 30128, 22 September, which has a molt score of 0 but has on its breast a mixture of lightly to moderately worn feathers with immature spotting, and unworn, unspotted feathers; and CAS 30384, 27 September, which has resumed a complete molt but has feathers on its crown divisible into a moderately to heavily worn group, presumably of the first nonjuvenal plumage, a lightly worn group, presumably from the early part of the second molt, and a fresh, unworn group apparently renewed after resumption of the second molt.

MOLT OF ADULT BACHMAN'S SPARROWS

Bachman's sparrow shows the same sequence of plumages and molts as Cassin's Sparrow. There is a body molt during spring and summer followed by a complete molt in autumn (Figs. 4, 7). Fifty-four percent of March specimens showed molting on throat, breast, side or face. Forty-four percent of April specimens were molting, but more than 80% of the May through August specimens showed molting involving all areas of the body, including the tertials and occasionally the central pair of rectrices (Fig. 7). Although only two birds from April through August were actually growing new tertials, 13 others had some that were newly-replaced, indicating that these feathers were molted in at least 21% of the birds. The first signs of this molt are in March when the average molt score jumps from the February value of 0.1 to 1.3. Scores stay steady through April, then climb to about six and remain steady through August (Table 3). Thus the body molt of Bachman's sparrow reaches an intensity of around six sooner and holds it longer than does Cassin's sparrow. As in the latter, this molt is prolonged as shown by a mixture of feathers in various stages of wear in an increasing proportion of birds as the season progresses (Table 3).

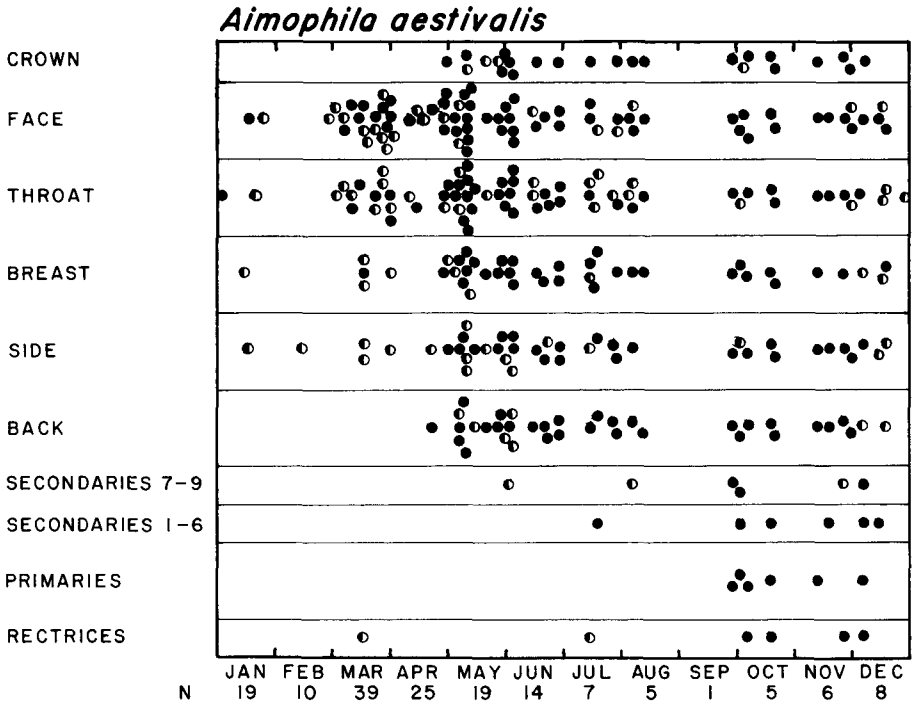

FIGURE 7. Occurrence of molting in adult Bachman's Sparrows. Symbols as for Figure 3.

Because nesting may occur from early April through August producing as many as three broods (Weston 1968), Bachman's Sparrow like Cassin's, has a body molt extending through a long breeding season. Individuals may suspend the molt during intense breeding efforts as suggested by three females with brood patches that were not molting (USNM 358003, 15 May; USNM 259106, 15 June; USNM 240559, 25 June). They all have a mixture of worn and unworn feathers on the back or breast, or both, indicating that partial feather replacement had taken place.

From late September through early December a complete molt occurs (Figs. 4, 7). There is little if any interval separating the end of the body molt and beginning of the complete molt. These data are consistent with H. L. Stoddard's observation (Burleigh 1958) that Bachman's Sparrow appears to be forever in molt, replacing lost feathers throughout the summer and fall, and even during winter months.

MOLT OF JUVENILE AND IMMATURE BACHMAN'S SPARROWS

I examined 36 specimens collected between 5 May and 13 December that can be classified as juvenile or immature. As with Cassin's Sparrow, a body molt begins shortly after fledging which replaces nearly all the body feathers, including the tertials in some birds (Fig. 8), but not the greater primary coverts. A few scattered juvenal feathers may remain on occiput and nape. In September, a complete molt begins which may be very rapid. All the body feathers are replaced again, along with the remiges and rectrices, so that all traces of juvenal feathering disappear. As with Cassin's sparrow, the heavily streaked juvenal breast plumage is replaced by a spotted plumage, which then is replaced by the unspotted adult plumage (Figs. 2, 6). In the series I examined there is less variability in the degree of spotting of the second plumage than in Cassin's Sparrow. Few adult birds retain any spotting, as only 7 of 66 January through March specimens have any traces of spotting on the breast, and none of these is as heavily marked as young birds.

One specimen shows that its second molt was interrupted for a time, perhaps during migration. USNM 363296, 3 October, Gulfport, Mississippi, was molting only on the face, but its crown and back have a mixture of unworn and lightly worn adult-like feathers, and primaries 1–3 are unworn, while 4–9 are heavily worn. A single juvenal feather is present on the nape.

DISCUSSION

I have interpreted the data as indicating that a postfledging body molt is followed by a complete molt during the young bird's first six months of age for the following reasons: (1) In both species, the juvenal body feathers nearly

all disappear with the growth of adult-like feathers during the months of June through September, while the juvenal remiges and rectrices (together with the greater primary coverts) remain and become progressively more worn. The heavily-streaked juvenal breast pattern changes to a spotted pattern in this period. (2) The majority of August and September specimens identifiable as immature birds (without juvenal body feathers but retaining juvenal remiges and coverts) are not molting or have very low molt scores, whereas the majority of October and November specimens are undergoing complete molts (Figs. 5, 8) and are losing their breast spotting (Figs. 2, 6). (3) I can find no sign of retention of any of the adult-like body feathers acquired in the earlier body molt through the later period of body and flight feather molt, since all specimens from November through January show a uniformly fresh coat of feathers, with the exception of the one January *A. cassinii* mentioned earlier. Otherwise, one should find a mixture of wear stages among the feathers on the backs of a few specimens that represent the youngest generation, which with a single body molt would have changed these feathers over a period of four or five months.

I have considered the possibility that the slow replacement of body feathers during the breeding season is the result of accidental feather loss, but conclude that it is a true molt, albeit a slow and extended one, for these reasons: (1) A majority of specimens show feather growth on various regions of the body throughout the months of the breeding season. (2) There is an accumulation of feathers in various stages of wear on the backs of up to 100% of specimens during the breeding season, but a lack of mixed wear in winter specimens. This is hard to explain as the result of accidental feather loss in the one season alone. (3) The elevated molt scores of breeding season birds contrast with the much lower scores of winter specimens, making it hard to explain the difference as a result of accidental feather loss. (4) I have scored species of the genus *Spizella* in the same way (Willoughby, unpubl.) and they show much lower molt scores during their breeding seasons. For each of these species, I list the number of May and June specimens examined, the average molt score and the range of molt scores, respectively: *S. arborea* 22, 0.7, 0–3; *S. breweri* 42, 1.2, 0–12; *S. pallida* 27, 1.6, 0–11; *S. pusilla* 20, 1.9, 0–4. Note how close these values come to those of winter specimens of Cassin's and Bachman's sparrows (Table 3). Thus the breeding season molt of Cassin's and Bachman's sparrows does not appear to be an artifact of my scoring methods.

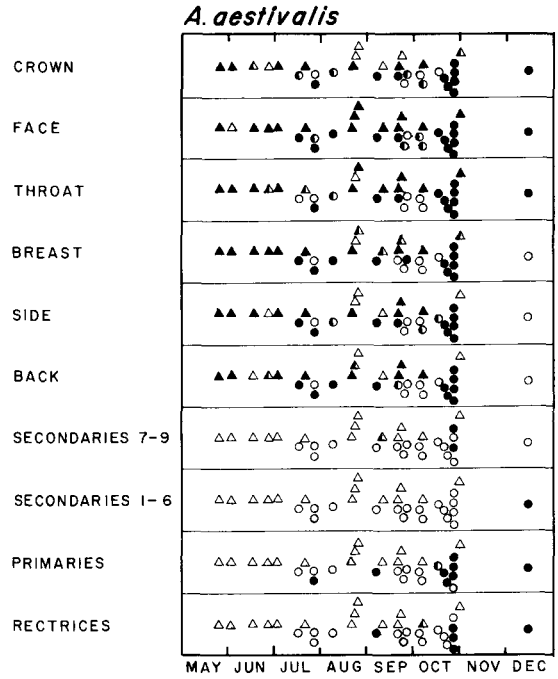

FIGURE 8. Occurrence of molting in juvenile and immature Bachman's Sparrows. Symbols as for Figure 5.

Wolf (1977) analyzed the molt cycles of *A. cassinii* with study skins. I agree with his conclusions on the general timing of molting (compare Fig. 4 with Wolf's fig. 6, p. 74). However I cannot agree with his conclusion that adults have only one molt, the complete postbreeding molt, and that new feathers noted on some specimens during the time when a prebreeding molt might have occurred appear to represent "adventitious replacement" (p. 60–61). I cannot agree with his conclusion that the postjuvenal molt of both species is a single complete one in which all or nearly all body feathers are replaced before the flight feathers and greater wing coverts are molted (p. 54, 58–59). It is clear that Wolf thought there is a single replacement of body feathers since he hypothesized that these birds stagger the renewal of body and flight feathers because of energy budget constraints (p. 75).

TERMINOLOGY FOR MOLTING AND PLUMAGES

In Figure 4, I have tried to apply the terminology for plumages recommended by Humphrey and Parkes (1959). A central purpose of the Humphrey-Parkes system is to express homologies of plumages and molts among species (Humphrey and Parkes 1959, 1963) and I have adhered to the following assumptions relating to this concept of plumage homology: (1) The homology of plumages is determined solely by the number of times feather follicles have been activated so that all plumages resulting from

the third cycle of growth, say, are homologous in all species. (2) During each molt a follicle is active only once, producing one new feather rather than two or more in succession. (3) When the remiges are molted only once in a cycle, they remain part of the basic plumage, whether or not their molt coincides with a body molt, and whether or not that body molt is prealternate, prebasic or presupplemental (Palmer 1972). (4) The molt into the first basic wings and tail, in this case, occurs during the first prealternate molt because the wing molt has been delayed, or "offset" (Palmer 1972), and this offset is carried over into subsequent plumage cycles.

If one observed the cycle of plumage replacement only in the adults, namely the body molt before (and in this case during) breeding and the complete molt following breeding, a pattern which is very common in the Emberizidae, one would want to designate the body molt prealternate producing an alternate plumage, and the complete molt prebasic producing a basic plumage. This would be the easiest way to homologize the plumages. Certainly the molts of these sparrows and the other Emberizidae having the ordinary plumage sequence are physiologically equivalent, posing the question whether the homologies implied in Figure 4 are correct. The plumage sequence illustrated could be derived by simultaneously delaying the first prebasic molt of the remiges so it begins after the first prebasic body molt is completed, while advancing the first prealternate molt from the spring into the preceding autumn. This would lead to the prediction that all birds in their first breeding season would skip the body molt, which they already went through, and would not have it again until their second breeding season. Thus the molt of older birds during the breeding season would fall into step and remain homologous with the prealternate and prebasic molts of other species.

I see little evidence for this in my data. Of 100 specimens of both species collected May through July, only two (both Cassin's in May) show no signs of a body molt either in progress or having recently occurred. It is possible, although unlikely, that my sample failed to include more than two yearlings, but the hypothesis could be tested by observing molt cycles in live birds through their first two or three years. Alternatively, the birds in their first breeding season might have two successive body molts, the second prebasic and second prealternate, while older birds had only one molt, the third and subsequent prealternate. This possibility could be tested by observing and following the fates of artificially marked groups of feathers in live birds. Other ways of deriving the observed plumage sequence might be (1) elimination of an ancestral first prealternate molt and advancing a second prebasic molt from the second autumn into the first autumn; (2) addition of a new, complete molt in the bird's first autumn; or (3) addition of a new body molt immediately following the juvenal plumage, but I see no way of verifying any of these last conjectures.

Because of these questions about the Humphrey-Parkes terminology in this case, many will prefer the older terminology originated by Dwight (1900) and later advocated by Stresemann (1963) and Amadon (1966), which names molts in relation to developmental and life-history events rather than hypothesized homologies. Using modifications consistent with Amadon's (1966) recommendations, I suggest the following terminology with the corresponding Humphrey-Parkes terms from Figure 4 in parentheses: Juvenal plumage—Postjuvenal molt (First Prebasic molt)—Immature plumage (First Basic plumage)—Immature molt (First Prealternate molt)—First Nonbreeding plumage (First Alternate plumage)—Prebreeding molt (Second Prebasic molt)—Breeding plumage (Second Basic plumage)—Postbreeding molt (Second Prealternate molt), and so forth. I use the conventional term Prebreeding molt although this molt extends through the breeding season, since it seems to start before breeding begins so that birds have acquired part of the resulting plumage by the time they breed.

COMPARATIVE AND ECOLOGICAL CONSIDERATIONS

The occurrence of the second complete molt after the first prebasic molt in Cassin's and Bachman's Sparrows appears to be a rather unusual sequence. Dwight (1900) did not describe such a molt sequence for any of the 151 species he studied. In their review of postjuvenal feather replacement, Humphrey and Parkes (1959) and Palmer (1972) cited no example of such a sequence being completed in rapid succession before birds are six months of age. Typically if the postjuvenal molt replaces only the body feathers, a bird does not replace the juvenal flight feathers until its first postbreeding molt, usually at one year of age.

Sutton (1935) described a "postjuvenal" body plumage in the Northern Cardinal (*Cardinalis cardinalis*) which is acquired by a molt of the juvenal body feathers, and which in turn is replaced during the molt of the juvenal remiges and rectrices to produce the "first winter" plumage, all within about the first three months of life. Sutton was unable to say whether all the juvenal body feathers were changed before the complete molt began. In the same paper Sutton stated that Henslow's Sparrow

(*Ammodramus henslowii*) has an incomplete postjuvenal body plumage, but his details are sketchy.

One other species is reported to have substantially the same sequence of molts and plumages as Cassin's and Bachman's Sparrows, the Black-headed Bunting, *Emberiza melanocephala.* Adults undergo a partial molt on the nesting grounds in June and July in which they molt feathers on the head, back, chin, throat, upper tail coverts and tertials (Dement'ev et al. 1954 p. 475). This apparently occurs during the breeding period, which begins in the second half of May and ends in July (Dement'ev et al. 1954 p. 474). Witherby et al. (1938 p. 121) noted the possibility, based on very limited material, that juveniles have a partial molt (not involving the wings and tail), and a few months later a complete molt. Dement'ev et al. (1954 p. 475) reported that juveniles have a partial molt in June and July, when only remiges and rectrices remain unreplaced, then in December undergo a complete molt which makes them like adults in appearance.

I have described analogous molt sequences in three larks (Alaudidae) of the Namib Desert, *Ammomanes grayi, Spizocorys starki,* and *Eremopteryx verticalis* (Willoughby 1971). These species have a postjuvenal body molt that is followed by a complete molt that begins about one month later so that all birds typically have replaced their body feathers twice and flight feathers once by the time they breed the following autumn. Adults have a postbreeding body molt followed by a complete molt synchronized with the molts of the young. Thus these larks and Cassin's and Bachman's Sparrows are alike in their molting except that the adult larks have their partial molt after, rather than during, the breeding season.

I suggested (Willoughby 1971) that these larks molt twice in order to renew plumage that becomes heavily worn in their abrasive desert habitat, and that the rapid postbreeding and postjuvenal body molts are timed to occur when insects and seeds are still abundant at the end of the rainy summer-autumn breeding season. The complete molts that follow are prolonged over several dry months (Willoughby 1971), and thus would require a small daily nutritional increment that could be sustained mostly by the grass seeds produced during the previous rainy season.

Compared to these larks and the Black-headed Bunting, the sparrows have a rather long breeding season. The timing of nesting in the Namib larks is influenced strongly by the occurrence of sparse rainfall sufficient to produce green vegetation and insects. Such rain usually falls only in the summer months in the Namib. The xerophilous Cassin's Sparrow occupies a range over which such necessary rainfall is not restricted to a short season. Rather, rainfall may occur in sufficient amounts from early spring through late summer, tending to be earlier in the eastern regions and later in the western regions. Observations by Phillips (1944), Ligon (1961), and Ohmart (1969, pers. comm.) suggest that this species is nomadic and breeds when and where it encounters suitable habitat. Ohmart (1969, pers. comm.) concluded that Cassin's Sparrow breeds in the spring in the eastern parts of its range, then moves into the western regions in late summer to continue breeding there. Bachman's Sparrow also has a long breeding season (Weston 1968). Therefore, it appears that these sparrows have accommodated the prebreeding molt to a long breeding season by spreading it over the breeding period, and thus perhaps gaining the benefit of replacing damaged plumage during the period of greatest wear. This keeps the plumage from becoming too severely degraded before the postbreeding molt can renew it. This hypothesis is supported by the plumage wear scores for Bachman's Sparrow, which remain at about 14 in May through August as a result of body feather replacement alone (Table 3). Cassin's Sparrow accumulates somewhat higher wear scores, leveling off at a value of 17 in July and August (Table 3). That Cassin's Sparrow attains greater levels of plumage wear in the breeding season might be attributed to a more abrasive desert habitat or its lighter pigmentation, or both. Regarding the latter, Burtt (1979) and Barrowclough and Sibley (1980) have shown that feathers lacking melanin pigments are more quickly abraded than are those containing melanins.

The occurrence of the body molt during the breeding season in these sparrows is unusual in temperate-zone landbirds. These two energy-demanding processes in the life cycle are typically separated temporally so they do not compete for food and essential nutrient resources (Foster 1975a, 1975b). What data I have on breeding condition of the specimens examined (brood patch present, notes by collector on breeding behavior or gonadal condition) suggest that some individuals suspend their molt during intensive breeding efforts, while others may not. For example, all six specimens of *A. cassinii* with breeding indications (three females, three males, collected 11 April through 5 July) show some molting, with an average score of 2.3. Five of these were molting on throat or face, or both, and one was molting its rectrices. On the other hand, of six *A. aestivalis* (four females, two males collected 30 April through 4 August) only one was molting (on throat and face), while all others display

mixtures of worn and fresh feathers on various parts of the body, indicating a molt had recently been in progress. The average molt score for this *A. aestivalis* group is 0.5.

Payne (1972) and Foster (1975a, 1975b) have reviewed the occurrence of molt during breeding and discussed the physiological and ecological implications. Although such molt is rare in temperate-zone landbirds, Foster (1975a) found it to some extent in 20% of neotropical landbird species she examined; and overlap of molting and breeding has been reported for many other tropical and Australian desert birds (Foster 1975b). Thus Cassin's and Bachman's Sparrows are not unique in this respect, but they apparently are the first North American passeriforms in which molting is reported to occur throughout a breeding season of several months duration. Since they resemble some neotropical landbirds in their molting and since other members of the genus occur in tropical and subtropical latitudes, one can speculate that these sparrows evolved from a neotropical ancestor, and thus retain an adaptive pattern that is atypical of temperate-zone birds.

Since the prebreeding molts of these sparrows are of low intensity and are prolonged through extended breeding seasons, they probably compete lightly with breeding for the available energy and nutrients but help to maintain plumage efficiency by replacing worn out feathers.

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